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THE PHYLOGENETIC RELATIONSHIPS OF THE ENDEMIC GENERA OF AUSTRALO-PAPUAN HAWKS

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ABSTRACT.—Six genera of accipitrids (*Erythrotriorchis*, *Hamirostra*, *Harpyopsis*, *Henicopernis*, *Lophoictinia*, and *Megatriorchis*), composed of a total of eight species, are endemic to the Australo-Papuan region. Traditionally, these were assigned to four subfamilies in the Accipitridae; however, a recent hypothesis suggested they together comprise an endemic radiation of closely related genera and species. We investigated these alternatives using phylogenetic analysis of DNA sequences of the slowly evolving nuclear RAG-1 exon. Bootstrapped maximum likelihood trees and a permutation likelihood ratio test provide robust evidence that these genera represent four clades placed in three divergent higher taxa of accipitrids: (1) *Hamirostra*, *Henicopernis*, and *Lophoictinia* comprise a monophyletic clade of pernine kites, (2) *Harpyopsis* is a harpy eagle, and (3) *Erythrotriorchis* and *Megatriorchis* represent two unrelated clades of accipiters. Parsimony and Bayesian analyses confirmed these results. The hypothesis that the six genera are monophyletic was firmly rejected. The data are consistent with a southeast Asian or Australo-Papuan origin for each of the four clades. These six genera each include only one or two species and are closely related to other monotypic taxa; an efficient classification would place most of these genera in synonymy.

KEY WORDS: Erythrotriorchis; Hamirostra; Harpyopsis; Henicopernis; Lophoictinia; Megatriorchis; *phylogeny*.

RELACIONES FILOGENÉTICAS DE GÉNEROS ENDÉMICOS DE HALCONES AUSTRALO-PAPUANOS

RESUMEN.—Seis géneros de accipítridos (*Erythrotriorchis*, *Hamirostra*, *Harpyopsis*, *Henicopernis*, *Lophoictinia* y *Megatriorchis*), compuestos por un total de ocho especies, son endémicos de la región Australo-Papuana. Tradicionalmente, estos géneros fueron asignados a cuatro subfamilias en Accipitridae; sin embargo, hipótesis recientes sugirieron que juntos comprenden una radiación endémica de géneros y especies relacionados cercanamente. Investigamos estas alternativas usando análisis filogenéticos de secuencias de ADN del exón nuclear de evolución lenta RAG-1. Árboles de máxima probabilidad de bootstrap y una prueba de radio de probabilidad de permutación proporcionaron evidencia robusta de que estos géneros representan cuatro clados ubicados en tres taxa divergentes más elevados de accipítridos: (1) *Hamirostra*, *Henicopernis* y *Lophoictinia* comprenden un clado monofilético de milanos perninos, (2) *Harpyopsis* es un águila harpía y (3) *Erythrotriorchis* y *Megatriorchis* representan dos clados de accipítridos no relacionados. Análisis de parsimonia y bayesianos confirmaron estos resultados. La hipótesis de que los seis géneros son monofiléticos fue firmemente rechazada. Los datos son consistentes con un origen del sureste asiático o Australo-Papuano para cada uno de los cuatro clados. Estos seis géneros sólo incluyen una o dos especies y están cercanamente relacionados con otros taxa monotípicos; una clasificación eficiente ubicaría a la mayoría de estos géneros en sinonimia.

[Traducción del equipo editorial]

The Australo-Papuan (Sahul) region possesses a high degree of endemism in birds and other elements of its biota, due in part to its long isolation from other major landmasses. In some cases these may date to the breakup of the Gondwanan supercontinent and many millions of years of isolation. Subsequently, a complex combination of plate collisions and the accretion of many terranes with differing historical origins have contributed to the unique biotic assemblage found in the region today (Hall 2001). More recently, the region was invaded by organisms from elsewhere, particularly southeast Asia (e.g., Schodde and Mason 1999). Nevertheless, a high degree of regional endemism remains, particularly noticeable given the short distance to Indo-Malayan influences, and is reflected in biogeographic

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generalizations such as Wallace's Line (Brown and Lomolino 1998).

