



Debating Liolaemidae diversity and classification, and a bit more: A response to Lobo *et al.*

DANIEL PINCHEIRA-DONOSO

Centre for Ecology and Conservation, College of Life & Environmental Sciences, University of Exeter, Streatham Campus, Exeter, Devon, UK. E-mail: D.PincheiraDonoso@exeter.ac.uk

Abstract

The Liolaemidae lizard evolutionary radiation has resulted from active spatial expansions into an extensive territorial area accompanied by active events of cladogenesis that have produced high levels of taxonomic and ecological diversity, especially within the *Liolaemus* genus. As a result, these lizards have been for decades the subject of intense taxonomic and systematic debates. Here, I provide an analysis of a recent paper where discussions on Liolaemidae diversity and classification involved biased and arbitrary interpretations and observations of two previously published monographs.

Key words: Liolaemidae, *Liolaemus*, *Phymaturus*, lizards

Introduction

Lizards of the Liolaemidae family have undergone a remarkable evolutionary radiation that has resulted in continuous debate primarily about the taxonomic richness and phylogenetic relationships of two of the three known liolaemid genera, *Liolaemus* and *Phymaturus* (the third being the monotypic *Ctenoblepharys*). In general, such discussions have only been aimed at advancing the study of these lizards, and as would be expected, authors that have made the most significant contributions (e.g. Laurent, 1983; Laurent, 1985; Etheridge, 1995) have concentrated on unsolved problems or on the development of novel perspectives. A recent discussion by Lobo *et al.* (2010) has not followed any of these latter aims, as it has mostly concentrated on presenting viewpoints extensively known by current liolaemid scholars, and has failed to create a legitimate environment of discussion as it is defeated by an often aggressive and offensive tone, and many biased and uninformed conclusions. This discussion focused exclusively on two liolaemid monographs published by myself and co-authors (Pincheira-Donoso & Núñez, 2005; Pincheira-Donoso *et al.*, 2008c).

Several general patterns can be extracted from Lobo *et al.*, although I will only summarize the most important ones. Firstly, the primary aim of Lobo *et al.*'s work is the discussion of the classification presented in our first work (Pincheira-Donoso & Núñez, 2005), which, by the way, is the result of my undergraduate work, and not my graduate thesis as suggested by these authors. Secondly, most of the aggressive commentaries appear to result from myself or co-authors simply having opinions and views about liolaemid problems that essentially differ from Lobo's (i.e. the senior author) previous work. Third, and more serious, there is a dangerously clear attempt of these authors to put several of our conclusions and views completely out of context, sometimes involving severe manipulations and omissions of information. This latter discussion is presented in a separated section. Below I discuss more specifically each of these points, while I have decided to leave out of this response other criticisms, such as their critiques that the limbs of lizards in our pictures are out of focus, critiques to our use of the term 'ovoviviparity' as they regard this term as 'rejected' (although it is extensively employed today in studies published in prominent international journals), or that when we present a picture of an Argentinean specimen of *L. fitzingerii* to mention the existence of this species in Chile, they criticize that the correct picture would be one of a Chilean animal (and not the Argentinean), and when we presented a picture of a Chilean specimen of the Chilean population known as *L. rothi* (later described as a new species), they criticize us because they think we should have provided a

picture of the Argentinean population instead! Likewise, I leave out other criticisms of similar irrelevance to the greater questions of Liolaemid systematic and phylogenetics that are of real interest to readers of this journal.

Responses to Lobo *et al.*'s claims

A considerable proportion of Lobo *et al.*'s paper criticizes, extensively, the fact that our first monograph (Pincheira-Donoso & Núñez, 2005) presented a morphological (and chromosome-based) subgeneric classification of *Liolaemus* that is not entirely matched by phylogenetic evidence. It has to be said, initially, that our classification was concluded after following several previous similar studies, and also, as any original proposal, following our own conclusions, that in some cases we or others have later found to be invalidated by newer evidence. However, Lobo *et al.*'s criticism is absolutely out-of-date, as the existence of these taxonomic mistakes has largely been demonstrated repeatedly by several phylogenetic studies where original hypotheses were presented after our work went to press (e.g. Espinoza *et al.*, 2004; Abdala, 2007; Pincheira-Donoso *et al.*, 2007a; Schulte & Moreno-Roark, 2010). Indeed, I myself have ignored this classification and have later employed instead more recently published phylogenetic hypotheses in my own studies where relationships among Liolaemidae lineages are required (Pincheira-Donoso *et al.*, 2007a; Pincheira-Donoso *et al.*, 2007b; Pincheira-Donoso *et al.*, 2008a, 2008b; Pincheira-Donoso *et al.*, 2008c; Pincheira-Donoso *et al.*, 2009). Any classification proposal or phylogenetic estimate is simply a hypothesis which is subject to refutation when new evidence or models arise. Therefore, most discussions in Lobo *et al.* do not present anything novel, do not present a different viewpoint, and as such, do not offer any additional contribution to our understanding of these lizards, as these points have repeatedly been made elsewhere. We all know now that peptic ulcer is caused by bacteria, but it would be absurd to write a paper to criticize today the work of those who claimed in the past that these ulcers were caused by stress or spicy food. In other words, after several authors have pointed out limitations in published works, it is very easy for others to come years later and 'find' and report these shortcomings.

