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A MOLECULAR PHYLOGENY OF KINGFISHERS (ALCEDINIDAE) WITH INSIGHTS INTO EARLY BIOGEOGRAPHIC HISTORY

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Abstract.—The phylogeny of kingfishers was reconstructed by comparing mitochondrial and nuclear DNA sequences representing 38 ingroup species. Analysis of the combined data and the nuclear data alone recovered the Alcedininae as the basal lineage in the family. This basal arrangement, and support for many relationships within the three subfamilies, allows discussion of biogeographic issues. The Australian region and Pacific islands display the highest diversity of kingfishers, but this diversity is not a reflection of a long history in the region. Rather, high diversity and endemism in the Australian region is inferred to result from relatively recent radiations from southern Asia. The most parsimonious explanation for the origin of New World taxa is two dispersal events from the Old World. Within the large *Halcyon* radiation, the phylogeny is well resolved and allows evaluation of generic assignments. The phylogeny supports splitting *Todiramphus* from *Halcyon*. *Todiramphus* and *Syma* are sister taxa, as are *Halcyon* and *Pelargopsis*. Thus, merging or retaining those genera is a more subjective decision. Although not fully resolved, relationships within the alcedinines indicate that *Ceyx* and *Alcedo*, as currently delimited, are not natural groups. *Received 9 December 2004, accepted 15 August 2005.*

Key words: Alcedinidae, biogeography, kingfisher, systematics.

Phylogénie Moléculaire des Alcedinidae avec un Aperçu de l'Histoire Biogéographique Ancienne

Résumé.—La phylogénie des Alcedinidae a été reconstruite en comparant des séquences d'ADN mitochondriales et nucléaires de 38 espèces de la famille. L'analyse des données combinées et des données nucléaires seules rétablit les Alcedinidae comme la lignée de base dans la famille. Cet arrangement de base, et le support pour de nombreuses relations à l'intérieur des trois sous-familles, conduisent à une discussion sur les questions de biogéographie. La région australienne et les îles du Pacifique affichent la plus grande diversité en Alcedinidae. Néanmoins, cette diversité n'est pas un reflet d'une longue histoire dans la région. La grande diversité et l'endémisme de la région australienne résulteraient des radiations relativement récentes de l'Asie du sud. L'explication la plus parcimonieuse pour l'origine des taxons du Nouveau Monde réside dans deux évènements de dispersion de l'Ancien Monde. À l'intérieur de la grande radiation *Halcyon*, la phylogénie est bien résolue et permet une évaluation des attributions génériques. La phylogénie supporte la séparation de *Todiramphus* avec *Halcyon*. *Todiramphus* et *Syma* sont des taxons frères, tout comme *Halcyon* et *Pelargopsis*. Par conséquent, rassembler ou maintenir ces genres est une décision plus subjective. Bien qu'elles ne soient pas complètement résolues, les relations entre les alcedinines indiquent que *Ceyx* and *Alcedo*, telles que définies actuellement, ne sont pas des groupes naturels.

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Kingfishers (Alcedinidae) are a family of ~90 species that range in size from the 9-g African Dwarf Kingfisher (*Ceyx lecontei*) to the ~500-g Laughing Kookaburra (*Dacelo novaeguineae*) (Woodall 2001). Despite their name, kingfishers are not all piscivorous. In fact, many species are found far from water and prey on a variety of terrestrial invertebrates and small vertebrates. Although a few species have adapted to temperate regions, kingfishers are a largely tropical group. Compared with some other widespread tropical bird groups, however, their diversity pattern is unusual. Kingfishers are most diverse in the Australian region, whereas some other speciose pantropical groups (e.g. barbets and trogons) do not occur east of Wallace's line. Many kingfisher species are not restricted to forest habitats and, as evidenced by their migratory behavior and presence on numerous Pacific islands, kingfishers seem to have substantial dispersal ability.

Distribution, behavior, and life-history characteristics make kingfishers attractive subjects for comparative evolutionary analyses. They have been the focus of studies on community ecology (Remsen 1991), cooperative breeding (Reyer 1980, 1984), retinal morphology (Moroney and Pettigrew 1987), skull morphology (Burton 1978), biogeography (Fry 1980a, b), and morphometry (Woodall 1991), yet none of these studies had the benefit of an explicit phylogenetic hypothesis for the family. Consequently, natural groups, primitive character states, ancestral areas, and convergent evolution have been inferred from taxonomic groupings, which rely heavily on plumage or behavioral characters. For example, one subfamily (Alcedininae) is divided into genera largely on the basis of feeding strategy (Delacour 1951, Fry et al. 1992, Woodall 2001), with terrestrial feeders assigned to *Ceyx* and aquatic feeders assigned to *Alcedo*. Unfortunately, terrestrial and aquatic species are not clearly delimited. Thus, some authors have added other genera (e.g. *Corythornis*) for species that display both feeding behaviors, and *Ceyx lepidus*, which has varying degrees of piscivory on different islands, has been included in both *Ceyx* (Dickinson 2003) and *Alcedo* (Schodde 1977, Fry et al. 1992). Other taxonomic groupings are similarly contentious, including a large Old World radiation of terrestrial sit-and-wait predators variously lumped into a single genus (*Halcyon*) or divided into as many as five genera.

