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MONOPHYLY OF THE FALCONIFORMES BASED ON SYRINGEAL MORPHOLOGY

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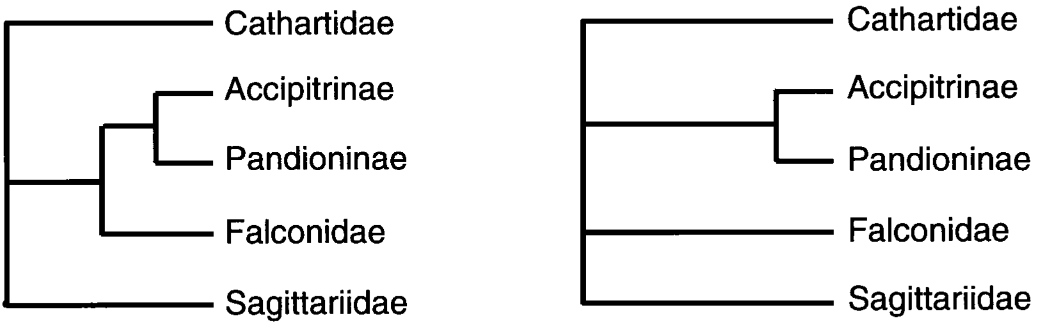
ABSTRACT.—The systematic relationships of the diurnal birds of prey (Falconiformes) are unresolved. The monophyly of the order has not been established, and the relationships of the families within the order and of genera within the three polytypic families are unclear. To derive a phylogeny for the order and to assess the usefulness of the syrinx for resolving the systematics of nonpasserines, I analyzed variation in syringeal morphology of genera within each of the currently recognized families in the order as well as among four orders of outgroups. The phylogeny derived from these syringeal data supports the monophyly of the Falconiformes. In addition, syringeal data provide strong support for the monophyly of three clades within the Falconiformes: the Cathartidae; the Falconidae; and an Accipitrinae-Sagittariidae-Pandioninae cluster. The Cathartidae are positioned as basal to the other two clades. Overall results indicate that syringeal morphology is conservative, with most of the informative variation occurring at higher systematic levels. *Received 10 May 1993, accepted 24 October 1993.*

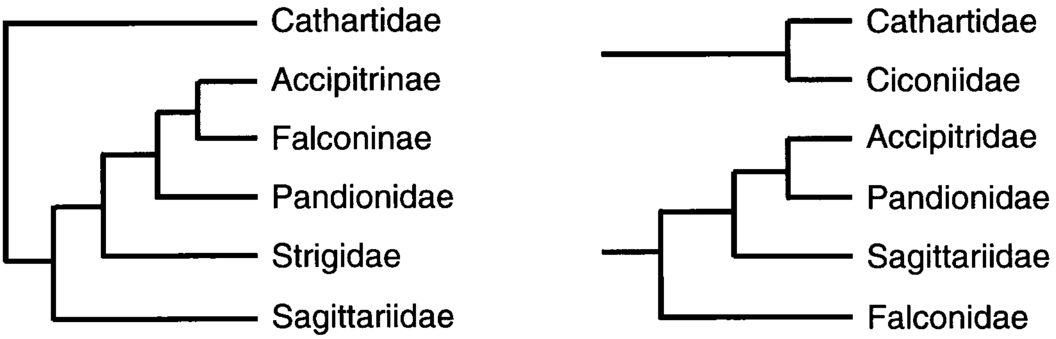
OF THE APPROXIMATELY 30 orders of birds, the order Falconiformes offers some of the more interesting systematic questions; the monophyly of the order is in question, as are relationships of families within the order, and of genera within each of the families. Falconiformes currently consists of 76 genera and 290 species divided into four families (Stresemann and Amadon 1979): Accipitridae, including Accipitrinae (hawks and eagles, 59 genera, 217 species) and Pandioninae (Osprey, monotypic); Falconidae (falcons, 10 genera, 62 species); Cathartidae (New World vultures, 5 genera, 7 species); and Sagittariidae (Secretarybird, monotypic).

Comprehensive reviews of the history of falconiform classification have been published previously (Jollie 1976, Sibley and Ahlquist 1990), and only a summary will be presented here. The order historically has been united by several external morphological characters (hooked beak and curved talons) and by several internal characters (biceps slip absent, ambiens present, caeca rudimentary; Beddard 1898). However, four current classifications disagree on the monophyly of the order, and on subordinal and familial relationships (Fig. 1). Two consider the order monophyletic (Stresemann and Amadon 1979, Storer 1971), while the other two propose either removal of the Cathartidae from the order (Sibley and Ahlquist 1990) or inclusion of Strigiformes (owls) within the order (Cracraft 1981).



Storer 1971

Stresemann and Amadon 1979



Cracraft 1981

Sibley and Ahlquist 1990

Fig. 1. Four recent, conflicting classifications of the Falconiformes.

The idea that the Cathartidae may not belong in the order has been proposed previously based on morphological and behavioral differences of this family from others in the Falconiformes. In addition, similarities of cathartids to other groups have been noted, including the Ciconiidae (Garrod 1873, Beddard 1898, Ligon 1967, Rea 1983), Pelecaniformes (Beddard 1898, Jollie 1976), Procellariiformes (Jollie 1976), and Gruiformes (Pycraft 1902). Friedmann (1950:6) stated that the Cathartidae were a primitive group not differentiated from the "primitive stock from which the Ciconiiformes, Pelecaniformes and Procellariformes have been developed."

Hypotheses of a falconiform-strigiform relationship have been advanced at various times, based on similarities of palatal and myological characters (reviewed in Sharpe 1891, Cracraft 1981, McKitrick 1991). Pandioninae (Sharpe 1891, Pycraft 1902) and Falconidae (Beddard 1898, Brown and Amadon 1968) have been suggested as links between falconiforms and strigiforms.

Relationships of the Falconiformes to other orders have also been proposed, including the orders Pelecaniformes, Ciconiiformes and Psittaciformes (reviewed in Sharpe 1891, Shufeldt 1909), Gruiformes (Shufeldt 1909), Cuculiformes and Columbiformes (Verheyen 1950, reviewed in Jollie 1977). The AOU (1983) *Check-list* places the Falconiformes between Anseriformes and Galliformes, whereas Sibley and Ahlquist (1990) position the order (with Cathartidae removed) as sister taxon to a group including the Podicipedidae, Sulidae, Phalacrocoracidae, and Phaethontidae.

Syringeal morphology had been used in the classification of the major subdivisions of the Passeriformes at the end of the nineteenth century (Ames 1971). Within the last 20 years, syringeal data have again become important in the systematics of oscines and suboscines (e.g. Ames 1971, Warner 1972, Lanyon 1984, Prum 1990, 1992), but have not strongly influenced the systematics of other orders. There have been no detailed reports on falconiform syringeal anatomy since Beddard (1903), and no systematic analysis of that anatomy.

I examined patterns of variation in syringeal morphology within the Falconiformes to assess the usefulness of the syrinx for systematics of nonpasserines (i.e. whether there are phylogenetically informative syringeal characters) and to answer two primary systematic questions: (1) Is the order monophyletic? (2) What are the relationships of the major clades within the order?

MATERIALS AND METHODS

Specimens.—I examined syringes from collections at the American Museum of Natural History (AMNH), the National Museum of Natural History (USNM), the Royal Ontario Museum (ROM), the University of Kansas Museum of Natural History (KUMNH), the Museum of Vertebrate Zoology of the University of California at Berkeley (MVZ), and the Louisiana State University Museum of Natural Science (LSUMNS), some of which I dissected from fresh or alcohol-preserved specimens. These were cleared and double-stained to distinguish cartilaginous and ossified tissue (Cannell 1988). Observations were made using a Wild M5A dissecting microscope, and drawings made with a camera lucida. Drawings were scanned into a Macintosh computer and final illustrations prepared using Aldus Freehand 2.0.

I analyzed 124 falconiform syringes and 66 syringes from purported outgroups (Appendix 1). Three of the five cathartid genera and all falconid genera were included. Within the Accipitridae, genera were chosen to represent each of the previously proposed subgroups; these totaled 60% of the currently recognized genera. In general, sampling within the ingroup was constrained by the availability of specimens. Two or more individuals from 27 species were analyzed to assess variation at the intraspecific level.

Analysis.—Variation in morphology was coded using both binary and multistate characters. Multistate characters were ordered if either of two criteria was satisfied. Similarity of derived states was the primary criterion used (Patterson 1982). Thus, transformation series were proposed if adjacent derived states were similar, and each succeeding state was a modification of the previous state (i.e. the derived states formed a nested set of synapomorphies). Transformation series also were proposed using ontogenetic information (character 7). Justifications used for ordering are discussed in the character descriptions (Appendix 2). Multistate characters were coded as unordered if states were alternative variations of a character.

