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MOLECULAR PHYLOGENETICS OF THE BUTEONINE BIRDS OF PREY (ACCIPITRIDAE)

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ABSTRACT.—**Phylogenetic relationships among birds of prey in the subfamily Buteoninae are not fully established but are of particular interest because the Buteoninae constitute one of the largest accipitrid subgroups and include multiple species of conservation concern. Genera previously included within the Buteoninae are *Buteo*, *Leucopternis*, *Buteogallus*, *Harpyhaliaetus*, *Busarellus*, *Parabuteo*, *Geranoaetus*, *Geranospiza*, *Ictinia*, *Rostrhamus*, *Kaupifalco*, and *Butastur*. We analyzed representatives from all buteonine genera and most non-*Buteo* (i.e., "sub-buteo") species with >3,000 bases of nuclear and mitochondrial DNA and found non-monophyly for the nominal genera *Buteo*, *Buteogallus*, and *Leucopternis*. The Old World Lizard Buzzard (*Kaupifalco monogrammicus*) is not closely related to buteonine taxa but is sister to goshawks in the genera *Melierax*, *Micronisus*, and *Urotriorchis*. Another Old World genus, *Butastur*, is sister to the clade including all other buteonine genera mentioned above. Investigation of several "superspecies" complexes within the genus *Leucopternis* revealed non-monophyly for the four subspecies of White Hawk (*L. albicollis*). On the basis of mitochondrial data, *L. a. albicollis* forms a clade with *L. polionotus*, whereas *L. a. costaricensis*, *L. a. ghiesbreghti*, and *L. a. williaminae* form a clade with *L. occidentalis*. Among taxa included as outgroups, we found two species in the genus *Circus* to be clearly nested within a clade of *Accipiter* spp. *Received 12 August 2006, accepted 31 May 2007.*

Key words: **Accipitridae, avian systematics, beta-fibrinogen intron 7, Buteoninae, mitochondrial DNA, molecular evolution,** phylogenetics.

Filogenética Molecular de las Aves de Presa Buteoninas (Accipitridae)

RESUMEN.—**Las relaciones filogenéticas entre las aves de presa de la subfamilia Buteoninae no están completamente establecidas, pero son de particular interés porque éste es uno de los grupos más grandes de accipítridos, e incluye varias especies de interés en conservación. Los géneros incluidos previamente en Buteoninae son *Buteo*, *Leucopternis*, *Buteogallus*, *Harpyhaliaetus*, *Busarellus*, *Parabuteo*, *Geranoaetus*, *Geranospiza*, *Ictinia*, *Rostrhamus*, *Kaupifalco* y *Butastur*. Analizamos representantes de todos los géneros de buteoninos y la mayoría de especies que no pertenecen al género *Buteo* (i.e., "sub-buteos") con más de 3,000 bases de ADN nuclear y mitocondrial, y documentamos la no monofilia del género nominal *Buteo*, de *Buteogallus* y de *Leucopternis*. La especie del Viejo Mundo *Kaupifalco monogrammicus* no está cercanamente emparentada con taxones buteoninos, y forma el grupo hermano del clado formado por los géneros *Melierax*, *Micronisus* y *Urotriorchis*. Otro género del Viejo Mundo, *Butastur*, es hermano del clado que incluye todos los demás géneros de buteoninos antes mencionados. La investigación de varios complejos de "superespecies" dentro del género *Leucopternis* reveló que las cuatro subespecies de *L. albicollis* no forman un grupo monofilético. Con base en los datos mitocondriales, *L. a. albicollis* forma un clado con *L. polionotus*, mientras que *L. a. costaricensis*, *L. a. ghiesbreghti* y *L. a. williaminae* forman un clado con *L. occidentalis*. Entre los taxones incluidos como grupos externos, encontramos que dos especies del género *Circus* están claramente anidadas dentro de un clado formado por especies de *Accipiter*.**

ONE OF THE largest groups in the family Accipitridae, the subfamily Buteoninae includes 24 "sub-buteo" species (Amadon 1982), two genera of kites (Lerner and Mindell 2005), and 25–28 species in the genus *Buteo* (Ferguson-Lees and Christie 2001, Dickinson 2003). The Buteoninae are of particular interest, because 11 species are of conservation concern (IUCN 2007), with one critically endangered species (*Buteo ridgwayi*) and two endangered species (*Leucopternis occidentalis* and *Harpyhaliaetus coronatus*). This subfamily also has included the sea and booted eagles (Grossman and Hamlet 1964) or the sea, booted, and harpy eagles (Friedmann 1950). Our

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recent molecular analysis, however, showed that the sea, booted, and harpy eagles form monophyletic groups separate from a clade of 10 sub-buteos, two kites, and three species in the genus *Buteo* (Lerner and Mindell 2005). Therefore, we do not consider any of the eagle groups members of Buteoninae. For the purposes of the present study, we consider Buteoninae to comprise *Buteo* and the nine sub-buteo and two kite genera previously proposed as, or found to be, close relatives of *Buteo*: New World hawks *Leucopternis*, *Buteogallus* (including *Heterospizias*), *Harpyhaliaetus*, *Busarellus*, *Parabuteo*, *Geranoaetus*, *Asturina* (now *Buteo*), and *Geranospiza*; Old World hawks *Kaupifalco* and *Butastur* (Amadon 1982); and the kites *Ictinia* and *Rostrhamus* (Lerner and Mindell 2005).

Although polyphyly of the sub-buteo group with respect to *Buteo* has long been suspected, only recently has it been shown that the genera *Buteo*, *Leucopternis*, and *Buteogallus* are not monophyletic with respect to each other (Riesing et al. 2003, Lerner and Mindell 2005, do Amaral et al. 2006). The full extent of polyphyletic relationships in Buteoninae is not known, because not all nominal species and subspecies have been included in a single analysis. Furthermore, previous analyses have not tested phylogenetic relationships in the Buteoninae in the context of the other major accipitrid clades. In particular, the placement of the Lizard Buzzard (*Kaupifalco monogrammicus*), Black-collared Hawk (*Busarellus nigricollis*), and genus *Butastur* remains to be assessed with molecular data in the broader context of the Accipitridae. The three species of *Butastur* have not previously been included in peer-reviewed analyses of molecular data sets. Neither *Kaupifalco* nor *Busarellus* formed close sister relationships with three other sub-buteo genera, 25 *Buteo* species, a booted eagle, and an accipiter in a study by Riesing et al. (2003) using mitochondrial NADH dehydrogenase subunit 6 (ND6) and pseudo-control region sequences. With a phylogeny generated from 191 osteological characters for 44 accipitrid taxa, Holdaway (1994) did not find a close relationship between *Kaupifalco* and any other accipitrid species. In the same study, *Busarellus* was sister to booted eagles *Hieraaetus* and *Polemaetus*, though nodal support values were not presented for the phylogeny.

Species status has been questioned for taxa in the subbuteonine genera *Buteogallus* (*B. anthracinus*, *B. subtilis*, and *B. aequinoctialis*) and *Leucopternis* (*L. schistaceus* and *L. plumbeus*; *L. kuhli* and *L. melanops*; and *L. albicollis*, *L. occidentalis*, and *L. polionotus*) where widespread taxa occupying similar niches have been divided into multiple subspecies or separate species without conclusive evidence one way or the other (Amadon 1982). A recent mitochondrial phylogeny found sister relationships for *L. kuhli*, *L. melanops*, and *L. albicollis*, and for *L. occidentalis* and *L. polionotus*, but not for *L. schistaceus* and *L. plumbeus* (do Amaral et al. 2006). Still, the other questioned groups in *Leucopternis* and *Buteogallus* have not been tested with molecular data, and further testing of most of these groups is needed to evaluate current taxonomy.

