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PHYLOGENETIC RELATIONSHIPS AMONG *HEMISPINGUS* TANAGERS

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Resumen. – Relaciones filogenéticas entre tángaras del género *Hemispingus*. – Las relaciones filogenéticas entre las tángaras del género *Hemispingus* no están completamente definidas. La monofilia del género es apoyada de manera incontroversial en un trabajo reciente basado en secuencias parciales de ADN del gen mitocondrial ND2. El género *Cnemoscopus* ha sido considerado como un grupo hermano del género *Hemispingus*. En este trabajo añadimos las secuencias correspondientes de ND2 de *H. parodii* y de *Cnemoscopus rubrirostris*, y analizamos los datos nuevamente. También analizamos secuencias parciales de citocromo *b* para un subconjunto de especies. Nuestra mejor hipótesis sugiere tres clados principales dentro del género: 1) aves ocráceas (*frontalis*, *melanotis*, *piurae*, and *trifasciatus*), 2) aves con cejas conspícuas (*calophrys*, *parodii*, *auricularis*, *atropileus*), y 3) aves semejantes a los chipes (Parulinae) (*xanthophthalmus* and *verticalis*). La posición de *H. superciliaris* (y suponemos que de *reyi*) es ambigua; los resultados apuntan a relaciones con el grupo de aves ocráceas o con las aves semejantes a los chipes. *H. rufosuperciliaris* (junto con *H. goeringi*) es la tángara conectada al nodo más profundo en la filogenia del género, ocupando una posición basal a los tres clados ya mencionados. Los análisis de ambos fragmentos de genes mitocondriales sugieren que *Cnemoscopus rubrirostris* es parte del grupo *Hemispingus*, y ocupa una posición basal en la filogenia del género. Aunque la mayoría de nuestros análisis sugieren que *Hemispingus* (+ *Cnemoscopus*) es monofilético, el género nunca es monofilético en análisis que incluyen muestras del género *Poospiza*, por lo que concluimos que los datos actuales no son suficientes para corroborar o rechazar la monofilia del género sin ambigüedad.

Abstract. – Phylogenetic relationships among *Hemispingus* tanagers are currently not well understood. Recent work based on partial mtDNA sequences of the ND2 gene supported unambiguously the monophyly of the genus. The genus *Cnemoscopus* has been considered sister to the genus *Hemispingus*. We added the corresponding ND2 sequences of *H. parodii* and *Cnemoscopus rubrirostris* to our previous data set, and reanalyzed it. We also analyzed partial cytochrome *b* sequences for a subset of species. Our best hypothesis suggests three main clades within the genus: 1) ochraceous birds (*frontalis*, *melanotis*, *piurae*, and *trifasciatus*), 2) conspicuous eye-browed birds (*calophrys*, *parodii*, *auricularis*, *atropileus*), and 3) warbler-like birds (*xanthophthalmus* and *verticalis*). The position of *H. superciliaris* (and presumably *reyi*) is ambiguous, with results placing it either with the ochraceous birds or with the warbler-like birds. The deepest *Hemispingus*, basal to these three clades, is *H. rufosuperciliaris* (and *H. goeringi*). Analyses of both mitochondrial gene fragments suggest *Cnemoscopus rubrirostris* is part of the *Hemispingus* assemblage, occupying a basal position in the phylogeny of the group. Additional analyses including *Poospiza* species, however, fail to recover a monophyletic *Hemispingus*. The current data available are thus insufficient to unambiguously confirm or reject monophyly of the genus. *Accepted 30 November 2002.*

Key words: *Hemispingus*, *Cnemoscopus*, nine-primaried oscines, aves, mtDNA, ND2, phylogeny, Andes, biogeography, speciation.

INTRODUCTION

Phylogenetic relationships among tanagers of the genus *Hemispingus* have been confusing. The taxonomic relationships among the 12 traditionally recognized species are far from clear. Recently, we presented a molecular phylogeny of this Andean genus based on partial mtDNA ND2 sequences. This work supported unambiguously the monophyly of the genus when compared to other "nine-primaried oscines", but could not resolve unambiguously the relationships within the genus (García-Moreno *et al.* 2001). It also suggested that more taxa might deserve species rank within the genus than currently acknowledged (e.g., *H. auricularis* and *H. piurae*; see Helbig *et al.* 2002). The molecular phylogeny, however, lacked samples of *Cnemoscopus*, which has been considered the sister group of *Hemispingus* (e.g., Isler & Isler 1987, Burns 1997, Yuri & Mindel 2002), and used sequences of *Ramphocelus* as outgroup. *Cnemoscopus* resembles typical *Hemispingus* tanagers in vocalizations and habits, but differs from them in having a uniform gray head with no ornamental pattern.

