Phylogenetic relationships of African sunbird-like warblers: Moho (*Hypergerus atriceps*), Green Hylia (*Hylia prasina)* and Tit-hylia (*Pholidornis rushiae*)

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Pholidornis, *Hylia*, and *Hypergerus* are monotypic songbird genera that share insectivorous feeding habits and a common habitat in West African forests. Each of these genera has some sunbird-like characters as well as other characters that suggest affinities to sylvioid warblers. We briefly review previous phylogenetic hypotheses for these taxa and then present an analysis based on over 2 000 bases of mitochondrial sequence data for a broad range of Old World songbirds representing most families in Sibley and Ahlquist's (1990) superfamilies Passeroidea and Sylvioidea. Our analyses confirm the placement of *Hypergerus* and its sister taxon *Eminia* within a larger monophyletic family of African warblers Cisticolidae. We also find strong support for a sister relationship between *Pholidornis* and *Hylia* and evidence that this clade represents just one lineage in a diverse assemblage of Old World warblers that is probably paraphyletic or polyphyletic with respect to other sylvioid families. While a definitive placement of the *Pholidornis/Hylia* clade within Sylvioidea was not possible, a number of specific previous hypotheses can now be rejected: *Pholidornis* and *Hylia* are not closely related to sunbirds Nectariniidae, estrildid finches Estrildidae, or honey-eaters Meliphagidae. Our study underscores the problems that may be encountered in avian systematics: on the one hand, repeated evolution of sunbird-like morphological features (slender bill, brush-tipped tongues and long hyoid bones) potentially misleads traditional classification, while on the other hand, the rapid diversification of lineages at different points in avian evolution reduces the phylogenetic signal in molecular sequence data, making difficult the reconstruction of relationships among taxa resulting from an adaptive radiation.

Introduction

Pholidornis, *Hylia*, and *Hypergerus* are monotypic songbird genera that share insectivorous feeding habits and a common habitat in West African forests. Each of these genera has some sunbird-like characters as well as other characters that suggest a relationship with sylvioid warblers and all three have had a turbulent history of systematic classification. *Pholidornis*, for example, has been proposed as a member of at least seven families (Sibley and Monroe 1990, Fry 2000); Sylviidae, Estrildidae, Dicaeidae, Nectariniidae, Remizidae, Hyliidae and Meliphagidae. Life histories of these enigmatic songbirds were described in recent volumes of the *Birds of Africa*, in which *Hypergerus* and *Hylia* are listed *incertae sedis* at the end of Sylviidae (Grimes *et al.* 1997, Keith 1997) and *Pholidornis* is described as a penduline tit (Remizidae) (Fry 2000).

The relationships of *Hypergerus* have been clarified in recent years as both the DNA-DNA hybridisation study of Sibley and Ahlquist (1990) and a recent molecular study focusing on Malagasy babblers (Cibois *et al*. 1999) agree on the placement of *Hypergerus* and its sister taxon *Eminia* with the African warblers (Cisticolidae). A sister relationship between *Eminia* and *Hypergerus* is also supported by behavioural evidence (Grimes 1974). The relationships of *Hylia* and *Pholidornis*, however, have not been addressed previously with molecular data.

We compared mitochondrial DNA sequences of these genera with that of representative Old World warblers and other African songbirds to test alternative hypotheses for their evolutionary relationships. Traditionally 'Old World warblers' has included warblers in the family Sylviidae, as well as an additional group, the Cisticolidae (Sibley and Ahlquist 1990, Sibley and Monroe 1990), which comprises not only *Cisticola*, *Prinia* and *Schistolais*, but also forest warblers such as *Camaroptera* and *Apalis*. Sibley and Ahlquist (1990) reported a close relationship between babblers ('Timaliidae') and *Sylvia* and included both within a subfamily Sylviinae. Additional families included in the superfamily Sylvioidea based on DNA-DNA hybridisation evidence are Sittidae, Certhiidae, Paridae, Aegithalidae, Hirundinidae, Regulidae, Pycnonotidae, and Zosteropidae (Sibley and Ahlquist 1990). With the exception of the first two, we include in our analysis at least one representative of each of these families as well as sunbirds (Nectariniidae) and estrildid finches (Estrildidae) to provide a broad test of the possible placements of *Hylia* and *Pholidornis* within the phylogeny of Old World songbirds.

We also consider the higher level structure of the sylvioid clade insofar as recent DNA sequencing studies raise questions about both the composition of sylvioid families and their relationships to each other (Cibois *et al.* 1999, 2001, Barker *et al.* 2002). For example, the Malagasy 'babblers' are not closely related to babblers elsewhere but derive from at least two separate colonisations of Madagascar by sylviine ancestors (Cibois *et al.* 1999). In addition, a variety of

Malagasy songbirds previously assigned to Timaliidae, Sylviidae, and Pycnonotidae fall within a single clade that may represent an endemic radiation (Cibois *et al.* 2001). In a higher level phylogeny of Passeriformes based on nuclear gene sequences, Barker *et al.* (2002) failed to corroborate the broadly conceived Sylvioidea of Sibley and Ahlquist's (1990), but found support for a clade comprising 'core' sylvioids, including representative Old World warblers. Our analysis includes a broader sample of sylvioid genera and families and focuses on additional testing of phylogenetic hypotheses within this group.

We present first a brief review of the status of *Pholidornis*, *Hylia*, and *Hypergerus* in earlier systematic work, with mention of the morphological and behavioural traits that are of relevance to their ecology and systematic relationships. We then focus on molecular evidence of their systematic relationships as provided by mitochondrial DNA sequence data. Finally, we discuss family-level relationships within the Sylvioidea and the diversity and diversification of African songbirds.

Hypergerus atriceps (Lesson 1831), Moho/Oriole Warbler

Mohos, *Hypergerus atriceps,* are large (26–32g) songbirds of forests and forest edge in Central and West Africa. Their feet are long, stout and strong; the birds cling to vines, feed by probing after insects into crevices of palms, and also come to the ground. Their main foods are grasshoppers and ants. *Hypergerus* pairs duet with clear loud ringing whistles (Bates 1930, Urban *et al.* 1997, Barlow *et al.* 1997, Borrow and Demey 2002).

