Muscular characters in the phylogeny of *Liolaemus* (Squamata: Iguania: Liolaemidae): a reappraisal

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Abstract

Liolaemus is one of the most speciosus genera of lizards, having more than 200 species. It is composed of small to moderate-sized lizards that live throughout most of austral South America. Many groups whose phylogenetic relationships have been controversial compose the genus. The proposed phylogenetic relationships of these lizards have been based on data-sets from many sources. In all of the morphological data-sets, three myologycal characters have been considered particularly important:1) insertion of the m. *tibialis anticus* hypertrophied in association with the presence of a sharp, bladelike process of the tibia, 2) medial head of the m. *flexor tibialis internus* covered by a hypertrophied m. *puboisquitibialis,* and 3) presence of melanic pigment within the medial portion of the epimysium of the m. *pterygomandibularis.* Important taxonomic and anatomical questions about these characters remain: 1) Can the size of the m. *puboisquiotibilis* be scored with only two character states? 2) Is there a close relationship between the hypertrophied m. *flexor tibialis internus* and the patch of the enlarged proximal postfemoral scales? and 3) Are these muscular characters exclusive to some of the groups of *Liolaemus* that have been proposed? Focusing on these questions**,** we have conducted a taxonomic and anatomic review of these characters in 42 species representing all of the proposed groups of *Liolaemus*. The analyzed samples show that variations in the considered muscular characters are much more gradual than previously stated. The only exception is the insertion of the m. *tibialis anticus* hypertrophied in relation to a bladelike hypertrophy of the tibia, which characterizes the *montanus* group of E theridge (1995). These characters seem to have the same phylogenetic information as any other morphological character. Although the coding we used is more complex, it shows more precisely the subtlety of the change in the character states.

Key words: *Liolaemus*, cranial and limb myology characters, phylogeny

Introduction

Liolaemus is one of the most speciosus genera of lizards. It is composed of small to moderate-sized lizards that live throughout most of austral South America. *Liolaemus* ranges from northern central Peru southward through Bolivia, Chile, and Argentina to northern Tierra del Fuego, and up the Atlantic coast of Uruguay and southeastern Brazil. Members of this genus occur at elevations from sea level to over 5000 m. *Liolaemus* may be insectivorous or herbivorous, but the majority of species appear to be omnivorous. The majority of liolaemid lizards live in arid or semiarid habitats, but the distributions of some *Liolaemus* extend into the humid forest of southern Chile, and along the Atlantic coast including several Brazilian islands. Liolaemids are almost entirely terrestrial, with most being microhabitat generalists, but some are highly specialized morphologically: some *Liolaemus* live their whole lives on aeolian sand, whereas others among crevices in boulder outcrops. Only *Liolaemus tenuis* (Duméril & Bibron) is commonly found on trees (Etheridge & Espinoza 2005).

Many groups whose phylogenetic relationships have been controversial belong to this genus. The proposed phylogenetic relationships of these South American lizards have been based on data sets from many sources: osteological and external morphology (e.g. E theridge 1995, 2000; Lobo & Abdala 2002; Abdala 2005); ethological (Halloy *et al.* 1998); myological (Moro & Abdala 1998); molecular (Schulte *et al.* 2000; Morando 2004; Abdala 2005) etc. In the morphological data sets that were used, three characters have been frequently considered:

Insertion of the m. *tibialis anticus* hypertrophied in association with the presence of a sharp, bladelike process of the tibia (proposed by Etheridge 1995).

Medial head of the m. *flexor tibialis internus* is covered by a hypertrophied m. *puboisquitibialis* (proposed by Etheridge 1995).

Presence of melanic pigment within the medial portion of the epimysium of the m. *pterygomandibularis* (proposed by Etheridge 1995).

These have been considered decisive characters in supporting many of the *Liolaemus* groups. Etheridge (1995) presented a taxonomic revision of the Liolaemidae that considered its three genera, *Ctenoblepharys*, *Phymaturus* and *Liolaemus* to form an unresolved polytomy. For the genus *Liolaemus*, he proposed an indented classification. *Liolaemus archeforus* Donoso-Barros & Cei and *L. kingii* Bell were considered basal, and the remaining species were placed in two large groups, the *nitidus* and *signifer* groups. The *nitidus* group included the basal species *L. magellanicus* Hombron & Jaquinot, plus a small *lineomamaculatus* group and a large *chiliensis* group, which was, for the most part, equal to the Chileno group of Laurent (1983). The *signifier* group included the basal species *L. anomalus* Koslowsky and *L. pseudoanomalus* Cei and a large *montanus* group, for the most part equivalent to the Argentino group of Laurent (1983). It was for the species of the *signifer* group that Etheridge (1995) employed the three morphological characters listed above: presence of pigmented epimysium of the m. *pterygomandibularis*