Modern phylogenetic hypotheses for kingfishers are few, and all are the byproduct of higher-level studies not specifically intended to examine relationships among kingfishers. Morphological comparisons (Maurer and Raikow 1981) indicated that Daceloninae was the basal subfamily, in agreement with a general consensus that this large and diverse group represented the ancestral morphotype, behavior, and geographic origin (Malesia). Sibley and Ahlquist's (1990) DNA–DNA hybridization studies recovered the Alcedininae as the basal clade, but these results have been questioned because of speculation that increased rates of molecular evolution in these small-bodied birds adversely affected the hybridization comparisons (Fry et al. 1992). A study based on DNA sequences of piciform and galbuliform birds (Johansson and Ericson 2003) included representatives of the three kingfisher subfamilies and found the Cerylinae basal. Thus, three studies using three different types of data have recovered each of the three potential basal relationships among kingfishers.

Here, I attempt to clarify higher-level relationships among the kingfishers. I compare DNA sequences of a mitochondrial and nuclear gene from 38 ingroup species and address three main questions. First, what are the historical relationships between major clades of kingfishers? Second, to the extent that taxon sampling allows, do current generic and subfamilial designations describe natural groups? Third, what are the biogeographic implications of the inferred higher-level relationships among kingfishers?

Methods

Taxon Sampling

Ingroup sampling (Table 1) included at least one species of all recently recognized genera of kingfishers except *Halcyon fulgidus*, a species from the Lesser Sunda Islands sometimes placed in its own genus *Carridonax*. Outgroup sampling included three families of coraciiforms: Coraciidae (*Coracias caudatus*), Momotidae (*Momotus momotus*), and Todidae (*Todus angustirostris*). Previous molecular studies (Sibley and Ahlquist 1990, Harshman 1994, Johansson and Ericson 2003) indicated that motmots and todies are the closest living relatives of kingfishers.

TABLE 1. Taxa included in the present study.

Species [a]	Common name	Voucher identification number	Source [b]	Locality [c]
	Ingroup: Daceloninae			
Actenoides lindsayi	Spotted Wood Kingfisher	433013	FMNH	Philippines
A. concretus	Rufous-collared Kingfisher	B36383	LSUMNS	Borneo
Tanysiptera galatea	Common Paradise Kingfisher	AM1008	KUNHM	New Guinea
Cittura cyanotis	Lilac Kingfisher	115589	ZMUC	Sulawesi
Melidora macrorrhina	Hook-billed Kingfisher	96077	KUNHM	New Guinea
Clytoceyx rex	Shovel-billed Kingfisher	5103	KUNHM	New Guinea
Lacedo pulchella	Banded Kingfisher	DOT10817	AMNH	Vietnam
Dacelo gaudichaud	Rufous-bellied Kookaburra	67921	UWBM	New Guinea
D. leachii	Blue-winged Kookaburra	60802	UWBM	Australia
D. novaeguineae	Laughing Kookaburra	DOT2409	AMNH	Australia
Pelargopsis (Halcyon) capensis	Stork-billed Kingfisher	4-1H	MNHN	Thailand
Halcyon badia	Chocolate-backed Kingfisher	DOT12426	AMNH	Liberia
H. malimbica	Blue-breasted Kingfisher	DOT12517	AMNH	CAR
H. senegalensis	Woodland Kingfisher	DOT12481	AMNH	CAR
Todiramphus (*Halcyon*) *leucopygius*	Ultramarine Kingfisher	DOT6654	AMNH	Solomon Is.
T. (H.) chloris	Mangrove Kingfisher	DOT6704	AMNH	Solomon Is.
T. (*H.*) *sanctus*	Sacred Kingfisher	DOT12594	AMNH	Sulawesi
T. (*H.*) *tutus*	Pacific Kingfisher	42503	UWBM	Cook Is.
T. (*H.*) *ruficollaris*	Mangaia Island Kingfisher	42791	UWBM	Cook Is.
Syma (Halcyon) torotoro	Lesser Yellow-billed Kingfisher	AM1036	KUNHM	New Guinea
	Ingroup: Alcedininae			
Ceyx (*Ispidina, Myioceyx*) *lecontei*	African Dwarf Kingfisher	DOT10589	AMNH	CAR
C. (*Ispidina*) *pictus*	African Pygmy Kingfisher	DOT10701	AMNH	CAR
C. erithaca	Oriental Dwarf Kingfisher	DOT9655	AMNH	Singapore
C. (*Ispidina, Corythornis, Ceycoides*) *madagascariensis*	Madagascar Pygmy Kingfisher	393192	FMNH	Madagascar
C. (*Alcedo*) *lepidus*	Variable Dwarf Kingfisher	DOT6641	AMNH	Solomon Is.
Alcedo (*Corythornis*) *leucogaster*	White-bellied Kingfisher	DOT10682	AMNH	CAR
A. (*C.*) *cristata*	Malachite Kingfisher	B39303	LSUMNS	Ghana
A. quadribrachys	Shining-blue Kingfisher	DOT6738	AMNH	Liberia
A. (*Alcyone, Ceyx*) *azurea*	Azure Kingfisher	96095	KUNHM	New Guinea
A. atthis	Common Kingfisher	DOT12586	AMNH	Sulawesi
	Ingroup: Cerylinae			
Chloroceryle aenea	American Pygmy Kingfisher	DOT11970	AMNH	Venezuela
C. inda	Green-and-rufous Kingfisher	DOT6182	AMNH	Bolivia
C. americana	Green Kingfisher	DOT6181	AMNH	Bolivia
C. amazona	Amazon Kingfisher	DOT2317	AMNH	Bolivia
Megaceryle (*Ceryle*) *maxima*	Giant Kingfisher	396319	FMNH	Gabon
M. (*C.*) *torquata*	Ringed Kingfisher	DOT8781	AMNH	Venezuela
M. (*C.*) *alcyon*	Belted Kingfisher	DOT10476	AMNH	California
Ceryle rudis	Pied Kingfisher	B39362	LSUMNS	Ghana
	Outgroup			
Coracias caudata	Lilac-breasted Roller		Genbank	
C. garrulus	European Roller		Genbank	
Momotus momota	Blue-crowned Motmot	RWD17160	AMNH	
Todus angustirostris	Narrow-billed Tody	NKK1014	AMNH	