Reichenow (1904) classified *Hypergerus atriceps* as a thrush in Turdinae, a group in which he included *Turdoides*, which are now regarded as babblers. Placement of *Hypergerus* with the babblers, Timaliidae, was subsequently suggested based on body form, the long tail and strong feet (Bates 1930, Sclater 1930). The slightly decurved bill of *Hypergerus* is similar to that of the babbler *Turdoides fulvus*, and the scaly plumage pattern of the head suggested to Bannerman (1936) the babblers *T. plebeja* and *Phyllanthus atripennis*. The French name 'Timalie à tête noire' (Morel and Morel 1990) reflects this classification, while one of the English common names, Oriole-babbler (Bannermann 1936), emphasises oriole-like aspects of the plumage, such as the dark head and body olive-green above and bright yellow below.

More recently, *Hypergerus* has been considered a large, perhaps 'overgrown' warbler (Chapin 1953) similar to the East African Grey-capped Warbler *Eminia lepida*. The nests and songs of *Hypergerus* and *Eminia* are similar, and both species duet (Van Someren 1956, Kunkel 1966, Grimes 1974, Zimmerman *et al.* 1996). Grimes *et al.* (1997) considered *Hypergerus* and *Eminia* to be of uncertain family association, and placed them *incertae sedis* after the warblers. As noted above, both DNA-DNA hybridisation (Sibley and Ahlquist 1990) and mitochondrial DNA sequences (Cibois *et al.* 1999) provide evidence for a relationship between *Hypergerus* and *Eminia* and their placement in Cisticolidae, although the two taxa were never compared directly by Sibley and Ahlquist (1990).

Several characteristics shared by *Hypergerus* and *Eminia* are suggestive of sunbirds. They have a brush-tipped tongue and an elongated hyoid complex with a slender epihyoid like the sunbirds *Anthreptes* and *Nectarinia*. The slender, decurved bill of *Hypergerus* resembles that of a sunbird, although it is stouter than in all sunbirds except the Asian spiderhunters, *Arachnothera,* and not as decurved as in most sunbirds. Also similar to sunbirds, their nest is a large, covered structure of thick wet grasses suspended from a branch, with a side entrance near the top and a long streamer hanging below, giving the entire nest an appearance of streamside debris (Lang 1969).

Pholidornis rushiae (Cassin 1855), Tit-weaver, Tit-hylia

Pholidornis are tiny birds (5g, Fry 2000) found in the forest canopy in West and Central Africa, where they feed on insects, particularly scale insects (Coccidae) and seeds (Fry 2000).

Pholidornis rushiae like the estrildid finch, *Parmoptila rubrifrons* (which was at that time also included in the genus *Pholidornis*), was once regarded as a flowerpecker Dicaeidae, a primarily Asian family (Sharpe 1885, Reichenow 1904). Other early systematic treatments considered *Pholidornis,* along with penduline tits, *Anthoscopus,* and antpeckers, *Parmoptila,* to be tits Paridae (Reichenow 1904). In his review of ploceid genera, Chapin (1917) included *Pholidornis* with the estrildine finches based on its morphological similarity to *Parmoptila*, which have domed nests and nestlings with gape globes and palate markings like other estrildines. *Pholidornis* nestlings, however, are unknown (Fry 2000). Sclater (1930) followed this course and listed *Pholidornis* between *Parmoptila* and *Nigrita* in the Ploceidae, which included estrildid finches. These accounts gave the bird its common name 'tit-weaver' (Chapin 1954). The nests of *Pholidornis* often are covered, hanging structures like those of weavers *Ploceus*, and the eggs are white as in the estrildid finches. One of the first nests found was built inside an old weaver nest (Bates 1930), a behaviour that several estrildid finches use in their breeding (Immelmann *et al.* 1965, Sorenson and Payne 2001). Other nests of *Pholidornis* are supported on a branch and are not pensile (Serle 1965). Chapin (1954) and Traylor (1968) listed *Pholidornis* with the Estrildidae, whereas other recent reviews of estrildid finches have not included *Pholidornis* (Immelmann *et al.* 1965, Goodwin 1982).

The hyoid bones of *Pholidornis* are long and flattened like a spring at the end, somewhat like the longer hyoid bones of sunbirds Nectariniidae (Bannerman and Bates 1924) but more closely resembling the hyoid of *Hylia* (Bates 1930). Bates (1930) defined a new family Hyliidae comprising the distinctive genera *Pholidornis* and *Hylia* (see below).

More recently, *Pholidornis* has been considered a penduline tit Remizidae on the basis of its behaviour (Vernon and Dean 1975, Fry 2000). *Pholidornis* live in social groups and roost together in a nest (Chapin 1954). They feed like penduline tits and have similar juvenile plumage, nests, and breeding behavior. At least four adults were seen to feed the young at one nest, suggesting cooperative breeding (Vernon and Dean 1975). *Pholidornis* young beg by quivering the wings, unlike estrildid finches (Immelmann *et al.* 1965), but recalling penduline tit behaviour (Vernon and Dean 1975).

The behaviour and songs of *Pholidornis*, however, also suggest a relationship to warblers of the family Sylviidae

(Brosset and Erard 1986). The songs consist of two clear trills, the second faster than the first, loud and stereotyped. The trill is characterised as "puipuipui-tjitjitjitjitjitjju", and sometimes is preceded by two grating notes "ruirui" (Dowsett-Lemaire and Dowsett 1991, Dowsett and Dowsett-Lemaire 1993, Chappuis 2000). Although these authors noted the similarity of *Pholidornis* song to that of African warblers, they listed *Pholidornis* as a remizid.

Hylia prasina (Cassin 1855), Green Hylia

Green Hylia, *Hylia prasina,* are small, 12–14g insectivorous birds of forests and forest edge in Central and West Africa. They feed in twigs and foliage, moving like an *Anthreptes* sunbird as they take scale insects (Coccidae) from twigs, arboreal ants from nests on the underside of leaves, and butterflies in flight, or feed on the ground near ants. Nests are large globular structures built on low branches, with the outer layer of twigs, a middle layer of fibers, an interior of white kapok, and a side entrance near the top. The eggs are white. *Hylia* roost together in a nest. The common calls are a pair of clear whistles "kee-kee" and a dry scolding rattle "trrit,trrrrrit" (Bates 1930, Brosset and Erard 1986, Barlow *et al*. 1997, Keith 1997, Chappuis 2000).