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and hyperophied medial head of the m. *flexor tibialis internus* were proposed synapomorphies for the entire *signifer* group; a sharp, bladelike process of the tibia associated with a hypertrophied m *tibialis anterior* was given as a synapomorphy of the *montanus* group (i.e., all species of the *signifer* group except *L. anomalus* and *L. pseudoanomalus*), and a patch of abruptly enlarged, spinose scales on the posterior medial surface of the thigh, bulged out in adult males due to hypertrophy of underlying m. *puboischisotibialis* were proposed as synapomorphies of the *boulengeri* group, a subset of the *montanus* group. A subset of the *boulengeri* group, the *wiegmannii* group, was also proposed based on certain head scale characteristics.

According to a DNA analysis of Schulte *et al*. (2000), Morando (2004), and Abdala (2005), *L. pseudoanomalus* is the sister species of the *wiegmannii* group, and *L. chacoensis* Shreeve, placed in the *chiliensis* group by Etheridge (1995), is closely related to *L. darwinii* (Bell), but neither has the tibial blade nor the hypertrophied m. *puboisquiotibialis*. *Liolaemus chacoensis* does, however, have enlarged proximal postfemoral scales but they do not form a distinct "patch". Several austral species (e.g. *L. magellanicus*, *L. lineomaculatus* Boulenger, *L. hatcheri* Stejneger, *L. sylvanae* Donoso-Barros & Cei) also have some enlarged proximal postfemoral scales but lack a hypertrophied m. *puboisquiotibialis*. These species, along with the *chiliensis* group, were included in the *nitidus* group by Etheridge (1995). Schulte *et al*. (2000), however, placed them as basal members of the *montanus* group.

Etheridge (2000) proposed a phylogenetic hypothesis for the *wiegmannii* group, included within an analysis of the *boulengeri* group. In his data set, he includes the perimysium pigmentation of the m. *pterygomandibularis* character (his character 38), considering only two character states: with and without pigmentation. The species *L. multimaculatus* (Duméril & Bibron), *L. rabinoi* (Cei), *L. riojanus* Cei, and southern populations of *L. cuyanus* Cei & Scolaro were scored as "without pigmentation**."** Lobo and Abdala (2002), and Abdala (2005) also scored that character for their analysis of 24 species of the most important groups of *Liolaemus,* and the *boulengeri* group respectively. In these latter analyses the character was scored following the proposal of Etheridge (1995). Moro and Abdala (1998) added one more state for this character (ligthly pigmented), having in their analysis only some overlap with that of Etheridge (1995).

Thus, important anatomical and taxonomic questions concerning these characters remain: 1) Is the size of the m. *puboisquiotibilis* scorable with only two character states: normal and hypertrophied? Or is variation continuous? 2) Is there a close relation between the hypertrophied m. *flexor tibialis internus* and the patch of the enlarged proximal postfemoral scales? 3) are these muscular characters exclusive to any of the many *Liolaemus* groups?

Focusing on these questions, we present in this study an analysis of the afore mentioned characters in 42 species representing each of the groups of *Liolaemus* proposed by Etheridge (1995), and one species of *Phymaturus*, the sister taxon of *Liolaemus*. We

consider the morphology of the aforementioned muscles, and their distribution in different taxa. We also include a quantification of the area corresponding to the hypertrophy of the *flexor tibialis internus* muscle.

Material and methods

Sixty specimens belonging to 42 species of *Liolaemus* and one species of *Phymaturus* (Appendix 1) were used in the analysis. Macroscopic observations of the muscles were performed following usual laboratory techniques, with the aid of a binocular dissection microscope. Muscles were classified using the terminology proposed by Russell (1988, 1993) and Hoyos (1990) for fore and hind limbs and cranial muscles after Moro and Abdala (1998). Descriptions of the muscles examined are included. Variations are included in Table 1. Discussion is included under remarks.

To obtain the quantification of the area of the hypertrophy of the muscles, photos of the thigh were taken with a digital camera. Photos taken using the same scale were processed using the "Image tool 3.0" program to obtain the hypertrophied m. *flexor tibialis internus* area, which is related to the area of the m. *puboisquiotibialis,* to eliminate the size distortion. The resultant ratios are given in Table 2.