A comprehensive analysis of the phylogenetic relationships among proposed buteonine genera and species is needed to address remaining questions about the group's evolutionary history. With complete taxonomic representation of genera and nearly all nominal species and subspecies of sub-buteos, we address four questions. (1) Are *Kaupifalco*, *Busarellus*, and *Butastur* closely related to other proposed buteonines? (2) What are the sister relationships among genera in Buteoninae? (3) To what extent are the genera polyphyletic? (4) Is there evidence of genetic divergence and reciprocal monophyly to support current taxonomy for species and subspecies of *Buteogallus* and *Leucopternis*?

Methods

We sampled at least one individual of each nominal genus and species, and nearly all subspecies, of sub-buteos. Our final sampling included 107 individuals representing 45 out of 55 buteonine species, 26 out of 176 non-buteonine accipitrid species, and 2 non-accipitrid outgroup species (Ferguson-Lees and Christie 2001, Dickinson 2003; Table 1). To test monophyly of Buteoninae, we included representatives of each recognized subfamily or primary clade of Accipitridae. We also included multiple representatives of *Circus*, *Melierax*, and *Accipiter* and one sample each for two monotypic genera (*Micronisus* and *Urotriorchis*) on the basis of finding a close relationship between these taxa and *Kaupifalco* using published ND2 and cytochrome-*b* (cyt-*b*) sequences (Lerner and Mindell 2005). To incorporate more *Buteo* spp. in our analyses and to compare our results with two recent molecular studies, we also sequenced ND6 from 42 of our buteonine samples and analyzed them in a data set with previously published ND6 sequences from an additional eight *Buteo* spp., eight *Buteo* subspecies, and three non-*Buteo* buteonine subspecies (Riesing et al. 2003, do Amaral et al. 2006; Table 1). Samples were identified to the subspecies level on the basis of specimen labels or collection locality. Common names follow the 7th edition of the *Check-list of North American Birds* and its supplements (American Ornithologists' Union [AOU] 1988) or the *Handbook of Birds of the World* (Thiollay 1994).

Total genomic DNA was extracted from blood or other tissue of contemporary specimens or from toe-pad tissue of museum specimens using a DNeasy tissue extraction kit (Qiagen, Valencia, California). Lab work involving DNA extraction and polymerase chain reaction (PCR) set up from museum samples was conducted in a facility reserved for ancient DNA at the University of Michigan Museum of Zoology using protocols developed for ancient DNA, including multiple extraction and PCR controls (Cooper and Poinar 2000). The PCR amplifications were conducted using primers we designed for the Buteoninae, as well as published primer sequences for avian mitochondrial cyt-*b*, ND2, ND6, the nonrepetitive part of the pseudo-control region, and nuclear BF-I7 (primer sequences are reported in Table 2). These genomic regions were chosen for their ability to resolve both recent and deep divergences and their comparability with published sequences (Sorenson et al. 1999, Prychitko and Moore 2000, Riesing et al. 2003, Lerner and Mindell 2005, do Amaral et al. 2006). The PCR products were gel purified using a QIAquick gel extraction kit (Qiagen), directly sequenced from both strands with ABI big dye terminator chemistry, and resolved on an ABI 3730 automated sequencer. Sequences were viewed as chromatographs in SEQUENCHER, version 4.5 (Gene Codes, Ann Arbor, Michigan), and aligned by eye in BIOEDIT sequence alignment editor (Hall 1999).

Corrected sequence divergence (csd) estimates among taxa were calculated using Tamura-Nei distances (Tamura and Nei 1993) in MEGA, version 2.1 (Kumar et al. 2001). Empirical base frequencies and nucleotide composition bias were calculated in PAUP* (Swofford 2004). Substitution saturation plots were constructed by

Table 1. Sample localities and sources for samples used in each data set.

Taxon[a]	Sample ID, tissue type[c]	Data set			Locality	Source[f]
		mt[d]	mt + bf	ND6[e]		
Accipiter bicolor guttifer[b]	B18875, T	√	√		Department of Santa Cruz, Bolivia	LSUMZ
A. cooperii[b]	1757, T	√	√		Unknown, USA	KUNHM
A. gentilis atricapillus	T786; 233684, T	√			Michigan	UMMZ
A. gularis	16971, T	√			Saitama Prefecture, Japan	LSUMZ
A. c. cirrocephalus	O.65038, T	√	√		New South Wales, Australia	AMS
A. n. nisus	4501, T	√			Entracque, Italy	KUNH
A. r. rufiventris	PBC-19, T	√	√		South Africa	PBC
Aegypius monachus[b]	1903, B	√	√		Captive, unknown	DZ
Asturina nitida–Buteo nitidus pallida	B9624, T	√	√	√	Nicolás Suarez, Bolivia	LSUMZ
Busarellus nigricollis leucocephalus	105267, M	√		√	Paraguay	UMMZ
Butastur indicus	65937, M	√			Ishigaki, Japan	UMMZ
B. rufipennis	A1290, T	√	√	√	Gambia	UMMZ
B. teesa	209040, M	√			Kampur, India	UMMZ
Buteo albicaudatus hypospodius	20414 , T	√	√	√	Texas	MSB
B. albigula	31984, T	√	√	√	Quebrada Lanchal, Peru	LSUMZ
B. jamaicensis[b]	T-2797, T	√	√	√	North America	UMMZ
B. lagopus sanctijohannis	KU3450, T	√	√		Kansas	KUNHM
B. (Percnohierax) leucorrhous	P526 (113928), D	√	√	√	Cotopaxi, Ecuador	ZMUC
B. lineatus	B1344, T	√	√		Unknown	LSUMZ
B. (Rupornis) magnirostris occiduus[b]	B2862, T	√	√	√	Department of Loreto, Peru	LSUMZ
B. oreophilus trizonotatus	WOB-17, B	√	√		South Africa	WOB
B. platypterus platypterus	36, T	√	√	√	Michigan	UMMZ
B. poecilochrous	HUA-08, B	√	√	√	Peru	HUA
B. polyosoma polyosoma	B5135, T	√	√	√	Las Pampas, Peru	LSUMZ
B. regalis	KU1767, T	√	√	√	Kansas	KUNHM
B. rufinus	54, T	√	√		Unknown	UMMZ
B. rufofuscus	JBZ-5, B	√	√	√	South Africa	JBZ
B. swainsoni	11, T	√	√	√	Unknown	UMMZ
Buteogallus aequinoctialis	116637, M	√			Matapica, Surinam	UMMZ
B. a. anthracinus[b]	B28575, T	√	√		Fort Sherman, Panama	LSUMZ
B. meridionalis	155624, M	√	√	√	El Pao, Venezuela	UMMZ
B. subtilis bangsi	132087, M	√	√		Pigres, Costa Rica	UMMZ
B. urubitinga ridgwayi	132082, T	√	√	√	Catalina, Costa Rica	UMMZ
Busarellus nigricollis leucocephalus	105267, M	√	√	√	Riacho Negro, Paraguay	UMMZ
Chondrohierax uncinatus[b]	147, B	√	√		Grenada	TPF
Circaetus cinereus[b]	PNZ-8, B	√	√		South Africa	PNZ
C. gallicus[b]	363, T	√	√		Unknown	TAU
Circus aeruginosus[b]	353, T	√	√		Unknown	TAU
C. ranivorus[b]	PBC-6, B	√	√		South Africa	PBC
Elanus leucurus majusculus	24997, T	√	√		Texas	LSUMZ
Geranoaetus (Buteo) melanoleucus australis[b]	HUA-03, B	√	√	√	Peru	HUA
Geranospiza caerulescens	4226 HLK, T	√	√		Peru	LSUMZ
G. caerulescens flexipes[b]	KU3110, T	√	√		Paraguay	KUNHM
Haliaeetus leucocephalus[b]	N42, T	√	√		North America	UMRC
Haliastur sphenurus[b]	SAM NTMT651, ABTC-27746, T	√	√		Northern Territory, Australia	SAM
Hamirostra melanosternon[b]	1, F	√	√		Australia	AMS
Harpyhaliaetus coronatus[b]	101669, M	√			Amambay, Paraguay	UMMZ
H. solitarius solitarius[b]	HUA-18, B	√	√	√	Peru	HUA
Ictinia plumbea	KU2900, T	√	√		Paraguay	KUNHM
I. mississippiensis	B1581, T	√			Lousiana	KUNHM
Kaupifalco monogrammicus meridionalis	214672, M	√			Mozambique	UMMZ
Leptodon cayanensis[b]	139, T	√	√		Paraguay	KUNHM
Leucopternis albicollis albicollis	P1517 (114919), D	√	√	√	Tigre Playa Sucumbios, Ecuador	ZMUC
L. a. albicollis	HUA-10, B	√	√	√	Selva Central, Peru	HUA
L. a. albicollis	HUA-11, B	√	√	√	Selva Central, Peru	HUA
L. a. albicollis	HUA-12, B	√	√	√	El Huayco, Peru	HUA
L. a. albicollis	117773, M	√			Surinam	UMMZ
L. a. costaricensis	B2312, T	√	√	√	Panama	LSUMZ
L. a. costaricensis	WHH-024, B	√	√	√	Panama	TPF
L. a. costaricensis	56218, M	√			Barro Colorado Island, Panama	UMMZ