Hylia usually has been considered either a sunbird (Bannermann and Bates 1924, Bannermann 1948, Sclater 1930, Brosset and Erard 1986) or a warbler (Reichenow 1904, Chapin 1953, Dowsett and Dowsett-Lemaire 1993). Characters suggestive of a sunbird relationship include a long hyoid with flattened epibranchial horns, a brush-tipped (or fimbriated) tongue, membrane-covered nostrils, and sunbird-like feeding behaviour (Bannerman 1921, Bannerman and Bates 1924, Brosset and Erard 1986). In contrast, the nest of *Hylia* is hidden in forks of bushes and is not suspended like a sunbird nest (Bates 1930). Based on the presence of a somewhat fimbriated tongue and very similar hyoid complex in *Pholidornis*, Bates (1930) proposed the new family Hyliidae comprising *Hylia* and *Pholidornis* and following the sunbirds, Nectariniidae.

Although Chapin (1953) noted that the nasal operculum, strong bill, and firm plumage of *Hylia* are unusual for a warbler, he returned *Hylia* to the Sylviidae, a course followed by most other recent authors (Sibley and Monroe 1990, Dowsett and Dowsett-Lemaire 1993, Keith 1997). Perhaps the most convincing argument for a warbler relationship is the colour plate in Zimmermann *et al*. (1996), where *Hylia* appears to be a large *Phylloscopus* warbler.

Other ideas about the relationships of *Hylia* have gained less support. Apparently through its proposed association with *Pholidornis* (Bates 1930), *Hylia* has been considered either a finch Estrildidae or a tit Paridae (Keith 1997) following the placement of *Pholidornis* in these groups by Chapin (1917) and Reichenow (1904), respectively. Beecher (1953) grouped *Hylia* and *Pholidornis* with the African honeyeaters Meliphagidae based on their jaw muscles and brush-tipped tongues. Although grouped together in the past, most recent treatments have placed *Pholidornis* and *Hylia* in separate groups (Sibley and Monroe 1990, Keith 1997, Fry 2000).

Molecular methods

Taxa and DNA Sequencing

Our choice of taxa (Table 1) was guided by previously proposed affiliations of *Pholidornis*, *Hylia* and *Hypergerus* (see above) and encompassed most families within Sibley and Monroe's (1990) superfamilies Passeroidea (Nectariniidae, Estrildidae, Ploceidae, Fringillidae) and Sylvioidea (Paridae, Remizidae, Hirundinidae, Pycnonotidae, Regulidae, Sylviidae, Cisticolidae, Aegithalidae). We treat some of the subfamilies in Sibley and Monroe (1990) as families here and in the following discussion (e.g., Remizidae, Estrildidae, Ploceidae). Of particular interest were the warblers (Sylviidae, Cisticolidae), various 'tits' (Paridae, Remizidae, Aegithalidae), sunbirds (Nectariniidae), and forest estrildids (*Parmoptila*, *Nigrita*) that have been proposed as relatives of *Hylia* and *Pholidornis*. We did not include honeyeaters or thrushes in the present analysis because these taxa were clearly not related to *Pholidornis* in a preliminary analysis that included representatives of *Entomyzon* and *Turdus*, as well as many other passerine lineages. Finally, we included a number of corvoid taxa as an outgroup, including representatives of Laniidae, Corvidae, and Vireonidae.

DNA sequences for some of the taxa included in our analysis were reported by Sorenson and Payne (2001; see Table 1). For new samples, genomic DNA extraction and DNA sequence data collection were carried out as described by Sorenson and Payne (2001). The mitochondrial genes for NADH dehydrogenase subunit 2 (ND2) and the small subunit ribosomal RNA (12S) along with portions of the transfer RNAs flanking each gene were amplified with primers L5216, H5766, L5758, H6313 (ND2), L1263, H1859, L1754, and H2294 (12S). *Pholidornis* DNA was obtained from feathers of two museum specimens collected in 1960 and 1973, respectively. For this taxon only, we designed additional primers to amplify shorter fragments in those regions where amplification with the original primers failed. Primers L5941, H6013 (ND2), L1512, H1530, L2010, and H2084 (12S) were used in combination with the above primers to complete data collection for *Pholidornis*. Primer sequences are provided in Table 2.

New sequence data collected in this study have been deposited in GenBank (accession numbers AY136555–AY136614).

Phylogenetic Analyses

We constructed a preliminary alignment of 12S and ND2 sequences and identified variable length 'gap regions' in which the homology of aligned nucleotides was uncertain; one portion of each the tRNAs flanking ND2 and 23 separate segments in the 12S alignment were delineated as gap regions. Phylogenetic parsimony analyses were conducted with gap regions excluded using PAUP* version 4.0b10 (Swofford 2000). The well-aligned portions of the data set comprised 1 829 characters with 852 variable sites, 735 of which were parsimony-informative. We also analysed the full data set (comprising 2 096–2 115 nucleotides per taxon) using optimisation alignment (Wheeler 1996) as implemented in the program POY (Gladstein and Wheeler 1996). Optimisation alignment combines sequence alignment with

Table 1: List of taxa included in our phylogenetic analysis. Family names from Sibley and Monroe (1990) are indicated in parentheses for groups they treated as subfamilies. Taxa included in Sorenson and Payne (2001) are indicated by an asterisk. DNA extracts obtained from feather are indicated by (f)