Results and discussion

M. *puboisquiotibialis*: it originates from the ischiopubic ligament. It has parallel fibers, and is very broad. It covers a wide ventral surface of the thigh. Although some separation of the fibers can be seen, in most cases the muscle is composed by only one large portion. It inserts fleshily on the 4th proximal portion of the tibia. At its insertion the m. *puboischiotibialis* is joined by a slip of the m. *flexor tibialis internus*. Both muscles unite in a pennate fashion.

Remarks. We considered, as Etheridge (1995) did, that a hypertrophied m. *puboisquiotibialis* covers the medial head of m. *flexor tibialis internus*. This is the definition of our character state "hypertophied" for this muscle. It should not be taken to mean a larger muscle. The variations of this character can be seen in Table 1.

We observed two character states for this muscle: normal (Fig. 3) and hypertrophied (Fig.1). We agree with Etheridge (1995) with respect to the sexual dimorphism present in *signifer* group. The muscle is hypertrophied in the species of the *boulengeri*, and *wiegmannii* groups, and *L. andinus* Koslowsky*, L. huacahuasicus* Laurent*, L. pulcherrimus* Laurent*,* and *L. multicolor* Koslowsky (*montanus* group), also in agreement with Etheridge´s observations. However, the hypertrophied muscle was also observed in some species of the *chiliensis* group (*L. bitaeniatus* Laurent, *L. robermertensis* Hellmich, and *L. pagaburoi* Lobo & Espinoza), and also in *L. kingii* and *Phymaturus*

somuncurensis Cei & Castro. Thus, this character is not exclusive to any *Liolaemus* group, but it is defined by in two character states.

M. *flexor tibialis internus*: it has two bellies. The most superficial one arises from the ilioischiadic ligament, ventral to the m. *puboischiotibialis*. This belly shares many fibers with the m. *puboischiotibialis* at its origin. It is flat, and covers the deep portion of the m. *flexor tibialis internus* and the m. *puboischiotibialis*. It inserts tendinously on the proximal portion of the tibia, ventral to the insertion of the m. *puboischiotibialis*. The deep portion arises also from the puboischiadic ligament, internal to the origin of the superficial portion; it is cordon-like, rather bulky, and inserts tendinously onto the latero-proximal extremity of the tibia. This muscle is covered dorsally by the m. *puboischiotibialis* and latero-ventrally by the superficial portion of the m. *flexor tibialis internus*.

Remarks. In many species of *Liolaemus* (Table 1), the superficial belly of this muscle has a bulged-out portion**.** It can be seen externally as a ventral protuberance of the thigh (Fig. 1). A patch of enlarged scales sometimes covers this protuberance (Table 1). Our character states were: m. *flexor tibialis internus* hypertrophy absent, small, or bulge-like. The bulge-like structure is observed in the *boulengeri* group. An exception is one male specimen listed as *L. cf. ornatus* from Catamarca province, which has no bulge. Etheridge (1993) designated as the type locality of *L. ornatus* Koslowsky, 3km W of Abra Pampa (Jujuy province). All specimens from that location have a large bulge of the m. *flexor tibialis internus*. Probably our scored differences are due to our examination of two different species. The hypertrophy is small in the *wiegmannii* group. Some species of the *montanus* group *(L. andinus,* and *L. huacahuasicus)* have no hypertrophy, whereas others have the bulge-like structure (e.g., *L. pulcherrimus).* This character is polymorphic in *L. multicolor*, as we have one specimen with, and one without a bulge (Table 1). Meanwhile the character states of hypertrophy**,** absent or small, are seen in the *chiliensis*, and *lineomaculatus* groups, and in *L. kingii*. We disagree with Etheridge (1995) with respect to *L. andinus* and *L. huacahuasicus* of the *montanus* group, which he described to be without hypertrophy.

We agree with Etheridge (pers. comm.) that some fibers of the m. *flexor tibialis internus* insert on the skin, resulting by their contraction in the overlying skin to form a larger bulge.

Considering the ratio between the areas of both muscles (Table 2), we found a range that shows great overlap among different species (Fig. 5, 2). In this range, it makes no sense to recognize only three character states (normal, lightly hypertrophied, and hypertrophied) since they all share the same morphological space. The most logical option is to consider variation in this character as continuous.

The groups formed using traditional character states are not in agreement with any of the phylogenetic groups established so far.

TABLE 1. Taxa and character states of myologycal traits analysed.

