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The enormous liolaemine radiation: paradoxical herbivory, viviparity, evolutionary cul-de-sacs and the impending mass extinction

By Darren Naish | June 26, 2013

A small liolaemine lizard, encountered in Rio. Liolaemus lutzae, I presume? Photo by Darren Naish.

Did I mention that I spent time in Rio de Janeiro recently? Ha ha, kidding. While there I didn't just look at birds and pterosaurs: I also pursued lizards when I could. Rio is home to a special, unique iguanian: Lutz's tree iguana *Liolaemus lutzae*, an omnivorous, burrow-dwelling, beach-living liolaemine endemic to the Brazilian coast. Liolaemines (or liolaemids) are one of many iguanian groups classically regarded as a iguanid 'subfamily' and currently treated in different ways by different authors. Most recently, Pyron *et al.* (2013) treated all 'iguanid' clades as 'families' and found Liolaemidae to be the sister-group to a leiosaurid + oplurid clade

While looking for animals in the gardens of the Museu Nacional, I encountered a small liolaemine (estimated length = c. 50 mm SVL, c. 110 mm in total). I actually found the lizard thanks to the predatory efforts of a cat, which I saw making a quick grab for the lizard, causing it to take refuge in a crevice on a tree. My initial hypothesis was that this might be a Lutz's tree iguana (my first-ever viewing of this distinctive species) and, having looked at photos online, I think that this is what it is. Please say if you know better.

Liolaemines have been covered on Tet Zoo before (on ver 2, back in February 2008) so now is a good time to recycle (and update) that text. Here it is...

My brilliant former pet, Ermentrude the liolaemine. He was most likely a member of the Chilean species Liolaemus nigroviridis. Photo by Darren Naish.

Liolaemus is a pretty interesting taxon (hey: just like all the others!). Occurring in South America from the Pacific to Atlantic coasts, and from Peru to Tierra del Fuego, its diversification appears to have occurred in the Andean and/or Patagonian highlands (Schulte *et al.* 2000). It's a huge group, containing over 220 named species and with some studies hinting at the possibility of a futher 200 or so still awaiting publication. Indeed some herpetologists think that the *Liolaemus* radiation will eventually exceed the *Anolis* (*sensu lato*!) one in terms of number of species.

Phymaturus verdugo, an Argentinean liolaemid named in 2003. You can see why these lizards are sometimes called Alpine (or Chilean) chuckwallas. Photo by Gdebandi, licensed under Creative Commons Attribution 3.0 Unported license.

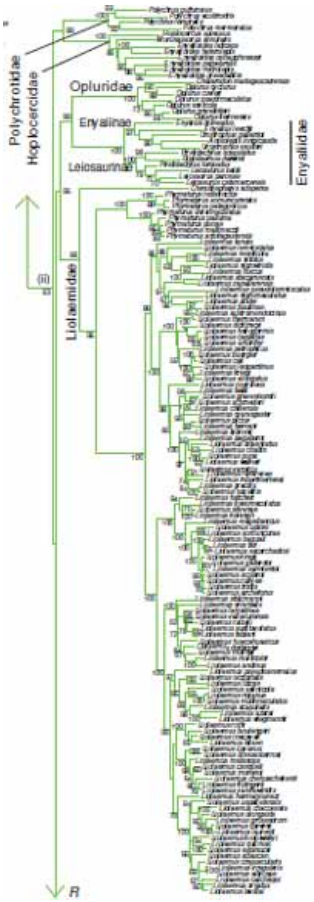
Unlike a few other iguanian clades (like the Australian dragons and anoles), diversification within liolaemines has apparently been slow and steady, rather than short and rapid (Harmon *et al.* 2003). While mostly inhabiting high altitudes, *Liolaemus* species dominate the scrubland lizard faunas of southern South America and in Chile it is typical to find four species partitioning the same habitat. Several species inhabit beaches, including *L. lutzae*. It is omnivorous, if not predominantly herbivorous as an adult (Rocha 1989, 1999), and has been very much affected by human development of its habitat. Some species inhabit places with strongly seasonal climates and can cope with very cold winters, and indeed *L. magellanicus* of Tierra del Fuego is the most southerly occurring lizard in the world. [Adjacent image of a *Phymaturus* species by Gdebandi.]

The viviparity cul-de-sac and... bad news for cool-adapted liolaemines?

Viviparity is present in about 55% of all known *Liolaemus* species, occurring in those high-altitude and/or high latitude taxa that have larger bodies (Cei *et al.* 2003, Pincheira-Donoso *et al.* 2013). It's generally thought that viviparity is advantageous for cool-climate lizards because the mother's thermoregulatory behaviour allows successful embryonic development in habitats frequently too cool for the successful incubation of shelled eggs. Conversely, viviparity is disadvantageous in warm climates since a female burdened with heavy embryos is relatively poor at running and more vulnerable to predation, and also slower at producing litters (Shine 2005). This doesn't mean that all warm-climate lizards must be oviparous and all cool-climate ones viviparous, of course: exceptions abound.