In this article, we re-analyze our molecular data set with the inclusion of sequences of *Cnemoscopus rubrirostris* and *Hemispingus parodii*, and present our best estimate of the phylogenetic relationships within this genus. *H. parodii*, which is a local endemic of the Vilcanota and Vilcabamba mountains near Cuzco, Peru (Weske & Terborgh 1974), was not available when we did our first phylogenetic analysis. We also explore the monophyly of the genus in the context of a broader taxonomic sampling.

MATERIALS AND METHODS

We complemented our previous molecular dataset (García-Moreno *et al.* 2001; Accession numbers AY039278-AY039300) with samples of *Cnemoscopus rubrirostris* from Loja, Ecuador, and Huanuco, Peru (voucher at Zoological Museum, University of Copenhagen), and *Hemispingus parodii* (2) from Cuzco, Peru (specimens at the Museo de Historia Natural, Universidad de San Antonio Abad del Cusco). We extracted DNA and amplified a 310 base pair fragment of the mitochondrial ND2 gene with the primers L5215 and H5578 (Hackett 1996) using standard protocols, as described elsewhere (García-Moreno *et al.* 2001). GenBank accession numbers for the new sequences are AY180913 and AY180914.

Phylogenetic analyses were carried out using PAUP* v.4b10 (Swofford 2002). We analyzed the data set under maximum likelihood (ML), maximum parsimony (MP), and minimum evolution (ME) criteria. For parsimony analyses, we did two kinds of searches: with all characters equally weighted and with transversions (tv) up-weighted 10x over transitions (ti) (the estimated ratio was 11. 03, see below), although different weighting schemes yielded results consistent with this one. We did several rounds of heuristic searches with 50 random stepwise additions of sequences. For minimum evolution, we estimated the shortest tree starting from a neighbor-joining tree using both uncorrected distances and several corrected distances available in PAUP*. For the likelihood analyses, we performed heuristic searches starting from a neighbor-joining tree. We used Modeltest (Posada & Crandall 1998) to select the appropriate likelihood models for analysis with and without several outgroups (for *Hemispingus* only: HKY + G model, ti/tv = 11.03, shape parameter = 0.25). The appropriate likelihood settings were also applied for the estimation of maximum likelihood distances in minimum evolution searches.

To estimate the reliability of the inferences, we performed bootstrap analyses with each of the methods: one hundred replicates with 50 random additions of sequence for parsimony (weighted and equal weights) or

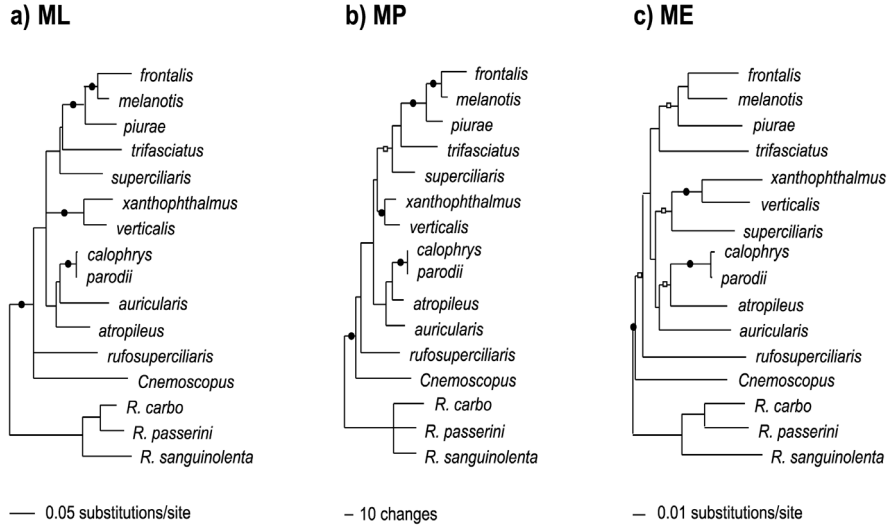

FIG. 1. Optimal *Hemispingus* phylogenies retrieved with different analyses using the closest outgroup. (a) Maximum likelihood under HKY model (transition:transversion ratio of 11.03; gamma parameter shape of 0.25); (b) Maximum parsimony with transversions weighted 10x over transitions; (c) Minimum evolution with uncorrected (p) distances. Other analyses resulted in similar but not identical topologies. Black dots on the branches indicate bootstrap support higher than 70%; open boxes on the branches indicate bootstrap support higher than 50%.