I used outgroup information to polarize characters (Maddison et al. 1984). However, the relationships of other orders to the Falconiformes are unclear, and the choice of an appropriate outgroup is not readily apparent. Species from four orders of birds were included in the analysis. A comprehensive subset of genera in the Ciconiiformes and Strigiformes was examined because there are phylogenetic hypotheses of relationships of these orders to the Falconiformes. In addition, species within the Pelecaniformes were added because several authors suggested a relationship of this order to the Falconiformes (Beddard 1898, Shufeldt 1909, Friedmann 1950, Jollie 1976). Because monophyly of the Falconiformes could not be assumed, species from these other orders were not treated as outgroups in the analysis, nor was there a constraint on monophyly imposed in the analysis (Maddison et al. 1984). Species within the Galliformes were used to root the cladogram. I used PAUP 3.0s (Swofford 1991) to derive the most-parsimonious resolution of the data. The size of this data set precluded the use of exact algorithms for resolving the data; therefore, the heuristic algorithm was used. However, this option does not guarantee optimality and may identify a solution that is only locally optimal. To increase the probability of finding solutions that were globally optimal, analyses were repeated varying both the branch-swapping and taxa-addition options.

Three indices were used to assess the congruence of the characters hypothesized as synapomorphies (Farris 1989): (1) consistency index, which is the minimum amount of change of a character divided by the amount observed on the tree; (2) rescaled consistency index, which is a linear rescaling of the consistency index so that values vary from 0 to 1; and (3) retention index, which is the proportion of original characters remaining as synapomorphies. Consensus methods were used to summarize information from the set of most-parsimonious trees. I used strict-consensus trees, which include groups found in each of the most-parsimonious cladograms, and majority-rule trees, which include groups found in a defined proportion of cladograms. Consensus trees must be interpreted with care as they may not be parsimonious reconstructions of the original data (Swofford 1992). Nevertheless, consensus trees remain an efficient way for highlighting congruent clades, and the characters and taxa causing incongruence.

RESULTS

Syringeal morphology.—The main components of a typical accipitrid syrinx (i.e. supporting elements, membranes, and muscles) are illustrated in Figure 2. Definitions of syringeal struc-

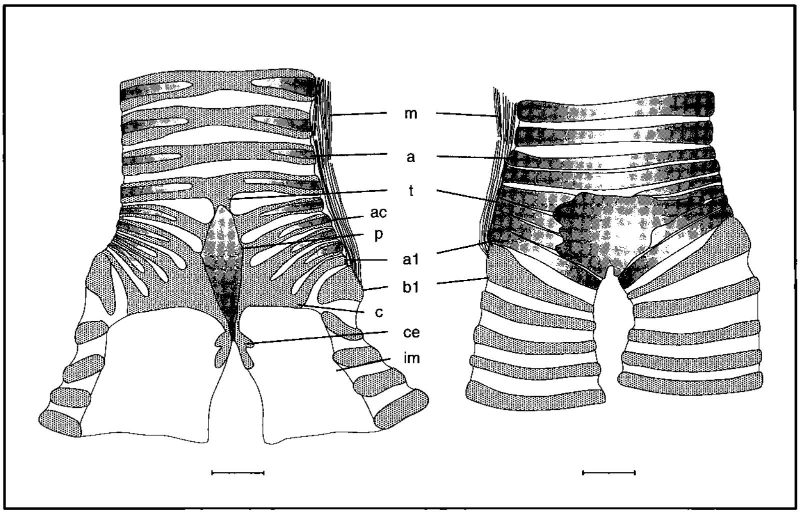


Fig. 2. Accipitridae syrinx (Broad-winged Hawk, *Buteo platypterus,* AMNH 20008). Left-dorsal view and right-ventral view. Abbreviations (numbers following refer to characters in Appendix 2): (a) *A* elements (1.2); (a1) A1 elements (3, 23); (ac) complete double *A* elements (5); (b1) B1 elements (34.4, 36); (c) accessory cartilaginous structure (44, 45.2); (ce) cartilaginous extension of A1 and A2 (12); (im) internal membrane; (p) pessulus (22.4); (t) tympanum (20, 21.1 24.2, 29.3); (m) M. tracheolateralis. See text for definitions of structural elements. In all illustrations, scale bar is 1 mm, stippling indicates cartilaginous tissue, and gray shading indicates ossified tissue.

tures follow Ames (1971) and include four types of supporting elements: *A* and *B* ringlike elements, the pessulus, and accessory cartilaginous structures. Ames (1971) used three criteria for defining *A* and *B* elements: composition, cross-sectional shape, and orientation of concavity. *A* elements are ossified and flattened in cross section, occurring on the trachea as single rings but sometimes extending onto the bronchi as paired double rings. They may be complete (forming a closed ring) or incomplete. In addition, they may be fused partially or completely near the tracheo-bronchial junction, forming a drum or tympanum. *B* elements are generally cartilaginous and *D*-shaped in cross section, occurring as paired rings on the bronchi. These may be complete rings or may have an opening on the medial surface of each bronchus. The pessulus, a cartilaginous or ossified bar, is located on the midsagittal plane between the bronchi. The dorsal and ventral ends of the pessulus may be free or may fuse to *A* or *B* elements. Finally, accessory cartilaginous structures occur on the craniad edge of the internal membranes.

The definitions of *A* and *B* elements differ from traditional terminology in which ringed structures are tracheal or bronchial rings (King 1989) based on the relative position of the structures to the tracheo-bronchial junction. There are no homologies that can be postulated using traditional names. For example, the external membrane in falconid genera is located between the second and third, third and fourth, or fourth and fifth bronchial rings. When these rings are recognized as *A* and *B* elements, however, this membrane is always between A1 and B1, a synapomorphy for the family. Definitions of rings as *A* and *B* elements have been used in systematic studies of oscines and suboscines (Ames 1971, Lanyon 1984, Prum 1990, 1992, 1993) and, in limited detail, to a broad range of orders (Cannell 1986). My analysis is the first application of these definitions to detailed structures in orders other than Passeriformes.

Ames' (1971) criteria for defining *A* and *B* elements are sufficient for most of the families used in this analysis. A1 and B1 can be differentiated by cross-sectional shape and composition in the Cathartidae, Ciconiidae, Ardeidae, Falconidae, and Strigiformes. However, because the first *B* elements in several Accipitridae species are highly ossified, these criteria alone could not always differentiate *A* and *B* elements. I used an additional criterion, the distinctive shape of the B1 element, for the accipitrids in this analysis. The first *B* element is wider medially than other *A* and *B* elements, with narrower ends. This was corroborated by the congruence of muscle insertion; the M. tracheolateralis always inserted on B1 when B1 was defined using these criteria.

In addition to structural elements, the syrinx is composed of two kinds of syringeal membranes. The internal membranes are located on the medial surface of the bronchi between the dorsal and ventral ends of incomplete *A* and *B* elements. These are considered to be the sound-producing structures (Gaunt and Gaunt 1985) and occur in all species examined except the ciconiids. The external membranes are on the lateral walls of the bronchi, usually between A1 and one or two of the first four *B* elements. Although the location of an external membrane is a synapomorphy for the Falconidae, the existence of external membranes is variable within most of the other families examined and may be correlated with structural modifications in elements bordering the membranes. Therefore, this character was of limited use in my analysis.

There are also two classes of syringeal muscles. Intrinsic muscles originate and insert on syringeal elements and are important in the systematics of the Passeriformes. These do not exist in falconiforms. The two extrinsic muscles originate outside the syrinx. The M. sternotrachealis originates on the internal surface of the coracoid or costal process of the sternum and inserts on several *A* elements on the trachea. The M. tracheolateralis originates on the lateral surface of the cricoid cartilage of the larynx and descends laterally down the trachea. In many taxa it is contiguous with or underlies the M. sternotrachealis, and the insertion of this muscle can be somewhat obscured as a result. Because muscle fibers are damaged in cleared specimens, the insertions of these muscles were not always apparent in specimens I examined and were of limited use phylogenetically. Where visible, the M. tracheolateralis inserts: on A1, B1 and possibly B2 in the Ardeidae; on B1 in the accipitrids (including *Pandion* and *Sagittarius*) and in the Strigiformes; and on the lateral membrane in the falconids. This muscle has been claimed to be lost in *Struthio, Casuarius, Dromaius, Rhea, Apteryx,* the Cathartidae, Ciconiidae, most Pelecaniformes, and some Galliformes (Beddard 1898, King 1989). Within the ratites, however, the muscle exists but ends where the M. sternotrachealis begins (King 1989). Similarly, I observed muscle fibers in a *Coragyps* syringeal specimen, laterally on the trachea, ending cranial to the junction. These muscles have also been described in *Cathartes* (Maynard 1897) and are probably the M. tracheolateralis, but this diagnosis must be confirmed in intact specimens.

Intraspecific variation in morphology.—Assessment of intraspecific variation revealed several characters that were polymorphic in species within the Falconidae and Accipitridae and were not used in this analysis. The number of *A* elements fused ventrally in the tympanum varied in *Buteo platypterus* (5, 6, or 7), in *Accipiter striatus* (5 or 6), and in *Falco sparverius* (3 or 4). The size of the ventral, ossified patch covering the fused tympanum rings varied within *Buteo* and *Leucopternis* species. Finally, the B1 element, although normally cartilaginous, was partially to totally ossified within several species, the amount of ossification varying intraspecifically.

