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PHYLOGENY OF THE FALCONIDAE INFERRED FROM MOLECULAR AND MORPHOLOGICAL DATA

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ABSTRACT.—Molecular data and variation in syringeal morphology were used to infer a phylogeny for the family Falconidae and to address three issues currently of interest in systematics: (1) the treatment of multiple data sets in phylogenetic analysis, (2) *a priori* analysis and differential weighting of molecular data, and (3) the reliability of molecular versus morphological data in phylogenetic analysis. Problems in recovering phylogenetic signal caused by rapidly changing sites in the molecular data were not solved by combining data sets. Differentially weighting saturated partitions of the sequence data, prior to phylogenetic analysis, provided a phylogeny congruent with morphological analysis. Molecular data provide substantially more informative characters than morphological data. However, morphological data provide a higher proportion of unreversed synapomorphies. A reclassification of the family based on the phylogeny results in two subfamilies: (1) the Herpetotherinae, (forest-falcons [*Micrastur*] and Laughing Falcon [*Herpetotheres cachinnans*]); and (2) the Falconinae, which includes the tribes Falconini (Spot-winged Falconet [*Spiziapteryx circumcinctus*], pygmy-falcons [*Polihierax*], falconets [*Microhierax*], and the genus *Falco*) and Caracarini (caracaras). The phylogeny also indicates that two genera, *Daptrius* and *Polihierax*, are polyphyletic, and these two are split. Finally, a biogeographic hypothesis derived from the phylogeny implies that the origin and early diversification of the family occurred in South America. *Received 12 November 1997, accepted 18 June 1998.*

THE FALCONIDAE, one of three families in the order Falconiformes (the diurnal birds of prey), includes some of the fastest and most spectacular birds in the world (Brown and Amadon 1968). Although the family is renowned for the hunting ability of its species (e.g. the Peregrine Falcon [*Falco peregrinus*]), foraging habits within the family are diverse. Thus, the Neotropical caracaras (*Daptrius, Milvago, Polyborus,* and *Phalcoboenus*) are scavengers that subsist mainly on carrion or invertebrates.

In addition to adaptations related to foraging habits, the four caracara genera share other morphological traits (Friedmann 1950) and historically have been considered to be closely related (Sharpe 1874, Gurney 1894, Swann 1922, Peters 1931). Classification of the other genera in the family has been less stable (Sharpe 1874, Gurney 1894, Swann 1922, Peters 1931). Amadon and Bull (1988) allocated the 10 currently recognized genera into two subfamilies. The Falconinae included the speciose genus *Falco* and the smallest diurnal raptors, *Polihierax* (pygmy-falcons) and *Microhierax* (falconets). The Polyborinae included seven Neotropical genera: the four caracara genera, *Micrastur* (forest-falcons), *Herpetotheres* (Laughing Falcon) and *Spiziapteryx* (Spot-winged Falconet). The relationships of the latter three genera historically have been problematic (Sharpe 1874, Gurney 1894, Swann 1922, Peters 1931). The placement of these genera with the caracaras (Amadon and Bull 1988) is in conflict with results from four cladistic analyses: (1) an osteological study (Becker 1987; Fig. 1A), (2) a preliminary morphological analysis (Kemp and Crowe 1990; Fig. 1A), (3) an analysis based on syringeal morphology (Griffiths 1994a; Fig. 1B), and (4) an analysis based on cytochrome-*b* sequences (Griffiths 1997; Fig. 1C). Based on Griffiths (1994a), the AOU (1998) reclassified the family, placing *Herpetotheres* and *Spiziapteryx* within the Falconinae and *Micrastur* in its own subfamily.

In this paper, I reanalyze the syringeal data, incorporating new information. Having collected both morphological and molecular data, I then examine a controversial issue in phylogenetic inference, the appropriate analysis of multiple data sets. This controversy spans a continuum of ideas. At one end is the idea that data sets should be analyzed separately. The

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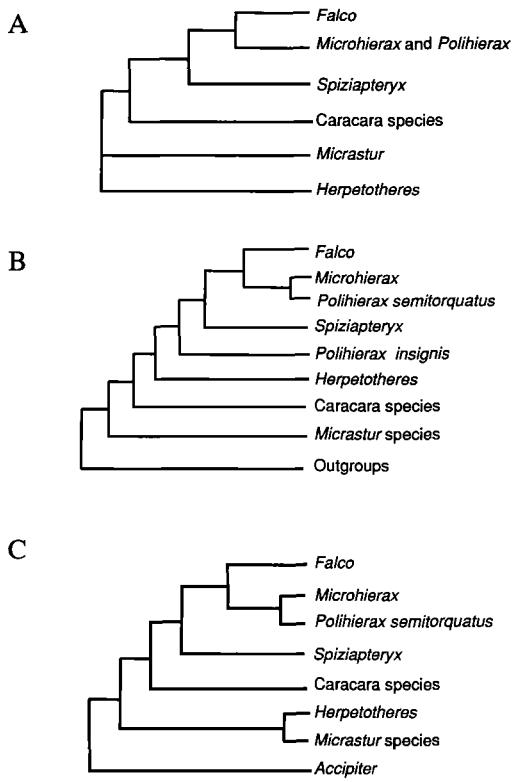

FIG. 1. Phylogenetic hypotheses inferred from cladistic analyses of the Falconidae. (A) Phylogeny inferred from osteological data (Becker 1987) and a preliminary analysis of skins and characters from literature (Kemp and Crowe 1990). (B) Phylogeny inferred from syringeal morphology (Griffiths 1994a). (C) Phylogeny inferred from differentially weighted cytochrome-*b* sequences (Griffiths 1997).

congruence of phylogenies inferred from each data set (taxonomic congruence) then provides a measure of the reliability of the phylogenies (Lanyon 1993, Miyamoto and Fitch 1995). At the opposite end is the idea that multiple data sets should be combined for phylogenetic analysis (total evidence or character congruence; Kluge 1989).

Between these two extremes, proposed methods for analyzing multiple data sets include: (1) conditional combination of data sets, i.e. combination only if the data sets are not significantly heterogeneous (Bull et al. 1993, Huelsenbeck et al. 1996); or (2) unconditional combination of data sets with differential weighting of characters to accommodate heterogeneity (Chippindale and Wiens 1994). Differential weighting is, in itself, controversial. Proponents of total evidence propose giving all characters equal weight initially in phylogenetic analysis. Assessments of character reliability derived from phylogenetic inference (i.e. successive approximations; Farris 1969, 1989; Carpenter 1988) can then be used to weight characters differentially (*a posteriori* weighting). *A priori* differential weighting is criticized for incurring unwarranted assumptions about process or requiring partitions of data for weighting that may be arbitrary (Eernisse and Kluge 1993, Brower and DeSalle 1994, Chippindale and Wiens 1994).

As part of the empirical exploration of the analysis of multiple data sets, I examine the effects of differential weighting on phylogenetic inference. I then compare the morphological and molecular data. The phylogeny inferred from these data is used to reclassify the Falconidae and two genera within that family. Finally, the phylogeny provides a framework for discussing the biogeography of the family.