Specie	M. *puboisquiotibialis*	M. *flexor tibialis internus* hypertrophy	M. *tibialis anticus*	patch	M. *pterygomandibularis* epimysium
L. abaucan ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. albiceps ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. albiceps ♀	normal	bulge-like	hypertrophied	present	pigmented
L. boulengeri ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. canqueli ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. cf. boulengeri ♀	normal	bulge-like	hypertrophied	present	pigmented
L. cf. boulengeri ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. cuyanus ♂	hypertrophied	bulge-like	hypertrophied	present	no pigmented
L. darwinii ♂	hypertrophied	bulge-like	hypertrophied	present	polimorphism
L. fitzingerii ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. inacayali ♀	normal	bulge-like	hypertrophied	present	pigmented
L. irregularis ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. koslowskyi ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. loboi ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. sagei ♂	hypertrophied	bulge-like	hypertrophied	present	pigmented
L. uspallatensis ♀	normal	bulge-like	hypertrophied	present	pigmented
L. xanthoviridis ♀	normal	bulge-like	hypertrophied	present	no pigmented
L. cf. anomalus ♂	normal	small	normal	present	pigmented
L. cf. ornatus ♂	hypertrophied	small	hypertrophied	present	no data
L. chacoensis ♀	hypertrophied	small	normal	present	pigmented
L. pseudoanomalus ♂	normal	small	normal	present	pigmented
L. salinícola ♂	hypertrophied	small	hypertrophied	present	pigmented
L. scapularis ♂	hypertrophied	small	hypertrophied	present	pigmented
L. bibroni ♀	normal	absent	normal	absent	few pigmented
L. bibroni ♂	normal	absent	normal	absent	few pigmented
L. bitaeniatus ♂	hypertrophied	absent	normal	absent	few pigmented
L. cf andinus ♀	hypertrophied	absent	hypertrophied	absent	no pigmented
L. chaltin ♀	normal	absent	normal	absent	almost without pigmentation
L. chaltin ♂	normal	absent	normal	absent	almost without pigmentation
L. huacahuasicus ♂	hypertrophied	absent	hypertrophied	absent	pigmented
L. lineomaculatus ♀	normal	absent	normal	absent	few pigmented
L. lineomaculatus ♂	normal	absent	normal	absent	few pigmented

to be continued.

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TABLE 1 (continued).

Specie	M. *puboisquiotibialis*	M. *flexor tibialis internus* hypertrophy	M. *tibialis anticus*	patch	M. *pterygomandibularis* epimysium
L. magellanicus ♀	normal	absent	normal	absent	few pigmented
L. magellanicus ♂	normal	absent	normal	absent	few pigmented
L. multicolor ♀	normal	absent	hypertrophied	absent	pigmented
L. multicolor ♂	hypertrophied	bulge-like	hypertrophied	absent	pigmented
L. neuquensis ♀	normal	absent	normal	absent	almost without pigmentation
L. neuquensis ♂	normal	absent	normal	absent	almost without pigmentation
L. petrophilus ♂	normal	absent	normal	absent	few pigmented
L. puna ♀	normal	absent	normal	absent	almost without pigmentation
L. puna ♂	normal	absent	normal	absent	almost without pigmentation
L. robertmertensis ♂	hypertrophied	absent	normal	absent	no pigmented
L. escarchadosi ♀	normal	absent	normal	absent	few pigmented
L. escarchadosi ♂	normal	absent	normal	absent	few pigmented
L. talampaya ♀	normal	absent	normal	absent	almost without pigmentation
L. talampaya ♂	normal	absent	normal	absent	pigmented
L. yanalcu ♂	normal	absent	normal	absent	almost without pigmentation
L. zullyi ♀	normal	absent	normal	absent	almost without pigmentation
L. zullyi ♂	normal	absent	normal	absent	almost without pigmentation
L. kingii ♂	hypertrophied	bulge-like	normal	absent	few pigmented
L.cf. pulcherrimus ♂	hypertrophied	bulge-like	hypertrophied	absent	pigmented
L. bibroni ♂	normal	small	normal	absent	few pigmented
L. ceii ♀	normal	small	normal	absent	few pigmented
L. elongatus ♀	normal	small	normal	absent	few pigmented
L. hatcheri ♀	normal	small	normal	absent	few pigmented
L. hatcheri ♂	normal	small	normal	absent	few pigmented
L. pagaburoi ♂	hypertrophied	small	normal	absent	few pigmented
Phymaturus sp ♂	hypertrophied	small	normal	absent	no pigmented
Diplolaemus darwinii ♂	hypertrophied	absent	normal	absent	no pigmented
Iguana iguana ♂	normal	absent	normal	absent	few pigmented