In many instances, however, it is not clear whether organisms in the Australian region are closely related and the product of local divergence, representing endemic radiations, or are the result of multiple independent invasions from the north and west. Resolving such cases requires phylogenetic analyses of the groups to determine whether the endemics of the Australian region comprise monophyletic clades.

One long-standing enigma has been the relationships of six genera of hawks, comprising eight species (e.g., Dickinson and Remsen 2013), restricted to the Australo-Papuan region. These include the monotypic genera *Hamirostra*, *Harpyopsis*, *Lophoictinia*, and *Megatriorchis*, together with *Erythrotriorchis* and *Henicopernis*, both of which contain two species. Although traditional treatments, such as that of Peters (1931), placed these genera in four diverse subfamilies within the Accipitridae, Amadon (1978) regarded their relationships as problematic. He pointed out, for example, that *Erythrotriorchis* and *Megatriorchis* had tail:wing ratios inconsistent with those of typical accipiters, and that although *Lophoictinia* looked like a milvine kite, *Hamirostra* had buteonine proportions. Nevertheless, Stresemann and Amadon (1979) adopted a sequence similar to that used by Peters (1931), and subsumed *Erythrotriorchis* and *Megatriorchis* into *Accipiter*, placed *Harpyopsis* with the large harpy (*Harpia*, *Morphnus*) and monkey-eating (*Pithecophaga*) eagles, put *Henicopernis* adjacent to the Eurasian honey-buzzards (*Pernis*), and placed both *Hamirostra* and *Lophoictinia* with the milvine kites. Later, Amadon and Bull (1988) published a similar classification. However, these assemblages were not supported by any phylogenetic analyses, and first Olsen et al. (1993), and later Schodde (1993), suggested that the six genera might comprise representatives of an ancient Australian raptor fauna. Subsequently, Thiollay (1994) and Olsen (1995) postulated that the six genera actually might represent a single clade, possibly allied to *Accipiter*: a regional radiation of diverse accipitrids.

Gamauf and Haring (2004) investigated the relationships of *Pernis* and *Henicopernis*, but, using only 382 bp of the rapidly evolving mitochondrial *cyt-b* gene, they were unable to ascertain the relationships between the two. Griffiths et al. (2007) used DNA sequences from a nuclear protein-coding gene, RAG-1, to investigate the relationships among many genera of the Accipitridae. However, because those authors limited their survey to species for which freshly preserved tissue samples were available, they were only able to examine the relationships of three of these Austral endemic genera. They reported that *Harpyopsis* was close to the great or harpy eagles, as Amadon and Bull (1988) had suggested, but *Hamirostra* and *Lophoictinia* formed a clade restricted to Australia. Lerner and Mindell (2005) found the same relationships of these three genera using DNA sequences from two mitochondrial genes and a nuclear intron; they also did not have access to the remaining three genera and five species. Thus, were *Erythrotriorchis*, *Henicopernis*, and *Megatriorchis* found to be related to *Hamirostra* and *Lophoictinia* using DNA, there would be evidence for a significant radiation of raptors restricted to the Australia-New Guinea region, as suggested by Olsen (1995) on the basis of egg morphology.

Here we report on our investigation of the phylogenetic relationships of all the genera and species of Australia and New Guinea endemic hawks, using slowly evolving nuclear DNA sequences from the RAG-1 exon. This gene previously has proved useful for phylogenetic inference in hawks (Griffiths et al. 2007), falcons (Griffiths et al. 2004), and other nonpasserine birds (Groth and Barrowclough 1999); more generally, it has provided the basis for our current classification of all passerine birds (Barker et al. 2002, Barker et al. 2004).