MATERIALS AND METHODS

Morphological data.—Characters were derived from variation in syringeal supporting elements, membranes, and muscles (Griffiths 1994a). Supporting elements include ringlike elements on the trachea and bronchi (*A* and *B* elements; Ames 1971), the pessulus, and accessory cartilaginous structures. Homology of the ringlike elements was traditionally based on the relative position of these structures to the tracheobronchial junction (King 1989). This analysis postulates homologous elements following Ames' (1971) definitions of syringeal structures (Griffiths 1994b).

Data on variation in syringeal morphology for two species were added to the original data of Griffiths (1994a). The first, *Accipiter striatus* (Sharp-shinned Hawk; AMNH 18761), was substituted for *Gampsonyx swainsonii* to be consistent with the molecular data. The second, *Herpetotheres cachinnans* (LSUMNS 123200), recently became available. Because the *Herpetotheres* syrinx used to code characters for the original analysis (Griffiths 1994a) had been damaged, this new specimen was examined and the resulting information used to recode two of the characters. Character 16, the modification of the ends of the B1 element, changed from one to zero. Character 3, dorsal fusion of the tympanum, changed from one to two. In addition, three characters (characters 5, 6 and 7) that were originally coded as binary representations of alternative character states were recoded as one unordered multistate character.

Syringeal character descriptions with these modifications are presented in Appendix 1. The final data

TABLE 1. Species included in the phylogenetic analyses.

Species	Combined analysis	Morphological	Molecular
Milvago chimachima	*	*	*
M. chimango	no	*	no
Polyborus plancus	*	*	*
Phalcoboenus australis	*	*	*
Daptrius ater	*	*	*
D. americanus	*	*	*
Spiziapteryx circumcinctus	*	*	*
Micrastur gilvicollis	*	*	*
M. semitorquatus	*	*	*
Polihierax insignis	no	*	no
P. semitorquatus	*	*	*
Microhierax erythrogonys	*	*	*
Herpetotheres cachinnans	*	*	*
Falco berigora	no	*	no
F. sparverius	*	*	*
F. mexicanus	no	*	no
F. peregrinus	*	*	*
F. rufigularis	no	*	no
F. biarmicus	no	*	no
F. columbarius	no	*	no
F. cenchroides	no	*	no
F. vespertinus	*	no	*
F. femoralis	*	*	*
Accipiter striatus	*	*	*
Otus asio	no	*	no
Pelecanus onocrotalus	no	*	no

matrix for the reanalysis consisted of 25 taxa and 23 characters, six of which were multistate (Appendix 2). Transformation series for multistate characters were proposed if adjacent derived states were similar, and each succeeding state was a modification of the previous state; that is, the derived states formed a nested set of synapomorphies. Multistate characters were coded as unordered if states were alternative variations of a character.

Molecular data.—The complete sequences for cytochrome *b* were collected for species from each of the 10 genera in the family (Griffiths 1997; Genbank accession numbers U83305 to U83320). Details of DNA extraction, primers used, PCR and sequencing protocols, and data analysis are described in Griffiths (1997). In that study, molecular data were differentially weighted prior to phylogenetic analysis by filtering saturated subsets of data. These partitions were identified in an assessment of saturation of substitutions within domains of cytochrome *b* (the transmembrane, 561 base pairs; two extra-membrane regions of 240 and 342 base pairs; Griffiths 1997). The filtered partitions were first- and third-position transitions, and first-position transversions and second-position transitions in the extra-membrane domains.

Combined data.—The syringeal morphological data were combined with cytochrome-*b* sequences (Griffiths 1997). Osteological characters (Becker 1987) were not included because the data matrix for that analysis and details of the analysis were not available. All 10 currently recognized genera were sampled for both molecular and syringeal characters (Table 1). However, taxon sampling was not identical between the two data sets. Some species sampled within the genus *Falco* varied between the two, and no tissue samples of *Polihierax insignis* (White-rumped Pygmy-Falcon) were available. An initial analysis was run that included all species. The number of missing characters in the morphological data set resulted in conflict in relationships among the *Falco* species and, therefore, thousands of most-parsimonious trees. The topology of the strict consensus tree from that analysis was the same as the topology produced when species with missing data were deleted from the analysis. Because this study was not an attempt to resolve relationships within the genus *Falco*, species not included in the molecular analysis were pruned from the combined data matrix for the phylogenetic tests.

Accipiter striatus (Accipitridae), the sister taxon to the Falconidae (Griffiths 1994b), was used to root the tree. The rationale for using one outgroup was detailed by Griffiths (1997). Basically, several species within the Accipitridae were included initially to determine the root (Smith 1994). In the final analysis, only one outgroup species was used. This rooted the cladogram in the same place and produced the identical phylogeny as the analysis with multiple outgroups. The additional outgroup species were delet-

ed to facilitate the detailed examination of change in molecular characters within the family.

To test the different methods proposed for combining data for phylogenetic inference, two sets of phylogenetic analyses were performed. In the first set (i.e. the total evidence test), all characters were weighted equally for an initial phylogenetic analysis. Data were then weighted again to assess the effects of *a posteriori* differential weighting. Weights were derived from the fit of the characters to a phylogenetic hypothesis, using two different methods. In the first method, the maximum value of the rescaled consistency index was used to reweight characters (successive approximations; Farris 1969, 1989; Carpenter 1988). In the second method, the characters were weighted concurrently with the analysis based on the homoplasy implied by each tree (Goloboff 1993). The weighting function used to evaluate trees was a modification of the consistency index.

The second set of analyses examined the effect of combining data using *a priori* differential weighting of characters to accommodate heterogeneity of data sets (unconditional combination; Chippindale and Wiens 1994). Molecular data were differentially weighted as in Griffiths (1997). Because the molecular phylogeny inferred in that study was congruent with the morphological phylogeny, the combined analysis was performed to determine the effect of the addition of the morphological data on support for nodes. Bootstrap analyses were performed on the molecular data and then on the combined data to provide heuristic measures for comparing nodal support.

Within these sets of analyses, the effect of ordering four of the morphological characters was examined. Ordering effectively weights character-state transformations by forcing intermediate steps in the transition from the first to the last character state. Thus, in each set, morphological characters were first treated as unordered, and then four of the six multistate characters were ordered. To determine the effect of ordering morphological changes on support for nodes, bootstrap analyses on the combined data were performed with morphological characters ordered and then unordered.

All phylogenetic analyses were conducted using the test version 4.0d54 of PAUP*, written by David L. Swofford. Each phylogenetic analysis employed the heuristic algorithm, which included 100 replicates that randomly varied the order in which taxa were added.