(Continued)

Table 1. Continued.

Taxon[a]	Sample ID, tissue type[c]	Data set: mt[d]	Data set: mt + bf	Data set: ND6[e]	Locality	Source[f]
L. a. costaricensis	85741, M	√			Nicaragua	UMMZ
L. a. costaricensis	199396, M	√			Honduras	UMMZ
L. a. ghiesbreghti	LM-0, B	√	√	√	Tikal National Park, Guatemala	TPF
L. a. ghiesbreghti	LM-1, B	√	√	√	Naranjol, Guatemala	TPF
L. a. ghiesbreghti	LM-2, B	√	√	√	Yucatan Peninsula	TPF
L. a. ghiesbreghti	210554, M	√			Oaxaca, Mexico	UMMZ
L. a. ghiesbreghti	94013, M	√			Chiapas, Mexico	UMMZ
L. a. williaminae	372349, M	√			Cesar, Colombia	USNM
L. a. williaminae (TYPE)	160392, M	√			Bolivar, Colombia	ANSP
L. kuhli[b]	B4598, T	√	√	√	South Rio Amazonas, Peru	LSUMZ
L. kuhli	101120, M	√			Brazil	FMNH
L. kuhli	297880, M	√			Peru	FMNH
L. kuhli	512908, M	√			Para, Brazil	USNH
L. lacernulatus	317243, M	√			Espirito Santo, Brazil	AMNH
L. melanops	B4493, T	√	√	√	Lower Rio Napo, Peru	LSUMZ
L. melanops[b]	B7167, T	√	√	√	Peru	LSUMZ
L. melanops	260137, M	√		√	Surinam	FMNH
L. melanops	471056, M	√			Caura, Venezuela	AMNH
L. occidentalis	BE5 HL, T	√	√	√	Unknown	UMMZ
L. occidentalis	B7805, T	√	√	√	Ecuador	LSUMZ
L. occidentalis	B7890, T	√	√	√	Ecuador	LSUMZ
L. occidentalis[b]	P1319 (114721), D	√	√	√	Esmeraldas, Ecuador	ZMUC
L. plumbeus	1939.12.9.295, M	√			Perme	BMNH
L. plumbeus	1955.6.n.20.2453, M	√	√		Ecuador	BMNH
L. polionotus	1895.4.1.510, M	√	√		Rio de Janeiro, Brazil	BMNH
L. polionotus	1887.5.1.558, M	√	√	√	Rio de Janeiro, Brazil	BMNH
L. polionotus	264120, M	√			Santa Catharina, Brazil	USNM
L. princeps zimmeri	B11751, T	√	√	√	Ecuador	LSUMZ
L. p. princeps	389182, M	√			Turrialba, Costa Rica	AMNH
L. schistaceus	B4946, T	√	√	√	S. Rio Amazonas, Peru	LSUMZ
L. schistaceus	217636, M	√			Bolivia	FMNH
L. semiplumbeus	B2291, T	√	√	√	Panama	LSUMZ
L. semiplumbeus	B2326, T	√	√	√	Panama	LSUMZ
L. semiplumbeus	35, T	√			Unknown	UMMZ
Lophoictinia isura[b]	0.7591, F	√			Australia	AMS
Melierax canorus	WOB-7, B	√	√		South Africa	WOB
M. poliopterus	MB-15, F	√			Unknown	TPF
Micronisus gabar gabar[b]	A765, T	√	√		Zimbabwe	UMMZ
Oroaetus isidori[b]	HUA-23, B	√	√		Peru	HUA
Parabuteo unicinctus harrisi[b]	40, T	√	√	√	Arizona	UMMZ
Rostrhamus s. sociablis[b]	KU5852, T	√	√		Guyana	KUNHM
Spizaetus ornatus vicarious[b]	B2267, T	√	√		Darien Province, Panama	LSUMZ
Torgos tracheliotus[b]	T-2046; 234705, T	√	√		South Africa	UMMZ
Urotriorchis macrourus	204470, M	√			Centre Sud, Cameroon	FMNH
Sagittarius serpentarius[b]	JBZ-12, B	√	√		South Africa	JBZ
Pandion haliaetus[b]	T-264; 225997, T	√	√		Michigan	UMMZ

[a] Scientific names in this table follow Dickinson (2003), with changes suggested by David and Gosselin (2002). Riesing et al.'s (2003) proposed generic changes are in parentheses after the traditional name.

[b] Sequence data from Lerner and Mindell (2005).

[c] Tissue type: blood (B), muscle or organ (T), museum toepad (M), feather (F), and DNA extract (D).

[d] GenBank sequence used in the mt data set: NC 003128.

[e] GenBank sequences used in the ND6 data set: NC 003128, AY213011, AY213034, AY213045, AY216914, AY216916–AY216919, AY216921–AY216924, 15990570, 29569538, 29569560; odd numbers 7407009–7407013, 7407023–7407029, 7407057–7407059, 76009021–76009069; even numbers 29569512–29569514, 29569518–29569524, 29569530–29569534, 29569542–29569554, 29569564–29569568, 29569572–29569576.

[f] Australian Museum Evolutionary Biology Unit, Sydney (AMS); American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, London (BMNH); Field Museum of Natural History, Chicago (FMNH); El Huayco, Lima (HUA); Johannesburg Zoo, Johannesburg (JBZ); Kansas University Natural History Museum, Lawrence (KUNHM); Louisiana State University Natural History Museum, Baton Rouge (LSUMZ); Museum of Southwestern Biology, Albuquerque, New Mexico (MSB); Predatory Bird Centre, Pietermaritzburg, South Africa (PBC); National Zoological Gardens of South Africa, Pretoria, (PNZ); South Australia Museum, Adelaide (SAM); Tel Aviv University Research Zoo, Tel Aviv (TAU); The Peregrine Fund, Boise, Idaho (TPF); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); University of Minnesota Raptor Center, Saint Paul (UMRC); National Museum of Natural History, Washington, D.C. (USNM); World of Birds Wildlife Sanctuary, Hout Bay, South Africa (WOB); Zoologisk Museum, Københavns Universitet, Copenhagen (ZMUC).

Table 2. Primer sequences used in the present study.