METHODS

RAG-1 sequences of *Harpyopsis novaeguineae* from Papua-New Guinea and *Hamirostra melanosternon* and *Lophoictinia isura* from Australia were reported by Griffiths et al. (2007). We were able to obtain recent tissue samples of *Henicopernis longicauda* and *Megatriorchis doriae* from Papua-New Guinea; tissue samples of *Henicopernis infuscatus* and the two species of *Erythrotriorchis* were not available, so we extracted DNA from toe pads from specimens of these species in the collections of the American Museum of Natural History, the Bishop Museum, and the Western Australian Museum. In Griffiths et al. (2007), a single species of *Circus* (*C. aeruginosus*) had been sequenced; for this study, we sequenced two additional species (*C. assimilis* and *C. cyaneus*) to improve our understanding of the relationship between *Accipiter* and *Circus*. The source and voucher information for the new taxa used in this study are provided in the Appendix.

DNA was extracted using standard procedures; previously described RAG-1 primers were used to amplify and sequence the exon from the fresh

tissues (Groth and Barrowclough 1999). Because the DNA from the toe pads was old, fragmented, and of poor quality, a novel set of 33 closely spaced RAG-1 primers (available from the authors) were designed to target the 5′ end of the gene from hawks. Previously obtained accipitrid RAG-1 sequences were used for this purpose (Griffiths et al. 2007). The labeled sequenced fragments of DNA were run out on an ABI 3730xl DNA Analyzer; contigs were assembled and aligned by eye using Sequencher software.

We examined the sequences for potential quality problems by checking for unexpected stop codons, indels not a multiple of three base pairs, and sequences with more than two chromatographic peaks at any single site. We checked sequences for contamination by foreign PCR product by examining the divergence between each pair of sequences using a sliding 300 bp window; unexpectedly similar or abnormally divergent pairs of sequences were flagged for further examination. We also checked for contamination by foreign PCR product by examining the distribution of heterozygosity among taxa for outliers. We examined the sequences for base composition heterogeneity among taxa by comparing the proportion of third codon positions that were either cytosine or guanine to those that were adenine or thymine.

The new sequences were added to the prior (Griffiths et al. 2007) RAG-1 dataset; this included sequences from four outgroups: Turkey Vulture (*Cathartes aura*), Prairie Falcon (*Falco mexicanus*), Gray Parrot (*Psittacus erithacus*), and Tawny Owl (*Strix aluco*). We inferred phylogenetic trees using likelihood methods using PAUP* version 4.0b10 (Swofford et al. 1996, Swofford 2001); for the initial analyses, all three amino acid codon positions were treated as a single data partition. Because several of the new sequences were obtained from toe pads and consequently were shorter than the sequences used in Griffiths et al. (2007), we treated nonsequenced base pairs, as well as gaps, as missing; multistate sites within taxa were treated as uninformative. We used the AIC criteria in Modeltest version 3.06 (Posada and Crandall 1998) to choose an appropriate initial likelihood model and set of parameter estimates for the evolution of the sequences. After an initial TBR heuristic search, starting with a neighbor-joining tree, we reestimated the likelihood parameters on the resulting maximum-likelihood tree and began a subsequent search for a new maximum-likelihood tree consistent with the reestimated parameters; this process was iterated until the resulting tree was consistent with the starting parameters (Sullivan et al. 2005). We used a χ^2 test to determine whether the maximum likelihood tree for these hawks was consistent with a clock-like model of DNA substitution (Huelsenbeck and Crandall 1997, Posada and Crandall 1998). We conducted a likelihood bootstrap procedure (1000 nonparametric replicates) using RAxML version 7.3.2 (Stamatakis 2006).

