

Kommentare / Comments

Taxonomy of *Metallura*

Recently, Heindl & Schuchmann (1998) published a detailed speciation scenario for *Metallura* hummingbirds. They suggested a scenario where the three main lineages of *Metallura*, and the sister genus *Chalcostigma*, all dispersed out of an area of origin in the Andes of Bolivia or south eastern Peru, with successive pulses of dispersal northwards and intermittent isolation of populations during the last twoglacial periods. A fairly detailed sequence of events is suggested. The results and interpretations of a molecular phylogenetic study of the same group (García-Moreno et al. in press) are mentioned in a final paragraph ('Alternative model and time scale'). This study also suggests a southern origin of the group, but provides evidence of strong population subdivision, especially of taxa inhabiting tree-line habitats (the *M. aeneocauda* species group, including the aberrant *M. phoebe*) since well before the onset of major glacial cycles 800,000 years ago. We would like to comment on some of the discrepancies between these two analyses of the same taxonomic group.

1) Heindl & Schuchmann contend the usefulness of the mtDNA data as a molecular clock.

Date estimation based on DNA alone is prone to errors (Hillis et al. 1996), but DNA estimates can be used as working hypotheses until more accurate dating can be established. Given that hummingbirds are scarcely represented in the fossil record, molecular data may be the best estimate we can obtain based on data that pertain directly to the group in question. The alternative would be to base the time estimates on pre-conceived idea about the role of Pleistocene glaciations, which does not offer a mechanism for critical hypothesis evaluation.

2) The rate of molecular evolution is not calibrated for hummingbirds, and the usefulness of the rate which we used (2 % substitution per million years) is therefore questioned.

As Heindl & Schuchmann state, the existence of a universal constantly ticking molecular clock is contentious. However, there is little controversy regarding the existence of clocks which work well within specific taxonomic groups (Li 1993). We therefore see no problem in using DNA sequences of related organisms to investigate their history, and in fact several other molecular studies of Andean birds suggest that vicariance patterns that are prominent today, were established long before the period of major glaciations (García-Moreno et al. 1998).

The 2 % substitution rate used by Klicka & Zink (1997) to estimate the age of divergence of North American song birds has been found reasonably constant among many different bird groups (note #11 in Klicka & Zink 1997, and references therein, Fleischer et al. 1998). Furthermore, based on several years DNA hybridisation work, Bleiweiss (1998 a, b) suggested that the nuclear DNA of hummingbirds evolves at a similar rate to that of other bird families, and that highland hummingbirds have a decidedly slower rate of molecular evolution. Although we agree with Heindl & Schuchmann that a more precise dating should be attempted using a local clock calibration, we tried to overcome the inherent error by estimating divergence dates using also other rates (10 % third position substitutions or 0.5 % third position transversions per million years; Irwin et al. 1991). Our estimates with these different rates are similar and both point to a divergence between mid elevation and highland species about 2–4 mya. This result holds for us even when correcting for net sequence divergence

between the two groups as suggested by Avise & Walker (1998).

It is important to bear in mind that, according to our estimation, the *Metallura* radiation started in the lower Pleistocene, as also suggested by Heindl & Schuchmann. However, neither molecular nor morphological data are good enough to associate individual speciation events with specific glacial maxima. Detailed interpretations based on a crude phylogeny and the current distribution patterns cannot lead beyond the speculative level of scenario building and can never provide a mechanism for rigorous evaluation of ideas (e. g., see García-Moreno et

al. 1998). Their interpretation of speciation among *Metallura* hummingbirds is full of speculation about possibilities – and many other likely scenarios could be thought of – but there are no facts supporting any of them.

3) The position of *M. phoebe* is contentious.

This is an aberrant, large, melanistic form which inhabit mist vegetation high above the Peruvian coastal desert. The DNA evidence supports its placement in a clade together with geographically adjacent forms living in south-western Ecuador thus suggesting a vicariance pattern even if the branching pattern within this clade is not fully resolved. Heindl & Schuchmann totally ignored this result in suggesting that *M. phoebe* colonised western Peru directly from the dispersal centre in Bolivia. The only evidence they produced was to refer to the existence of a melanistic Bolivian species in the genus *Aglaeactis*. Why not refer to the existence of a melanistic *Coeligena* in north-western Colombia? The characters they used to infer a phylogeny can be mapped without conflict into the DNA generated phylogeny (Fig.).

Heindl & Schuchmann (1998) provide an excellent and meticulous documentation of the phenotypic variation in *Metallura*. However, we find it peculiar that they use this to build a detailed narrative with a specific time scale, supporting a general idea about a Bolivian dispersal centre for Andean hummingbirds and a traditional view of speciation caused by glacial isolation. There is considerable evidence suggesting random segregation of pigment characters in birds inhabiting patchy Andean habitats (e.g., Remsen 1984, Remsen & Graves 1995, García-Moreno & Fjeldså 1999) and in the *Metallura* case the authors were aware that an alternative interpretation exists and is supported by fairly robust analysis. We earlier proposed that the Andean avifauna diversified in the upper Pleistocene (see e. g. Fjeldså 1992), but as attempts critically to evaluate a model (Roy et al. 1997) point in another direction we must reject the initial hypothesis. We do not think that biogeography is brought forward by sim-