Results

Morphological data.—Phylogenetic analysis of these data resulted in 54 most-parsimonious trees, which are summarized in the strict consensus tree (Fig. 2). There are two major clades:

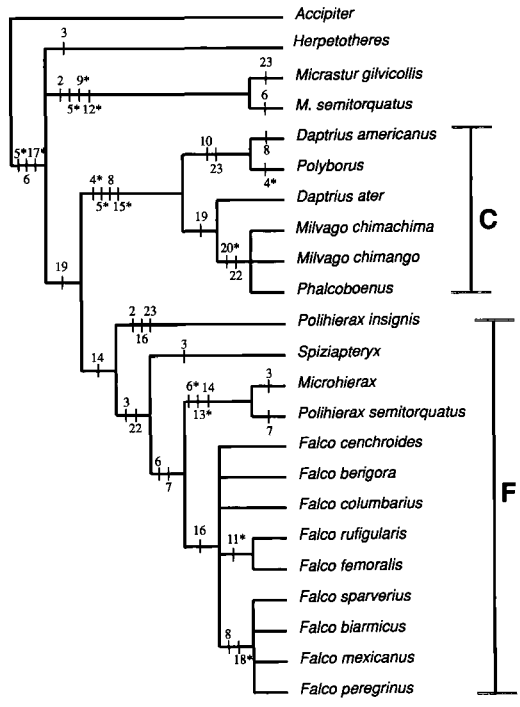

FIG. 2. Phylogeny of the Falconidae inferred from syringeal morphology; F = Falconinae, C = Polyborinae. Cladogram represents the strict consensus tree of 54 most-parsimonious trees of length 50; CI = 0.59 and RI = 0.81. Characters (Appendix 2) supporting each node are labeled. * = character with CI = 1.0. Characters 3, 4, 5, 6, 16, and 19 are multistate.

(1) caracaras; and (2) *Falco* species, including the two small falconets (*Microhierax* and *Polihierax*) and *Spiziapteryx*. *Herpetotheres* and *Micrastur* form a dichotomy basal to these two clades. This phylogeny is congruent with the osteological data (Becker 1987), the molecular data (Griffiths 1997), the morphological data (Kemp and Crowe 1990), and the original syringeal data in: (1) establishing these two clades, (2) placing *Micrastur* basal to these clades, and (3) placing *Spiziapteryx* in the Falconinae clade rather than with the caracaras. The position of *Herpetotheres* in this tree differs from the original syringeal analysis (Griffiths 1994a; Fig. 1B).

As with Griffiths (1994a), this phylogeny indicates that two genera, *Polihierax* and *Daptrius*, are polyphyletic. Differences in morphology, behavior, and habitat use between the two species in each of these genera have been described previously, and placing the species in each ge-

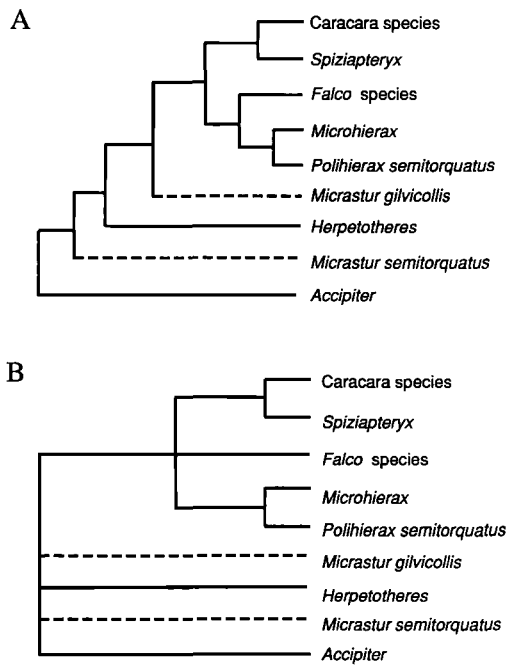

FIG. 3. (A) Phylogeny inferred from equally weighted molecular data (Griffiths 1997). (B) Phylogeny inferred from combined data sets with equally weighted molecular data. Strict consensus tree of five most-parsimonious cladograms (length = 1,089, CI = 0.46, RI = 0.45), morphological characters unordered. The same cladograms are inferred if morphological characters are treated as ordered. Dashed lines connect species in the genus *Micrastur*.

nus in either different subgenera or genera has been advocated (Brown and Amadon 1968).

Analysis of molecular data.—Results from the analysis of variation in cytochrome-*b* sequences are described in detail in Griffiths (1997). A summary is presented to serve as background for the combined analysis. Equal weighting (Fig. 3A) and differential weighting (Fig. 1C) of sequence data provided two different results. In the phylogeny inferred from the equally weighted molecular data (Fig. 3A), *Spiziapteryx* is the sister taxon to the caracaras, a result incongruent with that inferred from osteological and morphological data (Figs. 1A, 1B, 2). A more anomalous result is that the genus *Micrastur* is not monophyletic. Contrary to the results for *Daptrius* and *Polihierax*, polyphyly of the *Micrastur* species has not been suggested previously. The species within this clade are similar in morphology and habitat use and have been considered distinct from other genera in the family (Brown and Amadon 1968). In addition, the node supporting monophyly of the *Micrastur* species is one of the most strongly supported in the morphological phylogeny (Fig. 2), with four synapomorphies, three of these with a CI of 1.0. The alternative result, inferred using data weighted differentially prior to phylogenetic analysis, is congruent with the morphological hypotheses; i.e. the *Micrastur* species are monophyletic.

Combined data: Total evidence.—Combining equally weighted molecular data and morphological characters (either ordered or unordered) produced five most-parsimonious trees. The strict consensus of these five (Fig. 3B) is less resolved than the tree inferred from only molecular data (Fig. 3A), reflecting the conflict between the molecular data and the morphological data. Support exists for three clades: (1) the *Falco* species, (2) the caracara species and *Spiziapteryx*, and (3) *Microhierax* and *Polihierax*. There is no resolution of relationships among these clades nor of the relationships of the two *Micrastur* species and *Herpetotheres*.

A posteriori differential weighting, using assessments of character reliability derived from the phylogenetic analysis (i.e. successive approximations), or weights derived during phylogenetic analysis, produced one cladogram similar to that inferred from equally weighted molecular data (Fig. 3A). Results are the same with the morphological characters ordered or unordered. *Spiziapteryx* is sister taxon to the caracaras, and the genus *Micrastur* is not monophyletic.

Combined data: Unconditional combination.—Combining data sets with *a priori* differential weighting of molecular data (i.e. unconditional combination) produced two most-parsimonious cladograms. These differed only in resolution within the caracara clade (Fig. 4). Because step matrices were used for the molecular characters, summary statistics were not produced for these cladograms. As expected, this phylogeny is basically congruent with the separate analyses (*a priori* weighting of molecular data [Fig. 1C] and syringeal morphological data [Fig. 2]). Differences between the combined and separate analyses appear in two areas of the tree: (1) the sister taxa relationship of *Micrastur* and *Herpetotheres* is unresolved in the morphological analysis (Fig. 2); and (2) in one of the two trees, *Polyborus* and *Daptrius ameri-*

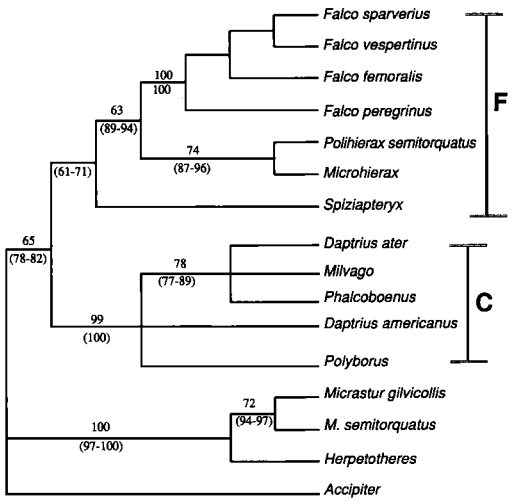

FIG. 4. Phylogeny inferred from combined data sets with *a priori* differential weighting of molecular data, and morphological characters ordered or unordered. F = Falconinae, C Polyborinae (caracaras). Strict consensus tree of two most-parsimonious cladograms. Bootstrap values at nodes are shown for the molecular data set and for the combined data sets; numbers above the branches are for the molecular data only, numbers below the branches are for the combined data sets. Range of numbers for the combined data sets are for ordered and unordered morphological characters (left = unordered, right = ordered).

canus are sister taxa, a result congruent with the morphological analysis. In the second tree, *Polyborus* is basal to the other caracaras.