FIGURE 1–2. 1, *Liolaemus darwinii*; m. *flexor tibialis internus* with a bulge-like hypertrophy; m. *tibialis anticus* with a blade-like hypertrophy. 2, *Liolaemus neuquensis*; normal m. *tibialis anticus*
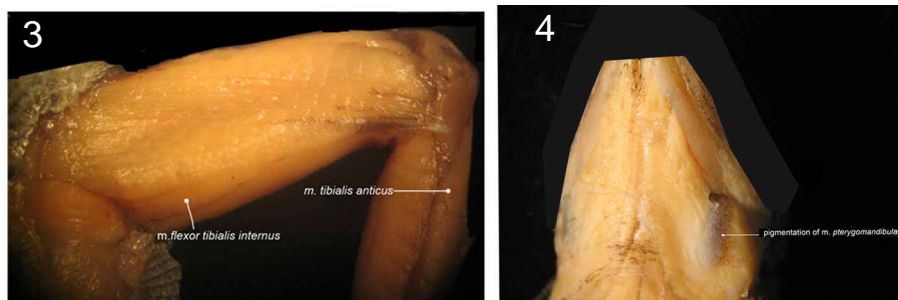

F**IGURE 3–4.** 3, *Liolaemus talampaya*; normal m. *flexor tibialis internus*. 4, *Liolaemus sagei*; Pigmented m. *pterygomandibularis*.

The underlying muscle may not bulge out the femoral patch although no species has a bulge without a femoral patch. In other words, members of the *boulengeri* group have a femoral patch, which usually but not always, is bulged out by the underlying muscle. It could also be inferred that both *L. anomalus* and *L. pseudoanomalus*, have femoral patches but no bulges (Table 1), the femoral scales being somewhat larger proximally, they grade gradually into smaller scales distally, so that there is no well marked "patch". This condition is not unlike that found in *L. hatcheri*.

M. *tibialis anticus:* it originates fleshly from the anterolateral internal face of the tibia, which is almost completely covered by the origin area of this muscle. It is a rather bulky muscle that inserts by a well-developed tendon on the proximal region of the metatarsal I.

TABLE 2. Areas (mm²) of m. *puboischiotibialis* and m. *flexor tibialis internus* and index of ratio between them.

