

## Assessing and dating Andean uplift by phylogeography and phylochronology: Early Miocene emergence of Andean cloud forests

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One possible way of dating the acquisition of altitude is to estimate the age of biotic evolutionary changes triggered by surface uplift and related environmental modifications. In the case of the Andes, considerable biotic radiations have occurred as new ecosystems were created by uplift, to the point that the Andean region now presents one of the world's highest biodiversity (Balslev, 1993). Between ~5°S and ~17°S, the rising Andes came to serve as a rain barrier: environments became drier in the west, and cloud forests developed along their eastern, windward side. This peculiar cool and moist environment directly results from orogeny and uplift since it is formed by orographic concentration of precipitation: the westward-moving Amazonian moist air is forced to rise by the topography and therefore cools down, and water vapor condenses as clouds, mist and rain. Thus dating related biotic basal radiations would date the synchronous emergence of cloud forests and provide an estimate of the time when Andean uplift became sufficient to significantly block Amazonian moisture.

Among the very diverse biota that are characteristic of Andean cloud forests are a number of bird genera referred to as mountain-tanagers. Here we use published molecular phylogenetic and phylogeographic information concerning these birds (Burns, 1997) in order to estimate the age of emergence of Andean cloud forests. Phylogenetic trees of tanagers (Passeriformes: Emberizidae: Thraupinae) based on mtDNA cytochrome *b* sequence data (Burns, 1997) evidence (1) that the group is monophyletic and of Caribbean origin (its basal taxa living in the Greater Antilles), and (2) that mountain-tanagers occur in two independent monophyletic clades, indicating that at least two distinct ancestors adapted to emerging cloud forests (Fig. 1).

Each of these two clades of mountain-tanagers display a ~6.0 % maximum divergence in 3rd codon position transversions, revealing that they branched off at about the same time, whereas this difference is ~11.9 % among all South American tanagers (Fig. 2; Burns, 1997). The age of branching of both mountain-tanager clades, which provides an estimate of the age of emergence of Andean cloud-forest habitats, is thus approximately equal to the age of the diversification, i.e. immigration into South America, of (the ancestor of) South American tanagers, multiplied by the factor  $6.0/11.9 = 0.504$ .

A molecular clock for tanagers can be calculated in at least two ways. Assuming that mtDNA evolutionary rates among birds are similar to those among mammals, Burns (1997) used the ~0.5 %/Ma rate of divergence in 3rd codon position transversions defined by Irwin et al. (1991), who observed a linear relationship between transversions in cytochrome *b* sequences and divergence dates among ungulates calibrated by fossils. This first method implies that immigration of the South American tanager ancestor from Caribbean islands would have occurred at ~23.8 Ma, and branching of both mountain-tanager clades at ~12.0 Ma (Burns, 1997).

Our preferred second method tentatively calibrates Burns's (1997) molecular data by an independent chronological tie-point. It has been proposed that two mammal groups, namely platyrrhine primates and caviomorph rodents, immigrated into South America from Caribbean islands (Marshall & Sempere, 1993). As