Cyan tree iguana (Liolaemus cyanogaster) of Chile, one of many viviparous liolaemine species; photo by jjsaez, licensed under Creative Commons Attribution-Share Alike 3.0 Unported, 2.5 Generic, 2.0 Generic and 1.0 Generic license.

The evolution of reproductive traits in *Liolaemus* has just been investigated by Pincheira-Donoso *et al.* (2013). They collected data from 153 species within the group (wow, that's *a lot* of fieldwork; it clearly involved looking at *thousands* of specimens) and concluded that the evolution of viviparity is, indeed, strongly associated with the invasion of cool regions. However, their phylogenetic work led them to argue that these lizards cannot switch from viviparity back to oviparity: there are a few places in squamate phylogeny where such a transition *might* have occurred, but general thinking is that it's essentially irreversible (Lee & Shine 1998).



Have you seen Pyron et al.'s (2013) ENORMOUS phylogenetic analysis of Squamata? 4161 species, representing all 'families' and 'subfamilies' (and it's open access: check it out). Here's the section of their iguanian tree that includes Liolaemidae - many, many Liolaemus species are included.

Given climate change, what does the future hold in store for these lizards? Pincheira-Donoso *et al.* (2013) suggest that a warming South America will encourage the invasion of higher elevations and higher latitudes by oviparous liolaemine lineages. Meanwhile, the many viviparous species will – if their evolution of viviparity truly is irreversible (in which case they've found themselves in an "evolutionary cul-de-sac") – be increasingly restricted in range. Eventually, they'll be competing directly with oviparous ones that will be competitively advantaged in a warmer climate (for the reasons discussed above). What then? Will there be a mass extinction of viviparous, cool-adapted liolaemines? "[T]hese predicted extinctions of viviparous species need not simply reduce *Liolaemus* diversity. We expect the genus to experience species turnovers in historically cold climates, where invasions by oviparous species (and extinction of viviparous [ones]) might drive new speciation events, resulting in new forms of high-latitude and high elevation *Liolaemus* fauna" (Pincheira-Donoso *et al.* 2013, p. 865).

Incidentally, at least one *Liolaemus* species is parthenogenetic, meaning that this trait has evolved in iguanians as well as in most other squamate lineages. Parthenogenesis has also been reported in *Phymaturus*, the sister-group to *Liolaemus*, but in that case it's only known to have occurred in captivity (Chiszar *et al.* 1999).

One subject which has been discussed quite a lot in lizards concerns which correlations, if any, occur between morphology and mode of life, with some studies on some groups finding no obvious correlations at all. Indeed some workers have reported exactly this for *Liolaemus* (Jaksic *et al.* 1980). Schulte *et al.* (2004) did further work of this sort on *Liolaemus* and found that different species had different escape strategies, and it was these escape strategies that tied to morphological differences.

Paradoxical herbivory

Orange-bellied lizard (Liolaemus pictus) of Argentina and Chile in its montane home. Is the montane liolaemine fauna set to change dramatically in future decades? It would seem so. Image by Nsimean, licensed under Creative Commons Attribution-Share Alike 3.0 Unported license.

Within the liolaemid radiation, the members of *Ctenoblepharys* are insectivorous, the species included within *Phymaturus* are entirely herbivorous while the largest clade within the group – *Liolaemus* – includes insectivores, omnivores and herbivores. The widespread herbivory present within *Liolaemus* is not well known and, indeed, it's repeatedly been missed or ignored in reviews of reptilian herbivory. Espinoza *et al.* (2004) drew attention to the fact that, contrary to predictions made on the basis of other herbivorous lizards (most of which are large, live in warm places and maintain high body temperatures), herbivory had repeatedly evolved at small body size and in cool-climate *Liolaemus* species. In fact, herbivory has probably evolved more times within *Liolaemus* than it has within any other squamate group, and about 66 times more rapidly than it has in non-liolaemid squamates (Espinoza *et al.* 2004, p. 16823).

It's obvious that there's a lot of interesting stuff to say about these lizards. New species are discovered on a regular basis, mostly due to surveying work in previously unexplored regions: *not* because of rampant splitting or the documentation of morphologically similar cryptic species. Ongoing work and the studies cited here mean that we're sure to see liolaemines being appreciated a lot more in coming decades – this is a *major* squamate radiation, the history and future of which need to become better appreciated and better understood.

For previous Tet Zoo articles on iguanians, see...

- Harduns and toad-heads; a tale of arenicoly and over-looked convergence
- Ermentrude the liolaemine
- 'Cryptic intermediates' and the evolution of chameleons
- Tell me something new about basilisks, puh-lease
- Amazing social life of the Green iguana
- The Squamozoic actually happened (kind of): giant herbivorous lizards in the Paleogene

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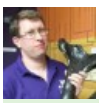

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