The Condor 96:127–140

SYRINGEAL MORPHOLOGY AND THE PHYLOGENY OF THE FALCONIDAE[1]

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Abstract. Variation in syringeal morphology was studied to resolve the relationships of representatives of all of the recognized genera of falcons, falconets, pygmy falcons, and caracaras in the family Falconidae. The phylogeny derived from these data establishes three major clades within the family: (1) the Polyborinae, containing *Daptrius, Polyborus, Milvago* and *Phalcoboenus,* the four genera of caracaras; (2) the Falconinae, consisting of the genus *Falco, Polihierax* (pygmy falcons), *Spiziapteryx* and *Microhierax* (falconets) and *Herpetotheres* (Laughing Falcon); and (3) the genus *Micrastur* (forest falcons) comprising the third, basal clade. Two genera, *Daptrius* and *Polihierax,* are found to be polyphyletic. The phylogeny inferred from these syringeal data do not support the current division of the family into two subfamilies.

Key words: Falconidae; phylogeny; systematics; syrinx; falcons; caracaras.

INTRODUCTION

Phylogenetic relationships form the basis for research in comparative and evolutionary biology (Pagel and Harvey 1988, Gittleman and Luh 1992). Patterns drawn from cladograms provide the blueprints for understanding biodiversity, biogeography, behavior, and parasite-host cospeciation (Vane-Wright et al. 1991, Mayden 1988, Page 1988, Coddington 1988) and are one of the key ingredients for planning conservation strategies (Erwin 1991, May 1990). For many orders of birds, however, these patterns or hypotheses are not available and the higher level systematics of many avian families and orders remain unresolved.

The Falconidae (falcons, caracaras and falconets) is an example of a family whose phylogenetic relationships are in question. Resolution of this phylogeny is particularly important since it is one of nine bird families identified as threatened in CITES appendix II (Norton et al. 1990). In addition, nine falconid species are listed by the International Council for Bird Preservation (ICBP) as vulnerable, rare or endangered.

Cladistic analyses of syringeal morphology (Griffiths, in press.) and osteology (Becker 1987) support the monophyly of the family, but systematic ambiguities exist at the intrafamilial level. Current classification allocates the 10 genera in the family into two subfamilies (Amadon and Bull 1988).

1. The Polyborinae. This includes seven genera: *Daptrius, Milvago, Polyborus* and *Phalcoboenus* (the caracaras), *Micrastur* (forest falcons), *Herpetotheres* (Laughing Falcon) and *Spiziapteryx* (Spot-winged Falconet).

2. The Falconinae. This includes three genera: *Falco, Polihierax* (pygmy falcons) and *Microhierax* (falconets).

Inclusion of the caracaras in the Polyborinae is not questioned (Sharpe 1874, Swann 1922, Peters 1931). The number of named caracara genera, however, has varied from two to four. Three other genera (*Spiziapteryx, Micrastur* and *Herpetotheres*) may not belong in the Polyborinae. *Spiziapteryx* had traditionally been associated with the pygmy falcons and falconets but was placed with the caracaras based on an assessment of osteological similarity (Olson 1976). Once thought to be related to hawks rather than falcons (Sharpe 1874, Swann 1922), *Micrastur* and *Herpetotheres* were later considered to be either one (Peters 1931) or, subsequently, two (Friedmann 1950) separate subfamilies within the Falconidae.

Composition of the Falconinae has also changed. *Polihierax, Spiziapteryx* and *Microhierax* were originally placed with *Falco* (Sharpe 1874, Swann 1922), then placed in a separate subfamily, the Polihieracinae (Peters 1931, Friedmann 1950). More recently, *Microhierax* and *Polihierax* were reunited with *Falco* (Stresemann and Amadon 1979).

Cladistic analyses of the family using osteology (Becker 1987) and allozyme frequencies (Boyce

[1] Received 6 May 1993. Accepted 7 October 1993.