starting with neighbor-joining for minimum evolution. For likelihood we only bootstrapped the data set with *Ramphocelus* as outgroup, and used the 'fast stepwise addition' option of PAUP*. This option, which does not perform branch swapping, appears to be a conservative underestimate of the branch support (Mort *et al.* 2000).

We compared alternative topologies under the likelihood criterion using the Shimodaira-Hasegawa test (SH; Shimodaira & Hasegawa 1999, Goldman *et al.* 2000), with one-tailed probabilities and 1000 RELL bootstrap replicates.

RESULTS

We successfully sequenced samples of *Hemispingus parodii* and *Cnemoscopus rubrirostris*, and added them to our previous data set (García-Moreno *et al.* 2001). Only two *Hemispingus* species are lacking in the present phylogeny, *H. reyi* and *H. goeringi*, both of them endemics of the Mérida mountains of Venezuela.

A first phylogenetic analysis included our *Cnemoscopus* and *Hemispingus* sequences as well as sequences of *Ramphocelus*, and also more distant representatives of the "nine-primaried oscines" (*Basileuterus* and *Chlorospingus*). The results of this analyses resulted in optimal topologies with *Cnemoscopus rubrirostris* being placed inside the *Hemispingus* clade, either associated with the *atropileus* group (ML, weighted parsimony, and ME) or close to *rufosuperciliaris* and sister to the *superciliaris*, *verticalis*, *xanthophthalmus* clade (9 out of 11 MP trees with equal weights, 2 out of 4 MP trees with weighted transversions). A clade comprising *H. melanotis*, *frontalis*, and *piurae* was retrieved in all optimal topologies. Also in all topologies

calophrys and *parodii*, and *xanthophthalmus* and *verticalis* appeared as sister taxa. *H. parodii* differed from *H. calophrys* only in 0.3 % divergence (a single A–G transition), which is a smaller order of magnitude than the divergence amongst other *Hemispingus* species (11–22 %, Table 1 in García-Moreno *et al.* 2001). The results did not change significantly when we increased the taxon sampling to include over 20 genera of parulid warblers, *Coereba*, and *Conirostrum* (Lovette & Bermingham 2002; Accession numbers AF383109–AF383147), with *Hemispingus* + *Cnemoscopus* forming a monophyletic clade sister to *Conirostrum*, and *Ramphocelus* basal to them. In a study addressing relationships among "nine-primaried oscines", *Ramphocelus* sequences also appear deeply seated on the same branch of tanagers as our ingroup (Yuri & Mindell 2002).

Analysis restricting the outgroup to *Ramphocelus*, resulted in *Cnemoscopus* basal to the *Hemispingus* clade separated by a very short internode (or unresolved in some trees). Bootstrap analyses supported the *Cnemoscopus* + *Hemispingus* clade in all replicates (100% in MP, ML, ME) – slightly lower when more outgroups were included (80% MP, 80–90% ME). Although less extensive, analysis using *Conirostrum* as outgroup, instead of *Ramphocelus*, gave the same results. Other branches with consistently high bootstrap support were those uniting *H. calophrys* and *H. parodii*, and *H. verticalis* with *H. xanthophthalmus*, as seen in Figure 1. Overall, the results are highly concordant with the hypothesis put forward by García-Moreno *et al.* (2001) in their Figure 4, and there is high congruence among the results based on three different methods of analyses.

Comparison of the different topologies using the SH test could not reject alternative hypothesis concerning the basal branching order within *Hemispingus,* nor the particular position of *Cnemoscopus*, i.e., inside the *Hemispingus* clade or basal to it (two ML trees –Ln = 1652.25369; MP equal weights –Ln = 1656.65737 , $P = 0.531$; MP weighted –Ln = -1652.97349, $P = 0.833$; ME uncorrected distance –Ln = 1654.06521, $P = 0.759$; ME with ML distance –Ln = 1660.00209, $P = 0.294$). Nevertheless, the topology obtained with plumage characters (García-Moreno *et al.* 2001) would be rejected with a more conservative analysis (e.g., $\alpha = 90\%$; –Ln = 1667.42124, $P = 0.08$).