A second pattern in Lobo *et al.*'s work is that these authors' critiques often turn into harsh commentaries when our published viewpoints differ significantly from (particularly) Lobo's published viewpoints. There is a tendency throughout the paper to argue that we made something very wrong, especially when we have said something that is not in agreement with the papers authored or co-authored by Lobo. I truly understand that they defend Lobo's work, but I cannot understand that they appear to believe that his opinions and conclusions cannot be considered in different directions. Indeed, if we all followed Lobo *et al.*'s philosophy of a "science of agreements", where everyone should accept someone's conclusions and opinions, we would not know of progress in science. Hence, differences between authors are the fuel of science development. Several of these points of disagreement reflect how Lobo *et al.* challenged our opinions when we (in their view) failed to recognize Lobo's own work (see next section for more details). For instance, Lobo *et al.* criticize our opinion (in the 2008 monograph) that the first comprehensive phylogeny for *Phymaturus* lizards is that of Espinoza *et al.* (2004), which included most known species to date. They, in contrast, argue that "the first comprehensive phylogenetic analysis of *Phymaturus* was by Lobo & Quinteros (2005)", which, as can be seen, was actually published later. The reason for Lobo *et al.* to think that we failed to recognize Lobo & Quinteros is that Espinoza *et al.*'s phylogeny "was produced...to test hypotheses concerning the evolution of herbivory in Liolaemidae" but that Espinoza *et al.* "did not provide a discussion of the systematic implications of their topology". We prefer to see the broad picture. For us, it did not matter that Espinoza *et al.* did not focus on a systematic/taxonomic discussion, as the aim of a particular study should not have any effect on the topology produced. Hence, the fact that Espinoza *et al.* did not discuss the systematic implications of their phylogeny does not invalidate it. And the fact that Lobo & Quinteros's work was explicitly taxonomic, where systematic implications were discussed, does not mean it is the first phylogeny for the genus. A phylogeny is a phylogeny regardless of the context. Lobo *et al.* then proceed to bias the criticism. They inexplicably argue that we "dismissed [Lobo & Quinteros's phylogeny] for being based on morphology rather than DNA". This is entirely a false accusation. We never dismissed Lobo & Quinteros's work. Indeed, we recognized its value (although, maybe we did not offer enough praise), with sentences such as Lobo & Quinteros "presented the only known explicit study on phylogenetic relationships within *Phymaturus*" (explicit because that paper aimed to investigate this problem), "supported substantially the hypothesis of two major clades", or "these recent attempts [Espinoza *et al.* and Lobo & Quinteros]...represent substantial progress for future phylogenetic-based systematic and evolutionary research".

Criticism based on biased and incomplete use of information

In the following paragraphs I will discuss the points that I regard as most serious in Lobo *et al.*'s review, namely the arbitrary manipulation of information aimed to give an impression that is false. I number below these repeated situations found in Lobo *et al.*'s paper.

(1) Lobo *et al.* argued that the Figure 2 in our 2008 monograph is based on misused information taken from previous Liolaemidae phylogenetic studies (Schulte *et al.*, 2000; Espinoza *et al.*, 2004; Schulte *et al.*, 2004; Cruz *et al.*, 2005) that we cited to support the phylogeny shown in that figure: "two thirds of the relationships depicted in their figure [Fig. 2] are incongruent with the topologies recovered in those studies and other relevant phylogenetic hypotheses". We present herein a comparison of all these phylogenetic topologies (Fig. 1), including a more recent one provided by Abdala (2007) as well, to show that Lobo *et al.*'s assertions are unjustifiable (note that what we called '*boulengeri*' group is called '*chacoensis*' group by Abdala, who regarded as '*boulengeri*' group the entire clade including the sister lineages *boulengeri* and *anomalous* in our 2008 monograph. However, this is simply an alternative arrangement of names, as the phylogeny is exactly the same. Our nomenclature in this case is the same nomenclature used by Espinoza *et al.* 2004).