[a] Taxonomy follows Woodall (2001). Alternative generic assignments are included in parentheses.

[b] Institution abbreviations are: AMNH, American Museum of Natural History; LSUMNS, Louisiana State University Museum of Natural Science; FMNH, Field Museum of Natural History; KUNHM, University of Kansas Natural History Museum; UWBM, Burke Museum of Natural History, University of Washington; MNHN, Muséum National d'Histoire Naturelle, Paris; ZMUC, Zoological Museum University of Copenhagen.

[c] CAR = Central African Republic.

Sequencing

Genomic DNA was extracted from muscle tissue using proteinase K digestion following the manufacturer's protocol (DNeasy Tissue Kit; Qiagen, Valencia, California). The primers L5215 (Hackett 1996) and H6313 (Johnson and Sorenson 1998) were used to amplify the entire NADH dehydrogenase-2 gene (ND2) via polymerase chain reaction (PCR). Amplification of smaller fragments from the initial PCR products or whole genomic DNA was performed with the internal primers L5758 (Johnson and Sorenson 1998), ND2Hal (5′–GTTAGTAGGGTRAGTTTDGGG–3′), and ND2Alc(5′–AGGTAGAAGGTTATTAGGGTTAG–3′). An exon from the recombination activating gene (RAG-1) was amplified using primers from Groth and Barrowclough (1999). These genes have provided good resolution across varying taxonomic levels in birds (e.g. Groth and Barrowclough 1999, Barker et al. 2004, Moyle 2005). The nuclear exon evolves slowly and generally provides more phylogenetic signal than mitochondrial markers at deeper nodes in a phylogeny. The mitochondrial marker evolves more quickly and is useful for resolving more closely related taxa.

I purified PCR products with Perfectprep PCR cleanup kits (Eppendorf, Westbury, New York). Sequencing of purified PCR products was performed with BigDye Terminator Cycle Sequencing reagents (Applied Biosystems, Foster City, California). Primers used for PCR were also used for cycle sequencing reactions, resulting in bidirectional sequence for all taxa. Cycle sequencing products were run on an ABI Prism 3100 automated DNA sequencer (Applied Biosystems). The program SEQUENCHER 4.1 (Genecodes, Ann Arbor, Michigan) was used to reconcile chromatograms of complimentary fragments and to align sequences across taxa.

Data Analysis

Congruence between phylogenetic signal in the two genes was tested with the incongruence length difference test (Farris et al. 1994, 1995), implemented in PAUP*, version 4.0b10 (i.e. partition homogeneity test; Swofford 2002). The test excluded constant characters and ran for 1,000 bootstrap repetitions. PAUP* was also used to test the base composition of each gene using a chi-square analysis of base frequencies across taxa. To visualize the degree of divergence between ingroup and outgroup taxa, the extent of saturation, and relative substitution rates between RAG-1 and ND2, I plotted the uncorrected distance (*P*-distance) and maximum-likelihood-transformed distance of ND2 versus that of RAG-1 for all pairwise comparisons of taxa.

Maximum-likelihood (ML) and maximum-parsimony (MP) analyses were performed for each gene as well as the combined data using PAUP*. Heuristic searches employed tree bisection and reconnection (TBR) branch-swapping and 100 random-taxon-addition sequences. For each likelihood analysis, I used MODELTEST, version 3.5 (Posada and Crandall 1998), to determine the model of evolution and parameter estimates. Support for nodes in the ML tree was assessed by nonparametric bootstrapping (Felsenstein 1985) and re-analysis of the data (100 replicates). MRBAYES, version 3.0 (Huelsenbeck and Ronquist 2001), was used to estimate model parameters from the data and to evaluate support for specific relationships in the phylogeny. For the combined data set, a mixed-model approach was implemented to account for the potential difference in evolutionary model parameters between data partitions (genes in this case). A general time-reversible (Yang 1994a) model framework, with γ-distributed rates among sites (Yang 1994b) and invariant sites, was used for both partitions (from MODELTEST). All parameters (except topology) were unlinked between partitions. I ran four Markov chains for 25 million generations, as well as two 2-million-generation runs. The shorter runs were used to help evaluate stationarity, the condition in which parameter estimates (and likelihood scores) have converged on a value and the Markov chain is sampling in the vicinity of the ML parameter and tree space. All samples prior to reaching stationarity were discarded. Markov chains were sampled every 1,000 generations, yielding 25,000 parameter point estimates. These subsamples, minus the burn-in generations, were used to create 50% majority-rule consensus trees.

