

Short communication

Reconsideration of the phylogenetic relationships of the enigmatic Bornean Bristlehead (*Pityriasis gymnocephala*)

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1. Introduction

Of the myriad birds with uncertain phylogenetic affinities and convoluted taxonomic histories, perhaps none rivals the Bornean Bristlehead (*Pityriasis gymnocephala*) for the sheer number of families to which it has been allied and the resulting confusion as to its biogeographic history. The sole member of the genus is endemic to Borneo, where it is an uncommon resident of lowland and hill forests (Colenutt, 2002; Sheldon et al., 2001). It is seldom seen in the field, and long absences from suitable habitat punctuated by brief appearances of vociferous flocks suggest that the species is highly nomadic (Witt and Sheldon, 1994). It is a relatively large passerine with a heavy, hooked bill. The plumage is mostly black, but with red and yellow feathers around the head and thighs. Plumage of the neck and head is coarse and stiff, giving rise to the English name, and it has been of particular interest to feather anatomists because of its unusual structure (Prum and Brush, 2002). The Bristlehead's odd appearance and uncertain relationships led Mayr and Amadon (1951) to describe it as "one of the strangest members of all the Oscines."

Ahlquist et al. (1984) provided a thorough chronology of the various taxonomic assignments for *Pityriasis*, which we briefly recount. Early taxonomic treatments placed *Pityriasis* closest to the genera *Cracticus* and *Gymnorhina* (Gadow, 1883; Temminck, 1835), similarly sized and heavy-mandibled genera from Australia and New Guinea. The first dissenting view arose by the end of that century when Shelford (1899) suggested that it had affinities to *Eulabes* (= *Gracula*) and thus was a starling (Sturnidae). Confusion

soon followed. Sharpe (1903) retained *Pityriasis* in the true shrikes (Laniidae) along with *Cracticus* and *Gymnorhina*, but moved that family next to the helmet-shrikes (Prionopidae) and vangas (Vangidae). Mayr (1943) considered the retention of *Pityriasis* within the Gymnorhininae untenable, and suggested that it was likely closest to starlings or babblers (Timaliidae), although it had no close living relatives. Mayr and Amadon (1951) included it in the Prionopidae, Beecher (1953) placed it in the Cracticidae, Rand (1960) moved it back into the Laniidae, Smythies (1960) proposed similarities to Prionopidae, and shrike-babblers (*Pteruthius*), and Raikow et al.'s (1980) myology studies placed it sister to the Prionopidae. Its English name for much of the 20th century, "Bald-headed wood-shrike," suggested a relationship to true wood-shrikes (*Tephrodornis*). Several additional authors have offered hypotheses on its taxonomic affinities, but all are generally encompassed by the groups mentioned above. Thus, *Pityriasis* has been allied with no less than seven families spanning much of the oscine radiation (Barker et al., 2004).

Ahlquist et al.'s (1984) DNA–DNA hybridization results indicated that *Pityriasis* was most closely related to *Cracticus*, *Gymnorhina*, and *Strepera*, confirming the earliest taxonomic treatments. DNA–DNA hybridization yields a measure of genetic dissimilarity or distance between two taxa. The metric used by Ahlquist et al. (1984) was Delta T₅₀H. Higher Delta T₅₀H values indicate more distant relationships to the reference taxon. Using *Pityriasis* as the reference (labeled) taxon, Ahlquist et al. (1984) recovered T₅₀H values of 3.9, 4.0, and 4.4 for *Cracticus*, *Gymnorhina*, and *Strepera*, respectively. Using these DNA–DNA hybridization results, Sibley and Ahlquist (1990) reconstructed a clade with *Pityriasis* sister to the cracticids, both of which were in turn sister to the woodswallows (*Artamus*). These results were not unequivocal however. The woodswallows,

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which by all recent accounts are sister to the cracticids (e.g., Barker et al., 2004; Sibley and Ahlquist, 1990), and thus should have clustered with them, had higher Delta T_{50H} values from *Pityriasis* than an oriole (*Oriolus cruentus*), a triller (*Lalage nigra*), and a cuckoo-shrike (*Campephaga quiscalina*). Most recent taxonomic treatments have included *Pityriasis* with the cracticids (Inskipp et al., 1996; Sibley and Monroe, 1990), but Dickinson (2003) placed it between the ioras (Aegithinidae) and cuckoo-shrikes (Campephagidae).