I found no sexual dimorphism in the species for which this information was available. General patterns in ontogenetic variation were found. Ossification of the tympanum and *A* elements increased in adults compared to juveniles in *Tyto, Buteo, Falco, Pandion, Accipiter* and *Cathartes.* Fusion of the elements in the tympanum also increased slightly in adults compared to juveniles of *Pandion, Tyto* and *Falco.* Both of these patterns are consistent with observations in the Passeriformes (Ames 1971). An additional pattern was found in the Cathartidae. In nestling *Cathartes,* single *A* elements immediately cranial to the tracheo-bronchial junction are complete rings. In adults, these are incomplete, with gaps dorsally (character 7).

Phylogenetic analysis of Falconiformes.—Variation in syringeal morphology was coded initially for 103 taxa as 49 characters, of which 33 were binary and 16 were multistate (Appendix 2). Redundant species (those with identical character states) were merged, resulting in a final matrix of 88 taxa (Table 1). Analysis of these data resulted in more than 5,000 most-parsimonious cladograms, which is not unexpected for a matrix with more taxa than characters. The shortest trees found had a length of 195, consistency index of 0.401, rescaled consistency index of 0.358, and retention index of 0.865.

The strict-consensus tree (Fig. 3) indicates support for the monophyly of the order Falconiformes. Within the order, Cathartidae is basal to a clade of two sister taxa, the Falconidae

TABLE 1. Distributions in 88 taxa of states of 49 syringeal characters used in phylogenetic analysis. See Appendix 2 for descriptions.

Taxon	Character (1–49) 1234567890123456789012345678901234567890123456789
	Accipitridae
Accipiter cooperii	1010100000012011001114120000400003010012000120101
A. gentilis	1010100000010011001114120000400002010010000120011
A. virgatus	1010100000011011001114120000400002010001000120010
A. striatus	1010100000011011001114120000400002010010000120001
Aegypius	1010100000012011001112120000200003010000000120000
Aquila	1010100000010011001112110000300003010001000110000
Aviceda	1010100000002011001123110000300003010012000120000
Busarellus	2010100000012011001124130000400004010012000120000
Butastur	1010100000010011001113021000400001010001000120000
Buteo albicaudatus	1010100000010011001114120000300004010000000110000
B. buteo	0010100000010011001112120000300004010000000110000
B. jamaicensis	1010100000011011001114120000300004010000000120000
B. magnirostris	1010100000010011001112120000300003010000000120000
Buteogallus	1010100000010011001112110000300004010002000110000
Circaetus	1010100000011011001102110000300003010002010110000
Circus	1010100000012011001114120000400002010002000120010
Elanoides	1010100000011011001112120000300003010001000120000
Elanus	2010100000000011001122110000100003010000000110000
Gampsonyx	2010100000000011001122130000400001000000000110000
Geranospiza	2010100000010011001123120000300002010011000120100
Gypaetus	1010100000010011001112120000300003010000010121000
Haliaeetus	1010100000010011001112110000300003010000000110000
Haliastur	1010100000011011001112121000300003010001000120000
Harpagus	1010100000010011001112120000300005010001000120000
Henicopernis	1010100000010011001123120000300005010000000120000
Heterospizias	1010100000010011001112120000300003010002000120000
Hieraaetus	1010100000011011001113120000300003010001000120000
Ichthyophaga	1010100000012011001112120000300003010001000120010
Ictinia	1010100000011011001112120000300003010002000120100
Kaupifalco	1010100000011011001123120000400001010002000120000
Leptodon	2010100000010011001123130000300002000000000120000
Leucopternis kuhli	1010100000010011001113120000300003010000000120000
L. albicollis	1010100000010011001114120000300004010001000120000
Melierax	1010100000010011001112120000300005010000000120001
Milvus	1010100000011011001112121000300003010001000120010
Necrosyrtes	1010100000010011001112120000200003010000000111000
Neophron	1010100000000011001112121000200003010000010111000
Parabuteo	1010100000011011001114120000300004010001000120000
Pithecophaga	1010100000010011001112120000300003010000010110010
Rostrhamus	1010100000011011001122120000400004010001000120001
Spilornis	1010100000011011001112120000300003010002000120000
Spizaetus	1010100000011011001112121000300003010002010120000
Terathopius	1010100000011011001112110000300003010002000120000
Pandion	1010100000013011001115010000300001000002100120000
	Sagittariidae
Sagittarius	2010100000000011001122130000020000110002010120000
	Falconidae
Daptrius americanus	2010100000000011001121000100030010004100100130000
D. ater	2010100000000011001121000100030010004100100140000
Falco berigora	2010100001000011001121000202020010003300100130000
F. columbarius	2010100000000011001121000201020010003301100130000
F. mexicanus	2010100000000011001121000201020010003200100130000
F. rufigularis	2010100000000011001121000201020010003300100130000
F. sparverius	2010100001000011001121000201020010003200100130000
Herpetotheres	2010100000000011001121000101020010003000100000000

TABLE 1. Continued.

Taxon	Character 1 2 3 4 1234567890123456789012345678901234567890123456789
Micrastur gilvicollis	2010100000000111001121000110010010001100100130000
M. semitorquatus	2010100000000111001121000210010010001100100140000
Microhierax	2010100001000011001121000302020010002100100130000
Polihierax insignis	2010100000000011001121000110020010003200100140000
P. semitorquatus	2010100000000011001121000301020010002100100130000
Polyborus	2010100000000011001121000100030010004100100130000
Spiziapteryx	2010100000000011001121000102020010003000100130000
Cathartidae	
Cathartes	2010112100000011011000000000000000000000000000000
Coragyps	2010111100000011001000000000000000000000000000000
Vultur	2010112100000011010000000000000000000000000000000
Ardeidae	
Ardea	2011000000000011100000000000000000010000001000000
Bubulcus	2010000000000011100000000000000000000000011000000
Butorides	2010000000000011100000000000000010000000001000000
Egretta	1010000000000011100000000000000000000000001000000
Ixobrychus	2011000000000011100000000000000000000000001000000
Nycticorax	2010000000000011100000000000000000000000001000000
Ciconiidae	
Mycteria	2100000000000010000000000000001000000000000000000
Tytonidae	
Phodilus	2010000010000021010000000000000002000000000000000
Tyto	2010100010000011010000000000000002000000000130000
Strigidae	
Aegolius	2011000010100011010000000000000102000000000000000
Asio otus	2011000010100021010000000000000103000000000000000
A. stygius	2011000010100011010000000000000103000000000000000
Bubo virginianus	2011100010100021010000000000100103000000000000000
Ciccaba huhula	2011000010100021010000000000000102000000000000000
C. virgata	1011000010100021010000000000000102000000000000000
Ketupa ketupu	0011000010100021010000000000100103000000000000000
Ninox connivens	2011000010000011010000000000000103000000000000000
N. odiosa	2011100010100011010000000000100103000000000130000
N. jacquinoti	2011000010100021010000000000100103000000000000000
Nyctea	1011000010000021010000000000100103000000000000000
Otus asio	2011100010100021010000000000000103000000000000000
O. watsonii	2011100010100011010000000000000103000000000000000
Sulidae	
Sula	2010000000000011000000000000100000000000001000000
Pelecanidae	
Pelecanus	0010000000000000000000000000000000000001000000000
Galliformes	0010000000000011000000000000000000000000000000000

and the Accipitridae (including *Sagittarius* and *Pandion*). Two derived characters unite the three clades in the order. All species have complete, double *A* elements on the bronchi; these also occur in several strigiform genera (character 5). Species also have an ossified pessulus, which is connected dorsally and ventrally to *A* elements; the dorsal attachment is lost in *Vultur* (character 19). Four characters unite the Falconidae and the Accipitridae as sister taxa. Species in these families have a tympanum composed of *A* elements fused ventrally and dorsally, to which the pessulus is attached (characters 20, 22). In addition, these species have sheets of cartilaginous tissue forming a border cranially on the internal membranes (character 44). The tym-