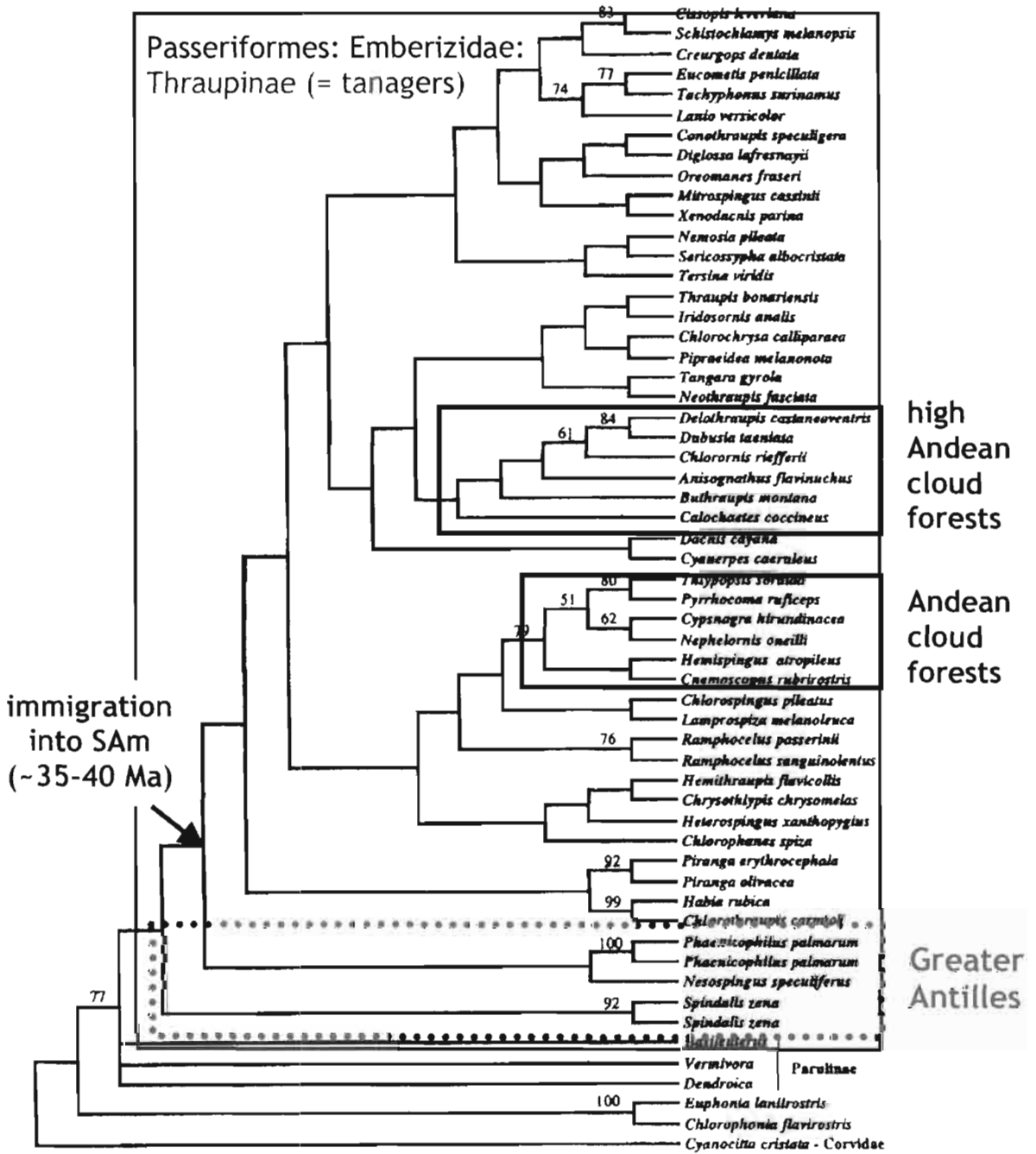


Figure 1. Phylogenetic tree of the Thraupinae (including outgroup species; strict consensus tree of the two most parsimonious trees resulting from an equally-weighted analysis); the phylogeny and phylogeographic information are from Burns (1997). The Thraupinae basal taxa are from the Greater Antilles (dotted green box). The two mountain-tanager clades (blue boxes) indicate that at least two ancestor taxa independently adapted to Andean cloud forests.