We conducted several additional phylogenetic analyses to confirm the standard maximum likelihood results; first, we performed a second maximum likelihood bootstrap (1000 replicates) analysis using RAxML in which first, second, and third codon positions were treated as separate partitions, each with its own model of substitution (three partition analyses). Second, we performed a parsimony bootstrap (100 replicates) analysis using PAUP* with five random additions of taxa and SPR branch-swapping within each replicate. Finally, we performed a Bayesian reconstruction using the program MrBAYES version 3.2.1 (Ronquist et al. 2012) for 10 million generations with 25% burn-in and chain-sampling every 1000 generations. A preliminary assessment of the sensitivity of the analysis to several branch length priors was conducted (Marshall et al. 2006). Convergence of chains was assessed using comparisons of log-likelihood scores and cumulative posterior probabilities.

We used a standard permutation procedure (SOWH-test) with a likelihood ratio test to determine whether the maximum likelihood topology obtained with our data was statistically superior to the likelihood of the hypothesis that all eight species in the six endemic genera formed a monophyletic clade (Hillis et al. 1996, Swofford et al. 1996). We compared the likelihood score of the best unconstrained tree given our data to that of the score of the best tree obtained subject to the constraint that all the members of the six endemic genera formed a clade. We generated 100 simulated parametric datasets using parameters obtained from the best constrained tree using SEQ-GEN vers. 1.3.2 (Rambaut and Grassly 1997). We obtained a null distribution of likelihood differences between constrained and unconstrained scores by comparing the differences between the likelihood of the best constrained tree and that of the best tree obtained in a new, unconstrained, TBR heuristic search for each of the 100 simulated datasets (Goldman et al. 2000).

RESULTS

We obtained 2872 bp of RAG-1 sequence from the fresh tissues of *Megatriorchis doriae*, *Circus assimilis*,

and *C. cyaneus*, and 2869 bp from *Henicopernis longicauda*; from the toe pad samples we obtained 714 bp from *Erythrotriorchis buergersi* and *E. radiatus*, and 711 bp from *Henicopernis infuscatus*. The sequences were easily aligned with the prior accipitrid RAG-1 sequences; a single three basepair deletion was required to align the two species of *Henicopernis* with the other samples. That single codon deletion coincided in position with a deletion previously described for *Hamirostra* and *Lophoictinia*. The initial (5′) basepair for all the new sequences corresponded to position 84 of the published chicken (*Gallus gallus*) RAG-1 sequence (GenBank M58530: Carlson et al. 1991). The new sequences have been deposited in GenBank; the accession numbers are provided in the Appendix.

The new sequences had base and amino acid compositions consistent with prior accipitrid RAG-1 sequences. No stop codons occurred in the aligned sequences and none of the sequences was unexpectedly similar to or divergent from any other. The patterns of heterozygosity provided no suggestion of contamination in the new sequences, including those obtained from toe pad samples; the maximum heterozygosity among the new samples was 0.003, for *E. radiatus*.

The AIC criterion in Modeltest suggested that GTR + Γ + I (general time reversal base pair substitutions with Γ-distributed evolutionary rates plus invariant sites) was the appropriate model for nucleotide substitution for this exon. We fixed the AIC estimated parameters for an initial heuristic likelihood search. The tree resulting from this first search was then used to reestimate the parameters for the model and start a second search. A tree with a superior likelihood score was not found; thus, the tree was consistent with its parameters (Sullivan et al. 2005). We computed the likelihood of this tree with and without the assumption of a molecular clock; clock-like substitution rates were rejected (χ^2 = 225.4, df = 70, $P < 0.005$).

The phylogenetic tree based on this single likelihood partition is shown in Fig. 1. It is quite similar to the tree reported by Griffiths et al. (2007) and is largely bifurcating with only a few multifurcations. All phylogenetic analyses placed the Australo-Papuan endemic genera in four positions on the tree; First, *Hamirostra*, *Lophoictinia*, and the two species of *Henicopernis* formed a clade embedded within the pernine kites; however, within the pernines, they were not sister to the honey-buzzard (*Pernis*). These four species also shared the only (3 bp) deletion found among the accipitrid sequences. Second, *Harpyopsis* was sister to the large Neotropical harpy eagles (*Harpia* and *Morphnus*). Third, the two species of *Erythrotriorchis* were sister to each other and in turn sister to several accipiters. Finally, *Megatriorchis* was sister to the clade of harriers (*Circus*) and that larger clade was sister to the Eurasian Sparrowhawk (*Accipiter nisus*).