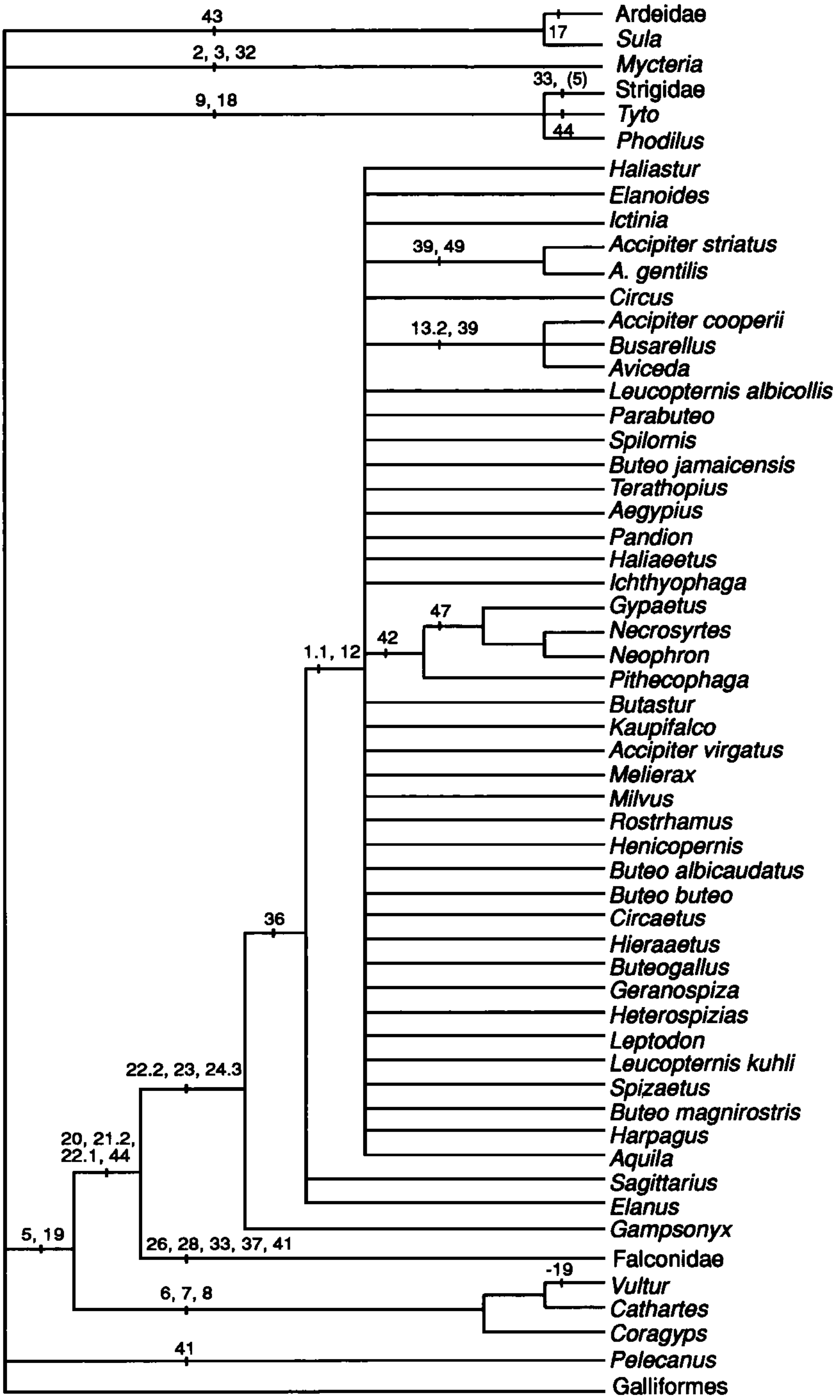


Fig. 3. Summary of strict-consensus tree derived from the set of 5,000 most-parsimonious trees found from analysis of syringeal data. Synapomorphies supporting nodes are numbered; descriptions of characters in Appendix 2.

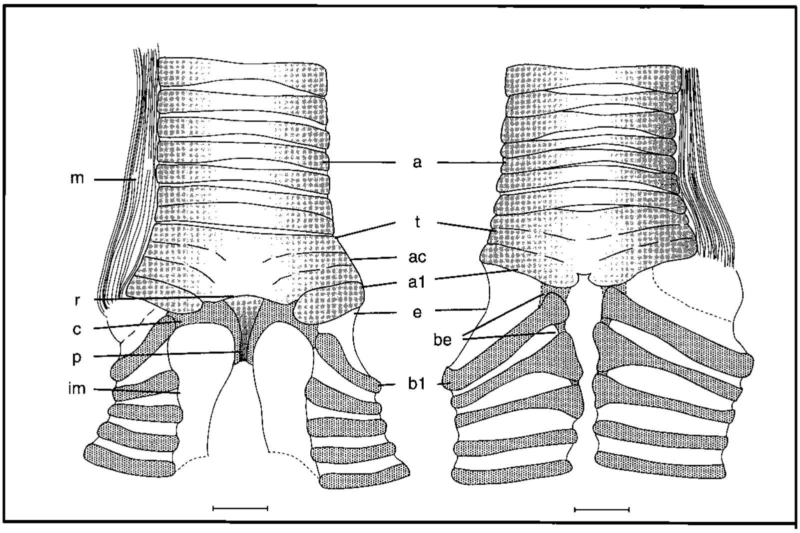


Fig. 4. Falconidae syrinx (Brown Falcon, *Falco berigora*, AMNH 193358). Left-dorsal view and right-ventral view. Abbreviations: (a) *A* elements (1.1); (a1) A1 elements (3); (ac) complete double *A* elements (5); (b1) B1 elements (33, 37); (be) fusion of element ends (38.3); (c) accessory cartilaginous structure (44, 45.3); (e) external membrane (41); (im) internal membrane; (p) pessulus (15, 16); (r) ossified ridge (9); (t) tympanum (20, 21.2, 26.2, 28.2, 30.2).

panum is ossified totally in falconid species and in the most basal accipitrid species, but an alternative pattern (lack of ossification dorsally) exists in most of the other accipitrids (character 21).

There is strong support for the monophyly of the Falconidae. The falconid syrinx (Fig. 4) is characterized by a completely ossified tympanum, an ossified pessulus fused dorsally and ventrally to the tympanum, a lateral membrane located between A1 and B1 on which the M. tracheolateralis inserts, B1 elements evenly wider than other *B* elements, and fusion of the ends of incomplete A1 and B1 elements (characters 26, 28, 33, 37, 41). A phylogeny of the Falconidae is presented in a separate paper (Griffiths 1994).

The three genera of cathartids included in

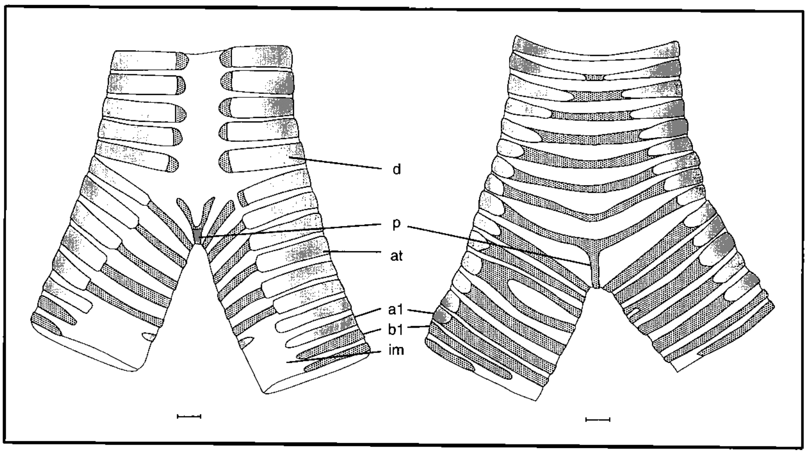


Fig. 5. Cathartidae syrinx (Turkey Vulture, *Cathartes aura*, AMNH 20933). Left-dorsal view and right-ventral view. Abbreviations: (a) complete double *A* elements (6, 8); (a1) A1 elements; (as) incomplete single *A* element (7); (b1) B1 elements; (im) internal membrane; (p) pessulus (16, 18).