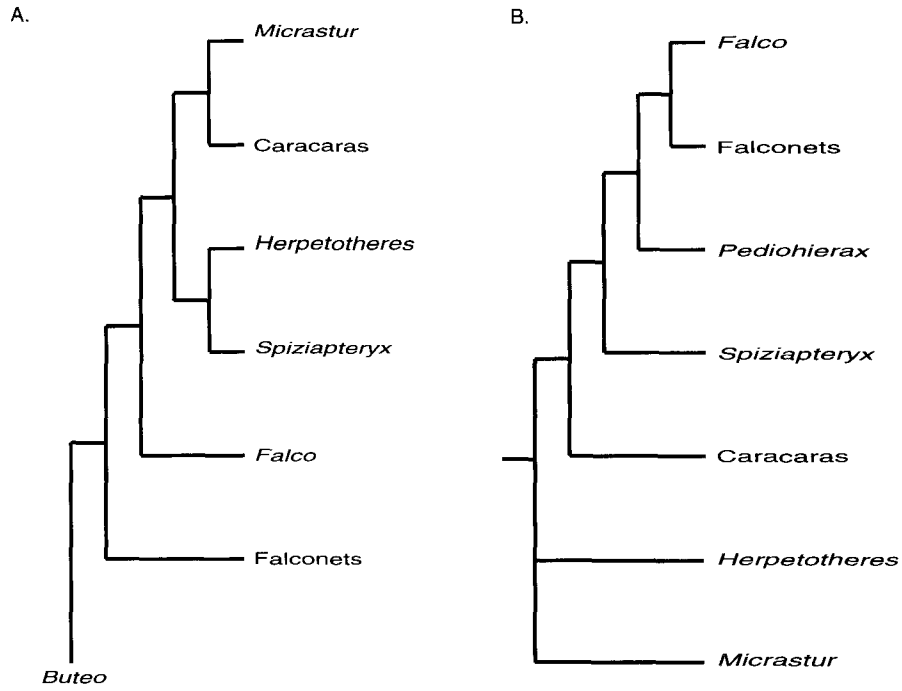

FIGURE 1. Alternative phylogenetic hypotheses for the Falconidae derived from (A) Allozyme data (Boyce 1989) and (B) Osteology (Becker 1987).

1989) produced two alternative hypotheses of generic relationships (Fig. 1). Osteological data placed *Micrastur* and *Herpetotheres* basal to the other genera, whereas allozyme data supported the falconets as the basal group.

I analyzed the variation in syringeal morphology of the Falconidae to derive a phylogenetic hypothesis for this family. Syringeal myology had been important in the classification of the major subdivisions of the Passeriformes at the end of the 19th century (see Ames 1971 for a detailed review), but the lack of intrinsic muscles in other orders obviated general taxonomic use of the syrinx. Within the last 20 years, application of staining techniques to the syrinx has made detailed observations of anatomy possible, and the use of syringeal data in systematics has intensified. However, this work was centered on the analysis of oscines and suboscines (Ames 1971, Warner 1972, Lanyon 1984, Prum 1990) and "higher birds" (Cannell 1986). There have been no previous analyses of falconid syringes.

MATERIALS AND METHODS

MATERIALS AND SPECIMENS

Syringes were obtained by dissecting fresh specimens and specimens originally preserved in formalin and stored in alcohol at the American Museum of Natural History (AMNH), the National Museum of Natural History (USNM), and the Louisiana State University Museum of Natural Science (LSUMNS). These were cleared and double stained to distinguish cartilaginous and ossified tissue (Cannell 1988). Additional cleared and stained specimens prepared by Dr. Peter Cannell were also used; these included specimens borrowed from the University of Kansas Museum of Natural History (KUMNH). Observations were made using a Wild M5A dissecting microscope and drawings made with a camera lucida.

All 10 currently recognized genera within the family (Stresemann and Amadon 1979) and 10 outgroup species were examined, a total of 44 specimens of 32 species (Appendix I). Species from the monotypic genera *Spiziapteryx, Polyborus* and *Herpetotheres* and both species in each of the genera *Daptrius, Milvago* and *Polihierax* were included. Sampling of species within the remaining polytypic genera was limited by the availability of alcohol preserved specimens (one of three species in *Phalcoboenus,* two of five in *Micrastur,* and one of five in *Microhierax*). An additional consideration limiting the number of species examined within the genus *Falco* (nine

of 38) was the minimal variation in syringeal morphology in these species.

Multiple individuals from six species were examined to assess variation at the intraspecific level. For the American Kestrel (*Falco sparverius*), collection data were available to allow assessment of both sexual and ontogenetic variation.