We retrieved from GenBank partial cytochrome *b* sequences (cyt *b*; 285 bp) of four *Hemispingus* species (*auricularis* AF006234, *melanotis* AF100537, *frontalis* AF100536, and *verticalis* AF100538), *Cnemoscopus rubrirostris* (AF006222), and *Ramphocelus* spp. (U15717, U15718, U15723). Phylogenetic analysis of this additional small data set yielded results congruent with the more extensive ND2 analyses presented here and elsewhere (García-Moreno *et al.* 2001), with *Hemispingus* (+ *Cnemoscopus*) forming a monophyletic clade and *Cnemoscopus* being associated with *H. atropileus* (as it did in some of our analyses with several outgroups).

We tested the idea put forward by Lougheed *et al.* (2000) that *Poospiza* may be the closest relative of *Hemispingus.* For this purpose, we added to the cyt *b* data set sequences of *Poospiza ornata*, *P. melanoleuca*, *P. whitii*, and *P. hypochondria* (AY005207, AY005209–AY005213), *Pyrrhocoma ruficeps* (AF006249), *Thlypopsis sordida* (AF006256) and *Nephelornis oneilli* (AF006243). None of 13 optimal likelihood trees (–Ln 1261.97615) showed *Poospiza* or *Hemispingus* as monophyletic clades. The SH test, however, could not reject monophyly of *Hemispingus* as a worse hypothesis (–Ln 1273.43289, $P = 0.188$), and it also accepted, although only marginally, the monophyly of *Poospiza* (–Ln 1277.72852, $P = 0.07$). We tried a similar approach with longer sequences (849 bp) but restricted to the two *Hemispingus* species for which complete cyt *b*