Region[a]	Primer ID	Sequence (5-3′)
Cyt-*b*[b]	H15370.leuc	GAT GTA GGG GAT RGC TGA GA
	L15287.leuc	CYC TYA TAG CAA CYG CCT TC
	H15599.leuc	AGG GAR AAG TAR GGR TGR AA
	L15508.leuc	CAC CTY ACC TTC CTC CAC GA
	L15718.leuc	CCC CAC ACA TCA AAC CAG A
	H15778.leuc	GGG ATT GAG CGT AGR ATR GC
ND2[b]	H5469.leuc	KAG RAG YGT RGA GGC TGT TG
	L5432.leuc	GCC ATC GAA GCY ACR ATC AA
	H6022.leuc	TGT RGY TRT TTC TTG YTT GG
	L5993.leuc	CAG GCT TCC TRC CCA AAT GR
BF-I7[c]	1H.bf.leuc	TAC TTG GTT GTG GAG CAG CA
	2L.bf.leuc	AGC CAA ATG TCC ATG CAG TT
	2H.bf.leuc	AAC TGA GCA CCT GTC TTC TGA G
	3L.bf.leuc	CAG TAA CAC ATA ATG GGT CCT GA
	3H.bf.leuc	TGG AAG GTG AAG CAG CTA AGA
	4L.bf.leuc	GCA ATT ATC ATT ATG AAC TGC AAG
	4H.bf.leuc	CCA TCC ACC ACC ATC TTC TT

[a] ND6: tPROfwd, tGLUfwd, tGLUrev, YCR2rev (Riesing et al. 2003).
[b] Cyt-*b*, ND2: L14996, H15646, L15560, H16064, L5219, H5766, H6313 (Sorenson et al. 1999).
[c] BF-I7: FIB-BI7U, FIB-BIL2, FIB-BIU2, FIB-BI7L (Prychitko and Moore 2000).

codon position and gene for mitochondrial loci in DAMBE (Xia 2000) using Tamura-Nei genetic distances (Tamura and Nei 1993) and pairwise numbers of transitions and transversions.

Phylogenetic reconstruction was done using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) separately on each gene or intron and then on multilocus data sets (see below). The MP trees were constructed in PAUP*, version 4.0b10 (Swofford 2004), using heuristic searches with starting trees obtained by random addition of taxa with 10 replicate searches and tree-bisection-reconnection (TBR) branch-swapping for 1,000 bootstrap replicates. Gaps were treated as a fifth state, and missing data were treated as uncertainties.

Nonparametric bootstrap ML analyses were conducted on unpartitioned data sets in GARLI, version 0.94 (Zwickl 2006). GARLI applies a genetic algorithmic approach similar to that of GAML (Lewis 1998). Sequence evolution models are implemented in a manner analogous to that conducted in PAUP* (Swofford 2004), such that resulting log likelihood scores are directly comparable to those that would be recovered in PAUP* analyses of sufficient length. We used MODELTEST, version 3.7 (Posada and Crandall 1998), to determine the best-fit model for each gene, intron, and codon position with the hierarchical likelihood ratio test, all characters equally weighted, and a neighbor-joining starting tree as implemented in PAUP* (Swofford 2004). The simplest model with the lowest Akaike's Information Criterion (AIC) was chosen for analyses. Bootstrap runs for ML analyses consisted of 500 pseudoreplicate heuristic searches with a GTR + I + G model.

Models with similarly low AIC values were applied separately for each gene, codon position, and intron in MRBAYES, version 3.1.2 (Huelsenbeck and Ronquist 2001), using four Markov chains sampling every 500 generations for 6 million generations. For each run, the distributions of parameter sampling were visualized and burn-in periods assessed in TRACER, version 1.1 (see Acknowledgments). Conservative burn-in periods of 10% were sufficient for all runs. In all cases, the resulting topologies were identical, regardless of the model used; therefore, the simplest model producing the most even distribution of sampling with the greatest number of independent samples (effective sample size [ESS] values in TRACER) was chosen for Bayesian inference (Alfaro and Huelsenbeck 2006).

We assessed four partitioning schemes for joint analyses of cyt-*b* and ND2: one partition including both genes, one partition for each gene (two partitions), one for each codon position (three partitions), and one for each codon position in each gene (six partitions). Similarly, ND6 was assessed as a single partition and as three partitions, each corresponding to a different codon position. Joint analyses with the nuclear intron forming a separate partition from the cyt-*b* and ND2 data were performed after the best partitioning strategy was determined (see below). Parameters were allowed to vary independently for each partition during MRBAYES runs. Harmonic mean log likelihoods for each partitioning scheme were calculated using the "sump" command in MRBAYES (Table 3). Bayes factors were calculated for each pairwise combination of partitioning schemes as an objective criterion for determining the best partitioning strategy for final analyses (Brandley et al. 2005). Three independent BI analyses using the partitioning strategy with the highest likelihood score were conducted to test for convergence on similar likelihood scores and topologies.

Results and Discussion

Sequence characteristics and phylogeny.—Numbers of parsimony-informative sites and variable but uninformative sites, respectively, were 487 and 48 out of a total 1,120 aligned base pairs (bp) of cyt-*b*, 564 and 74 out of 1,047 bp of ND2, 122 and 189 out of 981 bp of BF-I7, and 200 and 42 out of 519 bp of ND6. Empirical base frequencies correspond to those found in other avian studies (mitochondria: A, ~30%; C, ~35%; G, ~10%; T ~24%; BF-I7: A = 31%; C = 17%, G = 18%;

Table 3. Harmonic mean log-likelihood scores for each partitioning scheme.

Partition strategy	Number of partitions	Harmonic mean log likelihood
(A) mt data set		
No partitioning: (cyt-*b* + ND2)	1	–30,987.72
Gene: (cyt-*b*), (ND2)	2	–30,924.55
Codon position: (cyt-*b* and ND2 codon 1),(cyt-*b* and ND2 codon 2), (cyt-*b* and ND2 codon 3)	3	–29,934.30, –29,946.06, –29,937.33
Gene and codon position: (cyt-*b* codon 1), (cyt-*b* codon 2), (cyt-*b* codon 3), (ND2 codon 1), (ND2 codon 2), (ND2 codon 3)	6	–30,049.61
(B) ND6 data set		
No partitioning: (ND6)	1	–4,936.33
Codon position: (ND6 codon 1), (ND6 codon 2), (ND6 codon 3)	3	–4,767.79, –4,767.92, –4,768.40

T = 33%). The chi-square test of homogeneity showed no significant nucleotide composition bias across taxa.

Substitution saturation plots (not shown) show nearly linear increases of both transitions and transversions, with a steeper slope for transitions than for transversions, except for third-base-codon positions in ND6, which show some saturation beginning at a genetic distance of ~7%.

An insertion of three adenines was found in *Accipiter nisus* and *A. rufiventris* directly preceding the stop codon of cyt-*b*. Autapomorphic indels in BF-I7 ranged from 1 to 11 bp in length and were found in 12 species. Parsimony-informative indels were found for *Circus aeruginosus* and *C. ranivorus* (9-bp deletion), for *C. aeruginosus*, *C. ranivorus*, *A. bicolor*, *A. cirrocephalus*, *A. cooperii*, and *A. rufiventris* (1-bp deletion), and an insertion was found for five of these species (1 bp not shared by *A. cirrocephalus*). *Leptodon cayanensis*, *Rostrhamus sociabilis*, *Geranospiza caerulescens*, *Leucopternis schistaceus*, *Harpyhaliaetus solitarius*, and all four species in *Buteogallus* share a 2-bp deletion of TG or GT; all four *Buteogallus* spp., *H. solitarius*, and *L. schistaceus* share a 2-bp deletion. Because of ambiguity in the DNA sequence, we could not determine whether the 2-bp deletion (TG or GT) described above was synapomorphic for all nine sampled individuals, so the two bases were excluded from the analyses for all species. Missing data comprised <10 bp for all individuals, except in cyt-*b* for three individuals: *Butastur indicus* (216 missing bases), *L. p. princeps* (308 missing bases), and *Buteogallus aequinoctialis* (569 missing bases). No significant difference in topology or likelihood was found between analyses of the mitochondrial data set with and without these sequences; thus, mitochondrial analyses shown here include them. Sequences are available at GenBank (EU583221–EU583379); alignments and published trees can be found at TreeBASE (S2001).