Bootstrap analysis of the combined data indicates additional support for key nodes compared with the analysis of molecular data alone (Fig. 4). The position of *Spiziapteryx* in the *Falco* clade is not supported in the majority of bootstrap replicates with molecular data alone. When morphological data are added, that relationship is supported in 61 to 71% of the replicates. The support for monophyly of *Micrastur* increases from 72% to 94 to 97%, and the support for the sister-taxa relationship of the caracara and *Falco* clade increases from 65 to 78 to 82%. Ordering the four multistate morphological characters does not change the topology, but it provides stronger support for six of seven nodes on the cladogram (Fig. 4).

DISCUSSION

Analysis of multiple data sets.—One of the most contentious issues in systematics is the treatment of different data sets. Detailed reviews of this issue have been presented previously (Hillis 1987, de Queiroz et al. 1995, Miyamoto and Fitch 1995, Huelsenbeck et al. 1996), and only main points of the argument will be discussed. The two main questions to be answered are: (1) Should data sets be combined prior to any phylogenetic analysis? and (2) If not combined initially, should data sets be combined after initial analyses? The initial combination of data sets has been justified philosophically (i.e. the hypothesis with the greatest explanatory power is provided by the concurrent analysis of all relevant evidence; Kluge 1989). Analyzing data sets separately is disputed because the creation of separate data sets assumes that there are natural classes of data, an assumption that is not justified scientifically (Kluge 1989). This argument carries over into the appropriate method of weighting characters. *A priori* character weighting requires partitioning data and would therefore be unjustified by those who believe that data should be combined before analysis. *A posteriori* weighting, determined either iteratively or directly, is appropriate because weights are inferred through phylogenetic analysis.

Separate analysis of multiple data sets is supported by the argument that congruence among hypotheses from different data sets is a powerful tool for assessing accuracy of the hypotheses (Miyamoto and Fitch 1995). An assumption of this methodology is that dividing data into classes can be justified scientifically (e.g. different codon positions). Advocates of the initial separate analysis of data sets differ on the final treatment of multiple data sets. Opinions range from always keeping data sets apart (Miyamoto and Fitch 1995) to always combining data sets, after any conflicts are accommodated through differential character weighting (Chippindale and Wiens 1994). An intermediate position is to combine only congruent data sets, using either biological (e.g. gene trees for a species; de Queiroz et al. 1995) or statistical (significant differences among data sets; Huelsenbeck et al. 1996) criteria for determining incongruence. One problem with this approach is that the two criteria are not equivalent; data sets responding to different biological processes may or may not differ significantly. In addition, although various significance tests have been proposed (bootstrap [de

Queiroz 1993], tree lengths [Farris et al. 1995], and likelihood ratios [Huelsenbeck and Bull 1996]), the power and sensitivity to the assumptions of these tests are unknown.

If the goal of phylogenetic analysis is to provide the hypothesis with the greatest explanatory power, then comparing the various methods is unnecessary because only a combined analysis meets that goal. If the goal is accuracy of phylogenetic inference, then empirical tests comparing these methods are useful (de Queiroz et al. 1995). One implicit assumption of the total evidence approach is that the same underlying signal is contained in each data set (Hillis et al. 1996). Thus, any potential conflict among the hypotheses inferred from individual data sets will be overcome when data sets are combined, circumventing the need to address conflict among data sets (Brower and DeSalle 1994).

This is a testable hypothesis and is directly related to the idea of consistency; i.e. a consistent methodology will result in convergence to the correct topology as data are added (Felsenstein 1978, Penny et al. 1992). In this study, combining morphological and molecular data produced a phylogeny indicating polyphyly of the genus *Micrastur.* This result is inconsistent with cladistic morphological analyses and with generally accepted conclusions based on morphological, behavioral, and geographic data. Using assessments of character reliability to reweight the characters (*a posteriori* differential weighting) also resulted in polyphyly of *Micrastur.* This is not surprising; searches using *a posteriori* weighting are dependent on the values obtained from the starting tree and may become trapped in local optima (Swofford et al. 1996).

All phylogenetic methods can be inconsistent when the assumptions of the method are violated (e.g. Debry 1992, Huelsenbeck 1995, Swofford et al. 1996, Sullivan and Swofford 1997). These violations can be accommodated through the use of a more appropriate model or by differentially weighting data (e.g. Steel et al. 1993, Sullivan and Swofford 1997). The problem, then, lies in recognizing the conditions in a data set under which a phylogenetic method is inconsistent.

Inconsistency can be caused by characters with high rates of change and, subsequently, a low probability of recovering the homologous state at nodes (Kim 1996). These kinds of characters occur in the molecular data in this research. For these data, rates of change differ among partitions of sequences, with several partitions containing characters with high rates of change (Griffiths 1997). Substitutions are saturated in these partitions, and recovering phylogenetic signal is problematic (Griffiths 1997). When *a priori* differential weighting is used to correct for the high rates of change in these partitions, the phylogeny indicates monophyly of *Micrastur,* a result congruent with the morphological analyses.

These results support the intermediate position, the initial separate analysis of multiple data sets, and differential weighting to accommodate heterogeneity in rates of change. After these processes were performed, combining the congruent data sets increased the support for nodes in the phylogeny (Fig. 4).

Molecules and morphology.—Although the initial use of biochemical data in systematics was accompanied with assertions that molecular evidence was more reliable than morphological evidence (e.g. Sibley and Ahlquist 1987), the value of both morphological and molecular characters for systematics is now generally acknowledged (Donoghue and Sanderson 1992, de Queiroz et al. 1995; but see Hedges and Sibley 1994). For this analysis, each method has advantages and disadvantages. Informative molecular characters were an order of magnitude greater in number than morphological characters (328 vs. 23). The relative paucity of characters is the most substantial disadvantage of the syringeal data. For this analysis, there are 31 character states for 23 characters. There are few characters supporting most nodes, and the relationship of *Herpetotheres* and *Micrastur* is unresolved.