Results

The final data matrix included 38 ingroup species and 3,916 characters (1,044 ND2 and

2,872 RAG-1; Genbank numbers DQ111789–DQ111867). The ND2 sequence was three bases longer than usually reported, because of a one-codon insertion near the 3′ end of the *Alcedo cristata* sequence. The matrix included 930 parsimony-informative characters (414 RAG-1, 516 ND2), and both genes had skewed base composition (i.e. excess adenine in both genes and an excess of cytosine in the ND2 data), which was, however, homogeneous across taxa and typical of these genes in other birds (e.g. Groth and Barrowclough 1999, Kirchman et al. 2001). Aligned ND2 sequences appeared to be genuine mitochondrial sequence, rather than nuclear copies. Sequences contained no stop codons, overlapping fragments contained no conflicts, base composition was homogeneous across taxa, codon positions contained expected relative divergences (3>1>2), and highly suspect relationships were not evident. The partition homogeneity test results were not significant ($P > 0.05$). A plot of pairwise divergences (Fig. 1) between the two genes showed evidence of saturation in the ND2 partition. For *p*-distance, the slope noticeably decreased above ND2 divergences of ~15%. ND2 values remained between 20% and 25% for more than half the span of RAG-1 *p*-distance (~4.5% to 9.5%). Maximum-likelihood corrections produced a more linear relationship between pairwise distances for the two genes.

Higher-level Relationships

Parsimony, likelihood, and Bayesian methods produced congruent results. Topological differences occurred, but no conflicts received high support from bootstrapping or Bayesian analysis. Monophyly of the three traditional subfamilies of kingfishers (Alcedininae, Cerylinae, and Daceloninae) was strongly supported in all analyses (Figs. 2 and 3). The relationship among these three clades (Alcedininae basal to Cerylinae and Daceloninae) was the same across all combined analyses but did not always receive strong support. For example, posterior probability for the basal position of the Alcedininae from Bayesian analysis of the

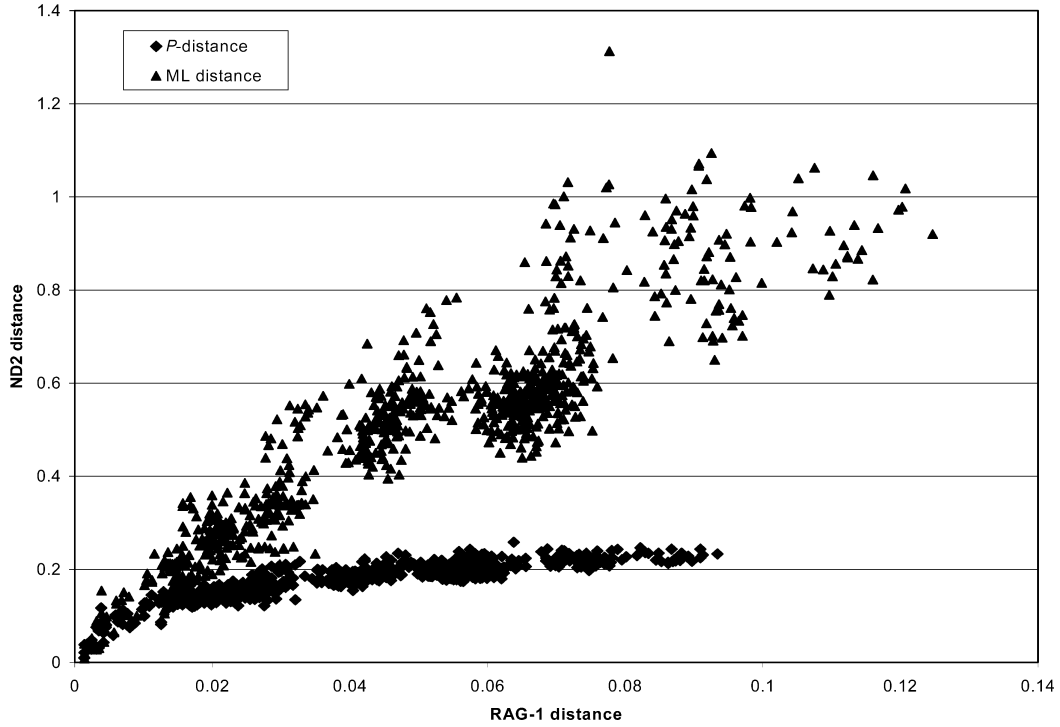

Fig. 1. Plot of pairwise values for uncorrected *p*-distance and ML-corrected distance. Maximum-likelihood model and parameter estimates from MODELTEST (see text).