already underlined by Burns (1997), the apparent Caribbean origin of tanagers obviously strengthens this scenario. Furthermore, it invites to search for a common interval of time at which immigration from Caribbean islands was made possible for both birds and these specific small-size mammals. This scenario does not require a land bridge because small-size birds can fly over seawater and small mammals can be rafted across, provided in both cases that island and continent are not unreasonably far away from each other. However, because of their ability to fly, island birds are expected to have reached the South American mainland earlier than rafted mammals. We therefore propose that the time of immigration of tanagers into South America was a few Ma

earlier than that of primates and rodents. Because the earliest known caviomorph rodent is dated ~31 Ma (Wyss et al., 1993), and because this age is only a minimum age for rodent immigration, we propose that the tanager immigration occurred at some time within the 35-40 Ma interval. This determines that speciation of the mountain-tanager ancestors, and hence the emergence of Andean cloud-forest habitats, would have occurred during the 17.6-20.2 Ma interval ( $= 18.9 \pm 1.3$  Ma), i.e. in the late Early Miocene (Fig. 2). The derived evolutionary rate of divergence in 3rd codon position transversions would hence be comprised between 0.30 and 0.34 %/Ma, a seemingly acceptable value for birds.

A  $18.9 \pm 1.3$  Ma age for emergence of Andean cloud forests is also preferred here because it is matched by geological (e.g., Sébrier et al., 1988) and other phylochronologic (Picard, 2005; Sempere et al., in prep.) data.

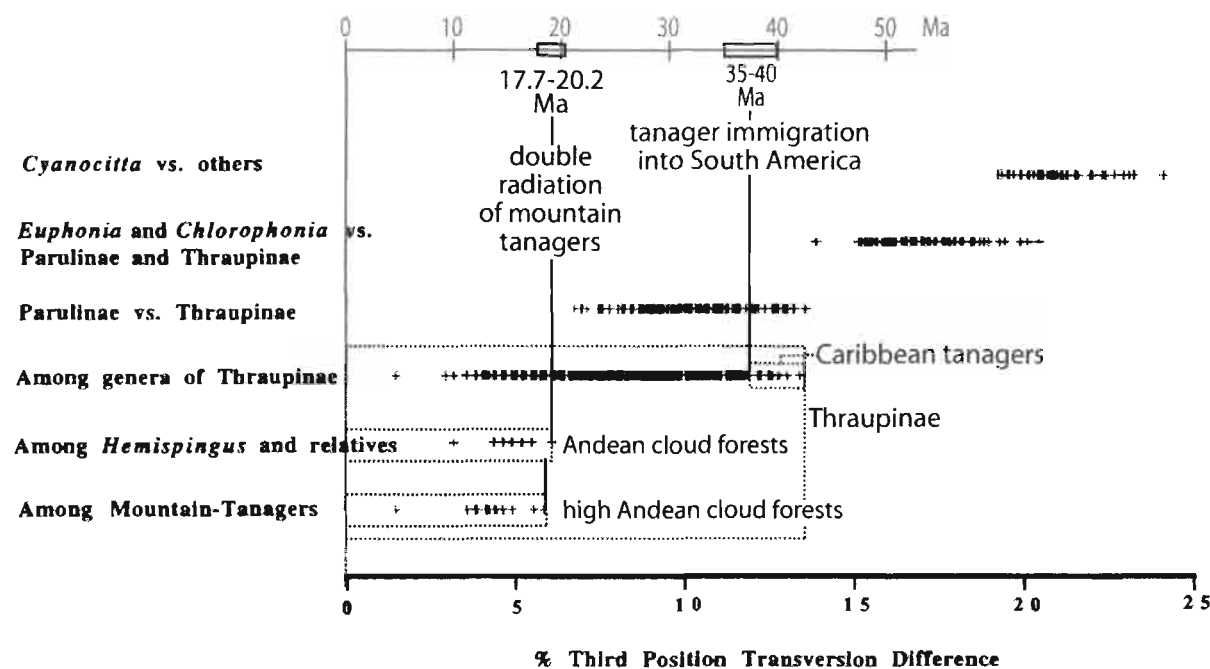


Figure 2. Preferred graphical estimation of age of mountain-tanager radiations, and hence of emergence of Andean cloud forests (see text). Graphical analysis is based on molecular data and phylogeographic information from Burns (1997). Radiation of South American tanagers from Caribbean tanagers is placed at start of higher density of pair divergence points.

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