Separate phylogenetic analyses of BF-I7 (not shown) produced a less-resolved tree than the other analyses. The relationships among major accipitrid clades were recovered with high support values (Bayesian posterior probability [BPP] = 1.00–0.97), as were most terminal sister relationships; however, the basal branching pattern within the Buteoninae was not resolved beyond finding three separate clades for the buteonine kites and *Geranospiza*, the species in *Buteogallus* sister to *L. schistaceus* and all other Buteoninae (BPP = 0.99). Also, the position of *Buteo* (or *Rupornis*) *magnirostris* was unresolved. Separate analyses of cyt-*b* and ND2 also produced trees with several buteonine polytomies: (1) a polytomy of three clades: *Busarellus*, *Geranospiza*, *L. princeps*, *L. plumbeus*, *Buteo* (or *Percnohierax*) *leucorrhous*, and *Parabuteo unicinctus*; the kites; and the *Buteogallus* spp., *Harpyhaliaetus* spp., and *L. schistaceus* and *L. lacernulatus*; and (2) a polytomy of the three remaining buteonine clades (clades diverging after node A in Fig. 1, described below). There were two main differences between the separate ND2 and cyt-*b* analyses: (1) *B.* (or *R.*) *magnirostris* diverged before all other Buteoninae in the cyt-*b* analyses (BPP = 1.00) but, in the ND2 analyses, was part of an unresolved polytomy with *B.* (or *P.*) *leucorrhous*, *Parabuteo unicinctus*, and a clade containing the later-diverging Buteoninae (species diverging after node A in Fig. 1, described below; BPP = 0.98); and (2) in cyt-*b* analyses, the *Butastur* spp. were part of a five-way polytomy with *Kaupifalco*, a clade of goshawks (genera *Melierax*, *Micronisus*, and *Urotriorchis*), a clade of accipiters and harriers (genus *Circus*), and a clade of sea eagles and buteonines (BPP = 1.00), whereas in the ND2 analyses the *Butastur* spp. were sister to the *Ictinia* spp. (BPP = 0.74). Because single-locus analyses produced topologies that were similar overall, we performed joint analyses of cyt-*b* and ND2 and of cyt-*b*, ND2, and BF-I7.

Three data sets were assembled. The mitochondrial or "mt" data set included 2,066 aligned (i.e., including indels) base pairs of mitochondrial DNA (1,020 bp cyt-*b* and 1,046 bp ND2) from 105 individuals of the family Accipitridae, representing 76 named species. The "mt + bf" data set included 3,048 bases of aligned combined mitochondrial and nuclear data (the mt data set appended to 981 bases of BF-I7) for 73 accipitrid taxa representing 56 nominal species. The "ND6" data set included 519 aligned bases of ND6 for 110 taxa representing 47 nominal species.

For the mt data set, the first codon position was modeled by HKY + I + G and the second and third codon positions were modeled by GTR + I + G. The mt + bf data set had four independent partitions: the three mitochondrial partitions described above and a separate partition for BF-I7 using the GTR + G model. For the ND6 data set, the first and third positions were modeled with GTR + G; the second codon position was modeled with HKY + G.

Bayesian consensus trees are shown in Figure 1A for the mt data set, in Figure 1B for the mt + bf data set, and in Figure 2 for the ND6 data set. Posterior probabilities (averages from three independent Bayesian analyses) and MP and ML bootstrap values are shown on the figures. The three different types of analyses produced largely congruent topologies; the few differences involved nodes resolved with low support in the BI analyses and not resolved in the MP or ML analyses. For instance, the branching pattern of the buteonine kites and *Geranospiza* was unresolved in MP and ML runs and supported by low posterior probabilities in Bayesian analyses (BPP = 0.51–0.77).

Nodes were supported with BPP ≥ 0.90 for 85% of mt and mt + bf nodes. Analyses resolved nearly all nodes in the mt + bf analyses with higher BPP values than with the mt data set alone, perhaps as a result of the larger number of base pairs in the mt + bf data set. For example, the placement of *Buteo* (or *Rupornis*) *magnirostris*