ANALYSIS

Variation in syringeal morphology was coded as both binary and multistate characters. The ordering of states for multistate characters was hypothesized using the similarity criterion and tested by examining the relationships of the character states to each other in the resulting cladograms (Lipscomb 1992).

Characters were polarized using outgroup information (Maddison et al. 1984). Multiple outgroups were used to ensure global parsimony, that is, that the phylogenetic hypotheses are the most parsimonious both within the Falconidae, and among the Falconidae and its sister taxa (Maddison et al. 1984).

The PAUP 3.0s computer program (Swofford 1991) was used to derive the most parsimonious resolution of the data. The size of the data set precluded exact search algorithms; therefore, a heuristic algorithm was used. However, this does not guarantee optimality. To avoid finding a solution that is only locally optimal, analyses were repeated varying both the branch swapping and taxa addition options. In addition, the effect of two different character optimizations was tested, ACCTRAN, which increases reversals, and DELTRAN, which increases parallelisms.

Three indices were used to assess the congruence of characters hypothesized as synapomorphies: (1) the consistency index, the minimum number of character state changes a character may show, divided by the number of changes observed on a particular tree, (2) the rescaled consistency index, a linear rescaling to allow the consistency index to vary between 0 and 1, and (3) the retention index, the proportion of hypothesized synapomorphies retained as homologies (Farris 1989).

Strict consensus trees, which only include groups found in all of the most parsimonious cladograms, were used to summarize the agreement in taxonomic relationships among the set of most parsimonious trees. Consensus trees must be interpreted carefully as they may not be parsimonious reconstructions of the original data.

RESULTS

SYRINGEAL MORPHOLOGY

The main structural components of the falconid syrinx are shown in Figure 2; Ames' (1971) definitions of syringeal components are used. These are as follows:

(1) A elements—occur on the trachea as single rings but may extend onto the bronchi as paired double rings. The rings may be complete or incomplete medially and are generally ossified in birds (Ames 1971, Cannell 1986). In the Falconidae, all genera have at least one incomplete double and one complete double ring and all A elements are completely ossified.

(2) B elements—occur on the bronchi and generally are cartilaginous. These are paired rings that may be either complete or incomplete medially. B elements are all incomplete medially (C rings) in the Falconidae.

(3) Tympanum—fused and ossified A elements occur near the tracheo-bronchial junction. In the Falconidae, from three to eight A elements are fused (Appendix II, Characters 2–7).

(4) Pessulus—a dorso-ventrally oriented cartilaginous or ossified bar located in the mid-sagittal plane of the trachea between the bronchi. It may be fused to other elements at the dorsal or ventral or both ends. In the Falconidae, the pessulus is always ossified and fused both dorsally and ventrally to the tympanum.

(5) Membranes—a. The internal or medial tympaniform membranes comprise the medial surface of the bronchial tubes, usually close to the tracheo-bronchial junction and supported at the edges by the ends of the divided A and B elements. The membranes may be continuous from the left to the right bronchus or may be separated by the pessulus. These are generally considered to be the sound producing structures (Gaunt and Gaunt 1985). b. The external or lateral tympaniform membranes are on the lateral walls of the bronchi, usually between one or two of the first four B elements. In the Falconidae, there is a large external membrane between A1 and B1.

(6) Musculature—a. Intrinsic muscles are short muscles which both originate and insert on syringeal elements. There are no intrinsic muscles within the Falconidae. b. Extrinsic muscles are longer muscles which originate away from the syrinx and insert on it. M. tracheolateralis originates on the lateral surface of the cricoid cartilage of the larynx and extends down the lateral