Taxon	Locality	Museum no.	Tissue no.
Remizidae (Paridae)			
Anthoscopus musculus	Kenya	UMMZ 213,072	213072 (f)
Pholidornis rushiae	Angola	DM 29184	A1073 (f)
	Cameroon	ZFMK 61.1422	B61.1422 (f)
Paridae			
Parus major	Japan	UMMZ 234,849	T1147
Aegithalidae			
Aegithalos caudatus	UK	UMMZ A571	A571
Hirundinidae			
Psalidoprocne petiti	Nigeria	UMMZ A877	A877 (f)
Tachycineta bicolor	Michigan	UMMZ 236,089	T1505
Regulidae			
Regulus satrapa	Michigan	UMMZ 235,942	T436
Pycnonotidae			
Bleda syndactyla	Nigeria	UMMZ 233,801	A301 (f)
*Pycnonotus barbatus**	Cameroon	UMMZ 232,528	A144
Cisticolidae			
Cisticola cantans	Gambia	UMMZ 235,853	A1110
*Cisticola fulvicapilla**	Zimbabwe	UMMZ A761 (photo)	A761
Prinia subflava	Gambia	UMMZ 235,854	A1109
Schistolais leontica	Guinea	UMMZ 235,855	A1409 (f)
Schistolais leucopogon	Cameroon	UMMZ 232,418	A243
Apalis flavida	Gambia	UMMZ 235,837	A1273
*Camaroptera brevicaudata**	Gambia	UMMZ A339	A339
Eminia lepida	Kenya	UMMZ 211635	211635 (f)
*Hypergerus atriceps**	Gambia	UMMZ A345	A345
Zosteropidae			
Zosterops japonica	Japan	UMMZ 234,850	T1149
Zosterops pallidus	South Africa	Durban Museum	A1085
Sylviidae			
Acrocephalus bistrigiceps	Japan	UMMZ 234,837	T1151
Sylvietta virens	Gambia	UMMZ 235,840	A1106
*Locustella ochotensis**	Japan	UMMZ 234,839	T1146
*Phylloscopus trochilus**	Gambia	UMMZ 236,529	A832
Turdoides plebejus	Gambia	UMMZ A569	A569 (f)
Panurus biarmicus	captive	UMMZ 235,044	BD4047 (f)
*Parisoma subcaeruleum**	Zimbabwe	UMMZ A769 photo	A759
Sylvia cantillans	Gambia	UMMZ 235,193	A523
Hylia prasina	Cameroon	LSUMZ 163,337	B-27195
Nectariniidae			
Anthreptes collaris	South Africa	Durban Museum	A1077
Nectarinia venusta	Cameroon	UMMZ 232,441	A197
Dicaeum trigonostigma	Philippines	FMNH 358,510	358510
Ploceidae (Passeridae)			
*Ploceus ocularis**	Malawi	NMM	A59
*Quelea quelea**	Cameroon	UMMZ 232,530	A168
*Sporopipes frontalis**	Nigeria	UMMZ 233,830	A287
Estrildidae (Passeridae)			
Nigrita canicapilla	Burundi	FMNH 358,180	F3686
Parmoptila jamesoni	Uganda	FMNH 385,327	F385327
*Amandava subflava**	Cameroon	UMMZ 232,471	A208
*Chloebia gouldiae**	captive	UMMZ 233,785	T807
*Hypargos niveoguttatus**	Zimbabwe	BWYO	A24
*Spermestes cucullatus**	Cameroon	UMMZ 232,476	A137
Fringillidae			
*Carduelis pinus**	Michigan	UMMZ 227,858	T540
OUTGROUP			
Laniidae			
*Corvinella corvina**	*Gambia*	*UMMZ A857*	*A857*
*Eurocephalus anguitimens**	Zimbabwe	UMMZ 202,542	202,542 (f)
*Lanius senator**	Gambia	UMMZ A525	A525
Oriolidae (Corvidae)			
Oriolus auratus	Gambia	UMMZ 235,196	A933
Vangidae (Corvidae)			
Platysteira cyanea	Guinea	UMMZ 235,808	A1414
Monarchidae (Corvidae)			
*Terpsiphone viridis**	Swaziland	UMMZ 215,126	215,126
Vireonidae			
Vireo olivaceus	Michigan	UMMZ	T978

DM = Durban Museum; FMNH = Field Museum of Natural History (Chicago); LSUMZ = Louisiana State University Museum of Zoology; NMM = National Museum of Malawi; BWYO = National Museum of Zimbabwe in Bulawayo; UMMZ = University of Michigan Museum of Zoology; ZFMK = Museum Alexander König, Bonn

Table 2: Primer sequences for the mitochondrial ND2 and 12S genes. L and H numbers refer to the strand and position of the 3' base in the published chicken sequence (Desjardins and Morais 1990). Degenerate sites are denoted by standard IUPAC codes. Many of these are revised versions of primers described by Sorenson *et al.* (1999)

Light strand primers		Heavy strand primers	
L1263	YAAAGCATGRCACTGAA	H1530	GTGGCTGGCACARGATTTACC
L1512	TAAGCAATGAGTGHAARCTYGACTTAG	H1859	TCGDTTRYAGRACAGGCTCCTCTA
L1754	TGGGATTAGATACCCCACTATG	H2084	NTTTACTDCTAAATCCDCCTT
L2010	TARHAMGACAGGTCRAGGTATAGC	H2294	TYTCAGGYGTARGCTGARTGCTT
L5216	GGCCCATACCCCGRAAATG	H5766	RGAKGAGAARGCYAGGATYTTKCG
L5758	GGCTGAATRGGMCTNAAYCARAC	H6013	AGTCATTTKGGKAKGAAKCCTG
L5941	ACTWTCMACYYTRATRACYRCATG	H6313	CTCTTATTTAAGGCTTTGAAGGC

tree search such that the phylogenetic information in gap regions can be used in an unbiased manner without a priori alignment. Parsimony searches in both PAUP* and POY were conducted with three different weighting schemes: equal weights for all changes or transitions down-weighted by 50% ('ts-50' analysis) or 80% ('ts-20' analysis) relative to transversions and indels. Gaps were treated as fifth character state in parsimony analyses. Bootstrap values (Felsenstein 1985) were determined from 500 randomly resampled data sets. Bremer support indices (Bremer 1988), defined as the number of additional steps in the shortest tree that does not include a given node present in the most parsimonious tree, were calculated for the ts-50 tree with the help of the program TreeRot (Sorenson 1999).