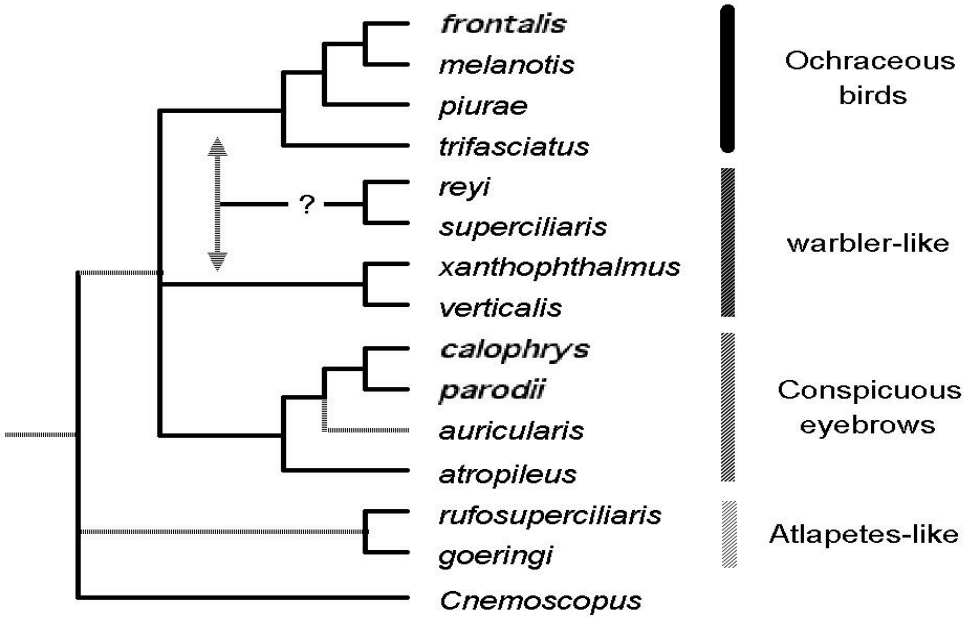

FIG. 2. Our best hypothesis for the phylogenetic relationships of the genus *Hemispingus*. Shaded branches are those for which there is good support but other arrangements are possible: although most analyses recover a monophyletic *Hemispingus* + *Cnemoscopus* clade, some analyses failed to do so, particularly when *Poospiza* was included; *H. rufosuperciliaris* (and by inference, *H. goeringi*) is assumed as the most basal *Hemispingus* proper, but in some analyses it associates basally with the ochraceous birds; *H. auricularis* is sometimes the most basal taxon of the conspicuous eyebrow group (see Discussion and García-Moreno *et al.* 2001). The arrows indicate alternative positions for *H. superciliaris* according to our analyses: *H. superciliaris* associates basally either to the ochraceous bird group or to the *xanthophthalmus-verticalis* clade. As no samples of *H. reyi* were available for our analysis, we connect it to its assumed closest relative with a question mark on the branch.

sequence are available (*frontalis* AF383020 and *auricularis* AF383019). The ML tree failed to recover monophyly of *Hemispingus* (–Ln = 3521.38015), and the best tree obtained when we enforced the monophyly of the genus was only marginally accepted (–Ln = 3529.96778, $P = 0.072$).

DISCUSSION

The results presented here fail to confirm unambiguously the monophyly of *Hemispingus* tanagers, inferred from partial mtDNA sequences, as was concluded in our previous study (García-Moreno *et al.* 2001). When using ND2 sequences, all methods of analyses recovered a *Hemispingus* + *Cnemoscopus* clade regardless of the outgroup chosen, and always with a high level of bootstrap support. Since the position of *Cnemoscopus* is not well established, often basal to *Hemispingus* but sometimes well within *Hemispingus*, our results suggest that *Hemispingus* may not be monophyletic with respect to *Cnemoscopus*. There is also conflicting information regarding the different genes. While analyses with ND2 always retrieved monophyly of *Hemispingus* (+ *Cnemoscopus*) against a broad array of outgroups

(see also García-Moreno *et al.* 2001), some analyses with cyt *b* sequences failed to do so. In particular, the inclusion of cyt *b* sequences of *Poospiza* resulted invariably in polyphyly of the genus *Hemispingus*, although we could not reject its monophyly as a worse hypothesis. Thus, our study is not conclusive regarding the monophyly of the genus. Although we have a good taxonomic sampling for the ND2 data set, the short sequences limit the power of discrimination between alternative hypotheses. On the other hand, the taxon sampling for the genus is far from complete for the cyt *b* data set, with only four *Hemispingus* species represented (+ *Cnemoscopus*), and even poorer (two *Hemispingus* + *Cnemoscopus*) for long cyt *b* sequences.

If we nevertheless assume the monophyly of the genus suggested by the ND2 data set, the internal branching order is still not completely resolved, although the addition of *Cnemoscopus* and *H. parodii* has improved the congruence of different phylogenetic methods and also in relation to our previous work (García-Moreno *et al.* 2001). For an assessment of the phylogenetic relationships within the genus *Hemispingus,* we base our conclusions on analysis using the closest outgroup available, i.e., *Ramphocelus* (or *Conirostrum*). Other genera included in this work, although useful for assessing the position of *Cnemoscopus* in relation to *Hemispingus*, are too distant to function as a proper outgroup of *Hemispingus* (see Burns 1997, Klicka *et al.* 2000, García-Moreno *et al.* 2001, Yuri & Mindell 2002). Our results suggests the following relationships (Figs 1 and 2):

Independent sequences of two mitochondrial genes suggest that *Cnemoscopus rubrirostris* may be part of the *Hemispingus* assemblage, occupying a basal position within the group. Genetic distances between *C. rubrirostris* and some *Hemispingus* species are smaller than some genetic distances between well-recognized *Hemispingus* species (e.g., Kimura-2-parameter distance for cyt *b*/ND2: *C. rubrirostris* vs *H. atropileus* 10/14%; *H. frontalis* vs *H. verticalis* 10/17%). Although genetic distances themselves are not a reliable indicator of relatedness, phylogenetic reconstruction methods based on different assumptions and different genes supported the inclusion of *Cnemoscopus* within the *Hemispingus* assemblage. This makes sense considering the similar song and habits of *Cnemoscopus* and *H. atropileus*, *auricularis*, *calophrys*, *parodii* and *trifasciatus.*