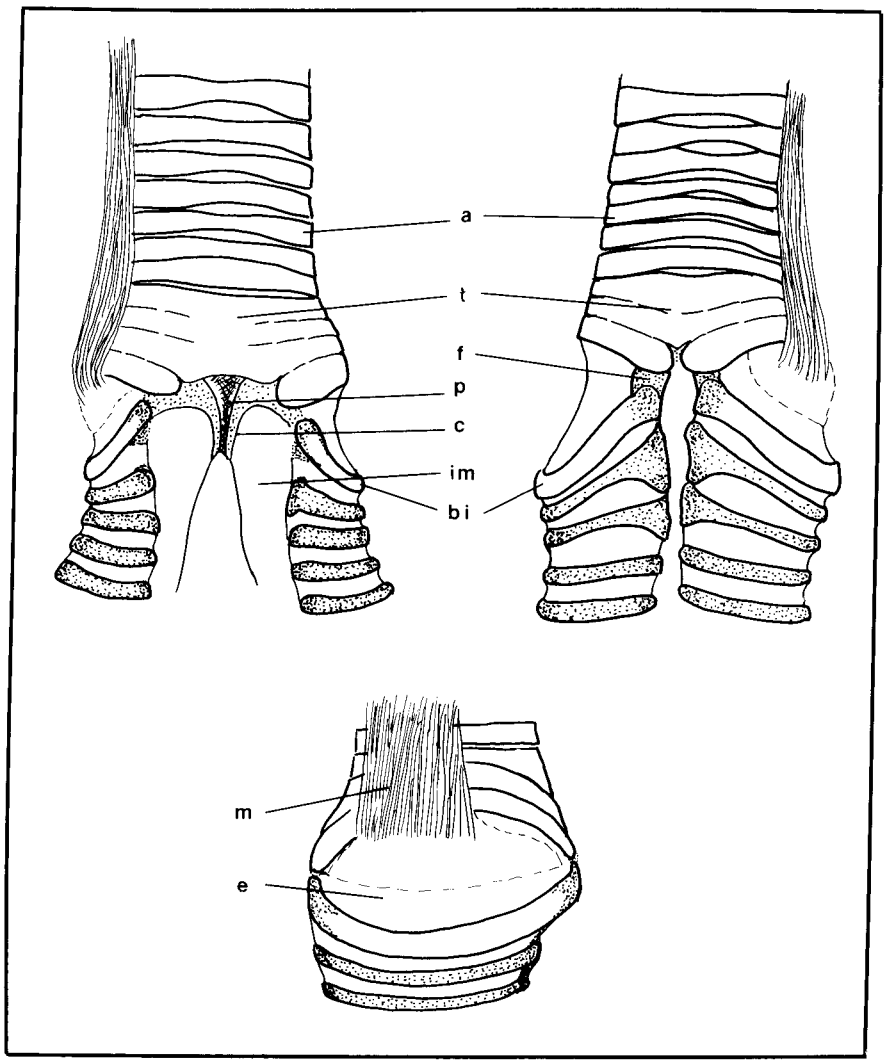

FIGURE 2. Syrinx of *Falco berigora* (AMNH 193358). Top: left, dorsal view; right, ventral view. Bottom: lateral view. Abbreviations: a (A elements), bi (double B1 element), c (cartilaginous border on internal membrane), e (external membrane), f (fusion of A1 and B1 elements), im (internal membrane), m (M. tracheolateralis), p (pessulus), t (tympanum). In all drawings: 1. stippling indicates cartilaginous tissue; 2. cross-hatching indicates dense ossified tissue; 3. the M. tracheolateralis is illustrated on one side only.

surfaces of the trachea, inserting in the syringeal region. In this family, the insertion is on the external membrane. M. sternotrachealis originates on the internal surface of the coracoid or costal process of the sternum, or on the internal surface of one or more ribs. It inserts on the lateral or ventral surface of the trachea or on the tissues surrounding the trachea, and may be continuous with, or overlap, the M. tracheolateralis.

PHYLOGENETIC ANALYSIS

Variations in syringeal morphology were examined for 32 taxa; 10 of these represented hypothesized outgroups of the Falconidae (five falconiform species and five species from three other orders of birds). After the initial character state coding, redundant outgroup species (those with identical character states) were deleted, resulting

TABLE 1. Data matrix of 25 syringeal morphological characters for 25 Falconidae and outgroup species.