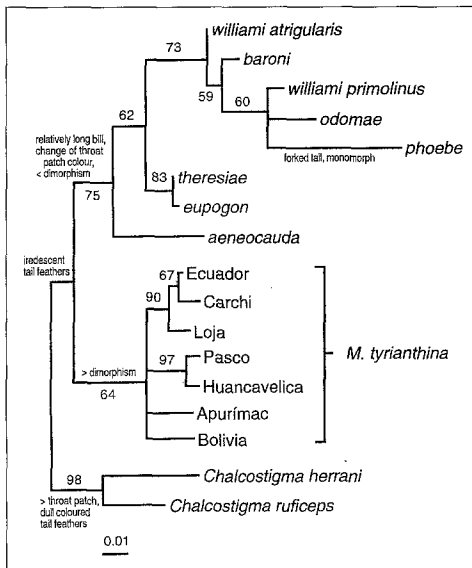


Fig. 1. Maximum likelihood tree obtained from 855 bp of combined DNA sequences of mitochondrial cyt b (345 bp), ND2 (290 bp) and ND5 (220 bp) genes (García-Moreno et al., in press) with the synapomorphies used by Heindl & Schuchmann (1998) in their phylogeny. Figures above the branches represent bootstrap values with the maximum likelihood algorithm after 200 replicates. Branches are drawn proportionate to the amount of change along the branch, and those with low bootstrap support (< 50 %) have been collapsed. Names in the *M. tyrianthina* clade refer to localities where the samples originated; Ecuador refers to a widespread haplotype found in all localities other than Carchi and Loja.

ply fitting phenotypic variation into a preconceived scenario.

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Reply from Karl-L. Schuchmann

As we stated in our *Metallura* paper (Heindl & Schuchmann 1998): “A major problem of the reconstruction of speciation and dispersal patterns is to apply a time scale to the processes of lineage divergence.” Alongside the traditional Pleistocene speciation models (habitat refuges serving as isolating mechanisms for speciation events during the recent ice ages, overview in Haffer 1974), molecular biologists estimate dates of taxa divergence from mitochondrial DNA sequence distances assuming a molecular clock, i. e., the number of substitutions which have occurred since two sequences diverged are calibrated by a nucleotide substitution model. Most of the recent approaches use the cytochrome b gene of the two taxa and propose a base substitution rate of 2 % per million years as a molecular clock ticking at a constant rate. These estimates have been shown to hold well for the divergence of primates and humans, and of chickens (*Gallus*) and partridges (*Alectoris*) (see references and critical remarks in Arbogast & Slowinski 1998). The substitution rate of 2 % per My has since been uncritically applied to molecular clocks for many other taxonomic groups to reconstruct phylogenies and

to postulate divergence time scales. As mentioned in our *Metallura* paper, substitution rates in the Trochilidae, and most of the other members of the class Aves, have not yet been calibrated and perhaps never will be owing to the lack of fossil records. Therefore, any estimates of dates of divergence are hypothetical, whether in the case of the Pleistocene speciation model which we favoured in our paper, or with respect to the concept of a constant-rate molecular clock. Arbogast & Slowinski (1998) give the following critical comment on the state of the art: "Accurately estimating dates of divergence from molecular data is, at best, a challenging process."

In general, our speciation scenario in *Metallura* covers the time of the late Pliocene and Pleistocene – a period of 3 million years (see summary: "High-Andean habitat fragmentations due to climate changes during the late Pliocene and Pleistocene presumably caused geographical isolation and differentiation of most *Metallura* populations."). This is within the general time frame (2–4 million years) suggested by García-Moreno et al. (in press). Only on page 470 of Heindl & Schuchmann (1998) do we speculate that differentiation in the genus *Metallura* perhaps occurred as late as the upper Pleistocene, driven mainly by glacial cycles. This is indicated to us by paleogeographical changes and vegetational shifts during glacial periods which are congruent with the phenotypic variation characters in *Metallura* taxa.

Based on phenotypic characters and patterns of biogeography, we postulate a sister-group relationship between *Metallura phoebe* and *Metallura aeneocauda*. This is not congruent with the proposed relationship indicated by García-Moreno & Fjeldså (their reply to Heindl & Schuchmann 1998), who consider *M. phoebe* closely related to the *M. williami* group, whereas *M. aeneocauda*, in their opinion, is not a close relative of that group. We consider *M. odomae* and *M. williami* to be members of the *M. aeneocauda* superspecies. These minor discrepancies cannot be resolved because of the different data interpretations.

Our suggested sister-group relationship is based on the criterion of parsimony, which assumes the smallest number of evolutionary changes, to minimise the probabilities of convergences and inversions. We assume that the long bill and reduced sexual dimorphism are the major characters shared between *M. phoebe* and *M. aeneocauda*.

We suggest that *M. phoebe* has a centre of origin in Cochabamba, Bolivia, as does another, unrelated, melanistic hummingbird, the endemic *Aglaeactis pamela* occurring in the same environment. For us, the congruence of distribution was the most striking argument. The melanistic *Coeligena* species from Colombia referred to by García-Moreno & Fjeldså surely cannot have been meant seriously.

In summary, we think that the analysis of phenotypic variation might help to explain patterns of phylogenetic biogeography. This traditional method is as valuable to science as the alternative methods of molecular biology, so long as we are aware that supposed divergences of taxa are not considered as facts but as useful alternative hypotheses. In general, the *Metallura* conclusions reached by us and by García-Moreno & Fjeldså are actually not far removed from each other when compared with many other ornithological studies, in which results obtained via molecular biology are rather in conflict with traditional findings.

My comments, for which I am solely responsible, profited from discussions with Walter Bock, N.Y., Brian Hillcoat, Neuss, and Leo Joseph, Philadelphia.

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