We also used the program MrBayes (Huelsenbeck and Ronquist 2001) for Bayesian inference of tree topology under a likelihood optimality criterion. For this analysis, we excluded both the gap regions noted above and all additional positions with gap characters in one or more taxa, leaving 1 815 positions for analysis. We used MODELTEST (Posada and Crandall 1998) to select the model of sequence evolution that best fit our data. We conducted four runs of 2 000 000 generations each, under the general time reversible model of sequence evolution with a portion of invariant sites and gamma distributed rate variation among sites. Each run comprised four simultaneous MCMC chains. Trees were sampled every 200 generations and, excluding a burn-in time of 100 000 generations, the resulting trees were summarised in a consensus cladogram. Parameter estimates obtained from MrBayes include base frequencies (A = 0.403, C = 0.355, G = 0.086, T = 0.156), relative transformation rates (A–C = 0.119, A–G = 3.520, A–T = 0.289, C–G = 0.100, C–T = 3.198, G–T = 1.0000), proportion of invariant sites (I = 0.465), and shape parameter for the G distribution (a = 0.523).

The various phylogenetic analyses were intended to evaluate the sensitivity of our results to changes in weighting scheme and model assumptions.

Results

Results of our phylogenetic analyses were mixed in terms of resolving relationships among sylvioid taxa. Figure 1 shows trees recovered in parsimony analyses with transitions down-weighted 50% and considering either well-aligned regions only (Figure 1A) or the full data set in optimisation alignment tree searches (Figure 1B). Both of these trees and

all other parsimony analyses were consistent in suggesting a basic division between Passeroidea and Sylvioidea with the exception of an unexpected placement of *Parus* basal to the rest of the ingroup (see below). Monophyly of many family-level taxa and a sister relationship between *Hylia* and *Pholidornis* were strongly supported, but higher level relationships within Sylvioidea were variable among analyses. In addition, representatives of the family Sylviidae formed a polyphyletic assemblage in all analyses, such that the sylviid lineages sampled here are mixed together with representatives of other sylvioid families.

Hypergerus and *Eminia* in Cisticolidae
All analyses suggested strong support for a *Hypergerus*/*Eminia* clade and its inclusion in Cisticolidae (Sibley and Ahlquist 1990). All cisticolid taxa in our study, including *Hypergerus* and *Eminia*, exhibit a shift in base composition towards a higher proportion of adenine and smaller proportion of cytosine residues in their mitochondrial light strand sequences as compared to other sylvioid taxa (Figure 2). Strong support for this clade in our analyses derives at least in part from this shared molecular characteristic of cisticolid species.

Within Cisticolidae, the topology of the clade comprising *Schistolais leontica*, *S. leucopogon*, *Camaroptera* and *Apalis* as shown in Figure 1 was recovered in all analyses, while the branching order between this clade and the other cisticolid lineages varied among equally parsimonious trees and among weighting schemes. The *Hypergerus*/*Eminia* clade was usually nested within cisticolids, but a sister relationship between this clade and all other cisticolids was either equally parsimonious or required a very small number of additional steps.

Position of *Hylia* and *Pholidornis* in Sylvioidea
A clade comprising *Hylia* and *Pholidornis* was found in all analyses and was strongly supported (Bremer support indices of 16, 16 and 12.6 in equal weights, ts-50 and ts-20 analyses on well-aligned regions). Poor resolution of the relationships among sylvioid lineages, however, prohibited a definitive placement of the *Pholidornis*/*Hylia* clade. Within the sylvioid clade, potential sister taxa for the *Pholidornis*/*Hylia* clade included *Acrocephalus* (equal weights and ts-50 parsimony analyses, Figure 1A), the cisticolid clade (ts-20 parsimony analysis), a clade comprising *Aegithalos* and *Phylloscopus* (all parsimony analyses including gap regions, Figure 1B), and *Phylloscopus* (Bayesian analyses).
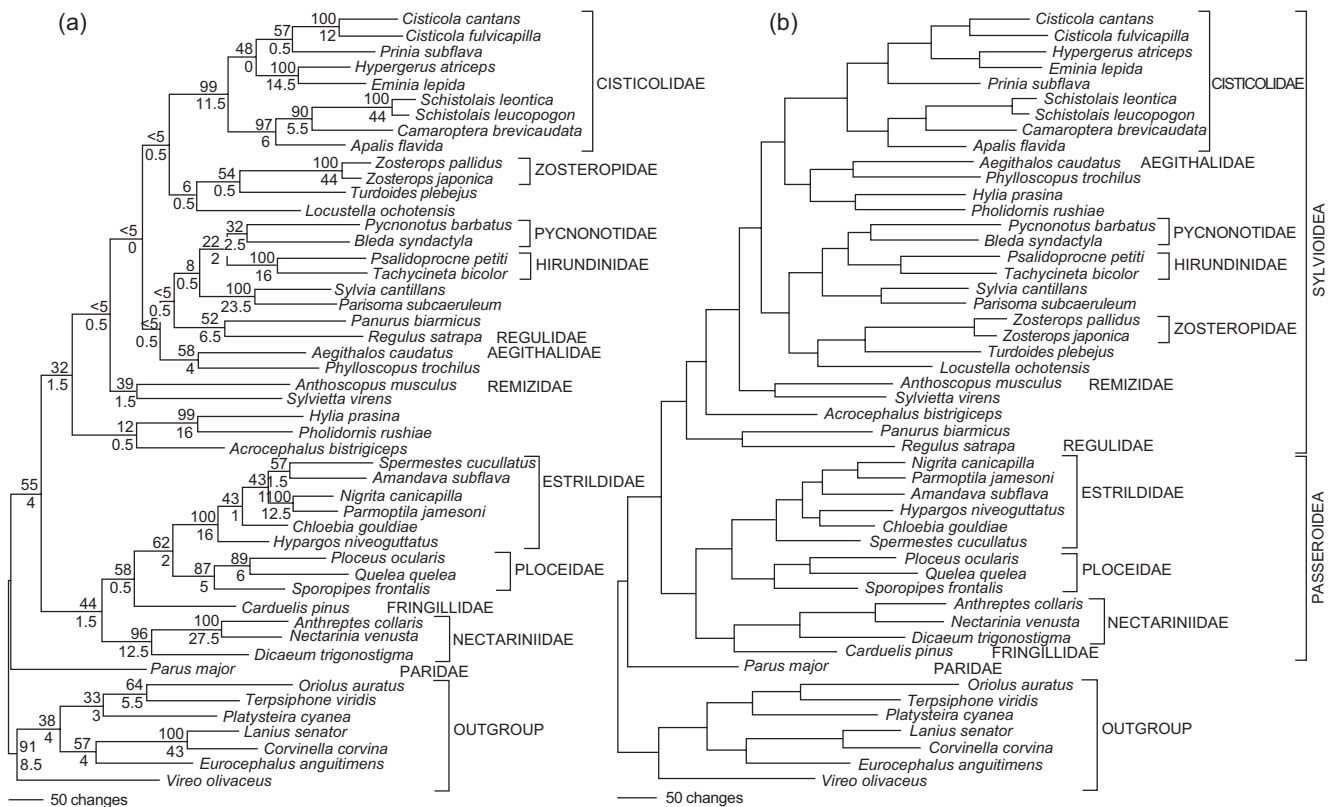
Figure 1: A. One of three most parsimonious trees found in a PAUP parsimony search excluding gap regions and down-weighting transitions 50%. Tree length = 8522; CI = 0.227; RI = 0.393. Bremer support indices and bootstrap values are shown below and above nodes, respectively. B. Most parsimonious tree found using optimisation alignment (POY) on the full dataset and down-weighting transitions 50%
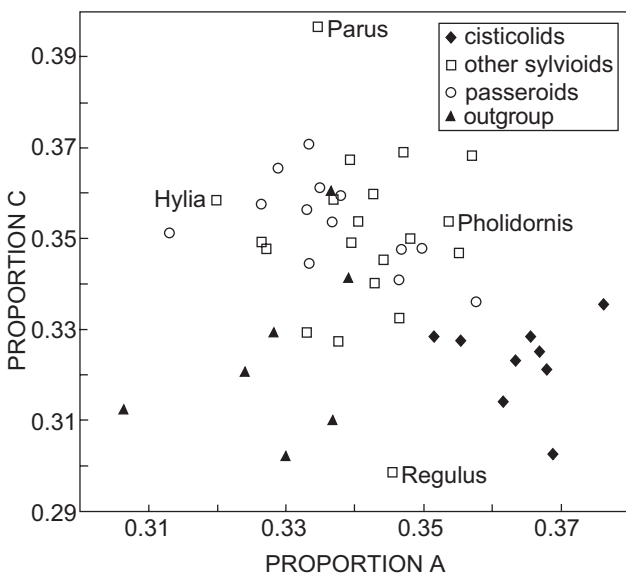
Figure 2: Proportions of adenine plotted against proportions of cytosine at variable positions in ND2 and 12S. Each point represents base composition for a single taxon