Taxa	Characters																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Pelecanus roseus	0	0	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	0	0
Gampsonyx swainsonii	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Daptrius americanus	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	2	0	1	0	1
D. ater	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0
Falco sparverius	1	0	1	0	0	1	0	2	1	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0
F. rufigularis	1	0	1	0	0	1	0	2	0	0	0	0	1	0	0	1	0	2	1	0	2	0	1	1	0
F. biarmicus	1	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	2	1	1	0	0	1	1	0
F. mexicanus	1	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	1	0
F. femoralis	1	0	1	0	0	1	0	2	0	0	0	0	1	0	0	1	0	2	1	0	2	0	1	1	0
F. cenchroides	1	0	1	0	0	1	0	2	1	0	0	0	0	0	0	1	0	1	1	0	2	0	1	1	o
F. berigora	1	0	2	0	0	1	0	2	1	0	0	0	0	0	0	1	0	2	1	0	2	0	1	1	0
F. columbarius	1	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	2	1	0	2	0	1	1	0
F. peregrinus	1	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	2	1	1	0	0	1	1	0
Herpetotheres cachinnans	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0
Micrastur gilvicollis	1	1	0	0	1	0	0	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	0	0	2	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0
Microhierax erythrogonys	1	0	2	0	0	1	0	3	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0
Milvago chimachima	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0
M. chimango	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0
Phalcoboenus australis	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0
Polihierax semitorquatus	1	0	1	0	0	1	0	3	0	0	0	0	0	0	1	0	0	0	1	0	2	0	1	1	0
P. insignis	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	2	0	1	0	1
Polyborus plancus	1	0	0	2	0	0	1	1	0	1	0	1	0	0	0	0	1	0	1	0	2	0	1	0	1
Spiziapteryx circumcinctus	1	0	2	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	1	1	0

in a data matrix containing 25 taxa, 22 falconid species and three outgroup species.

The 25 characters included in this analysis were coded first as 20 binary and five ordered multistate characters. The cladograms resulting from the analysis of this data matrix were examined to assess the congruence of the ordering of character states of the multistate characters. One of the five was highly incongruent; this character was reexamined and then treated as unordered. The final data matrix contained 20 binary, four ordered multistate and one unordered multistate character (Appendix II, ordered characters 3, 4, 8, 18, unordered character 21).

Analysis of this data matrix (Table 1) resulted in 27 most parsimonious cladograms of 50 steps, consistency index of 0.620, rescaled consistency index of 0.525 and retention index of 0.843. Because the consistency index is negatively correlated with the number of taxa, there is a maximum value expected for different numbers of taxa. The CI for this analysis compares favorably with the general result expected for 25 taxa (0.483, Sanderson and Donoghue 1989).

Congruence among the cladograms produced by this analysis is summarized in the strict consensus tree (Fig. 3); there are three polytomies (discussed below) reflecting the conflicting topologies in the 27 most parsimonious cladograms. This tree illustrates the distribution of derived characters and the effect of differing character optimizations (differences in character 10, Fig. 3).

CLADES WITHIN THE FALCONIDAE

The phylogeny derived from syringeal data does not support the monophyly of the two currently accepted Falconidae subfamilies. Rather, all trees are congruent in their support of three clades: (1) *Micrastur,* (2) the four caracara genera, and (3) a clade composed of *Herpetotheres, Spiziapteryx, Microhierax, Polihierax,* and the *Falco* species.

Four derived characters support the monophyly of the two species of *Micrastur* (Fig. 4); three of these are unambiguous synapomorphies. The *Micrastur* tympanum has minimal fusion compared to other genera in the family (dorsal fusion, character 2, CI 0.5; ventral fusion, character 5, CI 1.0). The ends of the A1 elements are flattened and enlarged (character 11, CI 1.0). The

