Skeletal variation within the *darwinii* group of *Liolaemus* (Iguania: Liolaemidae): new characters, identification of polymorphisms and new synapomorphies for subclades

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Abstract. Fifty-five skeletal characters (continuous and discrete) were analyzed for species of the *L. darwinii* group: *L. albiceps*, *L. chacoensis*, *L. grosseorum*, *L. irregularis*, *L. koslowskyi*, *L. lavillai*, *L. ornatus*, *L. quilmes*, plus *L. inacayali* (*L. telsen* group) and *L. scapularis* (*L. wiegmannii* group). We report polymorphic intraspecific variation that has not previously been taken into account and we describe 21 new characters that provide original information across the group. We detected several morphological synapomorphies for the *darwinii* group and subclades. The enclosure of Meckel's cartilage by a dentary outgrowth on lingual side of lower jaw (a synapomorphy of the subgenus *Liolaemus sensu stricto* and of the *Phymaturus patagonicus* group) also occurs within the *L. darwinii* group. The morphology of maxillary teeth with three conspicuous cusps may be a potential synapomorphy of the subgenus *Eulaemus*. The morphology of maxillary teeth may have adaptive value. Characters that were studied in other groups of lizards were informative for *Liolaemus*.

Keywords. Cranial skeleton, postcranial skeleton, *L. boulengeri* group, evolution.

INTRODUCTION

Osteological characters are used for phylogenetic analyses and reconstructions and for investigating environmental adaptations because skeletons exhibit a very wide range of morphological variation at supraspecific levels. Detailed examples that illustrate their use in systematic and phylogenetic studies within Iguania are found in Etheridge (1965, 1967), de Queiroz (1987), Estes et al. (1988), Etheridge and de Queiroz (1988), Lang (1989) and Frost and Etheridge (1989), among others. Although this information was primarily used in phylogenetic reconstructions, it is also important for future works in studies of comparative biology, as it can document evolutionary changes of characters in the context of any hypothesized selective regime.

Lizards of the Family Liolaemidae extend from the Andes through Bolivia, Peru and Chile to the coast of Tierra del Fuego in Argentina (Donoso-Barros, 1966; Cei, 1986, 1993; Lobo and Quinteros, 2005; Abdala, 2007). Currently, this family has 298 species (Uetz, 2016) and comprises three genera: *Ctenoblepharys*, *Liolaemus*, and *Phymaturus* (Etheridge, 1995; Frost et al., 2001; Schulte et al., 2003; Espinoza et al., 2004). Within the subgenus *Eulaemus* of *Liolaemus*, there is the species-rich *L. boulengeri* group (Etheridge, 1995; Abdala, 2007), which is characterized by having a group of enlarged scales at the back of the thigh, so it is also called the "patch group". As a result of taxonomic and phylogenetic studies of the *L. boulengeri* group, numerous subgroups within it have been proposed (Avila et al., 2006; Abdala, 2007). One of these is the *Liolaemus darwinii* clade, which was

defined by Etheridge (1993) based on the presence of posterior teeth with straight-edged crowns and marked sexual dichromatism in which males exhibit a more colorful dorsal color pattern than females. This group was inferred to be monophyletic in different analyses, based on morphological and/or molecular characters (Abdala, 2007; Avila et al., 2006; Fontanella et al., 2012; Olave et al., 2014). Following Abdala's total evidence hypothesis (2007), the *L. darwinii* group consists of two clades (*L. grosseorum* and *L. ornatus* clades) and of five species basal to these ones (*L. abaucan*, *L. espinozai*, *L. koslowskyi*, *L. quilmes* and *L. uspallatensis*). The *L. ornatus* clade comprises 6 species (*L. albiceps*, *L. crepuscularis*, *L. calchaqui*, *L. irregularis*, *L. lavillai* and *L. ornatus*), which have a wide distribution in the Puna, Montes de Sierras y Bolsones and the northern part of the ecoregion of Monte de Llanuras y Mesetas of Argentina (Burkart et al., 1999). Lizards in this group are distinguished by being viviparous and having a large number of precloacal pores in females.

Information about osteological features of liolaemid lizards appears in detailed descriptions of the head skeleton of *Liolaemus lutzae*, *L. occipitalis*, and *L. signifer* (Beurman and Vieira, 1980; Simoes-Lopes and Krause, 1988). In addition, studies of the appendicular skeleton of *L. occipitalis* (Keller and Krause, 1986) and the skeleton of *L. lutzae* and *L. multiformis simonsii* (Beurman and Vieira, 1980) have been published. Osteological character states for *Liolaemus* and *Phymaturus* in the context of iguanian phylogenetic analysis at the generic level were recorded by Etheridge and de Queiroz (1988). Lobo and Abdala (2001; 2002) described the variation found in the skeleton of 24 species. They demonstrated the phylogenetic information contained in those characters, recovering main clades and subclades of *Liolaemus* formally recognized in the literature. Additional skeletal characters were reported recently by Núñez et al. (2003) in the description of two new taxa (*L. manueli* and *L. torresi*). Da Silva and Verrastro (2007) described the axial skeleton of *L. arambarensis* and González-Marín and Hernando (2013) described the postcranial osteology of *L. azarai*.

In the present contribution we report new characters and polymorphisms and we provide additional informative characters for the *Liolaemus darwinii* group and subclades therein. We report the evolution of some characters of special interest such as the enclosure of Meckel's cartilage (a character traditionally studied in iguanian lizards), the morphology of maxillary teeth, the cartilaginous extremity of cervical rib IV, and the bladelike process on the posterior distal tibia mentioned by Etheridge (1995) and Lobo and Abdala (2001).

MATERIALS AND METHODS

A total of 30 adult specimens of the *Liolaemus darwinii* group were studied (Appendix A). The species included were *L. albiceps*, *L. chacoensis*, *L. grosseorum*, *L. irregularis*, *L. koslowskyi*, *L. lavillai*, *L. ornatus*, and *L. quilmes*. We also included skeletons of *L. scapularis* (representing the *L. wiegmannii* group) and *L. inacayali* (*L. telsen* group) for outgroup comparisons, and examined characters described in Lobo and Abdala (2001, 2002) for 24 taxa belonging to different groups of *Liolaemus*. We studied specimens deposited in biological collections and collected some additional specimens of *L. ornatus*, *L. scapularis*, and *L. quilmes*, which were sacrificed by injection with 10% sodium pentothal. They were fixed in 10% formalin and finally preserved in 70% ethanol. They are deposited in the herpetological collection of the Museo de Ciencias Naturales of the Universidad Nacional de Salta (MCN), Instituto de Bio y Geociencias del NOA, and the Fundación Miguel Lillo (FML). The skeletons were prepared following the technique of differential staining of bone and cartilage (Wassersug, 1976). This allows the observation of cartilaginous structures that are not visible in the dry skeletons. Measurements were taken using digital calipers, 0.01 mm precision, under a stereoscopic microscope. In the case of smaller structures, the measurements were taken using a micrometer eyepiece. Nomenclature of bones, processes and foramina follow de Queiroz (1982), Keller and Krause (1986), Frost (1992), Etheridge (2000), Lobo and Abdala (2001), Lobo (2001, 2005) and Torres-Carvajal, (2004). In total, 55 characters, 19 continuous and 36 discrete, of the cranial and postcranial skeleton were examined. The discrete characters were coded as non-polymorphic binary, polymorphic binary, non-polymorphic multistate, and polymorphic multistate.