The statistical bootstrap and Bayesian posterior support values for the positions of the six enigmatic genera, in the various phylogenetic analyses, are provided in Table 1. Support for a *Hamirostra*, *Henicopernis*, *Lophoictinia* clade within pernines was uniformly greater than 90%. The position of *Harpyopsis* with the harpy eagles and *Macheiramphus*, while present in all the shortest and most likely trees, had little bootstrap support, but a Bayesian posterior probability of 0.94. The relationships of *Megatriorchis* and *Erythrotriorchis* with accipiters and harriers had bootstrap support greater than 80% and a Bayesian posterior of 1.0.

The SOWH permutation likelihood ratio test provided robust evidence that the six genera of Australo-Papuan endemics were not members of a monophyletic clade. The difference between the log-likelihoods of the constrained and maximum likelihood trees, $\delta = 192.84$, exceeded the entire distribution of 100 randomized parametric log-likelihood scores by a multiple of more than nine; thus, $P << 0.05$ for a monophyletic clade of endemics.

DISCUSSION

Phylogeny. There was no support for a monophyletic clade of all the endemic genera of Australo-Papuan hawks, as suggested by Olsen et al. (1993), Thiollay (1994), and Olsen (1995). Rather, with varying degrees of bootstrap and Bayesian support (Table 1), our data suggest the six genera belong to four clades. However, three of the genera and four of the species do form a clade within the pernine kites, and two other genera are closely associated with the genus *Accipiter*.

Thus, our results are generally in agreement with the opinions of Amadon (1978) and Amadon in Stresemann and Amadon (1979), who placed *Henicopernis* with the pernine kites; *Harpyopsis* with the two genera of harpies; and synonymized *Erythrotriorchis* and *Megatriorchis* with *Accipiter*. Other opinions expressed by Amadon in the Stresemann and Amadon (1979) classification have not withstood the test of time, and it is now clear that *Hamirostra* and *Lophoictinia* represent pernine, rather than