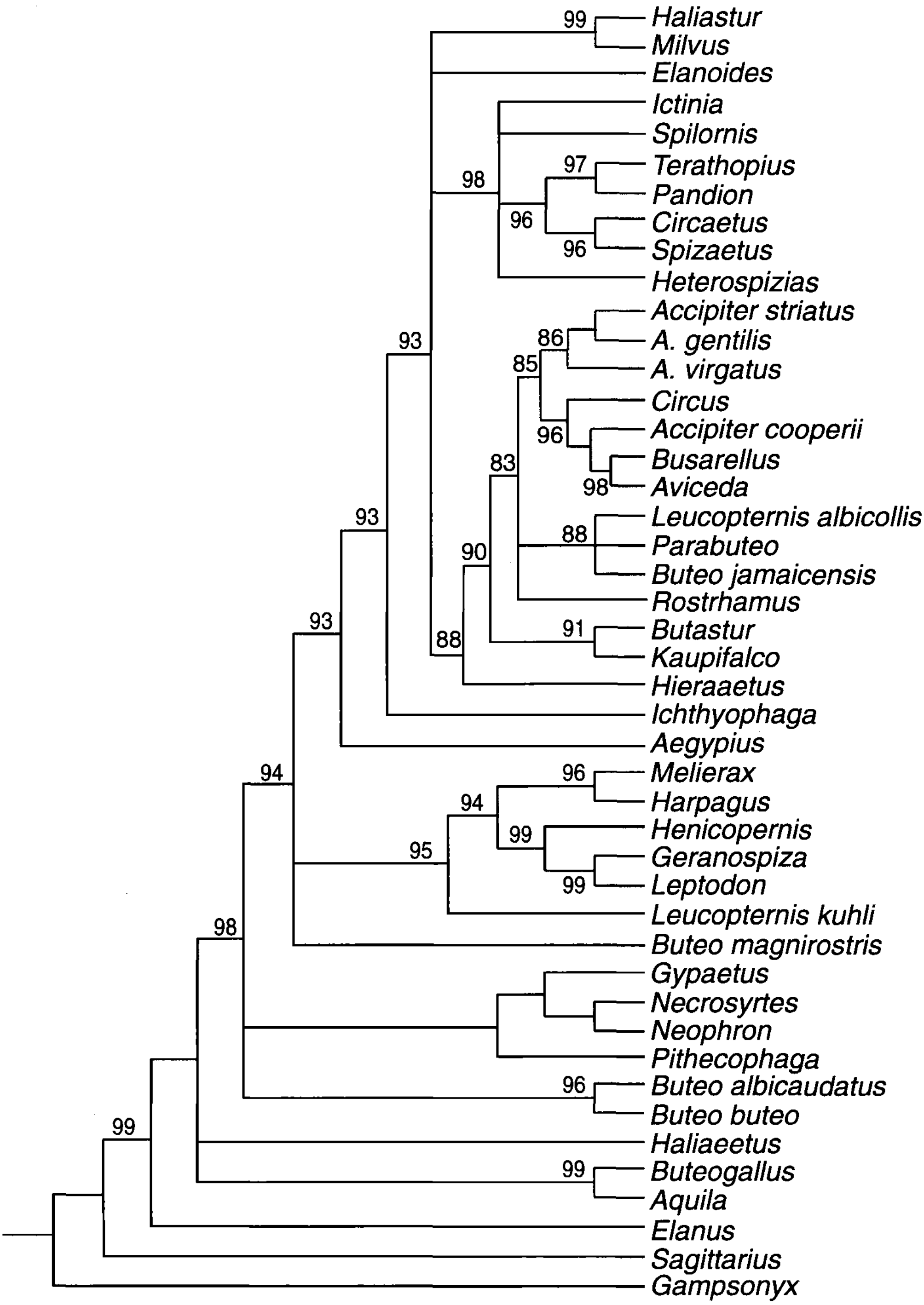


Fig. 6. An 80% majority-rule consensus tree of genera in Accipitridae. Clades illustrated are supported in at least 80% of the most-parsimonious trees. Numbers indicate percent support; nodes without numbers are supported in 100% of most-parsimonious trees.

my study are united by three unambiguous synapomorphies. *Coragyps* is the sister taxon to *Cathartes* (Fig. 5) and *Vultur*. Cathartid species are commonly considered as lacking a syrinx (Ligon 1967, Rea 1983, Gill 1990). Although the cathartid syrinx does lack some modifications occurring in other falconiform syringes, it has internal membranes, an ossified pessulus, characteristic ossification of *A* elements, and probably (as noted above) the M. tracheolateralis. The unique modifications characterizing cathartid syringes include dorsal gaps in the most caudal single *A* elements, and a minimum of four complete, medially thin, double *A* elements on the bronchi (characters 6, 7, 8).

Phylogeny of Accipitridae.—Syringeal data group *Sagittarius* and *Pandion* with the accipitrid genera; this clade is supported by three derived characters (characters 22.2, 23, 24.3). In these genera, A1 is not fused ventrally to the tympanum, although fusion and ossification of the tympanum is more extensive ventrally than dorsally. In addition, the dorsal attachment of the pessulus to the tympanum forms characteristic patterns different from the falconid pattern.

Limited sampling of genera and the lack of phylogenetically informative variation of the syrinx preclude my deriving a fully resolved phylogeny for the Accipitridae and impose constraints on the inferences that can be derived from this analysis. Nonetheless, there are some findings of interest, illustrated in the majority-rule tree (Fig. 6), and some results that indicate the need for further research.

Syringeal data support the polyphyly of the kites. The 17 genera currently considered to be kites have been grouped based on their predatory and social behavior and have been considered primitive to the other accipitrids (Brown and Amadon 1968), but the monophyly of this group has been questioned (Amadon and Bull 1988). There is support for the close relationship of the Old World milvine kites, *Haliastur* and *Milvus*, which are sister taxa in 99% of the trees (Fig. 6). Two kites, *Elanus* and *Gampsonyx*, currently grouped together with *Chelictinia* in the Elaninae (Brown and Amadon 1968) are not sister taxa, but are among the most basal accipitrid genera.

Butastur and *Kaupifalco* are thought to be closely related (Amadon and Bull 1988), and they are sister taxa in this analysis. Several other species groupings within the Accipitridae are not supported by syringeal data. The serpent eagles (*Terathopius*, *Spilornis*, and *Circaetus*) are in a clade with four other species and are not sister taxa. The five genera of sub-buteonines included in this analysis are widely separated. However, two taxa, *Parabuteo* and one of the *Leucopternis* species, form a monophyletic group with *Buteo jamaicensis*.

There are no syringeal characters uniting the four Old World vultures included in this analysis. *Aegypius* is separated from a clade of three genera (*Gypaetus*, *Necrosyrtes*, and *Neophron*), which are united by one unambiguous synapomorphy (character 47). Similarly, there are no derived characters supporting the monophyly of the two largest genera, *Accipiter* and *Buteo*. Three of the *Accipiter* species are clustered together, while the fourth, *A. cooperii*, is in a sister clade with *Circus*, *Busarellus* and *Aviceda*. There are also no characters supporting the sister taxa relationship of *Heterospizias* and *Buteogallus*, two species that have recently been synonymized (Amadon 1982).

Outgroup relationships.—I used outgroups in this study to polarize characters. Sampling of genera within the four orders of outgroups was not comprehensive enough, nor were enough orders included to derive a phylogeny at the ordinal level. Findings of my study, therefore, should be interpreted with care. Nevertheless, as a result of the more extensive examination of genera within the Ciconiiformes and Strigiformes, some conclusions can be drawn. Syringeal characters support the monophyly of each of the two families of Ciconiiformes included in the analysis but do not support the monophyly of the order. Three derived characters cluster the three genera of Ciconiidae (characters 3, 4, 47; Fig. 7), while one derived character (character 20) unites the six genera of the Ardeidae examined.

Syringeal data also support the monophyly of the Strigiformes. Of the two currently recognized families, Tytonidae and Strigidae, there are derived characters uniting only one, the Strigidae (characters 6, 12, 48, 52). *Tyto* and *Phodilus* are in unresolved positions relative to the Strigidae.

DISCUSSION

Systematics and the syrinx.—Syringeal data, in particular the variation in intrinsic musculature, have been important in the systematics of

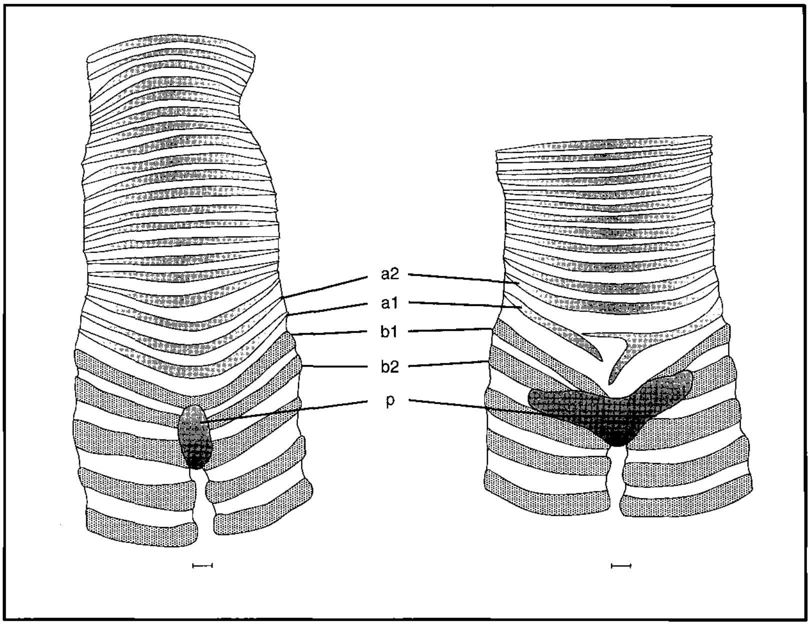


Fig. 7. Ciconiidae syrinx (White Stork, *Ciconia ciconia*, AMNH 1936). Left-dorsal view and right-ventral view. Abbreviations: (a1) A1 element; (a2) A2 element (2); (b1) B1 elements; (b2) B2 elements (31); (p) pessulus.

the oscines and suboscines, but these data have been virtually ignored in the systematics of most other orders of birds. This may have been the result of a perception that the structural elements of the syrinx offer minimal phylogenetic information, and that only the intrinsic muscles are informative. One goal of my research was to assess the usefulness of syringeal data in resolving phylogenetic relationships for orders other than the Passeriformes. This analysis has demonstrated that there is sufficient variation in the morphology of syringeal structural elements to derive credible phylogenetic hypotheses for the Falconiformes.

There are, however, a limited number of structures comprising the syrinx and a limit to the variation. Thus, the presence of major structural elements (e.g. presence of a tympanum, presence and location of lateral membranes, or different pessulus morphologies) provides synapomorphies defining orders or families of birds. Minor structural variants provide characters that define genera and resolve some generic relationships within families. These include changes in the shape of B1 or A1 elements, the shape of the ends of incomplete elements, and variations in the degree of ossification or fusion of the tympanum. Although there are not enough characters to resolve relationships within the Accipitridae, a family of approximately 60 genera and more than 200 species, there is sufficient variation to produce a robust phylogeny for a family with 10 genera (Griffiths 1994).