We add our data matrix to that of Abdala's (2007) Total Evidence analysis and performed a new phylogenetic analysis. Character evolution mapping and the optimization of new characters were performed using TNT (Goloboff et al., 2003) over the resulting tree (same topology as recovered by Abdala 2007; Fig. 1). We follow Abdala (2007) because it includes the taxa studied here (instead of Fontanella et al., 2012 or Olave et al., 2014; whose studies lacked many of the species of interest). Data on diet were taken from the literature (Aun and Martori, 1998; Espinoza et al., 2004; Semhan et al., 2013).

RESULTS

All morphological variation observed in the skeletons of *Liolaemus* is summarized in the following list of char-

acters, indicating the state of the character in each case. Variation of discrete and continuous characters is presented in Tables 1 and 2, respectively.

Updated list of osteological characters (modified from Lobo and Abdala, 2002)

1. Number of scleral ossicles: (0) 15; (1) 14; (2) 13. Polymorphic multistate.
2. Bones forming parietal foramen: (0) formed mainly by frontal bone; (1) mainly by parietal bone; (2) both bones participate approximately equally. Polymorphic multistate.
3. Shape of parietal foramen: (0) with regular edges; (1) with irregular edges. Polymorphic binary.
4. Ceratohyal process: (0) gradually widened; (1) abruptly widened; (2) hook-shaped. Polymorphic multistate.
5. Distal ending of ceratobranchial II: (0) narrow; (1) widened. Polymorphic binary.
6. Anterior process of arytenoid: (0) reaches the level of the anterior process of the cricoid; (1) does not reach that level. Polymorphic binary.

7. Number of tracheal rings. Continuous (Table 2).
8. Number of incomplete tracheal rings / total number of rings. Continuous (Table 2).
9. Number of pterygoid teeth. Continuous (Table 2).
10. Number of maxillary teeth. Continuous (Table 2).
11. Number of modified anterior maxillary teeth (heterodonty): in most species the anterior-most teeth of the maxilla are conical, elongated, and exhibit only one cusp. Continuous (Table 2).
12. Maxillary tooth morphology I (Fig. 2): (0) crowns with their anterior and posterior margins divergent, expanded crowns; (1) crowns with anterior and posterior margins straight. Non-polymorphic binary.
13. Maxillary tooth morphology II: (0) crowns without differentiated cusps, (1) three conspicuous cusps (all species studied here). Species of the *L. nigromaculatus* group (subgenus *Liolaemus sensu stricto*) were reported as having broad maxillary teeth without secondary cusps (Lobo, 2001). Non-polymorphic binary.
14. Meckel's groove (Fig. 3): (0) open; (1) fused, Meckel's cartilage is hidden by an extensive outgrowth of the dentary bone. This last character state was described as an apomorphy of the *L. chiliensis* group (sub-

Table 1. Discrete osteological characters and their variation within the *Leiolaemus darwinii* group. Intraspecific variation indicated by in brackets surrounding the relevant carácter states. Polymorphism in characters 1, 4, and 20, have not previously been reported.

	1	2	3	4	5	6	12	13	14	15	16	18	19	20	21	22	23	33
L. albiceps	[02]	0	[01]	1	0	[01]	0	1	0	1	[01]	1	0	0	1	1	[12]	0
L. chacoensis	[12]	[02]	[01]	1	0	0	1	1	1	[01]	[01]	1	0	0	[01]	0	[12]	0
L. grosseorum	2	0	0	1	0	0	1	1	1	1	[01]	1	0	0	[01]	1	[12]	0
L. inacayali	[12]	[01]	0	2	0	0	0	1	0	1	0	1	0	0	1	1	2	0
L. irregularis	1	0	[01]	1	0	[01]	0	1	0	1	[01]	1	0	0	[01]	1	2	0
L. koslowskyi	[12]	[012]	[01]	1	[01]	1	0	1	1	1	[01]	1	[01]	0	[01]	1	[12]	0
L. lavillai	1	1	1	1	0	0	1	1	1	1	1	1	[01]	0	1	1	1	0
L. ornatus	1	[12]	1	1	0	0	0	1	0	1	1	1	0	0	0	1	[123]	0
L. quilmes	1	[02]	1	[01]	0	[01]	1	1	1	1	[01]	1	0	[01]	[01]	1	1	0
L. scapularis	2	[02]	0	2	0	1	1	1	0	1	0	1	[01]	1	1	1	[12]	0

	34	35	36	37	38	39	41	45	46	47	48	49	50	51	52	53	54	55
L. albiceps	0	1	0	[01]	0	1	[012]	0	[01]	1	0	0	0	0	[01]	0	1	0
L. chacoensis	0	0	0	[01]	[01]	0	2	[01]	[01]	1	1	[01]	1	0	1	1	1	[01]
L. grosseorum	0	1	1	1	0	0	2	1	1	1	0	0	0	0	1	1	0	[01]
L. inacayali	0	1	0	1	1	0	2	0	1	0	0	0	0	0	1	1	0	0
L. irregularis	0	1	0	0	1	1	2	1	[01]	1	0	0	0	0	[12]	[01]	0	0
L. koslowskyi	0	1	0	1	1	0	0	[01]	[01]	1	0	0	0	0	[01]	1	1	1
L. lavillai	0	0	0	0	1	0	2	1	[01]	1	0	0	0	0	1	0	1	0
L. ornatus	0	1	1	0	0	0	0	1	1	1	0	1	0	[01]	[01]	[01]	1	0
L. quilmes	0	1	1	0	0	0	[02]	1	[01]	1	1	1	[01]	[01]	[01]	[01]	1	0
L. scapularis	0	1	1	1	0	0	2	1	[01]	1	0	0	0	0	1	[01]	0	0

Table 2. Continuous osteological characters (see text for character descriptions). Above: min-max. below: mean + standard deviation.