Interest in the relationships of *Pityriasis* extends beyond taxonomy, because some of the groups with which it has been allied occur far from Borneo. For example, the helmet-shrikes (Prionopidae) are restricted to Africa, the vangas (Vangidae) to Madagascar, and the butcher-birds (Cracticidae) to Australasia. None of these groups is currently represented in the Southeast Asian avifauna. Thus, deciphering the evolutionary relationships of the Bristlehead should yield insights into the biogeographic history of the Old World tropical avifauna. To resolve the relationships of *Pityriasis*, and shed light on its biogeographic history, we compared nuclear gene sequences of the Bristlehead with other taxa indicated as potential relatives by Ahlquist et al. (1984) or earlier taxonomic treatments. As a framework for these comparisons, we used the steadily expanding phylogenetic database for birds based on the RAG-1 and RAG-2 genes (Barker et al., 2002, 2004; Groth and Barrowclough, 1999), and thus placed our data within a larger matrix of passerine taxa.

2. Methods

2.1. Taxon sampling and sequencing

Ingroup sampling (Table 1) included broad representation from across the corvoid assemblage. Several sequences from previous studies (Barker et al., 2004; Beresford et al., 2005) were downloaded from GenBank, to which we added nine additional genera. We sampled most densely from a clade of shrike-like birds identified by Barker et al. (2004) that included several of the putative closest relatives of *Pityriasis* (e.g., *Cracticus*, *Prionops*). DNA was extracted, amplified, and sequenced using standard protocols (see Barker et al., 2004; Moyle, 2005). Two exons of the nuclear recombination-activating gene (RAG-1 and RAG-2), totaling just over 4 kb, were sequenced for all taxa. Primers for RAG-1 and RAG-2 amplification and sequencing were from Groth and Barrowclough (1999) and Barker et al. (2004).

2.2. Phylogenetic analyses

We analyzed the data matrix with maximum likelihood and Bayesian phylogenetic methods. For likelihood analyses, Modeltest 3.7 (Posada and Crandall, 1998) was employed to determine the simplest model of evolution and parameter estimates using the Akaike Information Crite-

Table 1
List of samples used in the study

Species	Source	ID No.	RAG-1	RAG-2
<i>Pomatostomus halli</i>	GenBank	—	AY443321	AY443209
<i>Corvinella corvina</i>	GenBank	—	AY443275	AY443131
<i>Pachycephala hyperythra</i>	GenBank	—	AY443310	AY443188
<i>Loboparadisea sericea</i>	GenBank	—	AY443294	AY443161
<i>Cracticus quoyi</i>	GenBank	—	AY443278	AY443135
<i>Gymnorhina tibicen</i>	GenBank	—	AY443289	AY443153
<i>Strepera graculina</i>	GenBank	—	AY443334	AY443230
<i>Artamus cyanopterus</i>	GenBank	—	AY443262	AY443108
<i>Artamus leucorhynchus</i>	GenBank	—	AY056980	AY443109
<i>Pityriasis gymnocephala</i>	LSUMNS	B50309	DQ376524	DQ376514
<i>Oriolus larvatus</i>	GenBank	—	AY057011	AY443184
<i>Oriolus cruentus</i>	LSUMNS	B36464	DQ376523	DQ376513
<i>Lalage leucomela</i>	GenBank	—	AY443292	AY443159
<i>Coracina novaehollandiae</i>	GenBank	—	AY443272	AY443128
<i>Hemipus hirundinaceus</i>	LSUMNS	B47036	DQ376527	DQ376517
<i>Dicrurus adsimilis</i>	GenBank	—	AY056991	AY443140
<i>Monarcha chrysomela</i>	GenBank	—	AY443304	AY443177
<i>Aegithina tiphia</i>	GenBank	—	AY056977	AY443104
<i>Lanioturdus torquatus</i>	GenBank	—	AY799819	AY799838
<i>Dryoscopus cubla</i>	GenBank	—	AY443284	AY443142
<i>Tchagra senegala</i>	AMNH	2168	DQ376528	DQ376518
<i>Telophorus dohertyi</i>	GenBank	—	AY443336	AY443234
<i>Prionops plumatus</i>	GenBank	—	AY443322	AY443211
<i>Bias musicus</i>	FMNH	385200	DQ376529	DQ376519
<i>Batis mixta</i>	GenBank	—	AY443263	AY443110
<i>Platysteira castanea</i>	AMNH	8185	DQ376531	DQ376521
<i>Philentoma pyrholopterum</i>	LSUMNS	B38609	DQ376525	DQ376515
<i>Tephrodornis gularis</i>	LSUMNS	B51360	DQ376526	DQ376516
<i>Vanga curvirostris</i>	GenBank	—	AY057040	AY443244
<i>Pseudobias wardi</i>	FMNH	356702	DQ376530	DQ376520
<i>Xenopirostris xenopirostris</i>	FMNH	356663	DQ376532	DQ376522