Nonetheless, *Pholidornis* and *Hylia* fell within a large clade of sylvioid taxa in all analyses except the equal weights parsimony analysis excluding gap regions, in which case they were joined with the warbler *Acrocephalus* to form a sister group to Passeroidea. In this analysis, *Parus*, *Regulus*, and *Panurus* were also basal to the other ingroup taxa.

Hylia and *Pholidornis* have been included in a number of different families over the past century (see above). We evaluated the strength of evidence against these previously suggested relationships by conducting tree searches in which *Pholidornis* and *Hylia* were constrained to fall within the same clade as various proposed relatives: including sunbirds, remizids, estrildids, and sylviids. Grouping *Pholidornis* and *Hylia* with estrildids increases tree length substantially (Table 3). This increase is as large as the Bremer support indices for some of the most strongly supported nodes in our analysis (e.g., nodes uniting the representatives of monophyletic families, such as Hirundinidae, Cisticolidae, Estrildidae, and Nectariniidae), indicating very strong evidence against the estrildid hypothesis for *Pholidornis* and *Hylia*. Intermediate values were obtained when *Pholidornis* and *Hylia* were constrained to the same clade as sunbirds (Nectariniidae) or the penduline tit, *Anthoscopus*. A smaller number of extra steps is required to group these two taxa with other lineages within the sylvioid clade, such as *Acrocephalus* or Cisticolidae, but the data do not discrimi-

Table 3: Tests of alternative phylogenetic hypotheses. The shortest trees compatible with previously suggested classifications of *Hylia* and *Pholidornis* were compared to the shortest unconstrained trees under three weighting schemes to determine the number of extra steps required to obtain various alternative hypotheses. For taxa that were not monophyletic in our analyses, the number of extra steps required to obtain monophyly of the specified group without *Pholidornis* and *Hylia* is indicated in parentheses. Analysis based on well-aligned regions only

	Equal weights	Transitions down-weighted 50%	Transitions down-weighted 80%
		Length of best unconstrained tree	
Hypothesis	6 370	4 261	2 987.2
Pholidornis and *Hylia* sister to:		Increase in tree length required for alternative hypothesis	
Estrildidae	26	19.5	15
Nectariniidae	9	3	2.8
Anthoscopus	6	4	3.2
Aegithalos+Phylloscopus	6	2	2
Cisticolidae	1	0.5	+1[a]
Acrocephalus	+1[a]	+0.5[a]	1
Pholidornis and *Hylia* within:			
Sylviidae	51 (52)	37 (36.5)	26.2 (26)
Sylviinae	28 (24)	18 (17.5)	14.2 (16)
Acrocephalinae	28 (33)	19.5 (21.5)	16 (16)
Timaliini	9 (9)	10 (10)	7.6 (9.4)
Paridae	19 (13)	16 (15.5)	12.6 (12)

[a] The specified relationship was found in the most parsimonious tree(s). The number given is Bremer support for the node joining the *Pholidornis*/*Hylia* clade with the specified sister group

nate between these potential alternatives. Including *Hylia* and *Pholidornis* within previously recognised sylvioid groups, such as Sylviinae or Acrocephalinae, generally requires a large number of extra steps (Table 3), but this is a function of constraining the monophyly of these groups regardless of whether *Hylia* and *Pholidornis* are also included (Table 3).

Higher level relationships within Sylvioidea

Our analyses provide limited insight into family-level relationships within Sylvioidea. The branching order among most sylvioid lineages is weakly supported (Figure 1A) and resolved in conflicting ways in different analyses. Bremer support values for many basal nodes are less than 2, suggesting a large basal polytomy for the sylvioid clade, and uncertain placement of the *Pholidornis*/*Hylia* clade. Nonetheless, monophyly of Cisticolidae, Hirundinidae and Zosteropidae were strongly supported in all analyses. The two bulbuls (Pycnonotidae) also formed a group in most analyses, but with lower support indices. Two other groups with strong support were a clade comprising *Sylvia* and *Parisoma*, corresponding to the tribe Sylviini (Sibley and Ahlquist 1990), and the *Pholidornis*/*Hylia* clade.