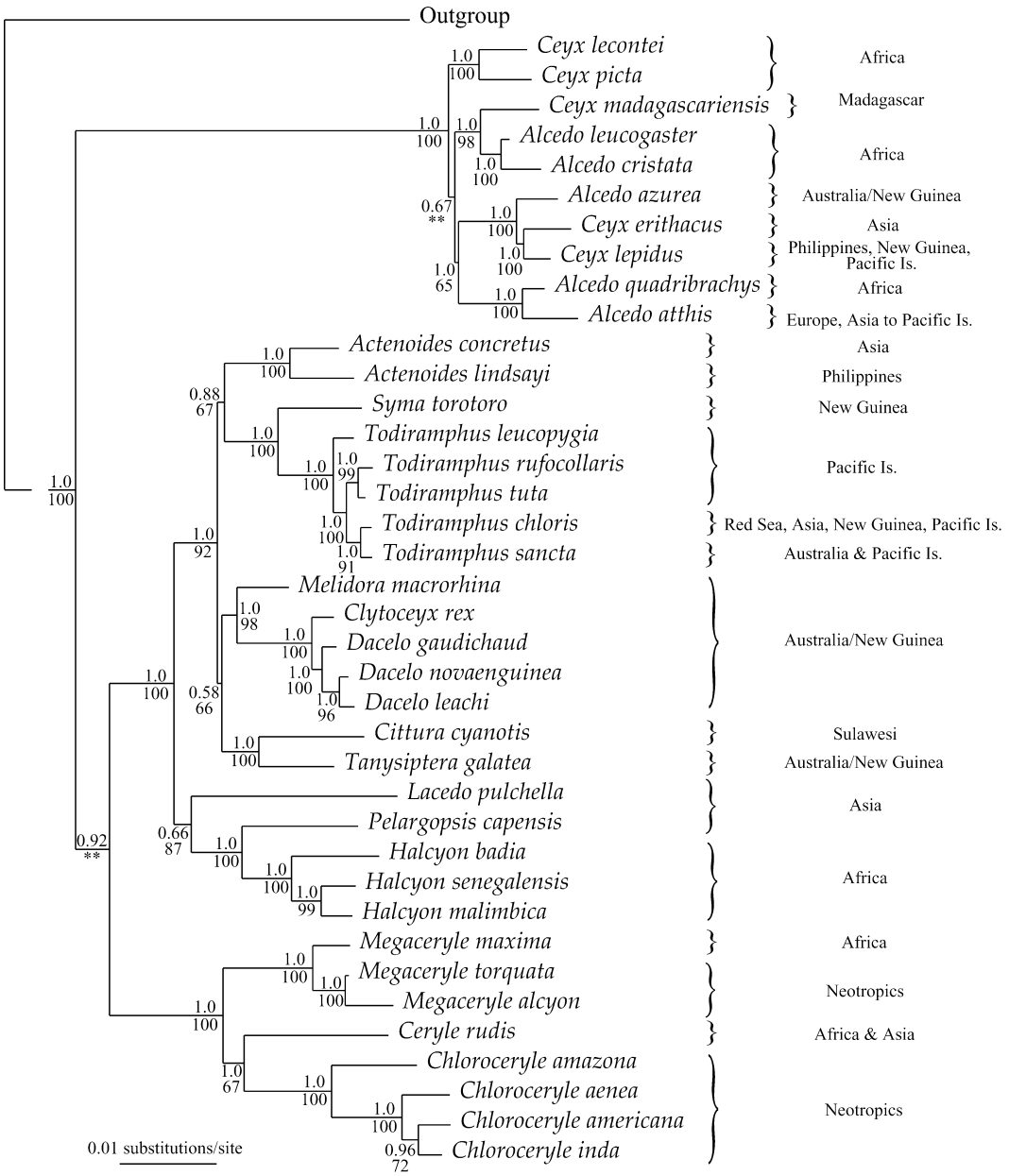

FIG. 2. Bayesian consensus tree of combined ND2 and RAG-1 data from mixed-model analysis. Numbers at nodes indicate Bayesian posterior-probability or maximum-likelihood bootstrap support. General distribution of each species is indicated to the right.

combined data (0.92) fell just shy of significance, and bootstrap support was <50%, but parsimony bootstrap analysis of RAG-1 alone was more persuasive (85%). It is apparent that resolution of this node relies heavily on the nuclear DNA sequence data. Analysis of the RAG-1 data alone (Fig. 3A) produced the same result as the combined analysis, but analysis of ND2 alone (Fig. 3B) produced an alternate basal topology (Daceloninae basal) with low branch support.