Institution abbreviations are as follows: Louisiana State University Museum of Natural Science (LSUMNS), American Museum of Natural History (AMNH), and Field Museum of Natural History (FMNH).

tion (see Posada and Buckley, 2004). A maximum likelihood heuristic search was conducted with PAUP*4.0b10 (Swofford, 2002) with 100 random taxon additions and TBR branch-swapping. Non-parametric bootstrapping (100 replicates) was used to assess support for nodes in the maximum likelihood phylogeny. Model parameters and phylogenetic relationships were simultaneously estimated in a Bayesian framework with MrBayes 3.1.1 (Ronquist and Huelsenbeck, 2003). We ran two independent runs of four Markov chains for 5 million generations each. Markov chains were sampled every 100 generations, yielding 50000 point estimates of parameters/run. Stationarity, the condition in which parameter estimates (and likelihood scores) have stabilized and the Markov chains are sampling in the vicinity of the maximum likelihood parameter and tree space, was determined by visually examining plots of parameter values against generation. All samples prior to reaching stationarity were considered “burn-in,” and discarded. The subsampled trees, minus the burn-in generations, were used to create a consensus tree.

In the Bayesian analyses a series of partitioning schemes was used to evaluate the effect of allowing different model parameters for different subsets of the data matrix (Nylander et al., 2004; Ronquist and Huelsenbeck, 2003).

We ran analyses using all data in a single partition, two partitions (by gene), three partitions (by codon position), and six partitions (by gene and by codon position). Results from each partitioning scheme were evaluated with Bayes factors (see Brandley et al., 2005 for a thorough discussion of the methodology and rationale). Bayes factors were calculated using the harmonic mean from the sump command within MrBayes. The appropriate number of model parameters was determined by running MrModeltest 2.2 (Nylander, 2004) on each data partition.

Alternative basal topologies were evaluated in two ways. First, the posterior distribution was searched for relationships that were not represented in consensus trees. The frequency that a relationship occurs in the posterior distribution should approximate the probability that the relationship exists given the data (and the model). Second, we tested an alternative topology against the ML tree using the Shimodaira–Hasegawa (SH) test (Shimodaira and Hasegawa, 1999) in PAUP*. The SH test is a one-sided, non-parametric test appropriate for testing a small number of topologies chosen a posteriori (Goldman et al., 2000; Shimodaira, 2002). It is a conservative test of tree topology, because it minimizes the type I error rate (Buckley, 2002; Shimodaira, 2002). The REL option in PAUP* was used to produce the test distribution. This technique uses the parameter estimates from the original data to calculate likelihood scores for each bootstrap replicate. The alternative topology tested was one in which *Pityriasis* was sister to the Artamidae/Cracticidae clade (see below).

3. Results

The data matrix contained 31 taxa and 4036 bp, of which 900 were variable and 374 parsimony informative. Results from the AIC criterion in Modeltest supported the use of a parameter rich model (GTR + I + G) for the combined data set in ML analyses. Parameter estimates for ML analysis were: Base = (0.3120, 0.2024, 0.2331), Rmat = (1.2795, 5.6971, 0.5870, 1.5999, 8.8591), Shape = 0.9413, and Pinvar = 0.4968. MrModeltest indicated that parameter rich models were appropriate for all partitions, with most differences due to accounting for invariant sites or gamma-distributed rate heterogeneity in the model (Table 2). Differences in Bayes factors (see Table 3) between one and two (by gene) partitions were negligible. Bayes factors do not have a traditional critical value like some statistical tests, but a 2ln Bayes factor difference of 10 or greater is generally accepted as strong evidence against the alternative hypothesis (Kass and Raftery, 1995). The 2ln Bayes factor difference for partitions accounting for codon position (3 and 6) compared to those not accounting for codon position (1 and 2) was over 300 (see Table 3). The difference between three and six partition models (−35.82) was taken as strong evidence that the simpler model (three partitions) was most appropriate for the data. All discussion of

Table 2

Data partitions, models selected, and the number of characters in each partition

Partition	Model	Number of characters
All data	GTR + I + G	4036
RAG-1	GTR + I + G	2884
RAG-2	GTR + I + G	1152
1st codon	GTR + I + G	1345
2nd codon	GTR + I + G	1345
3rd codon	GTR + G	1346
RAG-1 1st	GTR + I	961
RAG-1 2nd	GTR + I + G	961
RAG-1 3rd	GTR + G	962
RAG-2 1st	HKY + I + G	384
RAG-2 2nd	GTR + G	384
RAG-2 3rd	GTR + G	384

Bayesian analyses and results below refer to the three-partition model.