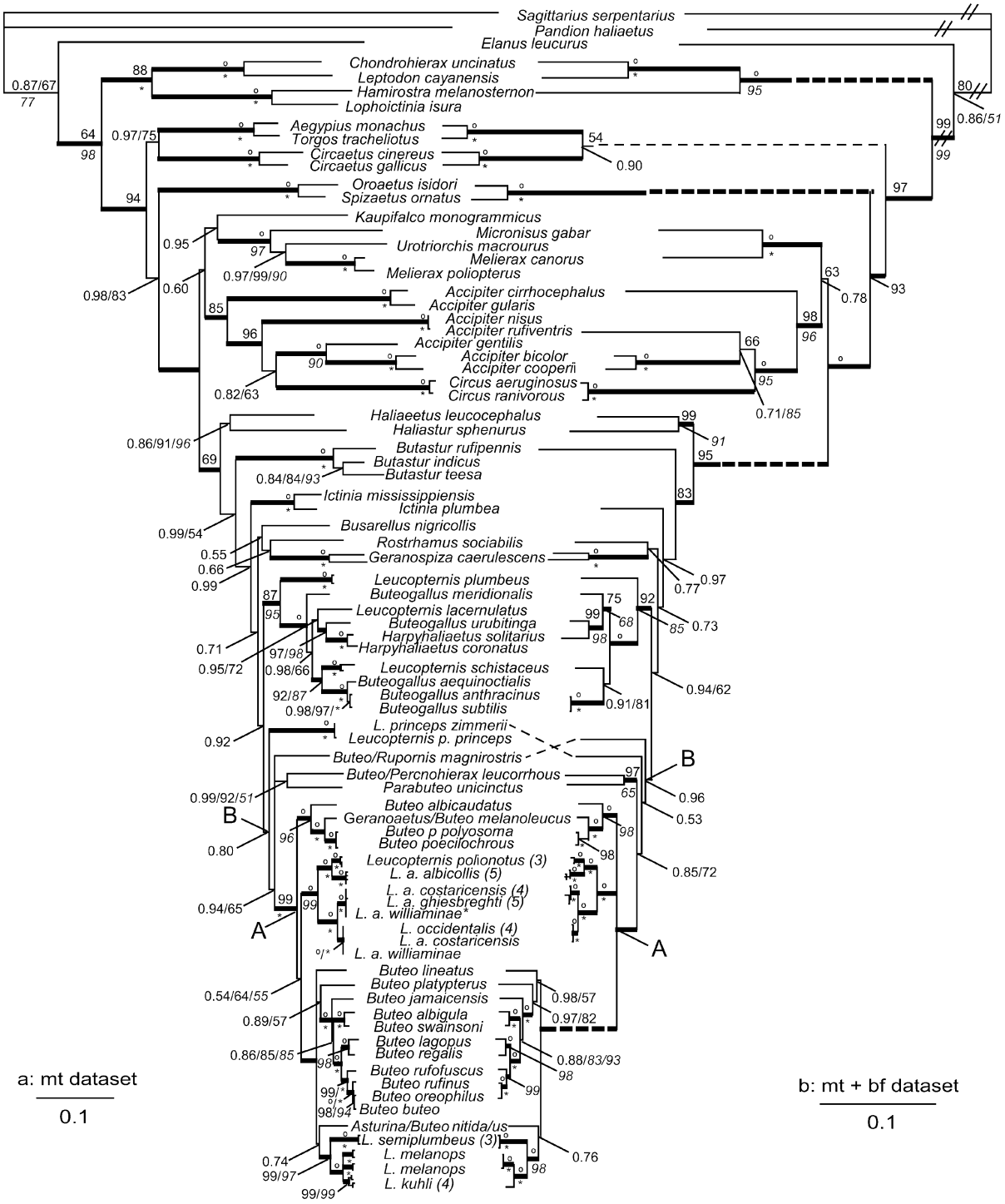

FIG. 1. Phylogeny for accipitrid taxa inferred from mitochondrial cyt-*b* and ND2 (a: mt data set) and nuclear BF-I7 (b: mt + bf data set). Topology shown is the Bayesian-inference majority-rule consensus tree from three independent runs. Bayesian posterior probability (BPP) values of 0.50–0.99 are shown above branches, and values of 1.00 are indicated by a bold line leading to the node. Maximum-likelihood (ML) values are above nodes, following BPP and preceding maximum-parsimony (MP) bootstrap values. Maximum-parsimony bootstrap values >50% are shown in italics below branches or following BPP or ML values. Bootstrap values of 100 are indicated by a circle for ML and by an asterisk for MP. Dashed lines are extensions of branch lengths, and double slash marks indicate branches reduced in length. *L. a. williaminae** denotes the type specimen.

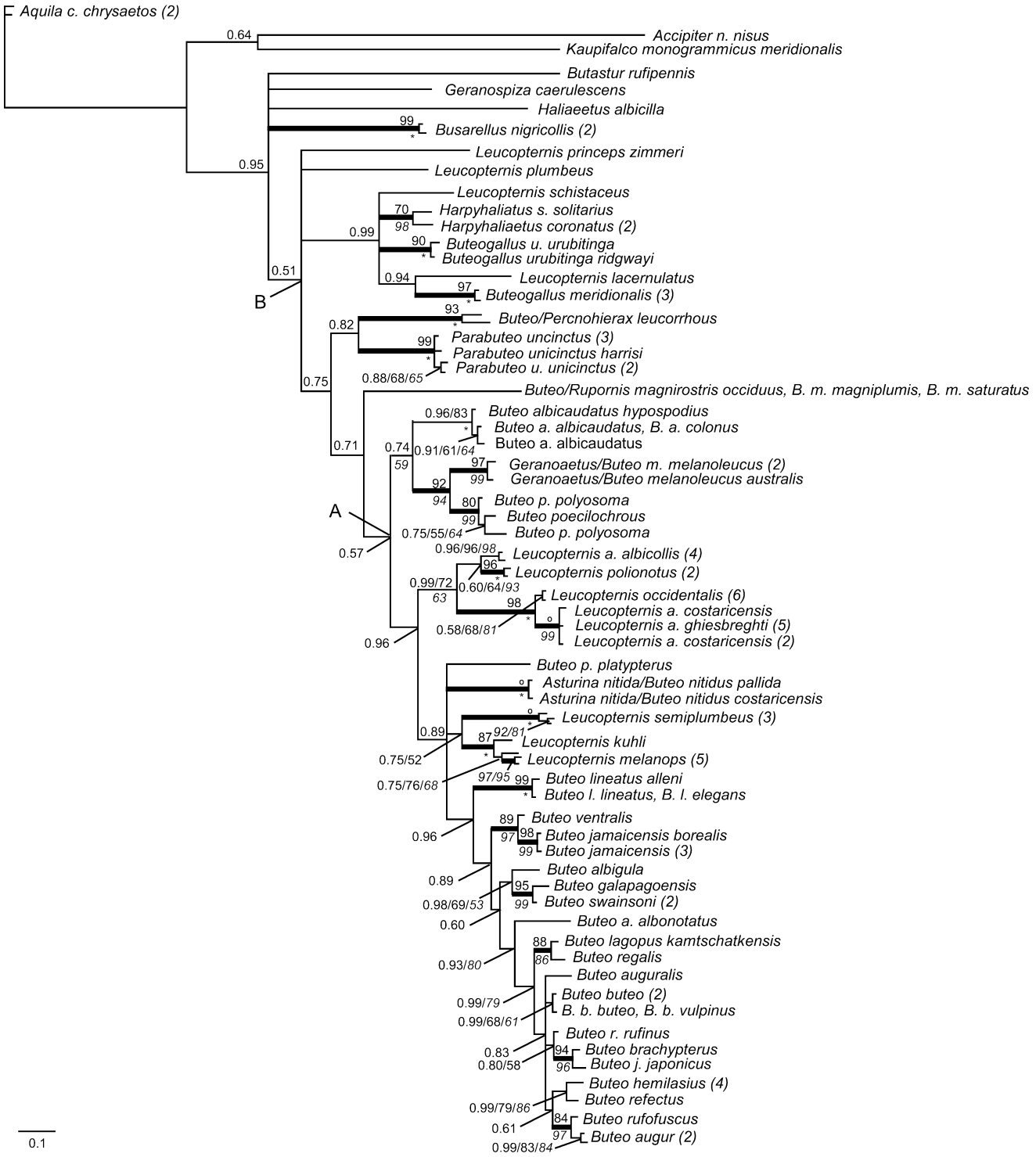

Fig. 2. Phylogeny for accipitrid taxa inferred from ND6 sequences. Topology shown is the Bayesian-inference majority-rule consensus tree from three independent runs. Bayesian posterior probability (BPP) values of 0.50–0.99 are shown above branches, and values of 1.00 are indicated by a bold line leading to the node. Maximum-likelihood (ML) values are above nodes, following BPP and preceding maximum-parsimony (MP) bootstrap values. MP bootstrap values >50% are shown in italics below the branches or following BPP or ML values. Bootstrap values of 100 are indicated by a circle for ML and by an asterisk for MP analyses.

and *B. lineatus* were unresolved in the Bayesian analyses of the mt data set but were resolved in the mt + bf analyses with high support (BPP = 0.96 and 0.98, respectively).

The phylogeny recovered in analyses of the ND6 data set (Fig. 2) largely agrees with the topologies in Figure 1, except for a polytomy of deeper divergences within and directly preceding the Buteoninae (i.e., placement of *Haliaeetus*, *Busarellus*, *Geranospiza*, and *Butastur*), which likely results from increased substitution saturation for this gene among older divergences. Within the Buteoninae, the positions of *L. princeps*, *L. plumbeus*, *Buteo p. platypterus*, and *Asturina nitida–B. nitidus* were unresolved. The ND6 analyses differ from the mt analyses in that they recover a sister relationship between *L. lacernulatus* and *Buteogallus meridionalis* and show an earlier but unresolved divergence of *B. platypterus.* This could reflect differences in taxon sampling between the analyses, differences between samples of *L. lacernulatus* (ND6 sequence from do Amaral et al. 2006), or differences in their molecular evolution, given that ND6 is the only mitochondrial protein-coding gene encoded by the light strand. Our ND6 analyses were concordant with previous studies (Riesing et al. 2003, do Amaral et al. 2006) except that we found a sister relationship between *B. r. rufinus* (not *B. auguralis* as in fig. 2 of Riesing et al. [2003]: MP bootstrap = 83, neighbor-joining support = 82) and a clade containing *B. brachypterus* and *B. j. japonicus* (BPP = 0.90; Fig. 2). Other differences between our analyses and those of Riesing et al. (2003) involve nodes supported by bootstrap values of <50% in their figures.