Chars	Liolaemus albiceps (N=4)	Liolaemus chacoensis (N=4)	Liolaemus grosseorum (N=2)	Liolaemus inacayali (N=1)	Liolaemus irregularis (N=4)	Liolaemus koslowskyi (N=3)	Liolaemus lavillai (N=2)	Liolaemus ornatus (N=4)	Liolaemus quilmes (N=5)	Liolaemus scapularis (N=2)
7	53-67 (61; 6)	52-52 (52; 0)	55-67 (61; 9)	52	56-75 (62; 9)	52-63 (59; 6.3)	49-60 (55; 7.8)	41-65 (55; 10.6)	47-57 (52; 5)	54-57 (56; 2.1)
8	0.2-0.3 (0.3; 0.04)	0.19-0.4 (0.3; 0.1)	0.23-0.25 (0.2; 0.01)	0.3	0.25-0.32 (0.3; 0.03)	0.16-0.27 (0.2; 0.05)	0.15-0.31 (0.2; 0.1)	0.2-0.39 (0.3; 0.08)	0.25-0.4 (0.3; 0.07)	0.17-0.26 (0.2; 0.06)
9	5-8 (7; 1.4)	0-4 (2.3; 1.7)	0-3 (1.5; 2.1)	7	5-6 (5.8; 0.7)	3-5 (4.3; 1.2)	4-4 (4; 0)	2-6 (3; 2)	1-3 (2.6; 0.9)	2-4 (3; 1.4)
10	16-18 (17; 1)	15-20 (17.6; 2)	16-18 (14; 1.4)	14	18-18 (18; 0)	16-16 (16; 0)	14-14 (14; 0)	16-16 (16; 0)	15-18 (17; 1.1)	12-14 (13; 1.4)
11	0-0 (0; 0)	0-0 (0; 0)	0-0 (0; 0)	0	0-0 (0; 0)	0-0 (0; 0)	0-0 (0; 0)	0-0 (0; 0)	1-1 (1; 1)	2-3 (2.5; 0.7)
17	3-7 (4; 2)	2-4 (3; 1.4)	2-4 (3; 1.4)	5	3-4 (3.5; 0.6)	2-3 (2.7; 0.6)	3-4 (3.5; 0.7)	4.58-5.5 (5; 0.4)	2-2 (2; 0)	3-4 (3.5; 0.7)
24	2.5-4 (3.3; 0.8)	0.3-0.4 (0.4; 0.04)	0.4	0.3	0.34-0.39 (0.38; 0.02)	0.33-0.37 (0.36; 0.02)	0.38-0.4 (0.39; 0.01)	0.36-0.39 (0.37; 0.01)	0.36-0.41 (0.39; 0.02)	0.3-0.4 (0.4; 0.04)
25	0.7-1 (0.8; 0.1)	0.6-0.8 (0.7; 0.08)	0.7-0.8 (0.7; 0.04)	0.7	0.7-0.9 (0.8; 0.06)	0.7-0.9 (0.8; 0.08)	0.8-0.81 (0.78; 0.04)	0.75-0.77 (0.76; 0.01)	0.74-0.85 (0.78; 0.05)	0.72
26	0.2-0.24 (0.21; 0.03)	0.18-0.23 (0.21; 0.02)	0.18-0.21 (0.2; 0.02)	?	0.24-0.3 (0.27; 0.03)	0.22-0.25 (0.24; 0.02)	0.24-0.27 (0.26; 0.02)	0.28-0.3 (0.29; 0.01)	0.19-0.28 (0.24; 0.04)	0.19-0.22 (0.21; 0.02)
27	1.8-3 (2.2; 0.5)	1.5-2.2 (1.8; 0.3)	2.8-3.4 (3.1; 0.5)	2.2	2-2.6 (2.3; 0.3)	1.7-3.5 (2.6; 0.9)	2.5-2.6 (2.6; 0.05)	1.9-3.8 (2.7; 0.9)	1.9-3.1 (2.3; 0.5)	1.7-2.4 (2.1; 0.5)
28	0.03-0.07 (0.05; 0.02)	0.01-0.09 (0.04; 0.04)	0.02-0.02 (0.02; 0)	0.05-0.05 (0.05; 0)	0.03-0.06 (0.05; 0.01)	0.02-0.09 (0.06; 0.04)	0.04-0.06 (0.05; 0.01)	0.04-0.08 (0.05; 0.02)	0.04-0.05 (0.05; 0.01)	0.02-0.06 (0.04; 0.02)
29	0.06-0.19 (0.13; 0.06)	0.1-0.26 (0.19; 0.07)	0.07-0.12 (0.1; 0.04)	0.19-0.19 (0.19; 0)	0.05-0.17 (0.11; 0.07)	0.06-0.19 (0.12; 0.07)	0.07-0.1 (0.09; 0.02)	0.03-0.17 (0.11; 0.06)	0.1-0.18 (0.14; 0.06)	0.05-0.2 (0.13; 0.06)
30	0.23-0.34 (0.29; 0.06)	0.26-0.33 (0.29; 0.03)	0.34-0.34 (0.34; 0)	0.27-0.27 (0.27; 0)	0.31-0.38 (0.34; 0.03)	0.28-0.34 (0.31; 0.03)	0.33-0.33 (0.33-0)	0.24-0.34 (0.28; 0.05)	0.35-0.35 (0.35; 0)	0.31-0.41 (0.35; 0.04)
31	0.04-0.11 (0.08; 0.04)	0.06-0.11 (0.09; 0.03)	0.1-0.1 (0.1; 0)	0.07-0.07 (0.07; 0)	0.05-0.11 (0.08; 0.03)	0.07-0.09 (0.08; 0.01)	0.06-0.07 (0.07; 0.01)	0.08-0.1 (0.09; 0.01)	0.06-0.06 (0.06; 0)	0.06-0.12 (0.08; 0.02)
32	0.76-0.93 (0.84; 0.09)	0.61-1.01 (0.82; 0.17)	0.76-0.79 (0.78; 0.02)	1-1 (1; 0)	0.72-1.04 (0.88; 0.14)	0.54-0.81 (0.66; 0.14)	0.83-0.89 (0.84; 0.04)	0.79-0.94 (0.86; 0.07)	0.84-0.88 (0.86; 0.03)	0.81-0.94 (0.88; 0.06)
40	8-7 (7.25;0.5)	6-3 (4.7;1.3)	5-3 (4;1.4)	6-6 (6; 0)	6-8 (6.7; 0.9)	5-12 (9;3.6)	5-8 (6.5; 2.1)	7-3 (4.7;1.7)	5-5 (5;0)	5-11 (6.6;2.5)
42	-4 (5.7;1.5)	4-4 (4;0)	5-5 (5;0)	4-4 (4;0)	4-6 (4.5; 1)	6-3 (4.67;1.63)	4-5 (4.5; 0.71)	8-7 (7.25;0.5)	7-7 (7;0)	5-4 (4.8;0.5)
43	6-6 (6; 0)	5-6 (5.7; 0.5)	6-6 (6; 0)	6-6 (6; 0)	6-6 (6; 0)	4-6 (4.7; 1.1)	6-6 (6; 0)	5-6 (5.25; 0.5)	5-6 (5.75; 0.5)	3-6 (15.4; 1.3)
44	20-22 (21; 0.8)	20-22 (20.5; 1)	18-20 (19; 1.4)	17-17 (17; 0)	22-24 (23; 1.1)	20-20 (20; 0)	18-18 (18; 0)	20-21 (20.75; 0.5)	18-20 (19; 1.4)	18-21 (19.8; 1.6)

genus *Liolaemus*) and it is the condition exhibited by the *Phymaturus patagonicus* group according to Etheridge (1995), Lobo et al. 2012 (its Fig. 7D). Non-polymorphic binary.

15. Cervical rib III: this rib, when present, is very small and remains cartilaginous. (0) present; (1) absent. Polymorphic binary.