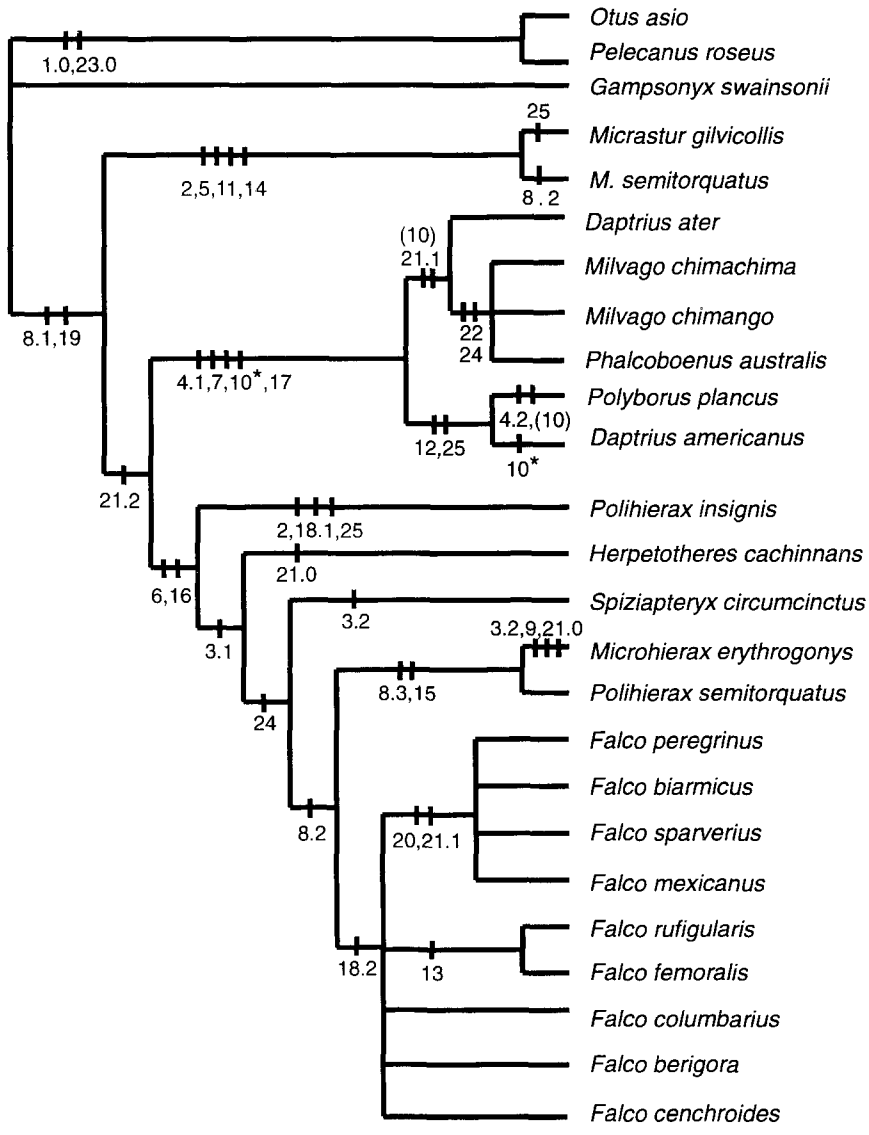

FIGURE 3. Strict consensus tree derived from the 27 most parsimonious cladograms. There are three polytomies: 1. *Milvago* and *Phalcoboenus*. 2. The *Falco* species *berigora, columbarius, cenchroides* and two clades. 3. The *Falco* species *sparverius, biarmicus, mexicanus,* and *peregrinus.* Character support for each node is indicated: states for the five multistate characters (3, 4, 8, 18, 21) are shown as decimals following the number. Optimization of character 10 is ambiguous; in the alternative DELTRAN optimization, characters states marked with asterisks are eliminated, character states in parentheses are acquired. The effect is to delay the transformations and to eliminate reversals.

B1 elements are straight medially; B1 ends ascend abruptly (character 14, CI 1.0) and fuse totally with A1 ends, forming an inflexible frame for the lateral membrane.

Monophyly of the clade of six species of caracaras also has strong support (three unambiguous synapomorphies, characters 4, 7, 17). Ventral and dorsal tympanum fusion is most extensive in the caracaras (characters 4 and 7, CI 1.0), in number of elements fused and degree of fusion of each element (Fig. 5). The B1 elements also have a characteristic shape: thick in circumference and concave medially with ends that ascend gradually (character 17, CI 1.0). Fusion of B1 to A1