The topology produced using maximum likelihood analysis (Fig. 1) was identical to that produced with Bayesian analysis. A large clade was evident that included species from the Artamidae, Cracticidae, Prionopidae, Vangidae, and Malaconotidae. This clade of shrike-like birds was initially identified by Barker et al. (2004) in their much broader analysis of passerine relationships. The best-supported portion of this clade was the Artamini (Fig. 1, clade A), with *Artamus* basal to *Cracticus*, *Gymnorhina*, and *Strepera*. High bootstrap values and posterior probabilities supported all of the nodes defining relationships among these genera, including the basal node. Notably, *Pityriasis* was not reconstructed as part of this clade. Instead, it was placed in one of the two clades (Fig. 1, clades B and C) sister to the Artamini. These clades encompass an assortment of families including Malaconotidae, Vangidae, Prionopidae, and several Asian genera (*Tephrodornis*, *Philentoma*, *Aegithina*, and *Hemipus*). All analyses placed *Pityriasis* within clade B, as the sister group to the Common Iora (*Aegithina tiphia*), although this relationship had low bootstrap support (63%) and non-significant Bayesian posterior probability (0.82).

The node uniting clades B and C (node A, Fig. 1) is crucial to evaluating the relationships of *Pityriasis* and several other taxa. This node separates *Pityriasis* from the artamids and cracticids, the taxa with which it has most recently been allied. In Bayesian analyses, partitioning the data by codon position resulted in a posterior probability of 0.96, indicating strong support for clade A + B. In contrast, ML bootstrap support for this node was relatively low (62%). DNA–DNA hybridization analysis (Sibley and Ahlquist, 1990) placed *Pityriasis* within the artamines, and sister to the cracticids. Strong support for the artamines (clade A, Fig. 1) rejects this hypothesis. However, low bootstrap support for node A (Fig. 1) leaves open the possibility that some analyses may have reconstructed *Pityriasis* sister to the artamines. To test this hypothesis, the nature of relationships between *Pityriasis* and the artamines was examined in several ways. A Shimodaira–Hasegawa test of the

Table 3
Likelihood scores ($-\ln$) and Bayes factor comparisons for data partitioning schemes

Analysis	Partitions	ML score	Arithmetic mean	Harmonic mean	2 ln Bayes factor	Node A PP
ML	1	14530.03972				
Bayesian	1		14557.47	14593.75	NA	0.90
	2		14555.26	14597.42	-7.43	0.91
	3		14380.57	14424.81	345.22	0.96
	6		14395.03	14442.72	-35.82	0.97

Bayesian partitions are as follows: 1 = all data together, 2 = data partitioned by gene, 3 = data partitioned by codon position, 6 = data partitioned by gene, and codon position. Bayes factors refer to the difference between a model and the next simpler model. A negative value indicates support for the simpler model. PP = posterior probability. Node A refers to Fig. 1. NA = not applicable, there is no simpler model available for Bayes factor comparison.