16. Cartilaginous extremity of cervical rib IV (Fig. 4A-B): (0) bifurcated; (1) not bifurcated. Polymorphic binary.

17. Number of postxiphisternal elongated ribs: According to Etheridge (1995), *Liolaemus* species exhibit the most common pattern of postxiphisternal ("inscriptional ribs posterior to xiphisternals"), with their free endings bearing an elongated cartilage. Continuous (Table 2).

18. Posterior process of the sternum: (0) present; (1) absent (all species studied here). State (0) reported only for the *L. pictus* group by Lobo and Abdala (2001). Non-polymorphic binary.
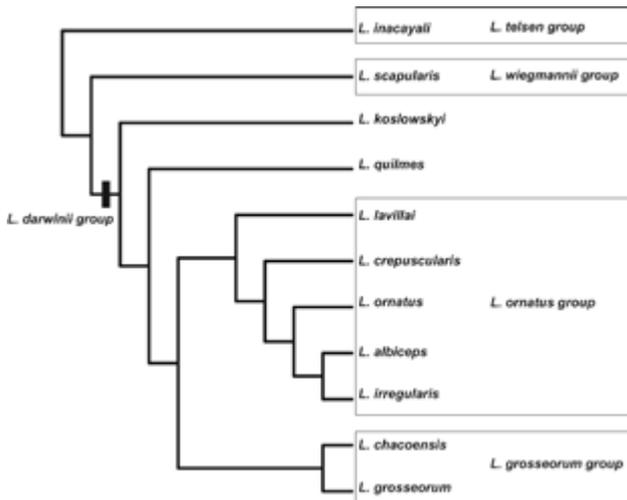
Fig. 1. Phylogenetic relationships recovered for the *Liolaemus darwinii* group.

Fig. 3. Evolution of Meckel's groove within the *Liolaemus darwinii* group. (A) Character states optimized on the recovered topology, (B) Meckel's groove of lower jaw closed, (C) open Meckel´s groove (C). Scale = 2 mm.
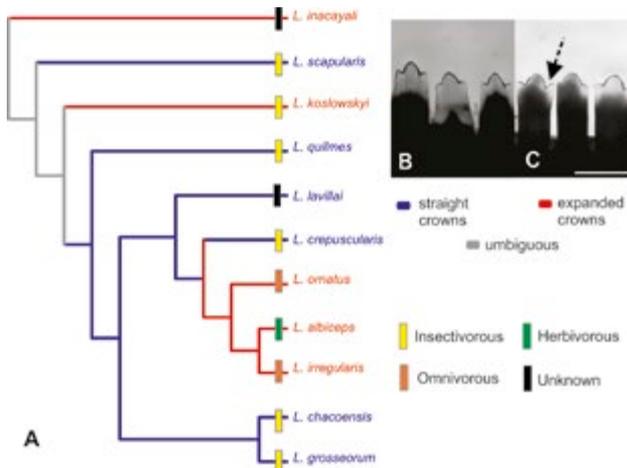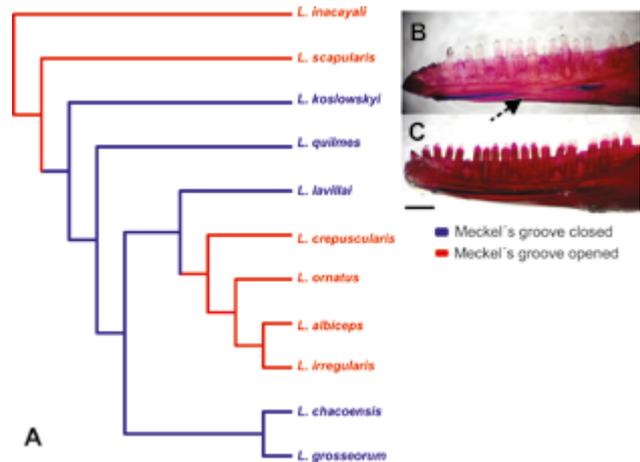

Fig. 2. Evolution of morphology of maxillary crowns and diet within the *Liolaemus darwinii* group. (A) Character states optimized on the topology recovered, (B) maxillary teeth with straight crowns, (C) maxillary teeth with expanded crowns. Dietary data for *L. inacayali* and *L. lavillai* were not found in the literature. Scale = 1 mm.

19. Clavicles: (0) without fenestra; (1) with fenestra. Polymorphic binary.
20. Sternal fenestra (Fig. 4C-D) located in the posterior half of the sternum over the posterior half of interclavicle: (0) single; (1) divided, as described by Etheridge (2000) for species of the *L. wiegmannii* group. Polymorphic binary.
21. The posterior end of hipoischium: (0) expanded; (1) unexpanded. Polymorphic binary.
22. Bladelike process on posterior distal tibia: (0) absent; (1) present. The presence of the bladelike process

on the posterior distal tibia was proposed as a synapomorphy of the *L. montanus* group by Etheridge (1995) and as a synapomorphy of the subgenus *Eulaemus* (including the *L. anomalus* group according to Lobo et al., 2010). Non-polymorphic binary.
23. Caudal vertebrae without "chevron": (0) caudal vertebra I; (1) caudal vertebrae I and II; (2) caudal vertebrae I-III; (3) caudal vertebrae I-IV. Polymorphic multistate.
24. Skull height / skull length. Continuous (Table 2).
25. Skull width / skull length. Continuous (Table 2).
26. Lateral rami of interclavicle / skull length. Continuous (Table 2).
27. Diameter of major coracoid fenestra / diameter of major scapular fenestra. Continuous (Table 2).
28. Preischial length / skull length. Continuous (Table 2).
29. Xiphisternal rod length / skull length. Continuous (Table 2).
30. Clavicle length / skull length. Continuous (Table 2).
31. Maximum clavicle width / skull length. Continuous (Table 2).
32. Sternal width / sternal length. Continuous (Table 2).
33. Orientation of the pubis: (0) facing forward, forming an acute angle with vertebral column; (1) perpendicular to the vertebral column. State (0) only reported for *L. pseudoanomalus* (Lobo and Abdala, 2001). Non-polymorphic binary.
34. Membranes over coracoid fenestrae: (0) without ossification; (1) with ossification. Non- polymorphic binary.
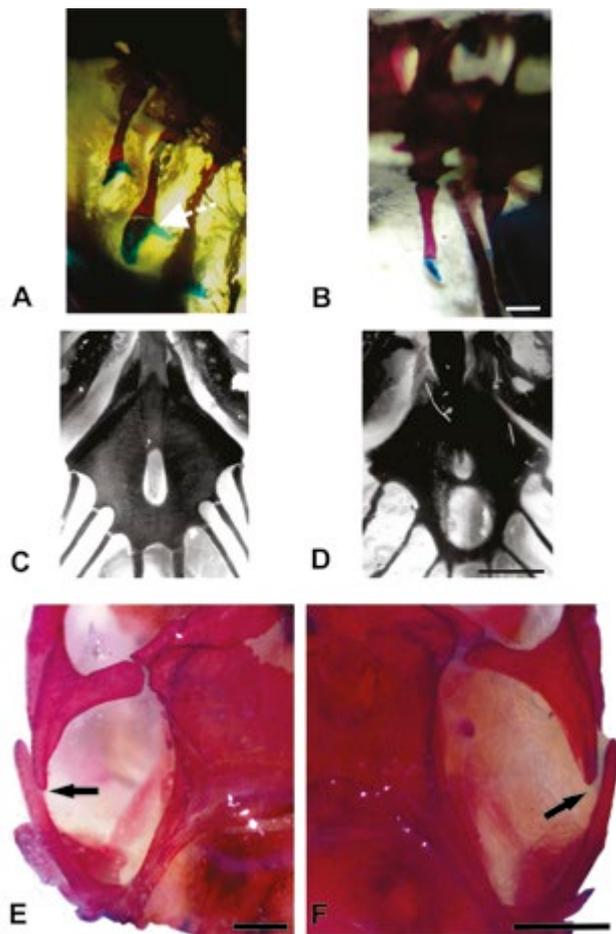
Fig. 4. Skeletal characters exhibiting variation within the *Liolaemus darwinii* group. (A-B) Cartilaginous extremity of cervical rib IV: bifurcate (A) in *L. scapularis* (MCN2431) and non-bifurcate (B) in *L. ornatus* (MCN 3545). Scale = 2 mm. (C-D) Sternal fenestra: single (C) in *L. ornatus* (MCN 3546) and divided (D) in *L. quilmes* (MCN 3524). Scale = 2 mm. (E-F) Temporal fenestra: open, without contact between postorbital and squamosal (E) in *L. ornatus* (MCN 3548) and closed, with contact between postorbital and squamosal (F) in *L. koslowskyi* (MCN 574). Scale = 1mm.