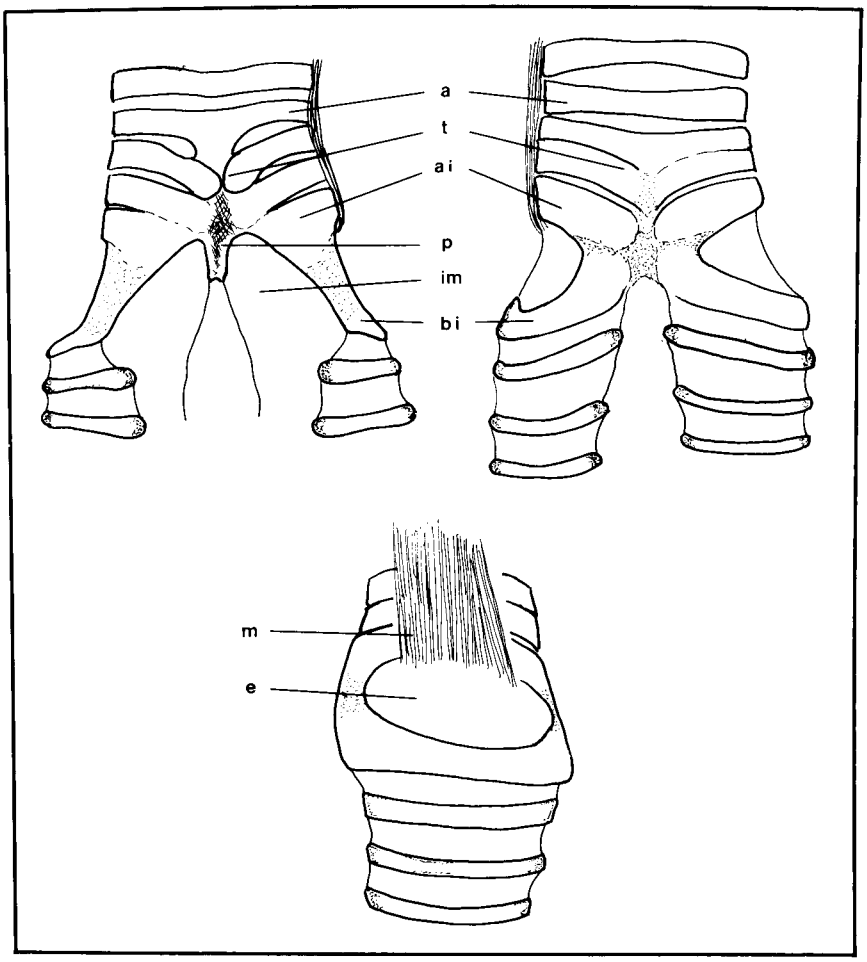

FIGURE 4. Syrinx of *Micrastur semitorquatus* (USNM 507797). Top: left, dorsal view; right, ventral view. Bottom: lateral view. Abbreviations: a (A elements), ai (double A1 elements), bi (double B1 elements), e (external membrane), im (internal membrane), m (M. tracheolateralis), p (pessulus), t (tympanum).

ends is not as strong as in *Micrastur*; a cartilaginous bridge connecting the ends allows some flexibility and movement.

The third clade comprises the current subfamily Falconinae (the falcons, pygmy falcons and falconets), with the addition of *Spiziapteryx* and *Herpetotheres*. Two derived characters unite the clade: (1) the pattern of ventral fusion of the tympanum (character 6, CI 1.0), and (2) the broad knobbed ends of the B1 element (character 16, CI 0.5). Within the clade, *Spiziapteryx* is sister taxon to *Falco* and two of the falconet species. *Herpetotheres* is sister taxon to the *Falco*-falconet clade, while *Polihierax insignis* (Asian Pygmy Falcon) is basal.

All trees are also congruent in the resolution of the interrelationship of these three clades. *Micrastur* is supported as the basal clade while one synapomorphy unites the caracara and Falconinae clades (character 21, CI 0.33, Fig. 3).

MONOPHYLY OF FALCONID GENERA

Syringeal data suggest that three genera are not monophyletic. Two of the genera, *Polihierax* (Fig. 6) and *Daptrius* are polyphyletic; the two species within each of these genera are not sister taxa. *Daptrius americanus* (Red-throated Caracara) is more closely related to *Polyborus plancus* (Crested Caracara), whereas *Daptrius ater* (Black Caracara) is closer to the *Milvago* clade.

Similarly, *Polihierax semitorquatus* (African Pygmy Falcon) forms a clade with *Microhierax erythrogonus* (Philippine Falconet), while *P. insignis* (Asian Pygmy Falcon) is sister taxon to *Herpetotheres, Spiziapteryx, Falco* and the other falconet species.