The advantage of the syringeal data set is the proportion of unreversed synapomorphies; 15 of 31 characters states have a CI of 1.0, and 40% of the characters change only once in the phylogeny (Figs. 5A, 6A). Homoplasy is more prevalent in the molecular data. Of the 328 characters, only 10% (33) have a CI of 1.0, and only 5% change one time (Figs. 5B, 6B). Homoplasy obscures the signal in the more basal branches connecting the monotypic genera *Herpetotheres* and *Spiziapteryx;* differential weighting corrects these problems. It is possible that more sequence data would increase the signal at these

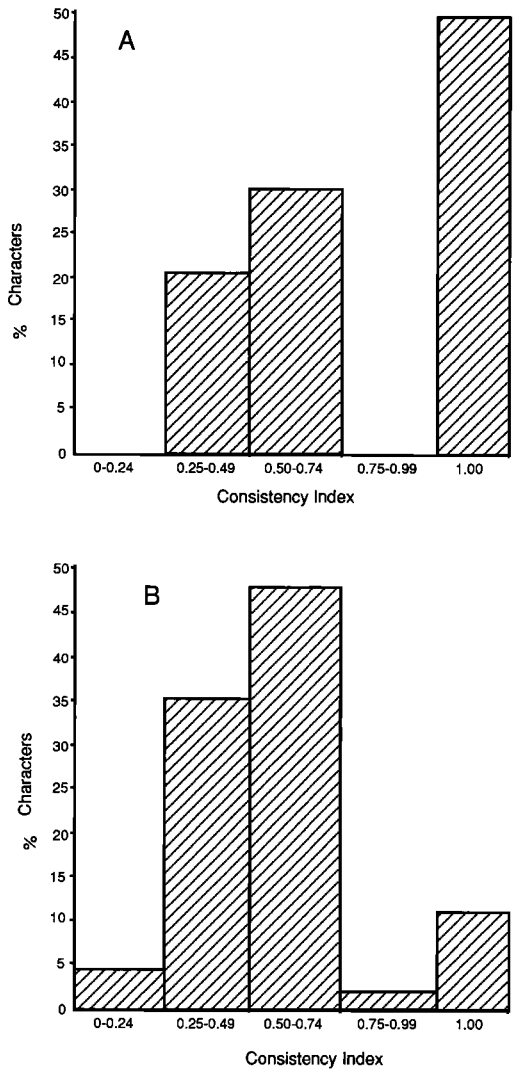

FIG. 5. The proportion of characters for each value of the consistency index. (A) Morphological data, (B) molecular data.

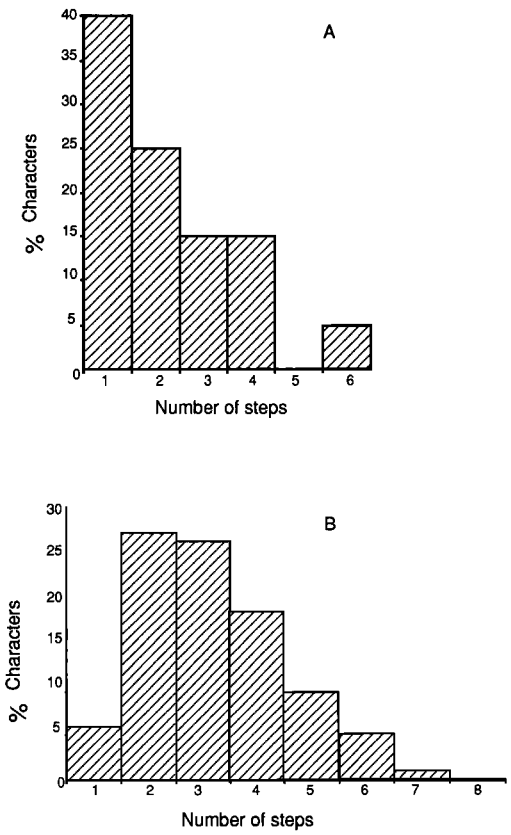

FIG. 6. The proportion of characters with a given numbers of steps. (A) Morphological data, (B) molecular data.

nodes. Alternatively, additional sequence data may not resolve these branches if the additional data have the same patterns of noise and signal as the present data (Bruns et al. 1992) or if the data do not fit the assumptions of the model used (Sullivan and Swofford 1997). Because these genera are monotypic, increased sampling of taxa within the family would probably not resolve the problem.

The results of my study support the general conclusion that both types of data are valuable for phylogenetic inference (Donoghue and Sanderson 1992, de Queiroz et al. 1995). Differentially weighted molecular data strongly support the sister relationship of *Herpetotheres* and *Micrastur,* which is unresolved in the morphological tree. The position of *Spiziapteryx* has weak support in the molecular tree. The inclusion of *Polihierax insignis* in the morphological analysis (Fig. 2) strengthens the support for *Spiziapteryx* within the *Falco* clade.

In this study, the molecular data were more homoplastic, thus disputing the assertion that molecular data are more reliable than morphological data for phylogenetic inference (Sibley and Ahlquist 1987, Hedges and Sibley 1994). The occurrence of saturated data partitions in the falconid sequences follows a pattern illustrated in studies of cytochrome *b* and other mitochondrial protein-coding genes (e.g. Kornegay et al. 1993, Hackett 1996, Yoder et al. 1996). The value of differential weighting for rapidly

evolving partitions of molecular characters, as shown in this research, has also been demonstrated previously (e.g. Simon et al. 1994, Sullivan and Swofford 1997). For morphological data, the level of homoplasy may also vary in partitions of data (e.g. in cranial versus postcranial osteology in birds; Livezey 1986). Finally, homoplasy may not be as prevalent in some morphological data sets because characters in these data are generally filtered before phylogenetic analysis (Livezey 1986, Novacek and Wheeler 1992, Griffiths 1994b).

Phylogenetic relationships in the Falconidae.—Cladograms inferred from variation in syringeal morphology and cytochrome-***b*** sequences both provide evidence that the two species in the genus *Daptrius* are not sister taxa. The suggestion that these two be split has been made previously based on differences in habitat use and foraging (Brown and Amadon 1968). The name *Ibycter* Vieillot 1816 (type, by monotypy, *Falco americanus* Boddaert 1783) is resurrected for *Daptrius americanus.* The name *Daptrius* Vieillot 1816 (type, by monotypy, *Daptrius ater* Vieillot 1816) is retained for *Daptrius ater.*

I also recommend that the two species of *Polihierax* be split based on polyphyly of this genus revealed by syringeal characters. The substantial differences of these species in size, plumage color, and tail shape have been noted previously, with the suggestion that they be placed in different subgenera (Brown and Amadon 1968). The name *Neohierax* Swann 1922 (type, by original designation, *Polihierax insignis* Walden 1872) is resurrected for *Polihierax insignis.* The name *Polihierax* Kaup 1847 (type, by monotypy, *Falco semitorquatus* A. Smith 1836) is retained for *Polihierax semitorquatus.*

The relationships revealed in the analyses of syringeal morphology (Fig. 2), DNA sequence data (Fig. 1C), and osteology (Fig. 1A; Becker 1987) are reflected in the phylogenetic classification presented below, which is a revision of the classification of AOU (1998):

FAMILY Falconidae
  Subfamily Herpetotherinae
    GENUS *Herpetotheres*
    GENUS *Micrastur*
  Subfamily Falconinae
    Tribe Falconini
      GENUS *Neohierax* (*incertae sedis*)
      GENUS *Spiziapteryx*
      GENUS *Falco*
      GENUS *Microhierax*
      GENUS *Polihierax*
    Tribe Caracarini (all genera *sedis mutabilis*)
      GENUS *Polyborus*
      GENUS *Ibycter*
      GENUS *Milvago*
      GENUS *Phalcoboenus*
      GENUS *Daptrius*

To minimize the number of higher taxa in this classification, taxa of equal rank within a monophyletic higher category are listed in order; each taxon is the sister group to the remaining taxa at that level (Raikow 1985). Problematic relationships are indicated by the placement of a taxon as *sedis mutabilis* (order within group is ambiguous and interchangeable) or *incertae sedis* (uncertain position) within the higher category (Raikow 1985).