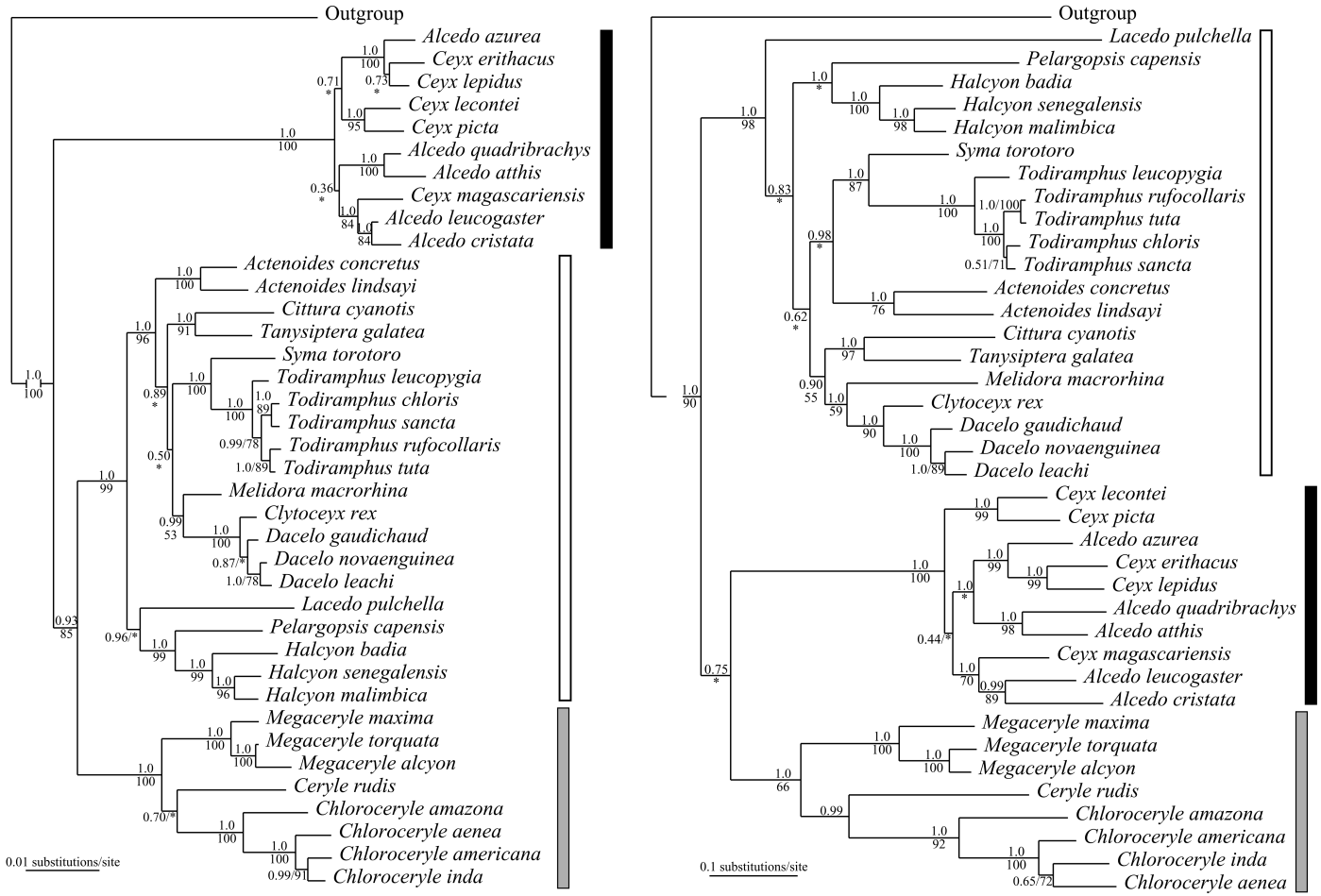

FIG. 3. Bayesian consensus trees of the RAG-1 (A) and ND2 (B) data analyzed separately. Numbers above nodes indicate Bayesian posterior-probability or parsimony-bootstrap proportions. Bootstrap proportions <50% are indicated with an asterisk. Bars indicate subfamilies: Alcedininae, black; Cerylinae, gray; Daceloninae, open.

Alcedininae

Basal relationships within the Alcedininae were not resolved with the current data. Bayesian analysis of the combined data (Fig. 2) essentially yielded a trichotomy at the end of a long stem lineage. The basal split, albeit with no support from any type of analysis, separated *Ceyx lecontei* and *C. picta* (both included in *Ispidina* at times) from the rest of the taxa. One of the two remaining groups, with high support at both nodes, placed the Madagascar Pygmy Kingfisher (*C. madagascariensis*) sister to a pair of African *Alcedo* species (*A. leucogaster* and *A. cristata*). The final clade of alcedinines sampled in the study included five species from Africa, Asia, and the Australian region, as well as the Common Kingfisher (*A. atthis*), one of the few kingfisher species that ranges far outside the tropics.

Cerylinae

Although the most depauperate of the three subfamilies, the Cerylinae arguably have the widest geographic distribution, occurring throughout the tropics of Africa, Asia, and the New World, as well as temperate regions of North America and Asia. Relationships within the Cerylinae were well resolved and divide the subfamily into two clades, both containing New and Old World taxa. One clade included the two New World species of *Megaceryle* sister to the one Old World *Megaceryle* species sampled. The second clade contained *Ceryle rudis* sister to the four species of *Chloroceryle*. Within *Chloroceryle*, plumage does not segregate species pairs as traditionally assumed (Fry 1980b, Fry et al. 1992, Woodall 2001). The two rufous-bellied species (*C. aenea* and *C. inda*) were not sister taxa, nor were the two white-bellied species (*C. amazona* and *C. americana*). Instead, *C. americana* and *C. inda* were sisters, and *C. aenea* and *C. amazona* branched off successively deeper in the clade.

Daceloninae

The Daceloninae are the most speciose and phylogenetically uncertain subfamily of kingfishers. All analyses supported monophyly of the Daceloninae, but uncertainty existed about relationships within the subfamily. Three well-defined lineages diverged at the base of the clade. The first was a sister grouping of *Halcyon* and the Stork-billed Kingfisher (*Pelargopsis capensis*). The second lineage included only the monotypic *Lacedo pulchella*. Bayesian analysis of the RAG-1 partition (Fig. 2A) yielded a significant posterior probability (0.96) placing *Lacedo* sister to the *Pelargopsis–Halcyon* clade, but support from combined analyses was far lower (0.66). This discrepancy may be due to the phylogenetic signal from the ND2 data (Fig. 2B), which reconstructed *Lacedo* as the basal branch in the Daceloninae, albeit with low support. When combined, the two genes cannot place *Lacedo* with any certainty.