In contrast, a number of other sylvioid clades recognised by Sibley and Monroe (1990) and represented by multiple taxa in our analyses did not form monophyletic groups. Representatives of the family Sylviidae were always polyphyletic and positions of taxa varied widely among analyses. Likewise, none of our analyses recovered the sylviid subfamilies Acrocephalinae (*Acrocephalus*, *Locustella*, *Phylloscopus* and *Sylvietta*) or Sylviinae (*Panurus*, *Turdoides*, *Sylvia*, *Parisoma*), the tribe Timaliini (represented by the babblers *Panurus* and *Turdoides*), or a clade corresponding to Paridae as defined by Sibley and Monroe (1990) (i.e. including both penduline tits and tits, represent-

ed here by *Anthoscopus* and *Parus*, respectively). Trees in which the monophyly of these groups was constrained generally required a large number of extra steps (Table 3).

Although weakly supported, the node connecting Green Crombec, *Sylvietta virens* (Sylviidae), with the penduline tit, *Anthoscopus musculus* (Remizidae), was found in all analyses and the group was placed close to the base of the sylvioid clade in parsimony reconstructions. Long-tailed tit, *Aegithalos caudatus* (Aegithalidae), grouped with Willow Warbler, *Phylloscopus trochilus,* in all parsimony analyses, while it was sister to the babbler *Panurus* in maximum likelihood analyses. Most parsimony analyses joined *Panurus* with *Regulus*, a result that may stem from strong base composition bias in the latter (see below and Figure 2). Two other results were consistent among most analyses: the second babbler in our sample, *Turdoides plebejus*, was sister to Zosteropidae, and *Acrocephalus* was the basal lineage in the sylvioid clade.

Base composition bias in *Parus* and *Regulus*

In all our analyses, the ingroup taxa were arranged in two clades generally corresponding to Sibley and Monroe's (1990) superfamilies Sylvioidea and Passeroidea. Due to the basal position of *Parus*, however, Sylvioidea appears paraphyletic with respect to Passeroidea. In parsimony analyses, similar results were obtained under all weighting schemes and with or without gap regions included. Likelihood-based analyses also placed *Parus* basal to the rest of the ingroup and also shifted the position of *Regulus* from the large sylvioid clade to the passeroid clade (*Regulus* sister to sunbirds, Nectariniidae). These unexpected placements of *Parus* and *Regulus* may be due to differences in base composition bias in these two taxa as compared to other taxa in the study (Figure 2). Among the ingroup taxa, *Parus* has the highest proportion of cytosine and the lowest proportion of thymine,

while *Regulus* has the highest proportion of thymine and the second-lowest proportion of cytosine, after the cisticolid *Schistolais leontica*. Exclusion of *Parus* and *Regulus* from the analysis results in reciprocal monophyly of Sylvioidea and Passeroidea and increased values of Bremer and bootstrap support for these two clades.

Interestingly, variation in the proportion of cytosine is greater in ND2 than in 12S, where the cytosine content of *Regulus* and *Parus* is roughly similar to that of other ingroup taxa. Optimisation alignment analyses based only on 12S sequences generally yield trees in which *Parus* is nested within the main sylvioid clade.

Discussion

Each of the monotypic songbird genera considered here, *Hypergerus*, *Pholidornis* and *Hylia*, have had a turbulent history of systematic classification, as previous authors focused on one or more morphological or behavioural characters that suggested affinities to various other songbird genera. While all three share some morphological features with sunbirds (Nectariniidae), such as elongated hyoids, brush-tipped or fimbriated tongues, and a decurved bill in the case of *Hypergerus*, sunbird-like morphologies have evolved independently in several passerine lineages. Brush-like tongues are found in both nectar-feeding and insectivorous birds in various families; e.g., *Myzomela* honeyeaters (Meliphagidae), *Dulus* palmchat (Bombycillidae), *Myzornis* babbler (Sylviidae), white-eyes (Zosteropidae), sugarbirds and sunbirds (Nectariniidae), most Hawaiian honeycreepers (Fringillidae), *Coereba* honeycreepers, some *Dendroica* wood warblers and *Icterus* orioles (Emberizidae). Frayed tongue tips are found in bushtits *Psaltriparus* (Aegithalidae) and in verdins *Auriparus* (Certhiidae), while the nectar-feeding flowerpeckers (Dicaeidae) have split tongues without a fringe (Gardner 1925, Scharncke 1931, 1932, Rand 1967, Liversidge 1967). Long hyoid bones also occur in some insectivorous birds such as woodpeckers, which thrust their tongue into crevices and extract insects (Gardner 1925). If simply coded as present or absent, the convergent evolution of these morphological features may yield misleading information about relationships. Nonetheless, the coding of component characters and evaluation of homology through more detailed morphological analyses may yield useful information for avian systematics.

Similarly, nest structures have not proved to be particularly reliable indicators of phylogenetic relationships, perhaps in part due to insufficient consideration of homology and component characters. In general form, however, nests may differ within genera or converge across families. For example, some *Apalis* have a pocket-shaped nest, with a shallow *(Apalis binotata)* or a deep cup *(Apalis jacksoni)*. *Camaroptera* have purse-shaped nests with leaves sewn together or held together with cobwebs. Some *Prinia* have deep purse-shaped nests, while *Schistolais leucopogon* has a bottle-shaped grass nest sewn between two large leaves of a plant or bush (Urban *et al.* 1997). The hanging nests of *Hypergerus* appear to be an elaboration of the nest tail in its East African counterpart *Eminia*; similar in structure, placement and materials, the nests of these two genera are consistent with their sister relationship, but are more suggestive of sunbird nests than the

nests of other cisticolids. In the same way, the unique form of the epibranchial horns in the hyoid complex of *Pholidornis* and *Hylia* is consistent with their sister relationship, but this character alone does not resolve the higher level relationships of the *Pholidornis*/*Hylia* clade.