This classification divides the family into two subfamilies. *Herpetotheres* is removed from the Falconinae and placed in a subfamily with *Micrastur.* Herpetotherinae (Lesson, 1843, type *Herpetotheres* Vieillot, 1816) has priority over Micrasturinae and is resurrected for that clade. The subfamily name Falconinae is retained and includes the tribes Falconini and Caracarini. The composition of the Falconini is not changed. Within that tribe, the relationship of *Neohierax insignis* is unresolved. *Polihierax semitorquatus* and *Microhierax* are sister taxa, a relationship supported by molecular sequences, syringeal morphology, and a morphometric analysis (Kemp and Crowe 1993). The Caracarini is a new tribe created to include the five caracara genera formerly placed in the Caracarinae. Relationships of the genera in this tribe are unresolved. Although there is support for the clade containing *Daptrius ater, Phalcoboenus* and *Milvago,* further resolution of the relationships among these three genera, and of this clade to the other two genera, await a detailed phylogenetic analysis of species and subspecies in that tribe.

Biogeography.—I used the phylogenetic classification as a framework for examining the biogeography of the Falconidae. Two approaches based on cladistic methodology can be used to infer biogeographic history. Cladistic biogeography (i.e. vicariance biogeography), the first approach, was developed as an alternative to "center of origin" and "improbable" dis-

persal scenarios prevalent in the 1970s (Nelson 1978, Bremer 1992). Vicariance biogeography is an attempt to recover the biogeographic pattern of an entire biota through the congruence of multiple cladistic hypotheses. For this method, an area cladogram representing the distribution of one group is interesting only to the extent that it confirms or conflicts with a general pattern. The alternative approach considers the historical biogeography of an individual group to be an important part of its natural history (Bremer 1992). Two methods, ancestral-area (Bremer 1992) and dispersal-vicariance analysis (Ronquist 1997), have been developed that use character optimization to interpret the biogeographic pattern of an area cladogram.

The ancestral-area methodology estimates the original distribution of a group by comparing the number of gains versus losses of areas under two models, forward (all gains) or reverse (all losses) Camin-Sokal parsimony (Bremer 1992). For example, if there are more gains than losses, the most-parsimonious interpretation is that the area was part of the ancestral distribution.

Dispersal-vicariance analysis uses Fitch optimization to reconstruct the history of biogeography by minimizing the dispersal-extinction events on the area cladogram. A step matrix, which specifies the cost of combinations of ancestral and descendant distributions (the difference between the distribution of the ancestor and each daughter area), is used in a three-pass algorithm to find the optimal reconstruction (Ronquist 1997).

I used the basic principles of the second approach to infer the biogeography of the Falconidae. The area cladogram, illustrating the distributions of the falconid genera mapped onto the phylogeny, is shown in Figure 7. The pattern of distribution of these genera enables a simple interpretation of biogeographic history for the family. Distribution of species in two of the three lineages, and the basal branch in the third, is limited to South America. Distribution of genera outside the Neotropics occurs only in the Falconinae. The sister taxa, *Microhierax* and *Polihierax semitorquatus*, occur in Southeast Asia and Africa, and the genus *Falco* contains species occurring in all regions of the world. The most-parsimonious explanation of this distribution pattern suggests that the origin and early diversification of the Falconidae occurred in the Neotropics.

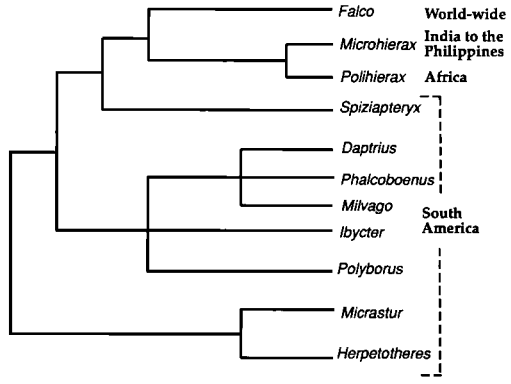

FIG. 7. Area cladogram of the Falconidae. Distribution of falconid genera mapped onto the phylogeny of the Falconidae.

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LITERATURE CITED

AMADON, D., AND J. BULL. 1988. Hawks and owls of the world: A distributional and taxonomic list. Proceedings of the Western Foundation of Vertebrate Zoology 3:294–357.

AMERICAN ORNITHOLOGISTS' UNION. 1998. Checklist of North American birds, 7th ed. American Ornithologists' Union, Washington, D.C.

AMES, P. L. 1971. The morphology of the syrinx in

passerine birds. Bulletin of the Peabody Museum of Natural History 37:1–194.

BECKER, J. 1987. Revision of *"Falco" ramenta* Wetmore and the Neogene evolution of the Falconidae. Auk 104:270–276.

BREMER, K. 1992. Ancestral areas: A cladistic reinterpretation of the center of origin concept. Systematic Biology 41:436–445.

BROWER, A., AND R. DESALLE. 1994. Practical and theoretical considerations for choice of a DNA sequence region in insect molecular systematics, with a short review of published studies using nuclear gene regions. Annals of the Entomological Society of America 87:702–716.

BROWN, L., AND D. AMADON. 1968. Eagles, hawks and falcons of the world. Hamlyn House, Feltham, United Kingdom.

BRUNS, T. D., R. VILGALYS, S. M. BARNS, D. GONZALEZ, D. S. HIBBETT, D. J. LANE, L. SIMON, S. STICKEL, T. M. SZARO, W. G. WEISBURN, AND M. L. SOGIN. 1992. Evolutionary relationships within the fungi: Analyses of nuclear small subunit rRNA sequences. Molecular Phylogenetics and Evolution 1:231–241.

BULL, J. J., J. P. HUELSENBECK, C. C. CUNNINGHAM, D. L. SWOFFORD, AND P. J. WADDELL. 1993. Partitioning and combining data in phylogenetic analysis. Systematic Biology 42:384–397.

CARPENTER, J. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4:291–291.

CHIPPINDALE, P. T., AND J. J. WIENS. 1994. Weighting, partitioning, and combining characters in phylogenetic analysis. Systematic Biology 43:278–287.

DEBRY, R. W. 1992. The consistency of several phylogeny-inference methods under varying evolutionary rates. Molecular Biology and Evolution 9:537–551.

DE QUEIROZ, A. 1993. For consensus (sometimes). Systematic Biology 43:368–372.