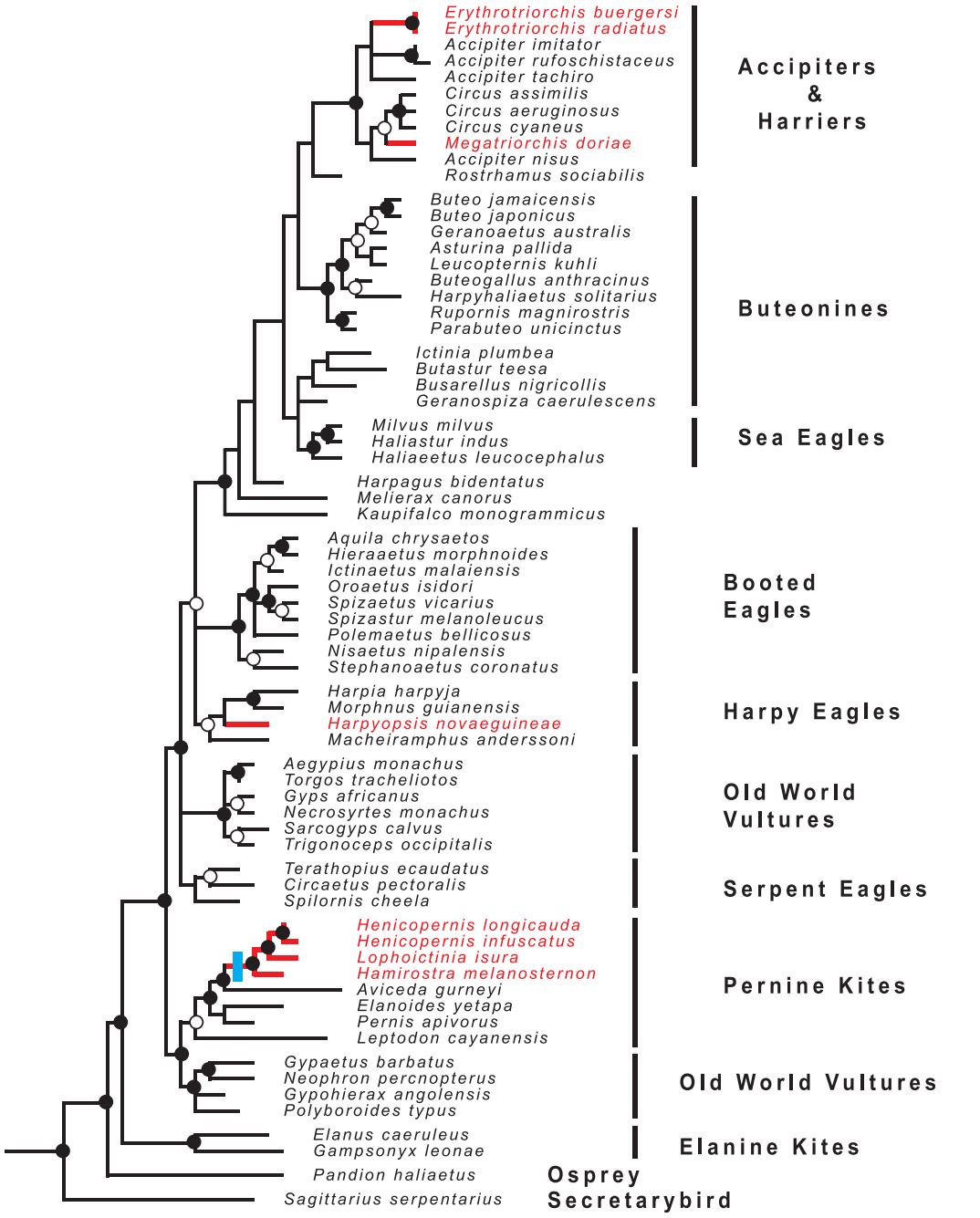

Figure 1. Maximum likelihood (single partition) phylogenetic tree for RAG-1 sequences for 68 species of accipitrids. Tree was rooted with four outgroups (not shown); branch lengths are drawn to scale. Positions of eight species in six genera endemic to the Australo-Papuan region are shown in red; position of a three basepair deletion delimiting four species of pernine kites is indicated by vertical blue bar. Likelihood bootstrap ranges are indicated for nodes with support of 50% or greater (open dots) and 80% or greater (solid dots). Some data used to infer this tree were originally presented in Griffiths et al. (2007).

Table 1. Statistical support for important clades of hawks under alternate phylogenetic analyses.

CLADE	LIKELIHOOD BOOTSTRAP (1 PARTITION)	LIKELIHOOD BOOTSTRAP (3 PARTITIONS)	PARSIMONY BOOTSTRAP	BAYESIAN POSTERIOR PROBABILITY
Hamirostra, Lophoictinia, and *Henicopernis*	91%	100%	100%	1.00
Hamirostra, Lophoictinia, and *Henicopernis* with Pernine kites	97%	98%	91%	1.00
Harpyopsis, Macheiramphus with harpy eagles	51%	52%	<50%	0.94
Megatriorchis and *Circus*	63%	64%	67%	1.00
Erythrotriorchis and *Megatriorchis* with Accipiters	90%	86%	82%	1.00

milvine, kites. The latter result was also discovered by Olson (1982).