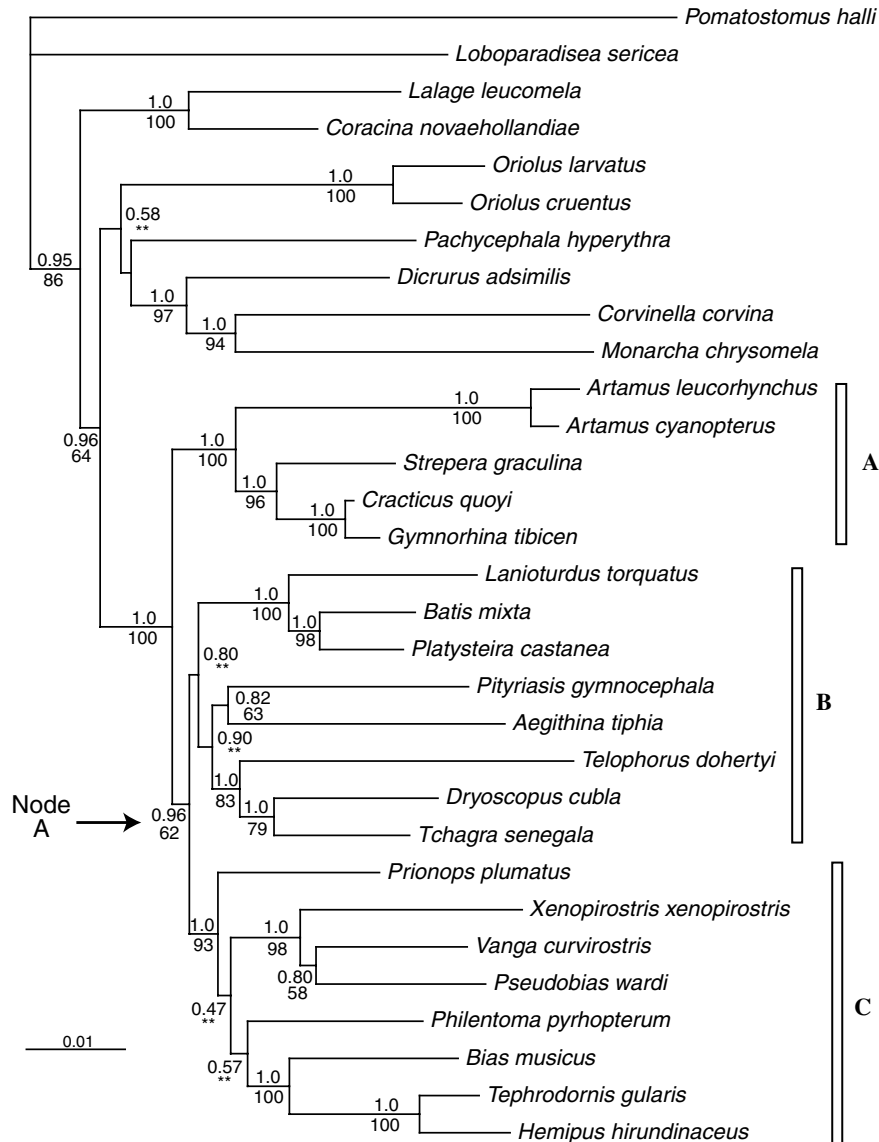


Fig. 1. Bayesian consensus topology from analysis of the combined data set. See text for model details. Upper numbers at nodes indicate Bayesian posterior probability; lower numbers indicate ML bootstrap proportion. Asterisks (**) indicate bootstrap support <50%. Clades A, B, and C are discussed in the text.

ML tree against one in which *Pityriasis* was sister to clade A returned a p value of 0.04, evidence that the alternate topology was a significantly worse explanation of the data than the ML topology. We also looked more closely at the posterior distribution of trees from the Bayesian analysis.

The 95% credible set of trees contained 3318 different topologies, yet none of those inferred a relationship of *Pityriasis* sister to the artamines. The 99% credible set of trees contained 6501 topologies, and again not one inferred a relationship of *Pityriasis* sister to the artamines. Of the total

7461 topologies included in the posterior distribution, only a single tree (#7283) placed *Pityriasis* with the artamines.

Although many relationships within clades B and C received low posterior probability or bootstrap support, a few well-supported nodes were evident. Interestingly, the clade of Malagasy vangas (*Vanga*, *Pseudobias*, and *Xenopirostris*), along with the African shrike-flycatchers (*Bias*) and helmet-shrikes (*Prionops*), also included three Asian genera (*Philentoma*, *Tephrodornis*, and *Hemipus*). DNA–DNA hybridization analysis (Sibley and Ahlquist, 1990) placed *Philentoma* and *Tephrodornis* in an unresolved clade with bush-shrikes, vangas, helmet-shrikes, *Batis*, and wattle-eyes, but our data were able to provide better resolution of the relationships, placing *Philentoma* and *Tephrodornis* closest to vangas, shrike-flycatchers, and helmet-shrikes. Our data also indicated that *Hemipus*, another Asian genus not included in Sibley and Ahlquist's (1990) sampling, is part of this clade. The close relationship between *Hemipus* and *Tephrodornis* was corroborated by a three-codon insertion in the RAG-1 sequence compared to all other species examined.