DE QUEIROZ, A., M. J. DONOGHUE, AND J. KIM. 1995. Separate versus combined analysis of phylogenetic evidence. Annual Review of Ecology and Systematics 26:675–681.

DONOGHUE, M. J., AND M. J. SANDERSON. 1992. The suitability of molecular and morphological evidence in reconstructing plant phylogeny. Pages 340–368 *in* Molecular systematics of plants (P. S. Soltis, D. E. Soltis and J. J. Doyle, Eds.). Chapman and Hall, New York.

EERNISSE, D. J., AND A. G. KLUGE. 1993. Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules and morphology. Molecular Biology and Evolution 10:1170–1195.

FARRIS, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18:374–385.

FARRIS, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5:417–419.

FARRIS, J. S., M. KALLERSJO, A. G. KLUGE, AND C. BULT. 1995. Testing significance of incongruence. Cladistics 10:315–319.

FELSENSTEIN, J. 1978. Cases in which parsimony and compatibility will be positively misleading. Systematic Zoology 27:401–410.

FRIEDMANN, H. 1950. The birds of North and Middle America. Part XI. Smithsonian Institution Bulletin 50:543–755.

GOLOBOFF, P. A. 1993. Estimating character weights during tree search. Cladistics 9:83–92.

GRIFFITHS, C. S. 1994a. Syringeal morphology and the phylogeny of the Falconidae. Condor 96:127–140.

GRIFFITHS, C. S. 1994b. Monophyly of the Falconiformes based on syringeal morphology. Auk 111: 787–805.

GRIFFITHS, C. S. 1997. Correlation of functional domains and rates of nucleotide substitution in cytochrome *b*. Molecular Phylogenetics and Evolution 7:353–365.

GURNEY, J. H. 1894. Catalogue of the birds of prey. R. H. Porter, London.

HACKETT, S. 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus*. Molecular Phylogenetics and Evolution 5:368–382.

HEDGES, S. B., AND C. G. SIBLEY. 1994. Molecules vs. morphology in avian evolution: The case of the "pelecaniform" birds. Proceedings of the National Academy of Sciences USA 91:9861–9865.

HILLIS, D. M. 1987. Molecular versus morphological approaches to systematics. Annual Review of Ecology and Systematics 18:23–42.

HILLIS, D. M., B. K. MABEL, AND C. MORITZ. 1996. Applications of molecular systematics. Pages 515–544 *in* Molecular systematics, 2nd ed. (D. M. Hillis, C. Moritz and B. K. Mable, Eds.). Sinauer Associates, Sunderland, Massachusetts.

HUELSENBECK, J. P. 1995. Performance of phylogenetic methods in simulation. Systematic Biology 44:17–48.

HUELSENBECK, J. P., AND J. J. BULL. 1996. A likelihood ratio test for detection of conflicting phylogenetic signal. Systematic Biology 45:92–98.

HUELSENBECK, J. P., J. J. BULL, AND C. W. CUNNINGHAM. 1996. Combining data in phylogenetic analysis. Trends in Ecology and Evolution 11: 152–158.

KEMP, A. C., AND T. M. CROWE. 1990. A preliminary phylogenetic and biogeographic analysis of the genera of diurnal raptors. Pages 161–175 *in* Proceedings of the international symposium on vertebrate biogeography and systematics in the tropics (R. Hutterer and G Peters, Eds.). Buseam A. Koening, Bonn, Germany.

KEMP, A. C., AND T. M. CROWE. 1993. Morphometrics

of falconets and hunting behaviour of the Black-thighed Falconet *Microhierax fringillarius*. Ibis 136:44–49.

KIM, J. 1996. General inconsistency conditions for maximum parsimony: Effects of branch lengths and increasing numbers of taxa. Systematic Biology 45:363–374.

KING, A. S. 1989. Functional anatomy of the syrinx. Pages 105–192 *in* Form and function in birds, vol. 4 (A. S. King and J. McLelland, Eds.). Academic Press, New York.

KLUGE, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Systematic Zoology 38:7–25.

KORNEGAY, J. R., KOCHER, T. D., WILLIAMS, L. A. AND A. C. WILSON. 1993. Pathways of lysozyme evolution inferred from the sequences of cytochrome *b* in birds. Journal of Molecular Evolution 37:367–379.

LANYON, S. M. 1993. Phylogenetic frameworks: Towards a firmer foundation for the comparative approach. Biological Journal of the Linnean Society 49:45–61.

LIVEZEY, B. C. 1986. A phylogenetic analysis of recent anseriform genera using morphological characters. Auk 103:737–754.

MIYAMOTO, M. M., AND W .M. FITCH. 1995. Testing species phylogenies and phylogenetic methods with congruence. Systematic Biology 44:64–76.

NELSON, G. 1978. From Candolle to Croizat: Comments on the history of biogeography. Journal of the History of Biology 11:269–305.

NOVACEK, M., AND Q. WHEELER. 1992. Extinct taxa: Accounting for 99.999% of the earth's biota. Pages 1–16 *in* Extinction and phylogeny (M. Novacek and Q. Wheeler, Eds.). Columbia University Press, New York.

PENNY, D., M. D. HENDY, AND M. E STEEL. 1992. Progress with methods for evolutionary trees. Trends in Ecology and Evolution 7:73–79.

PETERS, J. L. 1931. Check-list of the birds of the world, vol. 1. Harvard University Press, Cambridge, Massachusetts.

RAIKOW, R. 1985. Problems in avian classification. Current Ornithology 2:187–212.

RONQUIST, F. 1997. Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. Systematic Biology 46:195–203.

SHARPE, R. B. 1874. Catalogue of birds. British Museum, London.

SIBLEY, C. G., AND J. E. AHLQUIST. 1987. Avian phylogeny reconstructed from comparisons of the genetic material, DNA. Pages 95–121 *in* Molecules and morphology in evolution: Conflict or compromise? (C. Patterson, Ed.). Cambridge University Press, Cambridge, United Kingdom.

SIMON, C., F. FRATI, A. BECKENBACK, B. CRESPI, H. LIU, AND P. FLOOK. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the Entomological Society of America 87:651–701.

SMITH, A. B. 1994. Rooting molecular trees: Problems and strategies. Biological Journal of the Linnean Society 51:279–292.

STEEL, M. E., M. D. HENDY, AND D. PENNY. 1993. Parsimony can be consistent! Systematic Biology 42: 581–87.

SULLIVAN, J., AND D. L. SWOFFORD. 1997. Are guinea pigs rodents? The importance of adequate models in molecular phylogenetics. Journal of Mammalian Evolution 4:77–86.

SWANN, H. K. 1922. A synopsis of the Accipitres. Wheldon and Wesley, London.

SWOFFORD, D. L, G. J. OLSEN, P. J. WADDELL, AND D. M. HILLIS. 1996. Phylogenetic inference. Pages 407–514 *in* Molecular systematics, 2nd ed. (D. M. Hillis, C. Moritz and B. K. Mable, Eds.). Sinauer Associates, Sunderland, Massachusetts.

YODER, A. D., R. VILGALYS, AND M. RUVOLO. 1996. Molecular evolutionary dynamics of cytochrome *b* in strepsirrhine primates: The phylogenetic significance of third-position transversions. Molecular Biology and Evolution 13:1339–1350.