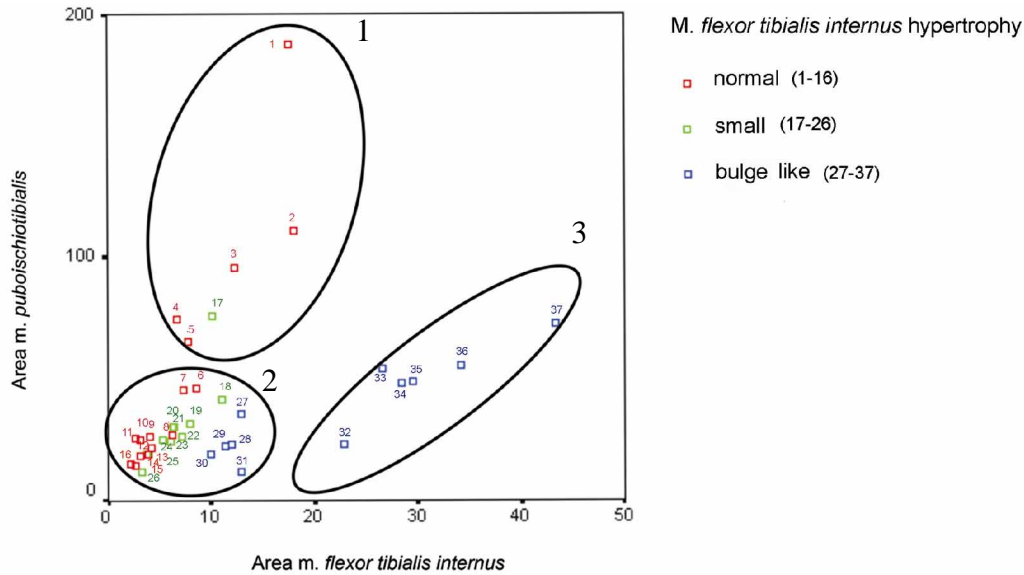| Figure 5	Species	Area m. *flexor tibialis interno*	Area m. *pub-oischiotibialis*	Index
1	*Iguana iguana*	17,6	187,78	11,0070339976553
2	*Liolaemus cei*	18,05	111,18	6,1595567867036
3	*Liolaemus zullyi*	12,34	96,03	7,78200972447326
4	*Liolaemus talampaya*	6,7	74,8	11,1641791044776
5	*Liolaemus talampaya*	7,74	65,06	8,40568475452196
6	*Liolaemus huacahuasicus*	8,53	45,99	5,3915592028136
7	*Liolaemus escarchadosi*	7,26	45,65	6,28787878787879
8	*Liolaemus petrophilus*	6,17	27,01	4,37763371150729
9	*Liolaemus neuquensis*	4,07	26,52	5,18095238095238
10	*Liolaemus lineomaculatus*	3,16	25,37	8,02848101265823
11	*Liolaemus robertmentensis*	2,68	25,86	9,64925373134328
12	*Liolaemus escarchadosi*	4,2	21,76	6,51597051597052
13	*Liolaemus bitaeniatus*	3,94	19,11	4,8502538071066
14	*Liolaemus magellanicus*	3,08	18,78	6,0974025974026
15	*Liolaemus chaltin*	2,66	14,68	5,5187969924812
16	*Liolaemus puna*	2,14	15,16	7,08411214953271
17	*Liolaemus elongatus*	10,05	75,76	7,53830845771144
18	*Liolaemus salinícola* ♀	11,06	41,27	3,73146473779385
19	*Liolaemus anomalus*	7,93	31,14	3,95964691046658
20	*Liolaemus hatcheri*	6,16	30,22	4,90584415584416
21	*Liolaemus albiceps* ♀	6,31	30,68	4,8621236133122
22	*Liolaemus scapularis*	7,22	26,12	3,61772853185596
23	*Liolaemus bibroni*	6,1	24,73	4,05409836065574
24	*Liolaemus pseudoanomalus*	5,26	24,82	4,71863117870722
25	*Liolaemus chacoensis*	3,71	18,84	5,07816711590297
26	*Liolaemus pagaburoi*	3,23	11,77	3,64396284829721
27	*Liolaemus multicolor*	12,92	35,34	2,73529411764706
28	*Liolaemus boulengeri* ♂	11,99	22,95	1,91409507923269
29	*Liolaemus abaucan* ♂	11,3	22,31	1,97433628318584
30	*Liolaemus inacayali*	9,97	19,01	1,906720160448144
31	*Liolaemus darwinii*	12,92	12,15	0,940402476780186
32	*Liolaemus salinícola* ♂	22,81	23,1	1,01271372205173
33	*Liolaemus albiceps* ♂	26,6	53,93	1,01271372205173
34	*Liolaemus canqueli*	28,45	47,98	1,68646748681898
35	*Liolaemus fitzingeri*	29,47	48,85	1,65761791652528
36	*Liolaemus sagei*	34,18	55,44	1,62200117027501
37	*Liolaemus cuyanus*	43,4	72,36	1,66728110599078

FIGURE 5. Ratio between areas of m. *puboischiotibialis* and m. *flexor tibialis internus*. m. *flexor tibialis internus* hypertrophy: 1. Absent; 2. Small; 3. Bulge-like

Remarks. In many species of *Liolaemus* (Table 1), the insertion of the m. *tibialis anticus* is hypertrophied in relation to a blade-like hypertrophy of the tibia (Fig. 2).

Our results are totally congruent with Etheridge (1995). The species of the *signifer* group, (*L. cf. anomalus*, *L. pseudoanomalus*); the *nitidus* group (i.e. the *chiliensis* (Lesson), and *lineomaculatus groups*), and *L. kingii,* have a normal muscle. *L. chacoensis* has a normal muscle also. This character state includes *L. chacoensis* within the *chiliensis* group, supporting Etheridge's (1995) view, in contrast to those of Laurent (1983), Schulte (2000), Lobo and Abdala (2002), Morando (2004), and Abdala (2005) who include *L. chacoensis* within the *boulengeri* group. The species of the *montanus* group, including its subset, the *boulengeri* group, have a hypetrophied muscle. The character is exclusive of the *Liolaemus montanus* group (sensu Etheridge 1995).

M. *pterygomandibularis*: it originates on the external ventral surface of the anterior end of the epipterygoid by means of a clearly visible, strong and wide tendon. It runs ventral to the pterygoid, and is pear-shaped and very bulky at its posterior end. The muscle inserts on the ventromedial surface of the retroarticular process of the jaw.