The third lineage in the Daceloninae was a diverse assemblage of mostly Australasian and Pacific taxa. Within this clade, relationships among some genera were strongly supported, but uncertainty existed at the base of the radiation. All analyses supported sister relationships between *Cittura* and *Tanysiptera*, *Syma* and *Halcyon* (the subset included in *Todiramphus*), *Dacelo* and *Clytoceyx*, and *Melidora* with (*Dacelo*, *Clytoceyx*). Bayesian analysis of the ND2 data yielded significant support for a sister relationship between *Actenoides* and *Syma–Todiramphus*, but this relationship lacked significant support from the RAG-1 partition or the combined analyses. The data did not produce significant support for other relationships among the main lineages in this clade.

Discussion

Higher-level Relationships

Phylogenetic analysis of nuclear and mitochondrial DNA sequences produced a robust hypothesis of kingfisher relationships. Combined analysis supported the Alcedininae as the basal branch in the kingfisher phylogeny, in agreement with Sibley and Ahlquist's (1990) DNA–DNA hybridization results. Fry et al. (1992) and Woodall (2001) speculated that the hybridization results may have been biased by a presumed faster rate of evolution among the small-bodied alcedinines. Visual inspection of the phylogeny (Fig. 2) confirms that the alcedinines sit farther from the base of the tree than the other subfamilies. This is not expected to greatly influence the present results because, unlike DNA–DNA hybridization methods, the current data and analytical methods are more adept at handling rate discrepancies.

Support for the basal node in the phylogeny derived exclusively from the RAG-1 partition. The ND2 data supported the Daceloninae as the basal lineage in the family (Fig. 3B), but there is reason to discount this result in relation to the RAG-1 and combined analyses. Kingfishers are an old family, arising in the Eocene or earlier according to the fossil record (Grande 1980, Houde and Olson 1988, Mourer-Chauviré 1995). In analysis of such a group, mitochondrial DNA, by virtue of its faster rate of evolution and among-site rate heterogeneity, is more likely to suffer from saturation effects (multiple superimposed substitutions) than nuclear DNA sequences. Saturation causes a decrease in phylogenetic signal at deeper nodes, and a concomitant increase in spurious signal. ND2 begins to show evidence of saturation by 15% uncorrected divergence (Fig. 1) and plateaus just above 20% divergence. Distance transformation using the ML model and parameter estimates established a more linear relationship between the two genes, but increased the variance (scatter) as well. A character- and model-based tree evaluation method (like ML) can emphasize phylogenetic signal from less-saturated characters, but no transformation can reconstruct informative character changes erased by homoplasy. Unlike mitochondrial DNA, the RAG-1 gene evolves at a much slower rate and has proved useful in deciphering distant relationships in several bird groups (e.g. Groth and Barrowclough 1999; Barker et al. 2002, 2004). The difference in phylogenetic signal provided by the two genes is reflected in the combined and separate analyses. Although the Daceloninae were basal in the ND2 analysis, this was based on relatively little informative phylogenetic signal. Nonparametric bootstrap resampling (<50%) and Bayesian posterior probability (0.75) provided little support for this conformation. By contrast, the basal node in the RAG-1 analysis received high-parsimony bootstrap support (85%) and a Bayesian posterior probability (0.93) just shy of significance. Mixed-model Bayesian analysis of the combined data yielded virtually the same posterior probability as the RAG-1 analysis, indicating that the nuclear sequence data is providing most of the phylogenetic signal at that deep node. In the combined data analysis, trivial posterior probabilities supported other basal arrangements (Cerylinae basal 0.01, Daceloninae basal 0.06).

Biogeographic History

Incomplete taxon sampling and uncertainty at the base of the alcedinine and dacelonine radiations preclude formal analysis of global kingfisher biogeography. Nevertheless, the current phylogenetic hypothesis and outgroup comparisons allow re-evaluation of the conventional wisdom on kingfisher biogeography and informed discussion about the family's origins. Kingfisher diversity reaches its maximum in the Australian region, which contains more species, endemic species, and endemic genera than any other region (Fry et al. 1992). The other tropical regions, in order of decreasing kingfisher diversity, are Asia, Africa, and South–Central America. This diversity pattern, along with the supposition that terrestrial sit-and-wait predators in tropical rainforests are likely to represent ancestral types, contributed to the idea that kingfishers arose in Malesia (Fry et al. 1992, Woodall 2001). The problem with this conclusion is that Malesia, a broad region stretching from the Malay Peninsula to New Guinea, comprises two distinct faunal regions and is divided by Wallace's line. Although it is possible that early kingfisher evolution straddled Wallace's line, the importance of this barrier in the biogeographic history of so many other groups indicates that Malesia may not be a cohesive biogeographic region in kingfisher evolution. Furthermore, the extensive archipelago between the Asian and Australian continental plates that constitutes much of Malesia did not exist until the early Miocene (Hall 1996), long after kingfishers first appeared in the Eocene fossil record of Europe and North America (Grande 1980, Houde and Olson 1988, Mourer-Chauviré 1995). Thus, lumping portions of the Asian and Australian tropics into a single region may obscure early biogeographic patterns of kingfishers.

Todies and motmots, the sister group of kingfishers, live in Neotropical forests. Considering that maximum kingfisher diversity occurs in the Australian region, this might indicate a southern origin for these taxa. A close look at their current distribution and the fossil record indicates otherwise. Todies are currently restricted to Caribbean islands, and motmot diversity is centered in Central America; neither family is predominantly South American. Furthermore, the fossil record of both families is restricted to

Europe and North America (Olson 1976, Becker 1986, Mourer-Chauviré 1995). Consequently, it is likely that todies and motmots are of northern origin, that they have become extinct in the Old World, and that their current distribution is relictual (Chapman 1923, Feduccia 1977). Thus, the sister group of kingfishers is most likely Laurasian, rather than Neotropical.