Old World taxa (Kaupifalco *and* Butastur) *and* Accipiter.—Three species in the genus *Butastur* form a monophyletic group (BPP = 1.00; Fig. 1A, B) diverging after the sea eagles but before the other sub-buteos, in a clade that is not closely related to *Kaupifalco*. By including representatives from each previously identified clade or subfamily of Accipitridae and expanding the sampling of harriers, accipiters, and goshawks, we found that *Kaupifalco* is sister to a clade including *Melierax*, *Micronisus*, and *Urotriorchis* (BPP = 0.95; Fig. 1A) and sister to an *Accipiter* sp. when the goshawks and other non-Buteonine genera were not included (BPP = 0.64; Fig. 2). *Kaupifalco* and *Butastur*, both described as sub-buteos by Amadon (1982), were later removed from the group by Amadon and Bull (1988). *Kaupifalco* was removed on the basis of observations by Kemp that the "voice and habits" of *Kaupifalco* are more similar to those of *Melierax* than to those of sub-buteos (Amadon and Bull 1988). Amadon and Bull (1988) also removed *Butastur* from Buteoninae, emphasizing its similarity to *Kaupifalco*. Our results confirm that *Kaupifalco* is indeed more closely related to *Melierax* than to sub-buteos but show that *Butastur* is more closely related to the sub-buteos than to the clade containing *Kaupifalco* and *Melierax*. Therefore, of the two Old World genera, we find support only for *Butastur* as a buteonine genus.

With this expanded sampling, we also found non-monophyly of the genus *Accipiter* when *Circus* spp. are included. In the mt data set, two *Circus* spp. are nested within a clade of seven *Accipiter* spp. (BPP = 0.82; Fig. 1A) or three accipiters (BPP = 1.00; Fig. 1B). This finding that *Circus* is nested within the larger *Accipiter* clade has not been published previously, as far as we know. Earlier studies including both genera, based on smaller sets of taxa and characters with less detailed searches, did not find *Accipiter* polyphyly but indicated reciprocal monophyly of the genera and a close but non-sister relationship instead (Wink and Seibold 1996, Wink and Sauer-Gurth 2004). Our finding of *Accipiter* polyphyly is also supported in analyses with greater sampling of species in both genera that are part of a larger consideration of Accipitridae (H. R. L. Lerner et al. unpubl. data).

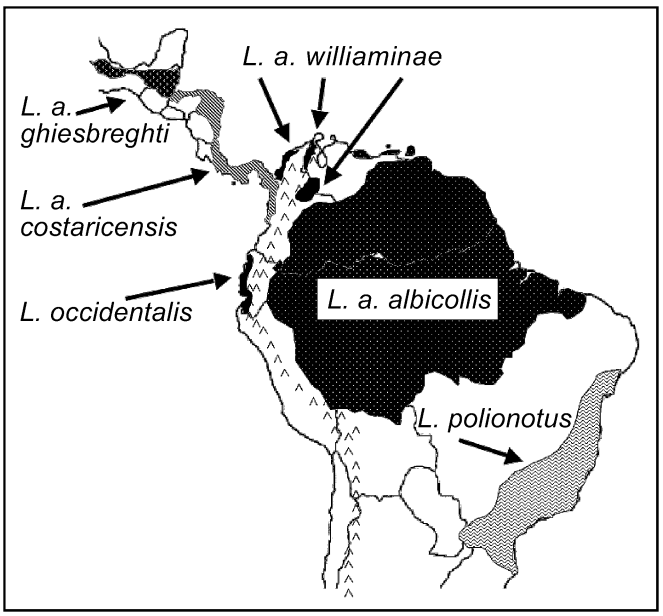

Fig. 3. Geographic distribution of White Hawk (*Leucopternis albicollis*) and related taxa, compiled from published descriptions and maps (Slud 1964, Wetmore 1965, Monroe 1968, Land 1970, Hilty and Brown 1986, Thurber et al. 1987, Sick 1993, Howell and Webb 1995, Ferguson-Lees and Christie 2001, Hilty 2003, Jones 2003, BirdLife International 2004).

Black-collared Hawk (Busarellus nigricollis).—*Busarellus* diverges early within the Buteoninae, after a clade of *Butastur* spp. and sister to *Rostrhamus* and *Geranospiza*, with low support in the mt analyses (BPP = 0.55; Fig. 1A) or unresolved with respect to *Butastur*, *Geranospiza*, and *Haliaeetus* (BPP = 0.95; Fig. 3). Previously proposed sister groups for *Busarellus* include milvine kites and sea eagles (Ridgway 1876, Olson 1982), sub-buteos *Buteogallus* and *Parabuteo* (Brown and Amadon 1968), or *Hieraaetus* and *Polemaetus* (Holdaway 1994). We did not find a well-supported close sister relationship for *Busarellus* here, but we confirmed its position within Buteoninae.

Relationships among and within genera of New World Buteoninae.—Divergence of *Ictinia* follows that of the sea eagles and the genus *Butastur* (BPP = 0.99, 0.97; Fig. 1). *Rostrhamus* is sister to *Geranospiza* but with low support (BPP = 0.66, 0.77; Fig. 1). With nearly complete sampling in *Leucopternis* and *Buteogallus*, we confirmed their non-monophyly (Lerner and Mindell 2005, do Amaral et al. 2006). Both *L. schistaceus* and *L. plumbeus* had been placed in the genus *Urubitinga* (Sharpe 1874, Ridgway 1876), now synonymous with *Buteogallus* (Peters 1931, AOU 1988), on the basis of morphological similarities with *B. urubitinga* and *B. anthracinus*. Here, we find that these two *Leucopternis* spp. are indeed more closely related to *Buteogallus* than

to other *Leucopternis* spp.; however, they are not sister taxa as proposed by Amadon (1982).

The clade including some *Leucopternis* spp., all *Buteogallus* spp., and both *Harpyhaliaetus* spp. shows a well-supported split between species that are dependent on aquatic habitats such as mangroves, marshes, forest, and wetlands (*B. aequinoctialis*, *B. anthracinus*, *B. subtilis*, and *L. schistaceus*) and mostly forest or open-vegetation habitats (*L. lacernulatus*, *B. urubitinga*, *H. solitarius*, and *H. coronatus*; Fig. 1) (BPP = 0.98 and 1.00; Ferguson-Lees and Christie 2001).

Leucopternis spp. are members of four different non-sister clades within the Buteoninae (Fig. 1; two species unresolved in Fig. 2). We found that *L. princeps* is more closely related to a large clade of *Buteo* and other *Leucopternis* taxa (BPP = 0.80 and 0.53, Fig. 1; unresolved in Fig. 2) than to a clade of *Buteogallus*, *Leucopternis*, and *Harpyhaliaetus* (fig. 1 in do Amaral et al. 2006: BPP = 0.68, bootstrap = 58). The lack of resolution for *L. princeps* in Fig. 2 and the difference between Fig. 1 and the results of do Amaral et al. (2006, their fig. 1) likely reflect differences in the size and informativeness of the data sets.

Genetic divergence among Buteogallus subtilis, B. anthracinus, *and* B. aequinoctialis.—The individual Mangrove Black Hawks (*B. subtilis*) and Common Black Hawks (*B. anthracinus*) we sampled had identical BF-I7 sequence, only a 1-bp difference in cyt-*b*, and another single difference in ND2, whereas the Rufous Crab-Hawk (*B. aequinoctialis*) was different from both of these species at 20 mitochondrial bases (2% csd). *Buteogallus subtilis* has been considered a subspecies of *B. anthracinus* and a member of a superspecies with *B. aequinoctialis* (Brown and Amadon 1968). Given that these three taxa are distributed in adjacent and sometimes overlapping ranges in similar habitat on the Atlantic and Pacific coasts and islands of the New World tropics, potential for interbreeding exists, and broader geographic sampling is needed before taxonomic revisions can be made.