Remarks. In many *Liolaemus* species, the perimysium of this muscle is very pigmented (Fig. 4). Some species have the perimysium lightly pigmented, and others have only very few pigmented points (Table 1). Most species of the *boulengeri* group present the epimysium very pigmented, except in *L. darwinii* (with both state characters, polymorphism), *L cuyanus* and *L. xanthoviridis* Cei & Scolaro. Etheridge (2000) reported the perimysium without pigmentation in *L. cuyanus*. Most species of the *montanus* group have a strongly pigmented perimysium, being absent only in *L. cf. andinus*. *Liolaemus*

kingii and the *lineomaculatus* group have the m. *pterygomandibularis* perimysium ligthly pigmented, and this is the case also for the *chiliensis* group. However it is very pigmented in *L. talampaya* Avila *et al.* and without pigmentation in *L. robermertensis* (both of the *L. chiliensis* group). Our results are not entirely congruent with those of Etheridge (1995), i.e., the perymysium is strongly pigmented in most, but not all members of the *signifer* group. In addition, it is also strongly pigmented in at least one species of the *nitidus* group.

General remarks

The analyzed samples show that variation in the muscular character is much more gradual than previously recognized. The only exception is the insertion of the m. *tibialis anticus* hypertrophied in relation to a bladelike hypertrophy of the tibia, which characterizes the *montanus* group of Etheridge (1995). Although the coding we used seems more complex, we think that it shows more precisely how subtle myology varies among the many different species of the genus. This continuity in myologycal characters makes them quite ambiguous, requiring the use of more aggressive search strategies for their cladistic analysis.

Acknowledgments

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Appendix 1

FML   Fundación Miguel Lillo
MCN   Museo de Ciencias Naturales
PT   Proyecto Tupinambis
ACUNSA   Anatomía Comparada Universidad Nacional de Salta

Diplolaemus darwinii: FML 16351. 48 km al Sur de Cerro Alto, por ruta provincial 23, camino a Comayo, departamento de Pilcaniyeu, Río Negro.
Iguana iguana without data.
Liolaemus abaucan: FML 25851–25856. Río Abaucan (S 27º 55'; O 67º 37'), departamento Tinogasta, Catamarca.
Liolaemus albiceps: MCN 668–675. Camino al Acay desde Estación Muñano, 8-9 km. 4100- 4200 m. Salta.
Liolaemus bibroni: FML 16345–346, 19 km al Oeste de Ingeniero Jacobacci, sobre ruta provincial 23, departamento 25 de Mayo, Río Negro.
Liolaemus bitaeniatus: FML 16772–779. Sierra de Medina, departamento de Burruyacú, Tucumán
Liolaemus boulengeri: FML 16334. 1 km de bifurcación de ruta nacional 40 y ruta provincial 17, sobre ruta provincial 17, camino a Corcovado, departamento de Languiñeo, Chubut.
Liolaemus canqueli: FML 16335. 11 km al Este de Pocitos de Quichaura, departamento Languiñeo, Chubut.
Liolaemus ceii: FML 16348–350. 1 km al Este de las puertas del Parque Nacional Laguna Blanca, departamento Zapala, Neuquén.
Liolaemus cf andinus: FML 16838–843. Río el Balcón. Catamarca.
Liolaemus cf. boulengeri: FML 16369–374. Tres Cerros, departamento de Puerto Deseado, Santa Cruz.
Liolaemus cf. elongatus: FML 16347, 27.7 km al Sur de Ingeniero Jacobacci, sobre ruta provincial 6, departamento 25 de Mayo, Río Negro.
Liolaemus cf ornatus: FML 16846. Laguna de Antofagasta, Antofagasta de la Sierra, departamento Antofagasta de la Sierra**,** Catamarca.
Liolaemus cf. pseudoanomalus: FML 16336–337. La laja, departamento Albardón, San Juan.
Liolaemus chacoensis: FML 28881–21883 Caspi Corral departamento Figueroa, Santiago del Estero.
Liolaemus chaltin: MCN 233–234. 2 km al Norte de Abra Pampa (S 22°41'819''; O 65°43'532''; 3510 m), departamento de Cochinoca, Jujuy.
Liolaemus darwinii: FML 13252–358. Valle Fértil, departamento de Valle Fértil, San Juan.
Liolaemus escarchadosi: MCN 1521–1533. Cordón de Los Escarchados, camino entrando por Estancia "La Martina", frente a Laguna "Los Escarchados" (S 50°22.471'; O 71°35.578'; 830 m), Santa Cruz.
Liolaemus fitzingerii: FML 16359–364. Gruta de Lourdes, Puerto Deseado, departamento Puerto Deseado, Santa Cruz.
Liolaemus hatcheri: MCN 838–845. Cerro Beltza (S 47° 59.617'; O 71°41.187'); Río Chico departamento de Río Chico, Santa Cruz.
Liolaemus huacahuasicus: FML 16826–836. Huaca Huasis (S 26°39'28.3''; O 65°44'36.4''), departamento Tafí Viejo, Tucumán.
Liolaemus inacayali: FML 16339–40. A 2.3 km al Sur de la intersección de ruta provincial 76 y 23, por ruta provincial 76, a 3.4 km al Sur de Ingeniero Jacobacci, departamento 25 de Mayo. (S 41° 20'022''; O 69° 28'23.3'', 898 m), Río Negro.
Liolaemus irregularis: PT 3367. 5 km al Oeste de San Antonio de los Cobres, departamento Los Andes, Salta.