(2) Lobo *et al.* accused that the ranges of morphological variation for *L. puna* used in our 2005 monograph to distinguish this species from *L. barbarae*, which we claimed to have been taken from the original description of the former species (Lobo & Espinoza, 2004), are actually different from the trait variation that they reported in that paper. In a previous paper, Quinteros & Lobo (2009) had also accused us for the same situation, questioning the origin of the data reported in our 2005 work. They then claimed that the origin of this information for *L. puna* is "unknown", "inexplicable", and "incongruent with data in Lobo & Espinoza". However, the source is not unknown or inexplicable. The answer, in fact, lies in the inconsistency of the ranges of morphological variation reported in the original description of *L. puna* by Lobo & Espinoza (2004). In our 2005 work, we took data on morphological variation of *L. puna* from the diagnosis (p.857-858) provided by Lobo & Espinoza for this species. Nevertheless, in the same paper, but in the section 'variation' (p. 859), Lobo & Espinoza (2004) provided different ranges of morphological variation for *L. puna*, which are the ranges referred by Lobo *et al.* and Quinteros & Lobo to support their accusations (similarly, note that Lobo *et al.* also provide inconsistent information on the number of known *Phymaturus* species: they refer 22 species in page 2, and 26 in page 22). Consequently, what is inexplicable is that different ranges of variation were reported in different sections of the same paper where *L. puna* was originally described (another accusation based on manipulated information is when Quinteros & Lobo inexplicably claimed that in our 2005 work, we reported the occurrence of *L. walkeri* in San Pedro de Atacama (Chile). However, our 2005 work clearly stated that the population previously recognized as *L. walkeri* from this area is in fact what we described as *L. barbarae*. Indeed, the conclusion of our monograph's discussion on *L. barbarae* is that all Chilean populations previously assigned to *L. walkeri* are *L. barbarae*, and hence, that *L. walkeri* is a species restricted to Peru).

(3) Lobo *et al.* claimed that we (2008) have used geographical information to suggest that *P. dorsimaculatus* is a synonym of *P. vociferator*, and proceed to develop a long discussion about why using geographical ranges is inappropriate to conclude taxonomic conspecificity (despite being something generally self-evident to most biologists). However, again, they have omitted an important part of the information we actually reported. *Immediately before* mentioning the geographical information as an additional signal to support our claim, we had suggested that (after studying specimens from both type localities) we found strong overlap between both populations in body size, scale counts, preloacal pores, coloration in males and females, and patterns of sexual dimorphism.

(4) Lobo *et al.* claimed that we (2008) have "misattributed" the use of "family Liolaemidae" to Frost & Etheridge (1989), where the correct reference should be Frost *et al.* (2001). Yet again, they omitted the fact that we actually cited Frost *et al.*: "Family Liolaemidae Frost & Etheridge 1989 (family status according to Frost *et al.* 2001)" (p. 18). The family was originally proposed by Frost & Etheridge as a subfamily (Liolaeminae), but later Frost *et al.* gave full family status to it. So, the references are correct, something that cannot be seen on the basis of the incomplete information arbitrarily provided by Lobo *et al.*

(5) Lobo *et al.* claim that our 2008 monograph is "largely an update of [our 2005 monograph]", and that the difference is "the inclusion of liolaemid species occurring outside Chile". Again, this is an incorrect statement, as we used a different, phylogenetically-informed, classification of the family in our 2008 work (see point number 1 above, and Fig. 1 in this response). Then, they make another peculiar statement about our 2008 work: "Several eco-

logical assertions are made (none that are novel), but no data or specific analyses are provided in support of this claim [sic]”. However, the table 1 in our 2008 work, where ecological (and more) information is given, is supported at the bottom of the table by more than 160 references.