Phylogenetic relationships.—Estimates of phylogenetic relationships of the five genera within the Cathartidae are ambiguous, but there is consensus that the smaller cathartids (*Cathartes* and *Coragyps*) are sister taxa to the other genera (Fisher 1944, Emslie 1988). Syringeal data support the basal position of *Coragyps*, whereas *Cathartes* and *Vultur* are sister taxa. A more complete taxonomic sampling is needed to resolve the phylogeny of the cathartids.

Syringeal data resolve relationships in the falconids (Griffiths 1994), but not the Accipitridae. One surprising result is the inclusion of *Sagittarius* and *Pandion* within the Accipitridae. *Sagittarius* is divergent in external morphology, behavior, and osteology from the other accipitrid genera, and has been considered closer to the Gruiformes than the Falconiformes (Pycraft 1902, Mayr and Amadon 1951). This divergence has been the justification for elevating *Sagittarius* to a monotypic family separate from the other clades within the order. *Pandion* has received similar taxonomic treatment. The distinctive treatment of these two species has not been supported by my phylogenetic analysis. Thus, the characters suggesting the distinctiveness of these two species may be autapomorphies and may suggest high rates of phenotypic evolution in these species relative to other accipitrids.

Monophyly of Falconiformes.—The composition of the Falconiformes has been a point of contention since the order was defined. At present, the most problematic taxon is the family of New World vultures (Cathartidae). There is a growing consensus that this family is the sister taxon to the Ciconiidae (Emslie 1988, Holdaway 1991), with three studies offered as support: Ligon (1967), Rea (1983), and Sibley and Ahlquist (1990).

Ligon (1967) and Rea (1983) each reviewed a range of characters for taxa in the Ciconiiformes and Falconiformes, and each concluded that Ciconiidae and Cathartidae were sister taxa. However, these studies were produced before cladistic methodology was in general use in ornithological analyses, and the data in these studies were not analyzed phylogenetically. Each study simply lists the taxa and the character states diagnosing the taxa.

There are additional problems with their conclusions because of the limited number of taxa sampled. Ligon listed 49 osteological characters and examined three genera within the Cathartidae, three within the Accipitridae, and six within the Ciconiidae. Of these, 27 cluster Ciconiidae with Cathartidae, and only 6 cluster Accipitridae with Cathartidae. I examined skeletons of 10 genera (*Ciconia, Leptotillus, Sarcorhamphus, Vultur, Hieraaetus, Buteo, Aquila, Accipiter,* and *Falco*) and researched additional anatomical studies. At best, only 8 of Ligon's 27 characters support grouping the Ciconiidae and Cathartidae. Several characters he used to unite ciconiids and cathartids, or to separate cathartids and accipitrids, occur in accipitrids or cathartids that he did not sample. Ligon listed basipterygoid processes as not present in the Accipitridae. However, they exist in several taxa (Shufeldt 1909, pers. obs.), and his illustration on page 5 shows these processes in *Necrosyrtes.* He lists a prominent foramen on the humeral shaft, and one pair of sternal manubrial fenestrae as occurring in Accipitridae only. These also occur in the Cathartidae.

Some of the described character states grade into one another. The curvature of the pelvic girdle is described by Ligon as having a slight angle above the antitrochanter in the Ciconiidae and Cathartidae, and a 45° angle in the Accipitridae. However, my observations indicate that the curvature in the Cathartidae is intermediate between the other two families. Using this character to unite the cathartids with either of the other two groups requires an extremely subjective decision. Similarly, the location of the anterior iliac crest is intermediate in the Cathartidae compared to the other two families, as is the crossing of the coracoidal sulci, the shape of the ilioischiatic fenestra, and the angle at which the bicipital crest joins the humeral shaft. In addition, several of Ligon's characters are composites that oversimplify variation or ignore variation in the accipitrids (e.g. the cathartids and ciconiids have a stocky or stout and sigmoidal humeral shaft). Within the accipitrids, the shaft is "often slender"; it appeared to be stocky in my observation of *Hieraaetus.*

Rea (1983) presented lists that are diagnoses of the Ciconiiformes (including the Cathartidae) and major groups within that order. His choice of characters has similar problems to Ligon's. For example, Rea listed characters uniting Ciconiidae and Cathartidae, which should be absent in Accipitridae, but are present in that family. These include the presence of M. ambiens (George and Berger 1966, McKitrick 1991), the presence of full spread-wing postures in sunning (Simmons 1986), and the absence of the accessory M. femorocaudal (George and Berger 1966). Some of his characters ignore or oversimplify variation. Thus, a "variably degenerate" syrinx unites Ciconiidae and Cathartidae. However, the syrinx is not one organ but a series of modifications of structures, and my analysis indicates that the variation in syringeal morphology cannot be described in one character. When fully described, the variations do not unite Ciconiidae and Cathartidae.

Finally, Rea (1983) listed characters uniting Ciconiidae and Cathartidae, which are, presumably, unique to those two families. However, these also can be found in other orders of birds. Thus, urohydrosis (urination used as a cooling mechanism), listed as occurring only in Ciconiidae and Cathartidae, also occurs in the Sulidae (order Pelicaniformes; Carboneras 1992). The pattern of macrochromosomes shared by Ciconiidae and Cathartidae are, in fact, more closely shared by the Cathartidae, Galliformes, Gruiformes, and Phoenicopteriformes (de Boer 1975).

M. pectoralis major is described as double in storks and cathartids. However, it is also double in Gruidae, Procellariiformes, and Pelecaniformes (George and Berger 1966). The most serious problem in both studies is that, without a phylogenetic analysis, none of the characters described by Ligon and Rea can be used to demonstrate a relationship between the Ciconiidae and Cathartidae; the characters may all be plesiomorphic or convergent. Determining whether any of their data are derived characters shared by these two families awaits an extensive survey of genera within each of these two families and other families within the two orders, and a phylogenetic analysis of the resulting data.

Sibley and Ahlquist (1990) used DNA-DNA hybridization data to generate phylogenies for all birds. Although widely cited, there are some problems with the methodology, analysis, and results of these data (e.g. Barrowclough 1992, Cracraft 1992, Lanyon 1992, Mindell 1992). One primary claim of these data is the sister-taxa relationship of the cathartids and ciconiids. Sibley and Ahlquist (1990) presented two different hypotheses of cathartid relationships: a Fitch tree (their fig. 338), which does not assume rate constancy, placed the cathartids with the strigiforms as a sister clade to the other Falconiformes; and an UPGMA analysis, which does assume rate constancy, placed the cathartids as sister taxa to the ciconiids. I reanalyzed the data in figure 338 of Sibley and Ahlquist (1990) using the same method they mentioned, the Fitch option of Phylip (Felsenstein 1990). My reanalysis produced a tree different from the one they reported, one that is congruent with the results of my syringeal analysis; the cathartids are sister taxa to the falconids and accipitrids (see also Mindell 1992). Sibley and Ahlquist (1990) dismissed their Fitch tree by concluding that different ages at first breeding cause problems. However, the additional assumptions, data, and corrections used to produce the UPGMA tree are not presented, and there is no way to assess the rigor of that hypothesis. In summary, the tree derived from my syringeal analysis fits the DNA-DNA hybridization data better than the tree reported by Sibley and Ahlquist (1990).

Although the notion that the cathartids should be removed from the Falconiformes is becoming acceptable (Emslie 1988, Snyder and Snyder 1991), the data and analysis offered in support of this notion are ambiguous at best. However, my phylogenetic analysis of syringeal data strongly supports inclusion of the cathartids within the Falconiformes. In addition, syringeal data provide support for the monophyly of three major clades within the Falconiformes: the Cathartidae, the Falconidae, and an Accipitrinae-*Sagittarius*-*Pandion* group.

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APPENDIX 1

Syringeal specimens examined. Specimens cleared and double-stained unless designated as unstained (UNS). Abbreviations for institutions from which specimens were borrowed are given in the Materials and Specimens section. Uncataloged specimens identified by a collector's number in brackets.