Molecular sequence data provide the potential for a very large number of characters for phylogenetic analysis and may help to resolve systematic questions in which morphological or behavioural convergence obscures historical relationships. In the present example, mtDNA sequences provide strong support for various groups of Old World songbirds and rule out some of the previously suggested hypotheses for *Hypergerus*, *Pholidornis* and *Hylia*, but leave higher-level relationships within the sylvioid clade largely unresolved.

As found by Cibois *et al.* (1999), *Hypergerus* and *Eminia* are strongly supported as sister taxa and are part of the African Warbler family Cisticolidae. The cisticolids traditionally were placed in Sylviidae, but were recognised as a distinct clade in DNA-DNA hybridisation studies by Sibley and Ahlquist (1990). Our mitochondrial data also provide clear support for this clade. Within Cisticolidae, our results support the recognition of a separate genus for *Schistolais leontica* and *S. leucopogon* (Wolters 1980, Irwin 1997), which have generally been included in *Prinia* in most previous treatments (e.g., Watson *et al.* 1986). We find *Prina subflava* to be more closely related *Cisticola*, whereas *Schistolais* are sister taxa to *Camaroptera* in a clade that also included *Apalis*.

Our analyses also provide strong support for a sister relationship between *Hylia* and *Pholidornis*, a result that is consistent with Bates' (1930) suggestion to place these taxa in their own family (Hyliidae). Ours are the first molecular data collected for these two taxa. Although neither taxon was sampled in the DNA-DNA hybridisation study of Sibley and Ahlquist (1990), Sibley and Monroe (1990) placed *Pholidornis* and *Hylia* in different families on the basis of behavioural information.

The *Pholidornis*/*Hylia* clade appears to be just one of many divergent lineages stemming from an ancient radiation of sylvioid songbirds. As such, the sister taxon of this clade is difficult to determine, but some of the previously suggested hypotheses for *Pholidornis* and *Hylia* can be rejected. Our analyses support a basal division between passeroid and sylvioid taxa and consistently place *Pholidornis* and *Hylia* within the sylvioid group. *Pholidornis* and *Hylia* therefore are not sunbirds Nectariniidae or finches Estrildidae. In addition, our preliminary analyses of a larger dataset rules out a close relationship to thrushes Muscicapidae or honeyeaters Meliphagidae.

The position of the *Pholidornis*/*Hylia* clade within Sylvioidea remains unresolved as do most of the higher level relationships within this group. The issue of placing *Pholidornis* and *Hylia* is complicated by the fact that monophyly of many previously recognised sylvioid groups is not supported, making tests of whether *Pholidornis* and *Hylia* are members of those groups (Table 3) essentially nonsensical. Alternative placements of the *Pholidornis*/*Hylia* clade in our analyses included sister relationships with Cisticolidae, *Acrocephalus*, *Phylloscopus*, or a clade comprising *Phylloscopus* and *Aegithalos*. None of our analyses grouped *Pholidornis* and *Hylia* with the remizid *Anthoscopus*, as proposed on behavioural grounds. At pres-

ent, we can conclude only that *Pholidornis* and *Hylia* are part of a diverse assemblage of Old World warblers that is likely paraphyletic or polyphyletic with respect to other sylvioid families (Figure 1).

Although providing limited resolution of higher level relationships within the sylvioid clade, our analyses provide relatively strong evidence against some currently recognised groups. The large number of extra steps required when monophyly of Sylviidae, Sylviinae or Acrocephalinae is constrained (Table 3) suggests that future analyses with larger character sets and a more comprehensive sampling of taxa will result in a significant revision of sylvioid classification. An important issue in the design of future molecular studies will be the choice of mitochondrial versus nuclear sequences. Although mitochondrial DNA has been used at all levels of avian systematics, the use of nuclear sequences (including both exons and introns) is increasing (e.g., Groth and Barrowclough 1999, Barker *et al.* 2002, Ericson *et al.* 2002). Nuclear genes offer lower substitution rates and therefore less homoplasy than mitochondrial sequences and may provide better resolution of family-level relationships.

Recently, Barker *et al.* (2002) presented a relatively well-resolved songbird phylogeny based on sequences of two nuclear genes, RAG-1 and c-*mos*. Focusing on basal passeriform relationships, their study included a smaller sample of sylvioid taxa than considered here but yielded results that were similar to ours in many respects. Their analysis also raises questions about the relationships of Old World warblers: two representatives of Sylviidae were paraphyletic with respect to a white-eye, *Zosterops*, while *Cisticola* was more closely related to a lark, *Alauda,* and a long-tailed tit, *Aegithalos*. Although their data set comprised over 3 400 bases of nuclear coding sequence, support indices for nodes within Sylvioidea were generally low.

Another potential advantage of nuclear sequences is that they may be less affected by lineage-specific changes in base composition. Variation among lineages in mitochondrial base composition bias can affect tree topology considerably (Naylor and Brown 1998, Sorenson and Payne 2001). As a form of non-independent character evolution, systematic shifts in base composition in selected lineages violate a basic assumption of all commonly used methods of phylogenetic analysis. Results in our study were likely affected by divergent base composition in at least three lineages (Figure 2): (1) support for the cisticolid clade may be inflated by the high proportion of cytosine and low proportion of adenine observed in all cisticolid taxa; (2) very high cytosine content in *Parus major* may have contributed to its placement basal to the rest of the ingroup; whereas (3) the opposite trend in *Regulus regulus* may help to explain highly variable placements of this taxon in analyses with different weighting schemes. Mitochondrial 16S rDNA sequences of several *Parus* and *Regulus* species (Sturmbauer *et al.* 1998) reveal a similar pattern of base composition divergence in these genera, suggesting that additional mitochondrial sequences for these taxa probably will not alleviate this source of systematic bias. We note that maximum likelihood models that account for variation among lineages in base composition have been developed (Yang and Roberts 1995, Galtier and Gouy 1998) but are too demanding computationally to be implemented for large sets of taxa.

Additional direct comparisons of nuclear and mitochondrial data sets for identical sets of taxa in analyses at various taxonomic levels are needed to guide future sequencing efforts. Regardless of the choice of molecular characters (nuclear versus mitochondrial), increased taxon sampling in future studies should improve phylogenetic analyses by reducing branch lengths and, in turn, uncertainty about character states at ancestral nodes.

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