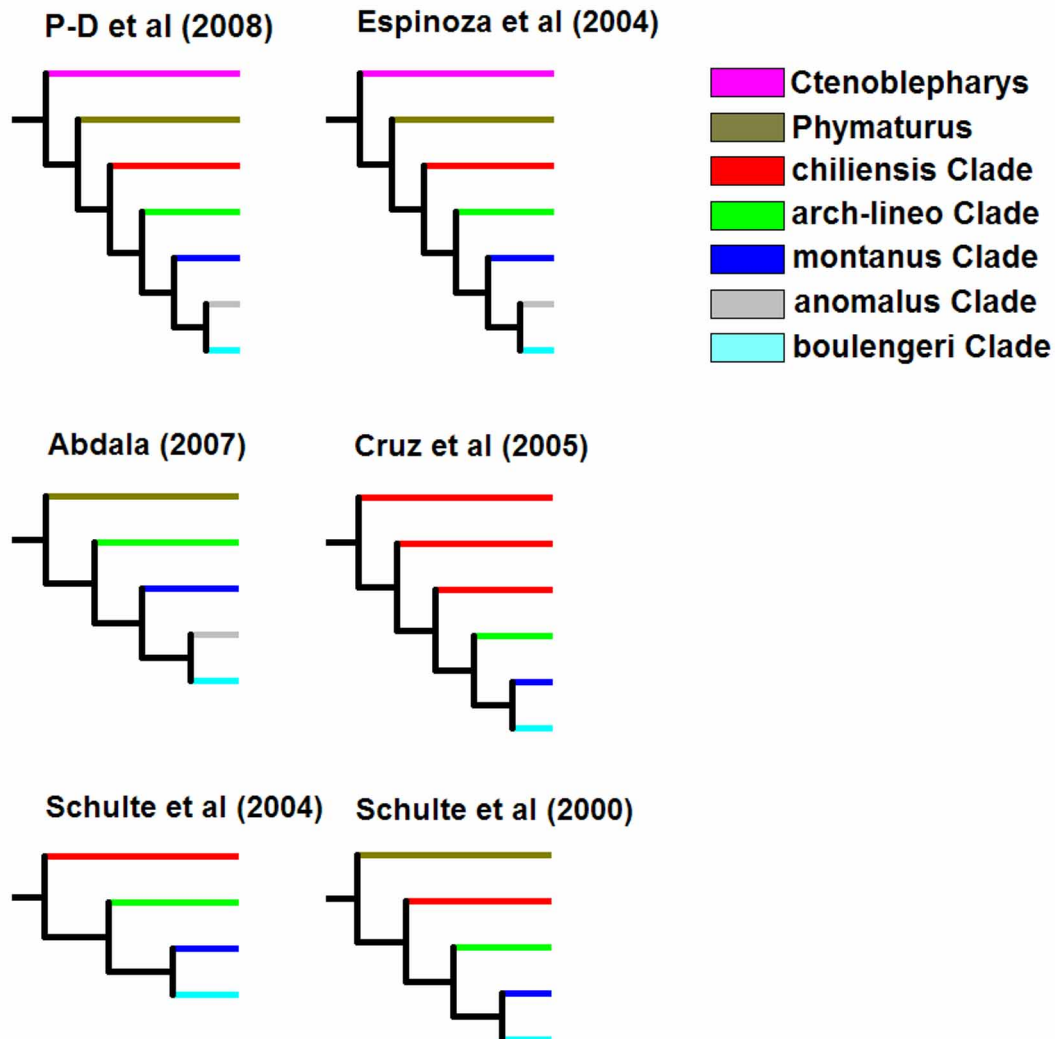


FIGURE 1. Phylogenetic topologies of major clades of the Liolaemidae family presented by Schulte *et al.* (2000, 2004), Espinoza *et al.* (2004), Cruz *et al.* (2005) and Abdala (2007), compared to the topology presented in Figure 2 of Pincheira-Donoso *et al.*'s (2008; abbreviated P-D *et al.*). Note that all topologies are essentially identical, except of that of Cruz *et al.*, which is in general highly similar in four of the six terminal branches depicted. Also, while Pincheira-Donoso *et al.*'s topology is entirely identical to Espinoza *et al.*'s tree, differences with the other four trees are almost entirely explained by different sets of clades included. For example, *Ctenoblepharys* and *Phymaturus* were not included in Schulte *et al.* (2004), while *Ctenoblepharys* was not included in Schulte *et al.* (2000). In both cases, however, the only species regarded by Pincheira-Donoso *et al.* (2008) and Abdala (2007) as member of the *anomalus* clade that was included in Schulte *et al.*'s (2000) and Cruz *et al.*'s (2004) studies, *L. pseudoanomalus*, is nested within the *boulengeri* clade. However, as declared by Pincheira-Donoso *et al.*'s (2008), the *anomalus* clade was recognized following phylogenetic evidence recently presented by Abdala (2007; see comments number 1 and 7 in the text for additional information). This comparative scheme demonstrates that Lobo *et al.*'s affirmation that two thirds of the phylogenetic tree presented by Pincheira-Donoso *et al.* (2008) differ from the rest of known (and cited) phylogenetic hypotheses known for Liolaemidae, is unjustified. Liolaemidae clades are detailed at the right hand side of the panel, where colours that identify lineages are shown. All groups identified as “clades” are lineages of the *Liolaemus* genus. The *archeforus-lineomaculatus* clade is abbreviated (arch-lineo clade). The name ‘*boulengeri*’ clade is the same used by Etheridge (1995) and Espinoza *et al.* (2004).