ACCIPITRIDAE: *Accipiter striatus*, AMNH 18761, 18762, 8686, 8482, 15938 imm. female, [CSG 9212, 9215], 1 Dec 1985 imm. female, (UNS) AMNH unnum. 1985 male, [CSG 9213]. *A. gentilis*, AMNH 17 Dec 1984 male, 11 Apr 1991 imm. male. *A. virgatus*, AMNH 8030. *A. cooperii*, AMNH 20007, 20623, [CSG 16, 9217, 9218, 9264 imm. female]. *Aegypius tracheliotus*, KUMNH 81668. *Aquila audax*, USNM 289389. *A. chrysaetos*, LSUMNS 126432. *Aviceda subcristata*, AMNH unnum. 1950. *Busarellus nigricollis*, LSUMNS 120424. *Butastur indicus*, AMNH 8497. *Buteo albicaudatus*, AMNH 8683. *B. buteo*, USNM 541690. *B. jamaicensis*, AMNH 18764, 20546, unnum. 1985. *B. magnirostris*, ROM 104270. *B. platypterus*, AMNH 18763, 8687, 20008, [CSG 9211], (UNS) AMNH 21464. *B. regalis*, AMNH 19629. *Buteogallus urubitinga*, LSU 114340. *Circus approximans*, AMNH 4-24. *C. macrourus*, USNM 615215. *C. cyaneus*, USNM 226415. *Elanoides forficatus*, AMNH [ROP 270]. *Elanus leucurus*, KUMNH 56804. *Gampsonyx swainsonii*, AMNH 8529. *Geranospiza caerulescens*, LSUMNS 120423. *Gypaetus barbatus*, AMNH 6398. *Haliaeetus leucocephalus*, KUMNH 46189, ROM 132599. *Haliastur indus*, AMNH 8496. *Harpagus bidentatus*, LSUMNS 114345. *Henicopernis longicauda*, USNM 615210. *Heterospizias meridionalis*, AMNH unnum. *Hieraaetus morphnoides*, AMNH unnum. *Ichthyophaga nana*, AMNH 8399. *Ictinia plumbea*, AMNH [ROP271]. *I. mississippiensis*, KUMNH 049239. *Kaupifalco monogrammicus*, USNM 615217. *Leptodon cayanensis*, LSUMNS 120426. *Leucopternis albicollis*, AMNH 8492, [ROP377]. *L. kuhli*, LSUMNS 114338. *Melierax canorus*, USNM 615216. *Milvus migrans*, USNM 615213. *Necrosyrtes monachus*, USNM 34631. *Neophron percnopterus*, USNM 615217. *Parabuteo unicinctus*, AMNH 19590. *Pithecophaga jefferyi*, AMNH 6396. *Rostrhamus sociabilis*, USNM 615212, AMNH [CSG 232, 711]. *Spilornis cheela*, AMNH 8616. *Spizaetus ornatus*, LSUMNS 3053. *Terathopius ecaudatus*, AMNH unnum.

PANDIONINAE: *Pandion haliaetus*, AMNH 8488 imm. male, 18808 female, [PFC445 female], USNM 615209.

SAGITTARIIDAE: *Sagittarius serpentarius*, YPM 3721, MVZ 4611.

FALCONIDAE: *Daptrius americanus*, AMNH 8667, [ROP266]. *D. ater*, KU068951. *Falco berigora*, AMNH 193358. *F. biarmicus*, AMNH 15927. *F. cenchroides*, AMNH 193394. *F. columbarius*, AMNH 19752, 14713. *F. femoralis*, LSUMNS 123309. *F. mexicanus*, KUMNH 053827. *F. peregrinus*, AMNH 8499, 19751. *F. rufigularis*, KUMNH 041874. *F. sparverius*, AMNH 8430 male, 8688 female, 8413 male, 15808, 15931, 16307, [CSG9210], (UNS) AMNH [CSG 21, 1216 male, 1217 imm. female]. *Herpetotheres cachinnans*, AMNH unnum. *Micrastur gilvicollis*, LSUMNS 98021. *M. semitorquatus*, USNM 507797. *Microhierax erythrogonys*, AMNH 8623. *Milvago chimachima*, LSUMNS 120427. *M. chimango*, USNM 346421. *Phalcoboenus australis*, USNM 511795, LSUMNS 120728. *Polihierax semitorquatus*, USNM 615218. *P. insignis*, AMNH 8627. *Polyborus plancus*, AMNH 9094. *Spiziapteryx circumcinctus*, LSUMNS 8 Sep 1990.

CATHARTIDAE: *Coragyps atratus*, AMNH 19607, (UNS) [PRS 245]. *Cathartes aura*, AMNH 20933, unnum. Dec 1985, [PFC443], nestling. *C. melambrotus*, LSUMNS 114336. *C. burrovianus*, USNM 227269. *Vultur gryphus*, AMNH 8498.

ARDEIDAE: *Ardea herodias*, AMNH 8933. *Bubulcus ibis*, AMNH 8624. *Butorides striatus*, AMNH 20736. *Egretta caerulea*, AMNH [PFC 427 imm. female]. *Ixobrychus sinensis*, AMNH 8621. *Nycticorax nycticorax*, AMNH 8625, 20335, (UNS) AMNH 8432.

CICONIIDAE: *Ciconia ciconia*, AMNH unnum. 1936. *C. nigra*, AMNH 6377. *Ephippiorhyncus asiaticus*, USNM 510447 (incomplete). *Mycteria americana*, AMNH 8513, (UNS) AMNH 9038, 9062, 9063, [MYC 85003, 85004, 85006-85009].

TYTONIDAE: *Tyto alba*, AMNH 14715, 8680, 8682, 20624, [CSG 9216]. *T. tenebricosa*, AMNH 7495. *Phodilus badius*, AMNH 6419.

STRIGIDAE: *Aegolius acadicus*, AMNH 8489, [CSG 9214]. *Asio otus*, AMNH 8312. *A. stygius*, AMNH 7466. *A. flammeus*, AMNH 8684. *Bubo bubo*, AMNH 7450. *B. shelleyi*, AMNH 8414. *B. virginianus*, AMNH 16092, [SC 957 imm.]. *Ciccaba huhula*, AMNH [SC 407]. *C. virgata*, (UNS) AMNH 7408. *Ketupa ketupu*, BM A1981. *Glaucidium brasilianum*, AMNH [SC 302, 410, 268]. *G. gnoma*, AMNH 7404. *Ninox jacquinoti*, AMNH 7422. *N. odiosa*, AMNH 7423. *N. connivens*, AMNH 7442. *N. philippensis*, AMNH 8490. *N. scutulata*, AMNH 8615. *Nyctea scandiaca*, AMNH 8836. *Otus asio*, AMNH 8310, 20625. *O. watsonii*, AMNH 8685. *O. nudipes*, AMNH 7438. *O. guatemalae*, AMNH 7437. *Pulsatrix perspicillata*, AMNH 2784. *Speotyto cunicularia*, AMNH 8679, 7447. *Strix varia*, AMNH 7439.

PHALACROCORACIDAE: *Phalacrocorax auritus*, (UNS) AMNH unnum.

SULIDAE: *Sula bassanus*, AMNH 8618, 8846. *Sula nebouxi*, (UNS) AMNH 8618.

PELECANIDAE: *Pelecanus roseus*, (UNS) AMNH 8619.

CRACIDAE: *Crax alector*, AMNH 15006, (UNS) [PFC 412].

PHASIANIDAE: *Tetrao parvirostris*, (UNS) AMNH 14100.

APPENDIX 2

Descriptions of 49 syringeal characters used in analysis. Derived states are described first. Characters 7, 26, 28, 38, 40 are multistate, ordered characters; justification for ordering follows descriptions. Characters 1, 13, 15, 21, 22, 24, 29, 30, 34, 37, and 45 are multistate unordered characters. Distribution of character states shown in Table 1. Characters illustrated in Figures 2, 4, 5, and 7.

A elements

1. *Ossification of* A *elements cranial to tracheo-bronchial junction.*—(1) Completely ossified in all genera in Falconidae and Cathartidae, and in most genera in Strigiformes, Ardeidae, and in several accipitrids. (2) Ossified ventrally and laterally, but cartilaginous dorsally in most accipitrid genera. (0) No ossification. Elements cartilaginous in *Pelecanus*, the two species of Galliformes, and in juveniles in Strigiformes, Accipitridae, Cathartidae and Falconidae.

2. A *elements immediately cranial to tracheo-bronchial junction thinner than subsequent elements and incomplete laterally.*—(1) In the Ciconiidae. (0) Not present. *A* elements complete rings in lateral view.

3. *Incomplete double* A *elements on bronchi caudal to tracheo-bronchial junction.*—(1) Yes. One or two present in species in all families examined except Ciconiidae. Gaps between ends of incomplete elements on medial walls of bronchi, forming lateral borders of internal membranes. (0) No *A* elements on bronchi in ciconiid genera.

4. *More than three incomplete double* A *elements.*—(1) At least four incomplete double *A* elements; in several genera in the Ardeidae; in all genera within the Strigidae. (0) No. A4 either single element or complete double elements.

5. *Complete double* A *elements on bronchi caudal to tracheo-bronchial junction.*—(1) Yes. In all genera in Cathartidae, Accipitridae and Falconidae; in several genera in Strigiformes. (0) Not present.

6. *More than three complete double* A *elements.*—(1) Yes. All cathartid genera have at least four complete double *A* elements. (0) No.

7. *Single* A *elements immediately cranial to tracheo-bronchial junction incomplete, with gap in element dorsally.*—(1) One or two *A* elements incomplete with small gaps between ends in *Coragyps* (2) More than three *A* elements incomplete with large gaps between the ends of each element, in *Cathartes* and *Vultur.* Unique to Cathartidae. Transformation from state 1 to 2 observed in ontogeny of *Cathartes.* (0) No. In all other families, single *A* elements complete when viewed dorsally.

8. *Medial cartilaginous section of complete* A *elements narrower than lateral, ossified section.*—(1) Yes. In Cathartidae. (0) No.

9. *Incomplete A1 elements wider laterally, thicker and more ossified than other double* A *elements.*—(1) Yes. In Strigiformes. (0) No.

10. *Dorsal ends of incomplete A1 elements connected medially forming ridge of ossified tissue.*—(1) In several *Falco* species and in *Microhierax.* (0) Not present.