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APPENDIX 1. Descriptions of syringeal anatomy and the 23 syringeal characters; 17 characters are binary and 6 are multistate. Characters 3, 4, 6, and 16 are ordered multistate; characters 5 and 19 are unordered multistate. In all cases, the hypothesized plesiomorphic state is state 0.

Tympanum: Fused *A* elements near the tracheo-bronchial junction

(1) Presence of a tympanum or tracheal drum
- [0] No fusion of A elements
- [1] Ossification and fusion of first A elements

(2) Dorsal fusion of tympanum by medial bar
- [0] Medial bar absent
- [1] First A elements fused medially by ossified bar

(3) Fusion along edges of A elements through ossification of cartilaginous borders separating elements
- [0] Ossified borders not apparent
- [1] Three or four A elements fused along margins of elements
- [2] Heavier fusion, margins somewhat obliterated, light sutures apparent

(4) At least five A fused entirely along edges
- [0] Light fusion or fusion absent
- [1] First five elements heavily fused, some sutures apparent
- [2] Sutures obliterated

(5) Degree of ventral fusion of tympanum
- [0] No ventral fusion of A elements
- [1] First three or four A elements fused partially along margins
- [2] First three or four A fused entirely along margins
- [3] At least five A elements fused entirely along margins, some sutures apparent

(6) Shape of fused and ossified tympanum (partially ordered character; state 3 is a modification of state 2)
- [0] Tympanum absent or not ossified
- [1] Tympanum graduated, widens caudally
- [2] Tympanum cylindrical
- [3] Tympanum cylindrical; A1 laterally flattened causing "pinching in" of most-caudal element

A Elements: Occur on the trachea as single rings but may extend onto the bronchi as paired double rings; they are ossified and flattened in cross-section

(7) Ridge covering dorsal A1 ends
- [0] Ridge absent
- [1] Ridge of ossified tissue forms medial ridge over A1 ends, covers dorsal ascent of pessulus

(8) Separation of dorsal A1 ends
- [0] A1 ends separated
- [1] Ends close medially, fused by ossified tissue

(9) Size of A1 ends
- [0] A1 single or width of ends similar to width medial
- [1] Dorsal ends very enlarged

(10) Flattening of paired A1 elements
- [0] A1 single element, or rounded half rings
- [1] A1 flattened dorsoventrally into parenthetical shape; laterally, A1 dorsal and ventral ends protrude

(11) Appearance of A1 on lateral view
- [0] A1 concave up medially
- [1] A1 flattened medially

B Elements: Occur as paired rings on the bronchi and are generally cartilaginous and D-shaped in cross-section

(12) Abrupt change in shape and orientation of B1 ends
- [0] B1 ends change gradually or are unchanged
- [1] B1 ends thick and wide, ascend abruptly in L-shape to fuse with A1

(13) Change in orientation of B1 ends
- [0] B1 ends change shape or ends maintain orientation
- [1] B1 ends thin, ascend gradually to fuse with A1

(14) Knobbing of B1 ends
- [0] No knobbing
- [1] Craniad edges knobbed, fused with A1 ends

(15) Gradual change in shape and orientation of B1 ends
- [0] B1 ends thin or L-shaped
- [1] B1 ends thicken; ends are rounded and ascend gradually to fuse with A1

(16) Fusion of B element ends
- [0] No fusion of B elements
- [1] B2 ends fused to B1/A1
- [2] B3 ends fused forming ridge bordering medial (internal) membrane

APPENDIX 1. Continued.

Muscles and Membranes
(17) Existence of lateral (external) membrane on bronchi
[0] Membrane absent
[1] Membrane present and located between A1 and B1
(18) Presence of cartilaginous bar on lateral membrane
[0] Bar is absent
[1] Bar is present M. tracheolateralis inserts on bar
(19) Presence of membranous extension of lateral membrane onto which M. tracheolateralis inserts
[0] Membranous extension is absent
[1] Thick, bulbous membrane on dorsal half of membrane
[2] Thick, bulbous membrane covers entire width of membrane
(20) Insertion of M. tracheolateralis onto lateral membrane
[0] Membrane absent or modified
[1] M. tracheolateralis inserts directly onto dorsal half of lateral membrane
(21) Cartilaginous border on (medial) membrane
[0] Border is absent
[1] Internal (medial) membrane has some cartilage on caudal border
(22) Complete border on internal membrane from A1 dorsal to A1 ventral ends
[0] Border absent or incomplete
[1] Thick, even, concave border on internal membrane from A1 dorsal to A1 ventral ends
Accessory Cartilaginous Structures: Occur on internal bronchial membranes
(23) Presence of thin, amorphous accessory structure extending from border
[0] Accessory structure absent
[1] Cartilage forms straight caudal edge from dorsal to ventral ends

APPENDIX 2. Data matrix of 23 synringeal characters for 22 falconids and 3 outgroup species.

Species	Character																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Accipiter striatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pelecanus onocrotalus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Otus asio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Daptrius americanus	1	0	0	1	3	1	0	0	0	1	0	0	0	0	1	0	1	0	2	0	1	0	1
D. ater	1	0	0	1	3	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0
Falco berigora	1	0	2	0	2	2	1	0	0	0	0	0	0	1	0	2	1	0	2	0	1	1	0
F. biarmicus	1	0	1	0	2	2	0	0	0	0	0	0	0	1	0	2	1	1	0	0	1	1	0
F. cenchroides	1	0	1	0	2	2	1	0	0	0	0	0	0	1	0	1	1	0	2	0	1	1	0
F. columbarius	1	0	1	0	2	2	0	0	0	0	0	0	0	1	0	2	1	0	2	0	1	1	0
F. femoralis	1	0	1	0	2	2	0	0	0	0	1	0	0	1	0	2	1	0	2	0	1	1	0
F. mexicanus	1	0	1	0	2	2	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	1	0
F. peregrinus	1	0	1	0	2	2	0	0	0	0	0	0	0	1	0	2	1	1	0	0	1	1	0
F. rufigularis	1	0	1	0	2	2	0	0	0	0	1	0	0	1	0	2	1	0	2	0	1	1	0
F. sparverius	1	0	1	0	2	2	1	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0
Herpetotheres cachinnans	1	0	2	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Micrastur gilvicollis	1	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	1
M. semitorquatus	1	1	0	0	1	2	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0
Microhierax erythrogonys	1	0	2	0	2	3	1	0	0	0	0	0	1	0	0	0	1	0	2	0	1	1	0
Milvago chimachima	1	0	0	1	3	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0
M. chimango	1	0	0	1	3	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0
Phalcoboenus australis	1	0	0	1	3	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0
Polihierax semitorquatus	1	0	1	0	2	3	0	0	0	0	0	0	1	0	0	0	1	0	2	0	1	1	0
P. insignis	1	1	0	0	2	1	0	0	0	0	0	0	0	1	0	1	1	0	2	0	1	0	1
Polyborus plancus	1	0	0	2	3	1	0	1	0	1	0	0	0	0	1	0	1	0	2	0	1	0	1
Spiziapteryx circumcinctus	1	0	2	0	2	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	1	1	0