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The *Phyllomedusa perinesos* group (Anura: Hylidae) is derived from a Miocene Amazonian Lineage

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Abstract

The *Phyllomedusa perinesos* group is composed of four species that inhabit cloud forests in the eastern Andean slopes. We estimated the phylogenetic relationships among them and their closest relatives using mitochondrial DNA sequences. Our results confirm the monophyly of the group and a close relationship with the Amazonian species *Phyllomedusa atelopoides* and *Phyllomedusa tomopterna*. A chronogram indicates that the group originated during the Miocene and the contemporary species diverged from their closest relatives during the Miocene and early Pliocene. The timing of the group's origin suggests that its evolution was linked to the rise of the eastern Andes. Based on the phylogeny we expand the species content of the group to include *P. atelopoides* and *P. tomopterna.*

Key words: Andes, Biogeography, Ecuador, Hylidae, Peru, Speciation

Introduction

The *Phyllomedusa perinesos* group was first defined by Cannatella (1982) to accommodate four species of leaf-frogs from cloud forests from the eastern Andean slopes from Ecuador and Peru: *P. baltea* Duellman & Toft 1979, *P. duellmani* Cannatella 1982, *P. ecuatoriana* Cannatella 1982, and *P. perinesos* Duellman 1973. The group was principally diagnosed by having purple coloration in the hands, feet, belly, flanks and concealed surfaces of the limbs (Cannatella 1982).

Two phylogenetic analyses of Phyllomedusinae each included two species of the *P. perinesos* group (*P. baltea* and *P. duellmani* in Faivovich et al. [2010] and *P. perinesos* and *P. duellmani* in Wiens et al. [2010]) and found that the two species were phylogenetically closest to each other. More recently, Pyron & Wiens (2011) re-analyzed the same sequences (originally published by Faivovich *et al.* 2010 and Wiens *et al.* 2005, 2010) and found moderate support (bootstrap = 59) for a clade composed of the three species, as the sister-group of *P. atelopoides*. Faivovich et al. (2010) and Pyron & Wiens (2011) found that the *P. perinesos* group + *P. atelopoides* are sister to *P. tomopterna*. Until know, *P. ecuatoriana* has not been included in a phylogenetic analysis and thus its evolutionary affinities have not been rigorously tested.

Herein we add new sequence data of *P. ecuatoriana* to determine its phylogenetic position and to resolve the relationships within the *P. perinesos* species group. The genetic data confirms the monophyly of the group and suggest that its origin was associated with the uplift of the Andean Eastern Cordillera.

Methodology

We estimated the phylogenetic position of *P. ecuatoriana* within the *P. perinesos* group based on new sequence

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By the early to middle Miocene, the Eastern Andean Cordillera had elevations below 700 m and by 4 Mya its elevations were below 40% of their current values (Gregory-Wodzicki 2000). Thus, by the time when the MRCA of the *P. perinesos* group originated (i.e., when its MRCA diverged from *P. atelopoides*, 18–24 My) the montane habitats characteristic of the group did not exist. The origin of the extant species was likely associated with the uplift of the Eastern Cordillera and a switch of ecological niche to inhabit montane forests with cooler temperatures. This scenario will suggest a parapatric mode of speciation along an environmental gradient. Similar speciation scenarios have been proposed for *Osteocephalus festae* and *Osteocephalus verruciger* (Ron et al. 2012).

In his review of the *P. perinesos* group, Cannatella (1982) hypothesized that speciation of the common ancestor of the group, was associated with vicariance associated with the Huancabamba Depression, a well-known biogeographic barrier in northern Peru (Duellman 1979; Parker *et al.* 1985). Our phylogeny supports that hypothesis because it shows that species on both sides of the depression are each other's closest relatives; however, alternative speciation scenarios are also possible. The importance of the Huancabamba Depression as a barrier promoting speciation in amphibians has yet to be confirmed. In frogs of the *Osteocephalus buckleyi* species group, the Huancabamba depression does not appear to represent a significant barrier (Ron *et al.* 2012).

It is worth reconsidering the definition and content of the *P. perinesos* group. Cannatella (1982) diagnosed the group as having purple coloration in the hands, feet, belly, flanks, and concealed surfaces of the limbs, which he postulated was a synapomorphy (Cannatella 1982). However, *P. atelopoides* has similar coloration, although with a lesser intensity of purple (Duellman *et al.* 1988:92).

We also note that several species in the *P. hypochondrialis* group (e.g., *P. palliata*, *P. nordestina*), which is the sister-group of the *perinesos* group + *P. atelopoides* + *P tomopterna*. (*sensu* Faivovich et al. [2010]) have purplish color on the flanks associated with orange regions. Thus, it is likely that the purple-orange coloration in the flanks is a synapomorphy for a clade that joins the *P. perinesos* group + *P. atelopoides* + *P. tomopterna* + *P. hypochondrialis* group (*sensu* Faivovich et al. 2010).

Duellman et al. (1988) did not make any direct comparisons with the species of the *P. perinesos* group. This molecular phylogenetic analysis then, is an example in which molecular phylogenies can illuminate the interpretation of the evolution of phenotypic characters.

Our phylogeny indicates that *P. atelopoides* and *P. tomopterna* are sequential sister-species to the *perinesos* group. Neither is assigned to a species group. For this reason we expand the content of the perinesos group to include *P. tomoptera* and *P. atelopoides*. As currently defined, the group lacks known morphological synapomorphies.

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