Biogeography. The six endemic genera of Australo-Papuan hawks are not all closely related and thus have multiple geographic histories. The *Hamirostra-Henicopernis-Lophoictinia* clade is sister to *Aviceda*, which has a paleotropical distribution from Africa east to Australasia. *Harpyopsis* is sister to two South American genera; all three are sister to *Macheiramphus* which is also paleotropical in distribution (Africa, southeast Asia to New Guinea). *Erythrotriorchis* appears to be sister to some Australo-Papuan accipiters. *Megatriorchis* apparently is sister to the nearly cosmopolitan harriers, and that clade in turn is sister to a widespread Eurasian *Accipiter* group (*A. nisus*). The association of harriers with *Megatriorchis* suggests that an Australo-Papuan origin of *Circus* is possible. At any rate, all six endemic Australo-Papuan genera of accipitrids, although not forming a monophyletic clade, do appear to have their origins in either southeast Asia or the Australo-Papuan region.

Taxonomy. Recent classifications (Stresemann and Amadon 1979, Dickinson and Remsen 2013) use three genera (*Hamirostra*, *Henicopernis*, and *Lophoictinia*) for a monophyletic clade of four species of closely related birds. Aside from differences expected among species in plumage, these genera differ in characters associated with their foraging activities, such as wing-tail ratios (Brown and Amadon 1968); however, basing genera on such characters results in a classification that emphasizes difference at the expense of hierarchy and so has little predictive value. A more useful classification would unite these four species in *Hamirostra*, the name with priority (Dickinson and Remsen 2013), and, by using a standard sequencing convention, convey hierarchy of relationship.

Our results and those of Lerner and Mindell (2005) and Griffiths et al. (2007) all indicate that *Harpyopsis* of New Guinea forms a clade with the Neotropical eagles *Harpia* and *Morphnus*; this relationship is also concordant with the sequence in traditional classifications (e.g., Stresemann and Amadon 1979). Again, three genera for three species add unnecessary complexity to the classification while obscuring hierarchy: three species in a single genus provides the same quantity of phylogenetic information as three monotypic genera, but with fewer names. *Harpia* Vieillot (April 1816) has priority over *Morphnus* Dumont de Sainte Croix (October 1816) and should be used for these three taxa. *Macheiramphus* probably should also be placed in this same genus.

The genera *Erythrotriorchis* and *Megatriorchis*, along with all the harriers (*Circus*), render the large genus *Accipiter* paraphyletic. *Accipiter* is currently the most speciose genus in the family Accipitridae with 46 species (Dickinson and Remsen 2013). Adding the additional 14 species in *Circus* plus the three in *Erythrotriorchis* and *Megatriorchis* to that 46 would create a single genus comprised of more than a quarter of all accipitrids. It would seem preferable to divide the latter into a few smaller genera, while incorporating *Circus*, *Erythrotriorchis*, and *Megatriorchis* into the new scheme. Unfortunately, this cannot be accomplished until we have a complete, species-level, phylogeny of *Accipiter*.

Future research. Many remaining and long-standing problems in accipitrid phylogeny, biogeography, and classification can only be resolved with a complete or nearly complete phylogeny for the large genus *Accipiter*. These birds are closely related and mitochondrial sequences are consequently appropriate for the research; the preliminary results of

Breman et al. (2013) suggest that as little as a kilobase of mtDNA sequence might be adequate for this purpose.

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Appendix. Specimen data.

SPECIES	MUSEUM[a]	GEOGRAPHICAL SOURCE	NO. BASES	GENBANK ACCESSION
Circus assimilis	WAMA 35959	Australia: WA	2872	KF437492
C. cyaneus	AMNH DOT13711	USA: NJ	2872	KF437491
Erythrotriorchis buergersi	BPBM 104612	Papua New Guinea	714	KF437488
E. radiatus	WAMA 14803	Australia: Qld	714	KF437489
Henicopernis infuscatus	AMNH 333700	New Britain	711	KF437487
H. longicauda	KUNHM 6902	Papua New Guinea	2869	KF437486
Megatriorchis doriae	KUNHM 6924	Papua New Guinea	2872	KF437490

[a] AMNH: American Museum of Natural History; BPBM: Bishop Museum; KUNHM: University of Kansas Natural History Museum; WAMA: Western Australian Museum.