New characters found in the present contribution

35. Temporal fenestra (Fig. 4E-F): (0) open (without contact between postorbital and squamosal); (1) closed (contact between postorbital and squamosal). Non-polymorphic binary.
36. Posterior edge of parietal (Fig. 5A-B): (0) convex; (1) forming a straight margin. Non- polymorphic binary.
37. Posfrontal shape (Fig. 5C-D): (0) triangular; (1) elongated, not triangular. Polymorphic binary.
38. Premaxillary shape (Fig. 5E-F): (0) nasal spine narrow and pars dentalis wide; (1) nasal spine wide and pars dentalis narrow (modified from Frost, 1992). Polymorphic binary.
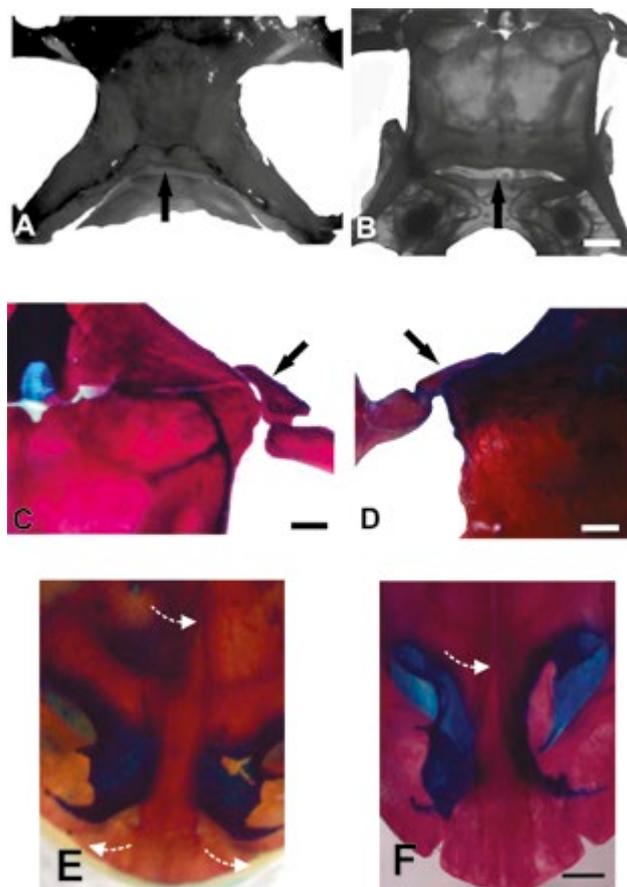
Fig. 5. Skeletal characters exhibiting variation within the *Liolaemus darwinii* group. (A-B) Posterior edge of parietal: convex (A) in *L. irregularis* (MCN 2443) and forming a straight margin (B) in *L. quilmes* (MCN 3527). Scale = 1mm. (C-D) Posfrontal shape triangular (C) in *L. quilmes* (MCN 3527) and elongated (D) in *L. inacayali* (MCN 500). Scale = 1mm. (E-F) Premaxillary shape: nasal spine narrow and pars dentalis wide (E) in *L. albiceps* (MCN 402) and nasal spine wide and pars dentalis narrow (F) in *L. koslowskyi* (MCN 573). Upper arrow indicates the width of the nasal spine and bottom arrows indicate the width of the area of premaxillary teeth. Scale = 2 mm.

39. Otic ramus of squamosal (Fig. 6A-B: (0) otic ramus located over the superior fossa of quadrate; (1) otic ramus inserted in the superior fossa of quadrate. Non-polymorphic binary.
40. Number of labial foramina (lateral view of maxilla). Continuous (Table 2).
41. Disposition of labial foramina (maxilla): (0) L-shaped; (1) forming two parallel rows; (2) forming a unique series in a single line. Polymorphic multistate.
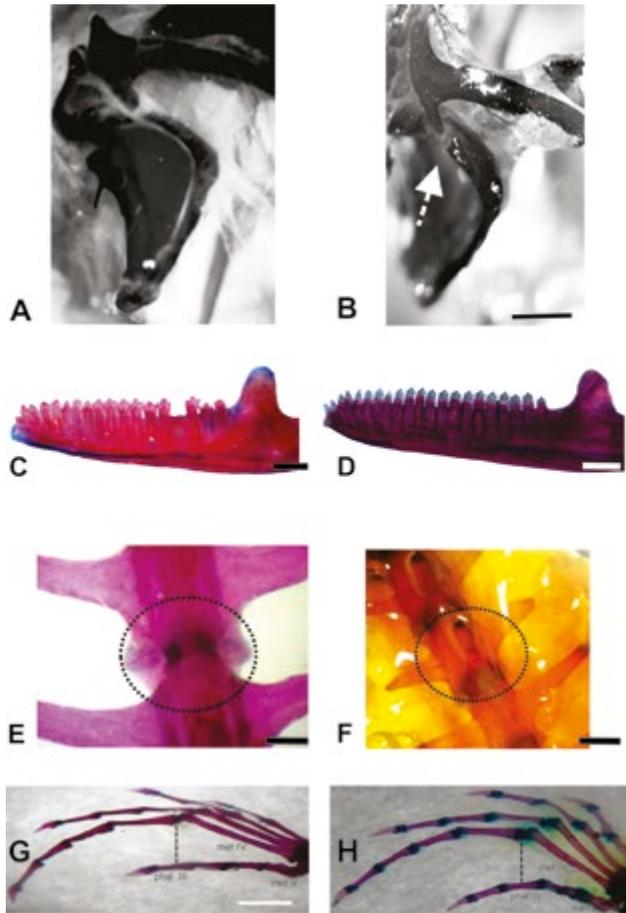42. Number of mental foramina of dentary (lateral view). Continuous (Table 2).