Diversity patterns within the kingfishers are also deceptive. Although the Australian region supports the highest kingfisher diversity, Australian taxa are not basal in the phylogeny. The basal subfamily in the kingfisher radiation is the Alcedininae, and the few Australian alcedinines (represented in this study by *Alcedo azurea* and *Ceyx lepidus*) are embedded among African and Asian taxa. Almost all the species endemic to the Australian region and Pacific islands are dacelonine, but within that subfamily two of the three basal lineages are entirely Asian and African. The third lineage contains all the diverse Australian and Pacific island taxa; yet, even here, major radiations are sister to Asian clades (e.g. *Actenoides* sister to *Syma–Todiramphus*). Consequently, the incredible kingfisher diversity east of Wallace's line is likely the result of a few relatively recent radiations from southern Asia. Fry (1980b) may be correct in surmising that the diversity of the dacelonine radiation was caused by the complex geography of Malesia in the Miocene, but the phylogeny indicates that crown-clade kingfishers had a substantial biogeographic history before that time.

Taxon sampling within the Cerylinae is relatively complete, lacking only Crested Kingfisher (*Megaceryle lugubris*) of Asia. It has been suggested that this subfamily arose as an offshoot of the Alcedininae as recently as the Miocene or Pliocene (Fry et al. 1992, Woodall 2001). In that scenario, an ancestor invaded the New World from Asia and subsequently split into the *Megaceryle* and *Chloroceryle* lineages. Extant Old World taxa are the result of re-invasions by the two lineages in the Pliocene or Pleistocene. Although this hypothesis correctly identifies the early split into *Megaceryle* and *Ceryle–Chloroceryle* lineages, the timing and direction of invasions is doubtful. In light of the phylogeny, initial diversification within the Old World and subsequent invasion of the New World is more parsimonious, requiring only two New World–Old World dispersal events. Divergence dates have not been estimated for the kingfisher phylogeny, owing to a lack of calibration points from the fossil record. However, branch-length comparisons and raw sequence-divergence between New and Old World clades of the Cerylinae are quite high (ND2: 10–17% *P*-distance, 14–40% ML distance) for an origin within the past 5 million years.

Implications for Taxonomy and Kingfisher Evolution

Even with the limitations imposed by incomplete taxon sampling, the current data clearly support or refute several proposed generic allocations. Inclusion of the New World species *alcyon* and *torquatus* within *Megaceryle* (Woodall 2001, Dickinson 2003), rather than *Ceryle* (Forshaw 1983), is strongly supported. *Ceryle rudis* has no close living relatives, but is closest to *Chloroceryle* rather than *Megaceryle*. The only missing species, *M. lugubris*, is assumed to group with the other *Megaceryle* species; its similarities in plumage and morphology to *M. alcyon*, *M. torquata*, and *M. maxima* led Fry (1980a) to consider them all part of a superspecies.

Within the Daceloninae, the data clearly demonstrate that *Halcyon* (*sensu* Forshaw 1983, Fry et al. 1992) is not a natural group. At least two genera are necessary to accommodate the traditional *Halcyon* species. The decision to split *Syma* off from *Todiramphus* and *Pelargopsis* off from *Halcyon* (Woodall 2001, Dickinson 2003) is not mandated by the phylogenetic results, but could be maintained to account for the degree of difference between the proposed genera. Bell (1981) and Fry (1980a) suggested that *Melidora* might have affinities to *Tanysiptera*, but the data support a more recent common ancestor with *Dacelo* and *Clytoceyx*. It is apparent that *Lacedo pulchella* has no close living relatives, and the data do not support a close connection to *Dacelo*, as proposed by Fry (1980a), or to *Tanysiptera*, as proposed by Forshaw (1983). One data partition (ND2) places *Lacedo* with *Pelargopsis* and *Halcyon*, but that result is contradicted by the RAG-1 results, which place *Lacedo* as the basal branch in the subfamily.

Ceyx and *Alcedo*, as delimited in most modern taxonomic treatments, are not natural groups. Members of both genera are interspersed in multiple well-supported clades. Thus, feeding strategy, bill shape, and plumage characters

are phylogenetically misleading. For example, the Madagascar Pygmy Kingfisher (*C. madagascariensis*) resembles Asian *Ceyx* species in plumage (rufous back), diet (mostly insects), and bill shape (dorsoventrally flattened), yet it is sister to two fish-eating *Alcedo* species from Africa, a relationship suggested by Traylor (1960). If the traditional taxonomic characters are misleading, what then are the common threads, aside from shared nucleotides, that unite clades? To some extent, the alcedinines are more cohesive geographically than previously believed. Traditional taxonomy indicated close relationships among species from different regions, but the phylogeny places many of those species into geographic groupings. For example, Azure Kingfisher (*A. azurea*) of Australasia is sister to Asian (*C. erithaca*) and Australasian (*C. lepidus*) species, rather than to other *Alcedo* taxa. Likewise, the Madagascar Pygmy Kingfisher (*C. madagascariensis*) is actually related to an African *Alcedo* clade, rather than the Asian *Ceyx* with which it had been grouped. Further evaluation of taxonomy, biogeography, and evolution in this subfamily awaits a phylogenetic hypothesis with complete taxon sampling (R. G. Moyle et al. unpubl. data).

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