Non-monophyly of nominal White Hawk subspecies (L. albicollis).—We sampled two to five (average = 4) individuals from the broad geographic range of each White Hawk subspecies, the Grey-backed Hawk (*L. occidentalis*) and the Mantled Hawk (*L. polionotus*; Fig. 3). The White Hawk was not monophyletic, with the nominate form (*L. a. albicollis*) more closely related to *L. polionotus* than to other subspecies of *L. albicollis* (BPP = 1.00, Fig. 1; BPP = 0.60, Fig. 2). Individuals of *L. a. albicollis* are 2.3% (mt csd) divergent from individuals of *L. polionotus*, a value similar to that found for other accipitrid sister taxa (Lerner and Mindell 2005: 95–98% sequence similarity for booted eagles; Johnson et al. 2006: 0.5–3.8% csd among *Gyps* spp.).

The three trans-Andean (i.e., occurring west of the Andean cordillera) subspecies of *L. albicollis* and *L. occidentalis* share mt haplotypes (Fig. 1A) and exhibit gradation of plumage coloration from nearly all-white birds in the north (*L. a. ghiesbreghti*) to heavy black coloration on the heads and wings of southern birds (*L. occidentalis*; H. R. L. Lerner et al. unpubl. data). Individuals of the most northern subspecies, *L. a. ghiesbreghti*, formed a clade sister to representatives of *L. occidentalis*, the most southern species; however, individuals of two White Hawk subspecies occurring in the center of the trans-Andean range for these taxa (*L. a. costaricensis* and *L. a. williaminae* from southern Central America and northern South America) were found in both clades. The subspecies *L. a. williaminae* has a very small range and is known from only a few museum specimens (the type specimen is indicated by an asterisk after the name on Fig. 1). The two clades identified in trans-Andean birds do not strictly correspond to current taxonomy, geography, or plumage coloration. These clades diverge by an average 1.2% (mt csd), which is similar to, but on the low end of, the divergence observed between other accipitrid sister-species pairs (Lerner and Mindell 2005, Johnson et al. 2006). Members of the trans-Andean clades differ from their sister clade containing *L. a. albicollis* and *L. polionotus* by 4.4% (average mt csd).

Analyses with greater sampling of individuals are needed, but the current set of relationships based on mitochondrial data (Figs. 1A and 2, but not Fig. 1B) support recognition of *L. a. albicollis* as *L. albicollis* and of *L. a. costaricensis*, *L. a. ghiesbreghti*, and *L. a. williaminae* as one or more distinct species. Four to six individuals of the endangered *L. occidentalis* form a monophyletic (Fig. 2) or unresolved group nested within a clade of individuals of *L. a. costaricensis*, *L. a. ghiesbreghti*, and *L. williaminae* (Fig. 1). None of these clades was recovered with nuclear intron data alone. This may reflect differences in expected coalescence times among maternally versus biparentally inherited loci, especially if these divergences are recent or if the effective population sizes are large (Hudson 1990). Using more variable loci, additional specimens, and population genetic methods could help in further taxonomic assessment and in distinguishing between alternative hypotheses, such as incipient speciation, secondary contact, or isolation by distance, for this clade. Given the status of the small and isolated populations of *L. occidentalis*, such analyses could be useful for conservation programs.

Genetic divergence between L. kuhli *and* L. melanops.—White-browed Hawks (*L. kuhli*) and Black-faced Hawks (*L. melanops*) are similar in appearance and are considered separate but closely related species (Hellmayr and Conover 1949, Amadon 1982). There were no shared mt or BF-I7 haplotypes between the species, and with mt data they are 1.8% divergent from each other. The polytomy in Figure 1A, however, precludes strong conclusions in this regard. The four individuals of *L. melanops* are nearly as divergent from each other as they are from individuals of *L. kuhli*, with 1.4% average csd, whereas the average csd among four conspecific individuals of *L. kuhli* is 0.56%. Using the more variable ND6 data set plus additional pseudo-control-region sequence, two individuals of *L. melanops* from Peru are 0.24% divergent from each other and, on average, 2.04% divergent from a Peruvian *L. kuhli*. These values are similar to, but on the low end of, those found between other closely related accipitrid species (see above).

Although the two species were originally described as allopatric, potential for hybridization exists, given that individuals of *L. melanops* have been trapped simultaneously with *L. kuhli* south of the Amazon river (Olalla collections of 1930 at the American Museum of Natural History [AMNH], and recent trappings described in Barlow et al. 2002). The two species, however, appear to be identifiable by plumage: about 20 specimens of each species examined at the AMNH were distinct in plumage, with no intermediate plumage types observed. Given the high level of genetic diversity within *L. melanops*, the lack of resolution of the mitochondrial data set, and the potential for hybridization, further analysis of these two species or this "superspecies" is warranted.

Phylogeny and taxonomy of the genus Buteo.—In Figure 1, all members of the nominal genus *Buteo* diverge after the node labeled "B." Following the early divergence of *L. princeps* and *B.* (*R.*) *magnirostris*, a sister relationship between *B.* (*Percnohierax*) *leucorrhous* and *Parabuteo unicinctus* is supported (BPP = 0.99 and 1.00, Fig. 1; BPP = 0.82, Fig. 2). The remaining *Buteo* species fall into two clades: (1) *B. albicaudatus*, *Geranoaetus melanoleucus*, *B. poecilochrous*, and *B. polyosoma* and (2) all others (11 species in Fig. 1 and 18 species in Fig. 2). The positions of *B. lineatus*, *Asturina nitida–Buteo nitidus*, and *B. jamaicensis* have not been resolved or well supported previously (nodes III [MP bootstrap = 58, neighbor-joining support = 90] and IV [support values <50] in Riesing et al. 2003). In Figure 1, we find that the divergence of *B. lineatus* (BPP = 0.98, Fig. 1B) is followed by that of *B. platypterus* (BPP = 0.97, Fig. 2B), and *Asturina nitida–B. nitidus* is more closely related to several species in the genus *Leucopternis* than to these two *Buteo* spp. (BPP = 0.74 and 0.76, Fig. 1; node III in Riesing et al. 2003). We also find that divergence of *B. jamaicensis* (BPP = 1.00, Fig. 1) is followed by divergence of the sister species *B. albigula* and *B. swainsonii* (BPP = 1.00 and 0.88, Fig. 1; BPP = 0.65, Fig. 2). Within the Buteoninae, we find that earlier divergences correspond to taxa with New World distributions followed by the sister pair of Nearctic *B. regalis* and circumpolar *B. lagopus* (BPP = 1.00, Figs. 1 and 2) and all Old World taxa diverging last (Figs. 1 and 2; see also Riesing et al. 2003).

We support the idea that taxonomy should reflect phylogeny. In that spirit, one proposal for redefinition of the genus *Buteo* includes all species descended from node A (Figs. 1 and 2, and Riesing et al. 2003). With the data set used by Riesing et al. (2003), this proposal would have required changing the generic names of three species (*Asturina nitida* to *Buteo nitidus, B. magnirostris* to *Rupornis magnirostris*, and *B. leucorrhous* to *Percnohierax leucorrhous*). Delimiting the genus *Buteo* at node A of Fig. 1 in our analyses would require changing the generic names of an additional six *Leucopternis* spp. as well as the genus *Geranoaetus*. We recommend delimiting *Buteo* earlier in the tree at node B (Fig. 1), so that it comprises a single clade including all current members of the genus *Buteo* sampled in both studies; this involves a change in genus name for two more species (*Parabuteo unicinctus* and *L. princeps*).

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