Fig. 6. Skeletal characters exhibiting variation within the *Liolaemus darwinii* group. (A-B) Otic ramus of squamosal located outside to the superior fossa of quadrate (A) in *L. irregularis* (MCN 2436) and otic ramus inserted in the superior fossa of quadrate (B) in *L. grosseorum* (MCN 508). Arrow indicates the insertion of the squamosal in the superior fossa of the quadrate. Scale = 2mm. (C-D) Lower jaw dentition homodont (C) in *L. inacayali* (MCN 500) and heterodont (D) in *L. quilmes* (MCN 3525). Scale = 1mm. (E-F) First chevron condition: incomplete (E) in *L. quilmes* (MCN 3524) and complete (F) in *L. albiceps* (MCN 402). Scale = 3mm. (G-H). Length of metatarsal IV with respect to toe V: reaches phalanx III (G) in *L. irregularis* (MCN 2431) and reaches phalanx II (H) in *L. inacayali* (MCN 500). Scale = 1 mm.

43. Number of premaxillary teeth. Continuous (Table 2).
44. Numbers of dentary teeth. Continuous (Table 2).
45. Lower jaw dentition (Fig. 6C-D): (0) homodont; (1) heterodont. Polymorphic binary.
46. First chevron shape (Fig. 6E-F): Chevron bones appear on anterior caudal vertebrae (Hoffstetter and Gasc, 1969). In *Liolaemus* the first chevron can appear on caudal vertebra III or IV. (0) incomplete; (1) complete. Polymorphic binary.
47. Length of metatarsus IV with respect to toe V (Fig. 6 G-H): (0) reaches phalanx II; (1) reaches phalanx
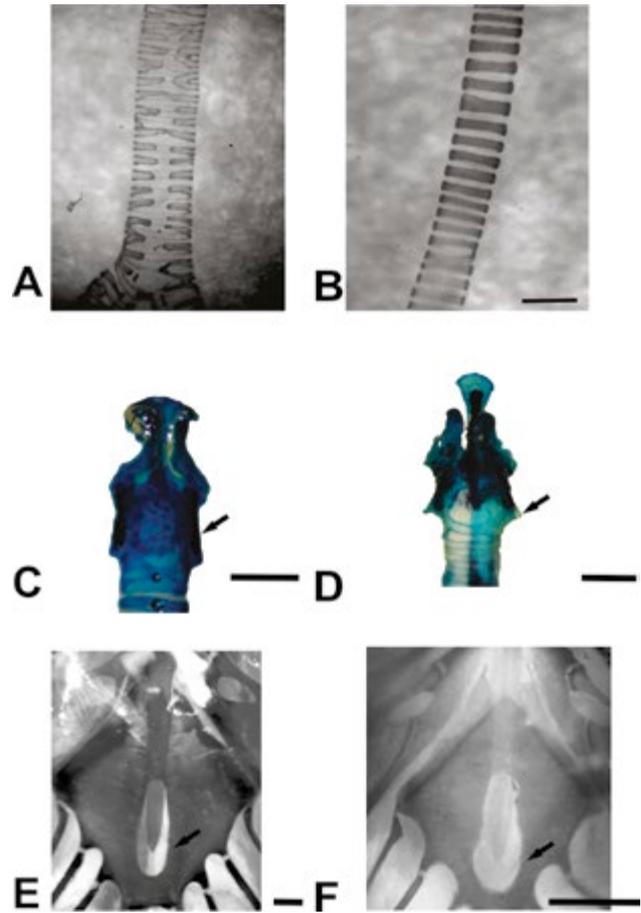

Fig. 7. Skeletal characters exhibiting variation within the *Liolaemus darwinii* group. (A-B) Presence of open intercalated tracheal rings: present (A) in *L. lavillai* (MCN 4351) and absent (B) in *L. grosseorum* (MCN 509). Scale = 1 mm. (C-D) Lateral processes of the cricoid: not pronounced (C) in *L. irregularis* (MCN 2443) and pronounced (D) in *L. albiceps* (MCN 457). Scale = 1mm. (E-F) Sternal fenestra shape: symmetrical not widened (E) in *L. albiceps* (MCN 457) and wider in the posterior half (F) in *L. chacoensis* (MCN 599). Scale = 1mm.

III (modified from Arias, 2012). Non-polymorphic binary.
48. Length of IV metacarpal with respect to finger V: (0) reaches phalanx I; (1) reaches phalanx II. Non-polymorphic binary.
49. Hipoischial fenestra: (0) absent; (1) present. Polymorphic binary.
50. Ischial fenestra (located close to the posterior margin of the ischium): (0) absent; (1) present. Polymorphic binary.
51. Number of sternal ribs: (0) three; (1) four. Polymorphic binary.
52. Number of branches of the xiphisternal rib: (0) three; (1) two; (2) none. Polymorphic binary.
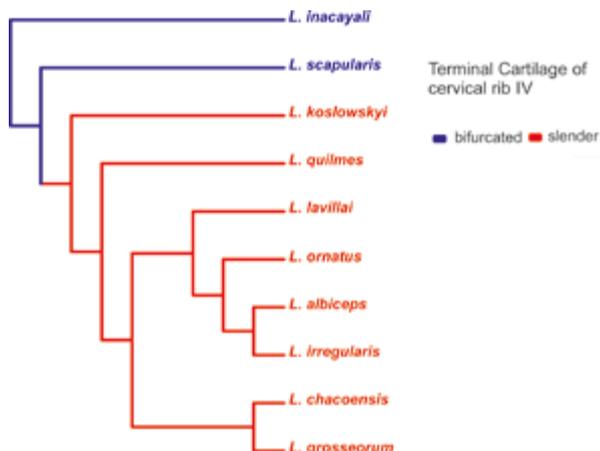
Fig. 8. Evolution of cartilaginous extremity of cervical rib IV. Potential synapomorphy of the *Liolaemus darwinii* group. Recovered Topology of the *L. darwinii* phylogeny. *Liolaemus crepuscularis* is excluded because of the lack of information on this character state.
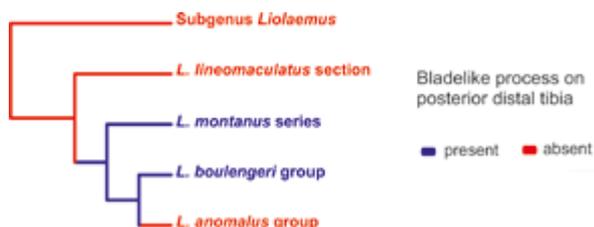

Fig. 9. Evolution of bladelike process on posterior distal tibia in *Liolaemus*. Note the secondary loss in the *L. anomalus* group. Tree modified from Schulte et al. (2000).

53. Open intercalated tracheal rings (Fig. 7A-B): (0) present; (1) absent. Polymorphic binary.
54. Lateral processes of the cricoid (Fig. 7C-D): (0) not pronounced; (1) pronounced. Non-polymorphic binary.
55. Shape of sternal fenestra (Fig. 7E-F): (0) symmetrical, not widened; (1) wider in the posterior half. Polymorphic binary.