4. Discussion

Analysis of nuclear exon data reconstructed *Pityriasis* as part of a large clade of African and Asian shrike-like birds, in conflict with DNA–DNA hybridization results that placed *Pityriasis* within the Australasian Artamini. The Bornean Bristlehead is therefore inferred to be part of a large radiation of vangas, bush-shrikes, helmet-shrikes, wattle-eyes, and assorted other genera. Such a relationship, although not commonly espoused, was suspected at least a century ago by Sharpe (1903), although his Prionopidae encompassed far more taxa than just the helmet-shrikes. More recently, Raikow et al. (1980) placed *Pityriasis* next to the Prionopinae based on appendicular myology, but they also included true shrikes (Laniidae) within this clade. Given the long branch leading to *Pityriasis*, the inability of our analyses to identify its sister taxon with any certainty, and the morphological disparity and geographic dispersion of the related taxa, it is not surprising that previous efforts to classify this unusual species resulted in such disparate conclusions. Assuming we have not omitted any living taxon that is closer to *Pityriasis* than those included in the study, the Bornean Bristlehead represents a relict lineage from the early diversification of these shrike-like birds across the Old World tropics. That it does not also occur on Sumatra, Java, or Malaya is a mystery, as the lowlands of those areas maintained subaerial connections to Borneo as recently as the last ice age, and they have no obvious competitors to exclude *Pityriasis*.

Partitioning the data by codon position resulted in a substantial improvement in likelihood scores in the Bayesian analysis, and resulted in higher posterior probabilities for some basal nodes. This finding mirrors the results of a study on scincid lizards (Brandley et al., 2005), document-

ing that partitioning biologically meaningful groups of characters (codon positions, stems, loops in rRNA's, etc.) can lead to better resolution of basal nodes in a phylogeny. Partitioning our data by codon position resulted in an increase in the posterior probability of node A (Fig. 1) from 0.90 to 0.96 (see Table 3), strengthening the interpretation that clades B and C are sister groups. Furthermore, results from a Shimodaira–Hasegawa test and an analysis of the posterior distribution of topologies (see results) provided strong evidence against a sister relationship between *Pityriasis* and the artamines (clade A, Fig. 1). Topologies in the posterior distribution that disagreed with our phylogenetic hypothesis (clades B and C sister, Fig. 1) did not involve *Pityriasis* moving closer to the artamines. For example, clades A and C were sister in 3.6% of the posterior distribution, which also results in *Pityriasis* distinct from the artamines.

This study added Asian genera to the clade of shrike-like birds identified by Barker et al. (2004). This group was first implied by Beecher (1953) who, using morphological evidence, included *Tephrodornis* in the Prionopidae, which was then linked with Vanginae, Pityriasidae, and Cracticidae. DNA–DNA hybridization comparisons (Sibley and Ahlquist, 1990) showed that *Tephrodornis*, *Philentoma*, and *Aegithina* were part of the bush-shrike/helmet-shrike clade, but they placed *Pityriasis* in the Cracticidae, which was far removed from the bush-shrikes and helmet-shrikes. *Hemipus* was not included in any DNA–DNA hybridization comparisons. Fuchs et al. (2004) examined the relationships among African helmet-shrikes and bush-shrikes with much denser sampling than our study, but they did not include any of the Asian genera. In addition to *Pityriasis*, the Asian genera in the helmet-shrike and bush-shrike clade now include *Aegithina*, *Tephrodornis*, *Philentoma*, and *Hemipus*. All are small groups (*Aegithina* is the most speciose with four species) with historically uncertain affinities, having been allied with leafbirds (Chloropseidae), fairy-bluebirds (Irenidae), honey-eaters (Meliphagidae), bulbuls (Pycnonotidae), muscicapid flycatchers (Muscicapidae), monarch flycatchers (Monarchidae), or cuckoo-shrikes (Campephagidae).

In addition to helping clarify the phylogenetic relationships of the Bornean Bristlehead, our data provide insight into the assembly of the Paleotropical avifauna. The fossil record (Boles, 1995) and molecular phylogenetics (Barker et al., 2002; Ericson et al., 2002) support an oscine origin and early diversification in Australasia. Basal corvoid families are predominantly Australasian and inferred dispersals out of that region are limited, but they generally led to speciose radiations across multiple continents. Barker et al. (2004) estimated the split between the Artamini (our clade A) and Malaconotinae (our clades B and C) occurred 28.5–23.5 million years ago (Ma), corresponding with dispersal into Africa. Although it certainly included African components, the addition of multiple Asian taxa to the malaconotines means that the dispersal event out of Australia cannot unequivocally be linked directly to Africa. The complex

composition of African, Asian, Malagasy, and Australasian taxa, combined with uncertain basal relationships means that we are unable with currently available data to decipher the biogeographic history of this clade.

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