11. *Ventral ends of incomplete A1 elements extend onto internal membrane forming amorphous, ovoid accessory cartilaginous structures.*—(1) In strigid genera. (0) Not present.

12. *Ventral ends of incomplete A1 and A2 elements extend onto cranial surface of internal membrane.*—(1) In accipitrid genera. (0) Not present.

13. *Modifications of caudal edges of dorsal ends of incomplete A1 elements.*—(1) Slight pointed cartilaginous extension of ends. (2) Large cartilaginous extension borders edge of internal membrane. (3) Ends fused to ends of B2 elements forming rings in *Pandion.* (0) A1 ends unmodified or single element.

14. *Dorsal ends of incomplete A1 elements flattened and enlarged forming a paddle shape.*—(1) In *Micrastur* species. (0) Not present.

Pessulus

15. *Pessulus composition.*—(1) Pessulus ossified. (2) Pessulus cartilaginous in several strigid genera. (0) Pessulus not present in *Pelecanus, Phalacrocorax, Podiceps, Spheniscus, Struthio, Casuarius, Dromaius,* or *Apteryx.*

16. *Pessulus an extension of* A *elements.*—(1) Yes. (0) No. Pessulus not present in *Pelecanus.* In Ciconiidae, pessulus an extension of B elements, an autapomorphy for that family and not included in this analysis.

17. *Ossified ridges at dorsal and ventral ends of pessulus.*—(1) In Ardeidae. (0) Not present.

18. *Dorsally, pessulus ends medially.*—(1) In Strigidae, *Vultur; Cathartes* polymorphic for this character (see character 19). (0) No.

19. *Dorsal and ventral ends of Pessulus extend caudally from* A *elements.*—(1) Yes. In all species within Falconidae and Accipitridae. In *Coragyps*, in some adult *Cathartes* and in juvenal *Cathartes.* (0) No.

Tympanum

20. *Fusion of* A *elements cranial to tracheo-bronchial junction.*—(1) In accipitrid and falconid genera and in *Sagittarius*, tympanum formed from lateral, ventral, and dorsal fusion of *A* elements. Patterns of fusion and ossification vary among families; described in following characters. (0) No fusion of *A* elements.

21. *Degree of dorsal ossification of tympanum.*—(1) Ossified medially and laterally only in most accipitrid genera. (2) Ossified completely in all falconid genera and several accipitrids. (0) Tympanum not present.

22. *Dorsal pessulus attachment to tympanum.*—(1) Narrow, more highly ossified medial strip extends

cranially connecting several *A* elements; in falconid genera. (2) Ossified narrowly, ends at or just above tracheo-bronchial junction; in some accipitrids and *Sagittarius*. (3) Ossified broadly, ends at or just above tracheo-bronchial junction in ovoid- or diamond-shaped pattern; in some accipitrids. (4) Ossified broadly, extends cranially connecting one or two single *A* elements medially; in some accipitrids. (5) Ossified broadly, extends cranially and laterally forming a cross-like pattern, in *Pandion*. (0) Tympanum not present.

23. *A1 not fused ventrally to tympanum.*—(1) In all accipitrids and *Sagittarius*. (0) A1 fused in the Falconidae. In other taxa, there is no tympanum.

24. *Pattern of partial dorsal fusion of* A *elements.*—(1) Slight fusion medially along caudal and cranial margins of two elements. (2) Medial, triangular-shaped cartilaginous plug fuses several elements. (3) Medial plug ossified, elements also fused somewhat along margins. Derived unordered states describe accipitrid tympanum. (0) Total fusion in Falconidae; in other taxa, no fusion of elements.

25. *More than seven rings fused to dorsal cartilaginous plug.*—(1) In five accipitrid genera. (0) Six or fewer rings fused in all other accipitrids and falconids. No dorsal fusion in other families.

26. *Shape of ossified and fused tympanum.*—(1) Graduated, widens caudally. (2) Almost cylindrical. (3) Almost cylindrical, A1 flattened laterally. In the Falconidae. State 3 modification of state 2. (0) No systematic variation in accipitrid tympanum shape. In other taxa, no tympanum present.

27. *Dorsal fusion of first two single* A *elements medially by ossified bar.*—(1) Yes. In *Micrastur*. (0) Not present.

28. *Dorsal fusion of first three or four* A *elements along their margins.*—(1) Margins apparent along edges of each ring. (2) Margins somewhat obliterated and only light sutures apparent medially. Derived states in falconid genera except *Micrastur*. State 2 modification of state 1; fusion increased. (0) No. Partial fusion in the accipitrids (character 29), and in *Micrastur* (character 27). In other taxa, no dorsal fusion.

29. *Pattern of partial ventral fusion of tympanum.*—(1) Slight medial fusion of *A* elements along margins. (2) Triangular-shaped ossified patch covers medial fusion of *A* elements. (3) Irregular, small ovoid ossified patch covers medial fusion. (4) Large ossified patch covers fusion of *A* elements medially and laterally. In Accipitridae, *Sula* and some Strigiformes. (0) Fusion total in falconids, lacking in other taxa.

30. *Pattern of total ventral fusion of tympanum.*—(1) First three or four *A* elements fused along margins. Spaces apparent between elements. (2) First three or four *A* elements fused lightly, sutures apparent along margins. (3) At least five *A* elements fused entirely along margins, sutures apparent only laterally. In falconids.

(0) Fusion partial in accipitrids, lacking in other taxa.

B elements

31. *All* B *elements complete rings.*—(1) In Ciconiidae. (0) In other taxa, *B* elements with medial gaps.

32. *B1 at oblique angle transversely.*—(1) In Strigidae. (0) In other taxa, B1 perpendicular to transverse plane.

33. *B1 evenly wider than other* B *elements, concave caudally.*—(1) In all falconids; in *Butorides*. (0) B1 not concave caudally in any other genera; same width as other *B* elements in all other taxa except accipitrids (character 35).

34. *Modifications of shape of incomplete B1 elements.*—(1) Wider at dorsal ends. (2) Slightly wider laterally, with narrowed ends. (3) Small arc-shaped extension on cranial margin laterally. (4) Large arc-shaped extension on cranial margin laterally. (5) Very wide dorsally, with slight narrowing at ventral ends. In accipitrids and some strigids. (0) Not present.

35. *B1, B2 and B3 concave cranially.*—(1) In *Sagittarius*. (0) No.

36. *B1 overlaps A1 laterally.*—(1) In accipitrid genera. (0) Membrane separates A1 and B1 in other taxa.

37. *Modification of shape of dorsal ends of B1 elements fusing with A1 elements.*—(1) Ends very thick and wide, ascend sharply in L-shape to fuse with A1 ends. (2) Ends thin, ascend gradually to fuse with A1 ends. (3) Knobbing of craniad edges; craniad extension fuses with A1 ends. (4) Ends thick, rounded, ascend gradually to fuse with A1. Derived states in falconid genera. (0) B1 elements complete in Ciconiidae; ends not modified in other species.

38. *Fusion of A1 and* B *ventral ends.*—(1) A1 and B1 ends fused. (2) B2 ends also fused. State 2 modification of state 1. (3) B3 ends also fused. State 3 modification of state 2. In falconid genera. (0) Not present.

39. *Fusion of B1 and B2 dorsal ends.*—(1) In *Accipiter* and three other accipitrid genera. (0) Not present.

40. *Fusion of B ventral ends forming ridge bordering internal membranes.*—(1) B1 and B2 ends fused. (2) B3 ends fused also. State 2 modification of state 1. (0) Not present.

Membranes and muscles

41. *External membrane between A1 and B1 elements.*—(1) In all falconid genera; in *Pandion* which has membrane between B1 and B2 also. (0) Not present.

42. *External membranes between B2–4 elements.*—(1) In several accipitrids and *Sagittarius*. These have external membrane between B1 and B2, also occurring in many accipitrid genera and not used as a character because generally small, with intraspecific and individual variation in its occurrence; may be an artifact of preservation. (0) Not present.

43. *M. tracheolateralis inserts laterally on A1.*—(1) In the Ardeidae and in *Sula*. (0) In Falconidae, M. tracheolateralis inserts on lateral membrane, in Accipit-

ridae and Strigiformes, inserts on B1. Not coded in analysis because correlated with other characters. See text for discussion of M. tracheolateralis in Galliformes, Cathartidae and Ciconiidae.

Accessory structures

44. *Cartilaginous border located on cranial edge of internal membrane, extending from dorsal to ventral ends of membrane.*—(1) Present. (0) Not present.

45. *Shape of cartilaginous border.*—(1) Narrow, thicker dorsally than ventrally. (2) Wide, thicker dorsally than ventrally. (3) Wide and even. (4) Narrow and even. (0) Not present.

46. *Border ossified.*—(1) In three taxa in Accipitridae. (0) Not present.

47. *Small cartilaginous paddle-shaped accessory structures extend onto internal membranes from dorsal A1 ends.*—(1) In several accipitrid species. (0) Not present.

48. *Small cartilaginous peaks extend caudally onto internal membranes medially.*—(1) In several accipitrid species. (0) Not present.

49. *Internal membranes almost parallel.*—(1) In *Accipiter* (0) No internal membranes in Ciconiidae. Internal membranes at angle to each other when viewed dorsally in all other species.