The deepest *Hemispingus* proper according to the mtDNA data is *H. rufosuperciliaris* (and presumably *H. goeringi* too, as shown by plumage patterns and proportions – see García-Moreno *et al.* 2001). This is also the most atypical *Hemispingus* by appearance (Cardiff & Remsen 1994). Proceeding upward in the phylogeny there are three clades, the relationships among which cannot be robustly resolved with the data at hand (considerably longer sequences would be needed to resolve confidently the short internodes separating them). One clade contains birds with conspicuous eyebrows (*H. atropileus*, *auricularis*, *calophrys*, and *parodii*), a second one contains birds with mostly ochraceous underparts (*piurae*, *melanotis*, *frontalis*), but also *trifasciatus* and *superciliaris* (and possibly the morphologically similar *H. reyi* from Venezuela), and the third one contains the sister species *xanthophthalmus* and *verticalis.*

The branching order in the *atropileus* group is only partially resolved. Although some methods place *H. auricularis* (Peru) as the basal taxon of the group, the maximum likelihood topologies put *H. atropileus* (Ecuador) at the base and the southern sisters *H. calophrys* and *H. parodii* as the most derived. This latter arrangement is interesting considering that *H. atropileus* (and hence also *H. auricularis*) was once regarded as conspecific with *H. calophrys.* Since *H. auricularis* is sympatric with *H. parodii* (inhabiting a lower altitude in the Cuzco mountains, see Weske & Ter-

borgh 1974), which in turn is close to *H. calophrys*, it should be clear that *H. auricularis* and *H. calophrys* are also different species. However, the very slight sequence divergence between the two southern populations, *H. parodii* and *H. calophrys*, may raise some concerns about the species ranks of these latter forms. They are allopatric, isolated by 150 km, in spite of continuous elfin forest habitat between them, so their genetic integrity is difficult to assess. The molecular data suggest a recent separation (upper Pleistocene or even later), while other speciation events in the genus appear to have occurred much earlier (García-Moreno & Fjeldså 2000). On the other hand, speciation events in the upper Pleistocene are well established for some other Andean groups (García-Moreno & Fjeldså 2000) and, considering the unique characters of *H. calophrys* (e.g., orange-yellow supercilium and throat, and yellow spot on black ear-coverts), we see no particular reason for lumping *H. parodii* with *H. calophrys* (see Helbig *et al.* 2002). We will instead emphasize that these two forms represent the most recent speciation event in a group which radiated perhaps as early as the Miocene/Pliocene and where most species have had plenty of time to re-distribute and segregate themselves in different ecological zones along the tropical Andes region (García-Moreno & Fjeldså 2000, García-Moreno *et al.* 2001).

The ochraceous bird group has a similar arrangement as the one presented by García-Moreno *et al.* (2001, Fig. 4), i.e., *H. piurae* basal to *H. melanotis* and *H. f. frontalis*. *H. trifasciatus*, which could not be placed unambiguously in our earlier study, appears now consistently at the base of this clade, and in several cases also closely related to *H. superciliaris*. *H. superciliaris* itself comes out as the most basal taxon of that clade, either by itself or together with *trifasciatus*.

The third clade within *Hemispingus* is formed by the sister species *verticalis* and *xanthophthalmus*. Interestingly, despite being sister species replacing each other north and south of the North Peru Low, the branch lengths in this clade are rather long (0.0561 mutations per site ± 0.020 for *xanthophthalmus*; 0.0436 ± 0.019 for *verticalis*). Other *Hemispingus* sister species show much shorter branches and must represent recent events (see the above-mentioned *H. parodii* – *H. calophrys* branch). This suggests that the speciation event for *H. verticalis* and *H. xanthophthalmus* was earlier than often assumed and that either this geographical replacement has remained stable for long periods of time, or the replacement as such may be a recent area of secondary contact resulting from the fluid state of the species' distributions over time.

The results presented here represent our best hypothesis. For a more complete resolution of the deeper nodes one will need to use considerably longer sequences and/or other markers. Similarly, longer sequence and a more comprehensive taxonomic sampling are needed to sort out the question of the monophyly of the genus. Our molecular set has limitations, as seen by the low bootstrap support for most branches and the lack of power to statistically discriminate between many competing hypotheses. Nevertheless, this is the most comprehensive phylogeny on the genus against which subsequent work should be compared, hopefully including the missing species *H. reyi* and *goeringii*, and some of the missing subspecies of *superciliaris* (with striking leap-frog patterns in pigmentation) and *melanotis*.

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