(6) Lobo *et al.* (p.13) develop a long discussion to support their criticism that the traits we (2005) regarded as diagnostic to distinguish the *Donosolaemus* subgenus (named after Roberto Donoso-Barros) from other *Liolaemus* lineages are inappropriate as they are not exclusive. Once Lobo *et al.* have arbitrarily made clear that we have used

inappropriate exclusive traits (in clear opposition to our real argument, as shown below), they describe how several traits included in our subgenera diagnoses are non-exclusive and found in several different lineages. However, Lobo *et al.* have once again misused and biased the information we explicitly provided in our works. Indeed, in our 2005 work, we *repeatedly insisted* on the fact that the groups we recognized were not based on *exclusive traits*, but on *exclusive combinations of traits*, which explains why different individual traits are observed in different groups (as we have also explicitly shown repeatedly in our work). This simply reflects our view that cladogenesis is a multivariate process where evolutionary change is not expressed in a single trait, but in the evolution of several traits simultaneously.

(7) Lobo *et al.* argue that we (2008) have “proposed” the *anomalous* clade, that “this grouping is not based on any of the cited studies”, and that “one could assume that the source of this grouping is Cei (1986)...or Abdala (2007)”. Again, the information has been manipulated by Lobo *et al.* Nothing has to be assumed, as we have actually made more than explicit that the sources for our recognition of an *anomalous* clade are the phylogenetic hypotheses presented by Espinoza *et al.* (2004) and Abdala (2007). Indeed, the group *anomalous* was explicitly proposed (and named) by this latter author. In our 2008 work, we included *L. anomalous*, *L. ditadai*, *L. duellmani* and *L. pseudoanomalous* as members of the *anomalous* group (p. 47). Initially, Espinoza *et al.* (2004) showed a lineage containing only *L. duellmani* and *L. pseudoanomalous*, and later, Abdala (2007) showed that *L. anomalous*, *L. ditadai* and *L. pseudoanomalous* are also members of a separate clade (Fig. 1, this study). Hence, we suggested (and insisted that more phylogenetic evidence is needed to consolidate this view) that recent phylogenetic evidence presented in these two studies “might” support the view of an *anomalous* clade, which again, was proposed by Abdala (2007). However, from Lobo *et al.*’s work, it looks like we have actually proposed an *anomalous* clade based on nothing, when the real scenario is that we have *only recognized* that the phylogenetic evidence presented by Espinoza *et al.* and Abdala might support an *anomalous* clade, as proposed by Abdala.

While I might extend this response considerably more, as many other statements of a similar nature are made in Lobo *et al.*, I am certain that the unfortunate and unnecessary non-constructive nature of their criticism will be clear to most readers. Lobo *et al.* finish their paper claiming that a better understanding of Liolaemidae relationships “will take the effort of many scientists working collaboratively for the mutual benefit of all”. Although this statement certainly represents a legitimate view, I might also conclude that their claim is likely to be conditioned by one factor: all studies have to offer warm and explicit praise to Lobo’s own previous work, or they may otherwise be at risk of being arbitrarily manipulated and relegated to the zone of “useless”, “not acceptable”, “lack of criteria”, and “fallacy” studies that “do a disservice” and “should not be tolerated”, as they claim in reference to our works. I and my co-authors would indeed welcome future collaborative efforts for the mutual benefit of all, including healthy debates and collegial critiques on points of disagreement, which lead to the increased understanding of the complex history and relationships among the liolaemids.

Acknowledgements

I am grateful to all colleagues who critically read this response.