DISCUSSION

In this contribution, twenty one new characters for the genus *Liolaemus* were studied (characters from 35 to 55). We also report additional states for characters previously described (Table 1). First, the number of scleral ossicles was previously reported by Lobo and Abdala (2001) as binary polymorphic (13 or 14 ossicles), whereas here we found a new state for *L. albiceps* (15 ossicles),

we consequently coded the character as polymorphic multistate. Second, the ceratohyal process was coded in Lobo and Abdala (2001) as non-polymorphic multistate (gradually widened, abruptly widened, and hook-shaped), whereas here we found in *L. quilmes* a polymorphism (gradually widened and abruptly widened). Third, according to Lobo and Abdala (2001), the sternal fenestra can be divided or single, without polymorphism. In this study we report a polymorphism in *L. quilmes*, which may have a divided or undivided sternal fenestra. The specimens of *L.* cf. *quilmes* included in Lobo and Abdala (2001) correspond to *L. crepuscularis* (Abdala and Diaz Gómez, 2006), a species distinct from that included in this contribution as *L. quilmes*.

Maxillary teeth with three conspicuous cusps were found in all specimens studied. This is consistent with Lobo and Abdala (2001), who found this character state in all specimens of the subgenus *Eulaemus*, whereas the species of the *L. nigromaculatus* group (belonging to the subgenus *Liolaemus sensu stricto*) show the maxillary teeth without differentiated cusps. This evidence allows us to consider tricuspid maxillary teeth as a potential synapomorphy of *Eulaemus*.

The number of tracheal rings for species of the *Liolaemus boulengeri* group reported by Lobo and Abdala (2001) ranges from 48 to 67. We extend this range to 41-75.

A potential synapomorphy for the *Liolaemus darwinii* group (Fig. 8) involves the morphology of the terminal cartilage of cervical rib IV, which is narrow and not bifurcated in *Liolaemus albiceps*, *L. chacoensis*, *L. grosseorum*, *L. irregularis*, *L. koslowskyi*, *L. lavillai*, *L. ornatus,* and *L. quilmes* (though polymorphic in the latter). Lobo and Abdala (2001) found this character to be polymorphic in *L. koslowskyi*.

Etheridge (1993) defined the *Liolaemus darwinii* complex based on the "possession of maxillary teeth crowns with straight edges" as an exclusive character of this group. *Liolaemus scapularis* (a member of the *L. wiegmannii* group), also shows tooth crowns with straight edges, so this character state is not exclusive to the *L. darwinii* complex, as Etheridge (1993) proposed. Moreover, our results indicate variation within this group (Fig. 2A) and according to recognized relationships (Abdala, 2007), this character has changed in the terminal subclade of the *L. darwinii* group (the *L. ornatus* group). Therefore, it can be considered a synapomorphy of the *L. ornatus* group (Fig. 2A-C).

Optimizing the character states of maxillary tooth crowns and the diet in the tree recovered, we found that an insectivorous diet and the straight-edged maxillary tooth crowns change together along the tree (Fig. 2A).

This can be interpreted as supporting a possible relationship between diet and tooth crown shape. Tooth morphology can reflect ecological adaptations and exhibit derived traits which may distinguish alimentary specializations (Hotton, 1965). We found that *L. scapularis*, *L. quilmes*, *L. lavillai*, *L. grosseorum* and *L. chacoensis* have straight crowns and are insectivorous. Lobo and Abdala (2001) cited straight crowns for *L. crepuscularis* (their *L.* cf. *quilmes*). Semhan et al. (2013) reported that *L. crepuscularis* feeds mainly on insects, but can fluctuate to omnivorous or herbivorous diets through the year based on prey availability. All other species studied here show expanded crowns, and their diet can be characterized as omnivorous or herbivorous (*L. albiceps*). The only exception to this association is *L. koslowskyi*, which has expanded crowns and an insectivorous diet (Aun and Martori 1998). Aun and Martori (1998) do not mention the season of the study, so it is not known if this taxon can change its diet as does *L. crepuscularis*. *Phymaturus* is the sister clade of *Liolaemus*, and has a strictly herbivorous diet (Lobo et al., 2010). Species of *Phymaturus* have teeth with expanded crowns (Lobo and Quinteros, 2005). The same phenomenon can be observed in non-liolaemid lizards. Hotton (1965) found that herbivorous lizards (*Dipsosaurus*, *Sauromalus*, and *Ctenosaura*) have highly cuspidate and antero-posteriorly widened teeth (similar to the expanded crowns of humans). In lizards that mainly feed on ants (*Phrynosoma*), Hotton (1965) described pointed and conical teeth, and in lizards that feed on bees and wasps (*Urosaurus* and *Callisaurus*), he described thin, cylindrical, sharp teeth. Herrel et al. (2004) observed that lacertids with omnivorous diets show teeth with wider crowns, whereas insectivorous species had slender and pointed teeth. In agreement with these results, we found that dentition seems to vary with diet. Nevertheless, further studies are needed in *Liolaemus* in order to confirm the hypothesis of correlation between straight crowns and insectivorous diet.

The exposure or not of Meckel's groove in liolaemid lizards was used by Etheridge (1995) as a character in his taxonomic proposal. He proposed this character as a synapomorphy of the *Liolaemus chiliensis* (subgenus *Liolaemus*) group which have a fused channel, and also for the *Phymaturus patagonicus* group within the sister genus of *Liolaemus* (Etheridge,1995; Lobo and Quinteros, 2005; Lobo et al., 2010). Lobo and Abdala (2001) viewed the groove as a potential synapomorphy of the *L. darwinii* group. Here, we found that Meckel's groove exhibits an additional change (reversal), being open in the *L. ornatus* group. Moreover, Lobo and Abdala (2001) found this character state for *L. crepuscularis*, a basal member of the *L. ornatus* group. Therefore, we can conclude that the

open Meckel's groove can be considered a synapomorphy of the *L. ornatus* group (Fig. 2A-C). The ancestral state would be the open Meckel's groove, already present in *Ctenoblepharys*, the basal genus of the Family Liolaemidae, and preserved in the *Phymaturus palluma* group. The hypothesis of the open Meckel's groove as the ancestral state is supported by the presence of this character state in other families related to Liolaemidae (e.g., Leiosauridae and Opluridae according to Pyron et al., 2013 and Reeder et al., 2015), but exhibiting polymorphism in many Iguanian families (Frost and Etheridge, 1989) such as Leiocephalidae (Etheridge, 1966) and Phrynosomatidae (Etheridge, 1964).

The bladelike process on the posterior distal tibia was described by Etheridge (1995), as a synapomorphy of the *Liolaemus montanus* group. In his proposal, Etheridge (1995) did not include the *L. anomalus* group inside the *L. montanus* group. In recent analyses (Espinoza et al., 2004; Abdala 2007), the *L. anomalus* group is inferred as more closely related to the *L. boulengeri* group. These two groups together are called the *L. boulengeri* series (included inside the *L. montanus* section in Schulte et al., 2000). The *L. anomalus* group lacks this tibial process, which we consider to be a secondary loss (Fig. 9). Here we found that every member of the *L. darwinii* group studied has the bladelike process on the distal tibia.