Liolaemus kingii: FML 16343–344. 11 km al Este de Pocitos de Quichaura, departamento Languiñeo. FML 16342. 4 km al Oeste de la intersección entre ruta nacional 40 y ruta provincial 12, Esquel, departamento Futaleufú, Chubut.

Liolaemus koslowskyi: FML 16805–809. Salar de Pipanaco, departamento de Pomán, Catamarca.

Liolaemus lineomaculatus: MCN 879–881. Perito Moreno, ruta del Oeste (S 46°30.402'; O 71°00.423'); Lago Buenos Aires, departamento de Lago Buenos Aires, Santa Cruz.

Liolaemus loboi: FML 16365–368. Kilómetro 1022, 149 km al Sur de Zapala, sobre ruta nacional 40, departamento Zapala, Neuquén.

Liolaemus magellanicus: MCN 852–861. Cordón de Los Escarchados, Camino entrando por La Martina (S 50°22.702'; O 71°36.868'; 960 m); Santa Cruz.

Liolaemus multicolor: FML 16341. Abra Pampa, departamento Cochinoca, Jujuy.

Liolaemus neuquensis: ACUNSA 753–754. Laguna Las Mellizas, frente a Pozo Geotérmico, 2.5 km. Al Sureste de Termas de Copahue, departamento Ñorquin, Neuquén.

Liolaemus pagaburoi: FML 16793–804. Ciénaga Grande, San José de Chasquivil (S 26° 41'35.5''; O 65° 39'37.5''), departamento Tafí Viejo, Tucumán.

Liolaemus petrophilus: MCN 1346. Cerro frente al Sombrero, departamento Paso de Indios, Chubut.

Liolaemus pseudoanomalus: PT 3876. departamento Castro Barros, 2.5 km al Este de Anillaco, La Rioja.

Liolaemus pulcherrimus: FML 16780–781. Palca de Aparzo, departamento Humahuaca, Jujuy

Liolaemus puna: MCN 225–227. Camino de Humahuaca a Chorcán (S 23°10'761''; O 65°11'709''; 4251 m), Jujuy.

Liolaemus robertmertensis: FML 16790–792. Estancia Río Blanco, 30 km al Sur de Andalgalá, departamento Pomán, Catamarca

Liolaemus sagei: FML 16375–379. 1 km al Este de las puertas del Parque Nacional Laguna Blanca, departamento Zapala, Neuquén.

Liolaemus salinícola: FML 16872–789. Medanitos por ruta 34 entre Fiambalá y Palo Blanco, departamento de Tinogasta, Catamarca.

Liolaemus scapularis: PT 4131. San Antonio 40 km Sur de Santa Maria sobre ruta Nacional 40, departamento Santa Maria, Catamarca.

Liolaemus talampaya: ACUNSA 216–233. Talampaya, La Rioja.

Liolaemus uspallatensis: FML 16474–475. Barreal Blanco, departamento Iglesias, San Juan.

Liolaemus xanthoviridis: FML 16338. 100 km al Norte de Camarones, departamento Florentino Ameghino, Chubut.

Liolaemus yanalcu: MCN 926. Camino al Acay desde estación Muñano. (5–6 km) departamento de Los Andes, Salta.

Liolaemus zullyi: MCN 1539–1541. 37 km al Sur de Los Antiguos, camino a Monte Cevallos (S 46° 46.237'; O 71°45.200'); departamento de Lago Buenos Aires, Santa Cruz.

Phymaturus antofagastensis: FML 16767-771. La Gruta, por ruta provincial 45, 20 km antes de Paso San Francisco, departamento de Tinogasta, Catamarca.