References

- Abdala, C.S. (2007) Phylogeny of the *boulengeri* group (Iguania: Liolaemidae, *Liolaemus*) based on morphological and molecular characters. *Zootaxa*, 1538, 1–84.
- Cruz, F.B., Fitzgerald, L.A., Espinoza, R.E. & Schulte, J.A. (2005) The importance of phylogenetic scale in tests of Bergmann’s and Rapoport’s rules: lessons from a clade of South American lizards. *Journal of Evolutionary Biology*, 18, 1559–1574.
- Espinoza, R.E., Wiens, J.J. & Tracy, C.R. (2004) Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the National Academy of Sciences, USA*, 101, 16819–16824.
- Etheridge, R. (1995) Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the taxonomy of Liolaeminae (Reptilia: Squamata: Tropiduridae). *American Museum Novitates*, 3142, 1–34.
- Frost, D.R. & Etheridge, R. (1989) A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *University of Kansas Museum Natural History, Miscellaneous Publications*, 81, 1–65.

- Frost, D.R., Etheridge, R., Janies, D. & Titus, T.A. (2001) Total evidence, sequence alignment, evolution of Polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). *American Museum Novitates*, 3343, 1–38.
- Laurent, R.F. (1983) Contribución al conocimiento de la estructura taxonómica del género *Liolaemus* Wiegmann (Iguanidae). *Boletín de la Asociación Herpetológica Argentina*, 1, 15–18.
- Laurent, R.F. (1985) Segunda contribución al conocimiento de la estructura taxonómica del género *Liolaemus* Wiegmann (Iguanidae). *Cuadernos de Herpetología*, 1, 1–37.
- Lobo, F. & Espinoza, R.E. (2004) Two new *Liolaemus* from the Puna Region of Argentina and Chile: further resolution of purported reproductive bimodality in *Liolaemus alticolor* (Iguania: Liolaeminae). *Copeia*, 2004, 850–867.
- Lobo, F., Espinoza, R.E. & Quinteros, A.S. (2010) A critical review and systematic discussion of recent classification proposals for liolaemid lizards. *Zootaxa*, 2549, 1–30.
- Pincheira-Donoso, D., Hodgson, D.J., Stipala, J. & Tregenza, T. (2009) A phylogenetic analysis of sex-specific evolution of ecological morphology in *Liolaemus* lizards. *Ecological Research*, 24, 1223–1231.
- Pincheira-Donoso, D., Hodgson, D.J. & Tregenza, T. (2008a) Comparative evidence for strong phylogenetic inertia in precloacal signalling glands in a species-rich lizard clade. *Evolutionary Ecology Research*, 10, 11–28.
- Pincheira-Donoso, D., Hodgson, D.J. & Tregenza, T. (2008b) The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? *BMC Evolutionary Biology*, 8, 68.
- Pincheira-Donoso, D. & Núñez, H. (2005) *Las especies chilenas del género Liolaemus*. *Taxonomía, sistemática y evolución*. Santiago: National Museum of Natural History Press.
- Pincheira-Donoso, D., Scolaro, J.A. & Schulte, J.A. (2007a) The limits of polymorphism in *Liolaemus rothi*: molecular and phenotypic evidence for a new species of the *Liolaemus boulengeri* clade (Iguanidae, Liolaemini) from boreal Patagonia of Chile. *Zootaxa*, 1452, 25–42.
- Pincheira-Donoso, D., Scolaro, J.A. & Sura, P. (2008c) A monographic catalogue on the systematics and phylogeny of the South American iguanian lizard family Liolaemidae (Squamata, Iguania). *Zootaxa*, 1800, 1–85.
- Pincheira-Donoso, D., Tregenza, T. & Hodgson, D.J. (2007b) Body size evolution in South American *Liolaemus* lizards of the *boulengeri* clade: a contrasting reassessment. *Journal of Evolutionary Biology*, 20, 2067–2071.
- Quinteros, A.S. & Lobo, F. (2009) The iguanian lizard *Liolaemus barbarae* Pincheira-Donoso and Núñez is a junior synonym of *Liolaemus puna* Lobo and Espinoza. *Journal of Herpetology*, 43, 336–339.
- Schulte, J.A., Losos, J.B., Cruz, F.B. & Núñez, H. (2004) The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae: Liolaemini). *Journal of Evolutionary Biology*, 17, 408–420.
- Schulte, J.A., Macey, J.R., Espinoza, R.E. & Larson, A. (2000) Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biological Journal of the Linnean Society*, 69, 75–102.
- Schulte, J.A. & Moreno-Roark, F. (2010) Live birth among Iguanian lizards predates Pliocene-Pleistocene glaciations. *Biology Letters*, 6, 216–218.