Characters that were studied in other groups of lizards were informative for *Liolaemus*, including shape of the premaxilla (Frost, 1992; Tropidurids); squamosal-quadrate joint (modified from Frost, 1992); metacarpal of IV finger reach the I or II phalange of V finger (modified from Arias, 2012; teiids); and presence of open tracheal rings (Lobo and Quinteros, 2005; Lobo et al., 2010; *Phymaturus*).

Here, we found the same variation in the shape of the premaxilla described by Frost (1992) for tropidurines: (0) narrow nasal spine - wide area of premaxillary tooth attachment and (1) broad nasal spine- narrow premaxillary tooth area. Frost (1992) found no relationship between the width of the area of premaxillary teeth and number of teeth in it. We found similar results for the *Liolaemus* species studied here, where the number of premaxillary teeth is constant regardless of the width of the area in which they are inserted.

Also, Frost (1992) described two states for the squamosal-quadrate articulation. These states are related to the width of the superior fossa of the quadrate, which may be relatively small or enlarged. In the *Liolaemus* species studied, it was observed that the superior fossa of the quadrate corresponds to the "relatively enlarged" state according to Frost (1992). All species except two (*L. albiceps* and *L. irregularis*) exhibit one of the states proposed

by Frost (1992): the otic ramus of the squamosal contacts (but is not inserted in) the posterior edge of the superior fossa of the quadrate. In contrast, *L. albiceps* and *L. irregularis* share the same state, with the otic ramus of the squamosal inserted in the medial part of the fossa (Fig. 6 B), thus reinforcing the hypothesis that they are sister species.

The character observed in teiids is related to the relative length of metacarpals, metatarsals and digits. Arias (2012) coded a character related to the length of toe V into three states: length of toe V exceeding that of metatarsal IV, equaling that of metatarsal IV, and not reaching the length of metatarsal IV. In all *Liolaemus* species studied here, the toe V always exceeds metatarsal IV in length, but there is variation as to which phalanx of toe V metatarsal IV reaches (Fig. 6 G-H). We recorded this character differently for one of the outgroup taxa (*L. inacayali*, where metatarsal IV reaches phalanx II) with respect to the *L. darwinii* group (in which metatarsal IV reaches phalanx III). Since we do not have samples of other members of the *L. telsen* group, we were not able to determine if this is a potential synapomorphy for that group. Similar variation to that described above for the hindlimbs was described for the forelimbs in *Liolaemus*. The length of metacarpal IV with respect to finger V, exhibited two states: reaches phalanx I or reaches phalanx II. Within the *L. darwinii* group, the character state in which finger V reaches phalanx II occurs independently in *L. quilmes* and *L. chacoensis*. It is clear that variation between fore and hindlimbs is independent.

The presence of intercalated open tracheal rings was only found in the members of the *Liolaemus ornatus* group. Therefore, this character state can be considered as a possible synapomorphy of this group. Nevertheless, the intercalated open tracheal rings were also found to be polymorphic in *L. scapularis* and in *L. quilmes*, species basal to the *L. ornatus* group. This character state was primarily proposed for *Phymaturus* (Lobo and Quinteros, 2005), but no polymorphisms were found in this genus.

While newly described characters have not yet been observed in many taxa, a general idea of the polarity of the optimized character was obtained. The study of new sources of variation and the distribution of characters described here in other taxa, as well as in the other two genera of *Liolaemidae* (*Phymaturus* and *Ctenoblepharys*) would allow us to hypothesize about relationships within this iguanian family. In this study we note that in the *Liolaemus darwinii* group the most informative characters are taken from the regions of the ribs, sternal plate, pectoral girdle, snout, jaw, larynx and hyoid arches. The literature shows that the osteology has been more thoroughly studied in the families Phrynosomatidae, Tropiduridae

and Corytophanidae within Iguania (Reeve, 1952; Etheridge, 1964; Presch, 1969; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Frost, 1992; McGuire, 1996; Reeder and Wiens, 1996; Torrez Carvajal, 2007; Frost et al., 2011) and osteological characters are observed mainly from the cranial skeleton. This shows a bias in the focus of skeletal variation studies, making it difficult to determinate the levels of variation across the whole anatomy of lizards.

Even if the literature emphasizes the idea of the importance of using osteological characters in different phylogenetic analyses and morphological descriptions (Conrad, 2008; Gauthier et al., 2012; Reeder et al., 2015), it is clear that there is not enough information yet to fully understand the patterns of morphological diversity across all existing iguanian families.

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APPENDIX A

Specimens examined. The acronyms used were MCN (Museo de Ciencias Naturales de la Universidad Nacional de Salta) and FML (Fundación Miguel Lillo).

Liolaemus albiceps (n=4): ARGENTINA: Salta: Los Andes: Camino al Acay desde Estación Muñano, 5-6 km, (24°18'31.6"S; 66°09'7"W) MCN 402, 407, 1452, 1453.

Liolaemus chacoensis (n=4): ARGENTINA. MCN 503, 504, 505, 599. No data.

Liolaemus grosseorum (n=2): ARGENTINA: Mendoza: San Rafael: Orillas del embalse el Nihuil, MCN 508, 509.

Liolaemus inacayali (n=1): ARGENTINA: Rio Negro: Ing. Jacobacci: 25 de Mayo, MCN 500.

Liolaemus irregularis (n=4): ARGENTINA: Salta: Los Andes: Aprox. a 11KM al SE de San Antonio de los Cobres por ruta 51 (24°8'53.44"S; 66°8'21.37"W). MCN 2431, 2436, 2443, 2446.

Liolaemus kingii (n=1): ARGENTINA: Santa Cruz. MCN 565. No data.

Liolaemus koslowskyi (n=3): ARGENTINA: La Rioja: Castro Barros: 6 km. E. De Anillaco (28°47'S; 66°52'W). MCN 573, 574, 576.

Liolaemus lavillai (n=2): ARGENTINA: Jujuy: extremo norte del Parque nacional los cardones, oeste de la Recta de Tin Tin. (25°05'09"S; 66°00'00"W). MCN 2688, 4351.

Liolaemus multicolor (n=1): ARGENTINA: Jujuy: Abra Pampa: Cochinoca. FML 2065.

Liolaemus ornatus (n=4): ARGENTINA: Jujuy: Castro Tolay: A 7 km de S de Rio las Burras. MCN 3545, 3546, 3547, 3548.

Liolaemus pseudoanomalus (n=1): ARGENTINA: La Rioja: Castro Barros: 6 km. E. De Anillaco (28°47'S; 66°52'W). MCN 526.

Liolaemus quilmes (n=5): ARGENTINA: Salta: Cachi: Cachi: A 7 Km Sur de Palermo entre Cachi adentro y Palermo, (24°58'41,9"S; 66°08'42,2"W). MCN 3524, 3525, 3526, 3527, 3528.

Liolaemus scapularis (n=2): ARGENTINA: Salta: Cafayate: Los Médanos. MCN 253, 283.