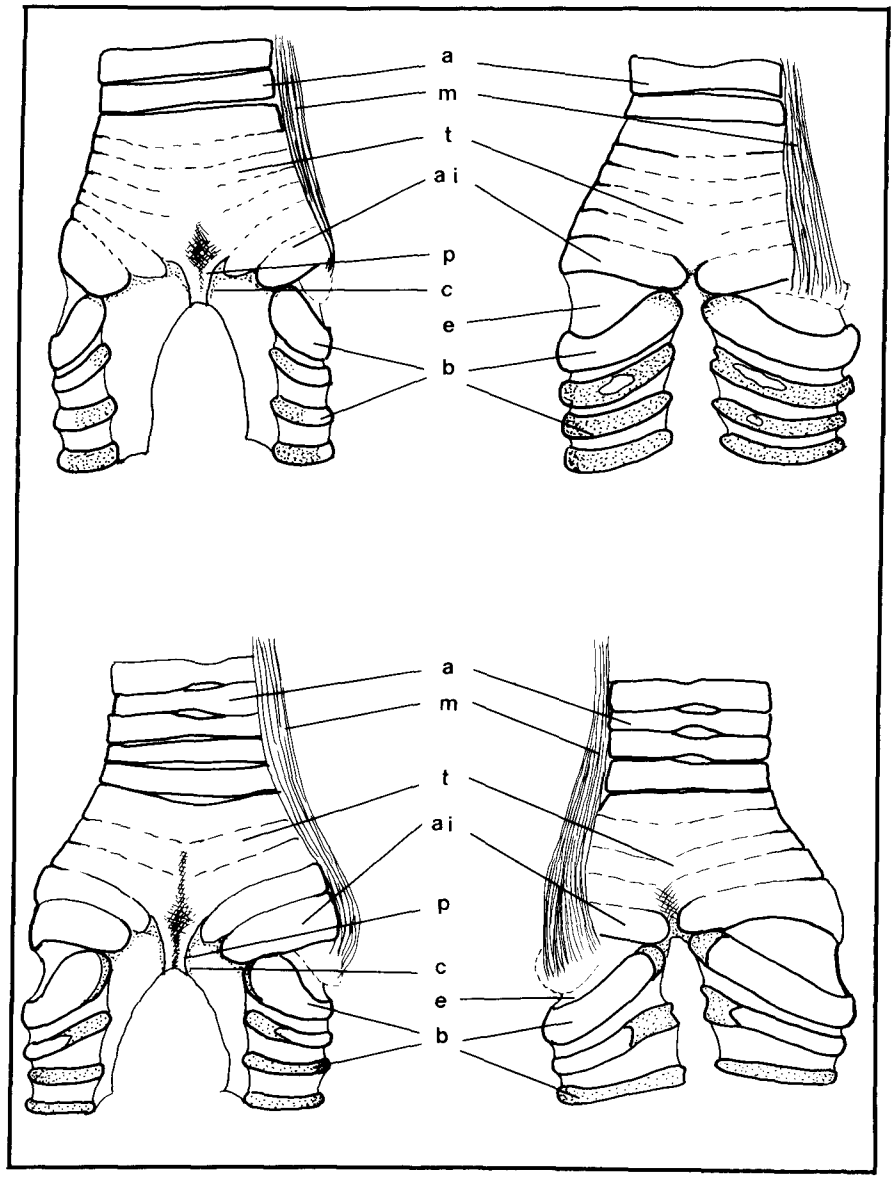

FIGURE 5. Syrinx of two caracaras. Top: *Milvago chimachima* (LSUMNS 120427). Bottom: *Daptrius ater* (AMNH 10128). Left, dorsal view; right, ventral view. Abbreviations: a (A elements), ai (double A1 elements), b (B elements), c (cartilaginous border on internal membrane), e (external membrane), m (M. tracheolateralis), p. (pessulus), t (tympanum).

The monophyly of *Milvago* is also uncertain. In this analysis, *Phalcoboenus australis* occurs in a polytomy with the two *Milvago* species. This clade is supported by two synapomorphies (characters 22 and 24); there are no syringeal characters that distinguish any of these three species (no autapomorphies).

These data support the monophyly of the *Falco* species examined for this study (nine of 38 species), but are unable to resolve the relationships of these species. One clade of four species, *F. mexicanus* (Prairie Falcon), *F. sparverius* (American Kestrel), *F. peregrinus* (Peregrine Falcon) and *F. biarmicus* (Lanner Falcon), is united by two synapomorphies (characters 20 and 21). Relationships of the other five *Falco* species, *F. cenchroides* (Australian Kestrel), *F. columbarius* (Merlin), *F. berigora* (Brown Hawk), *F. rufigu-*

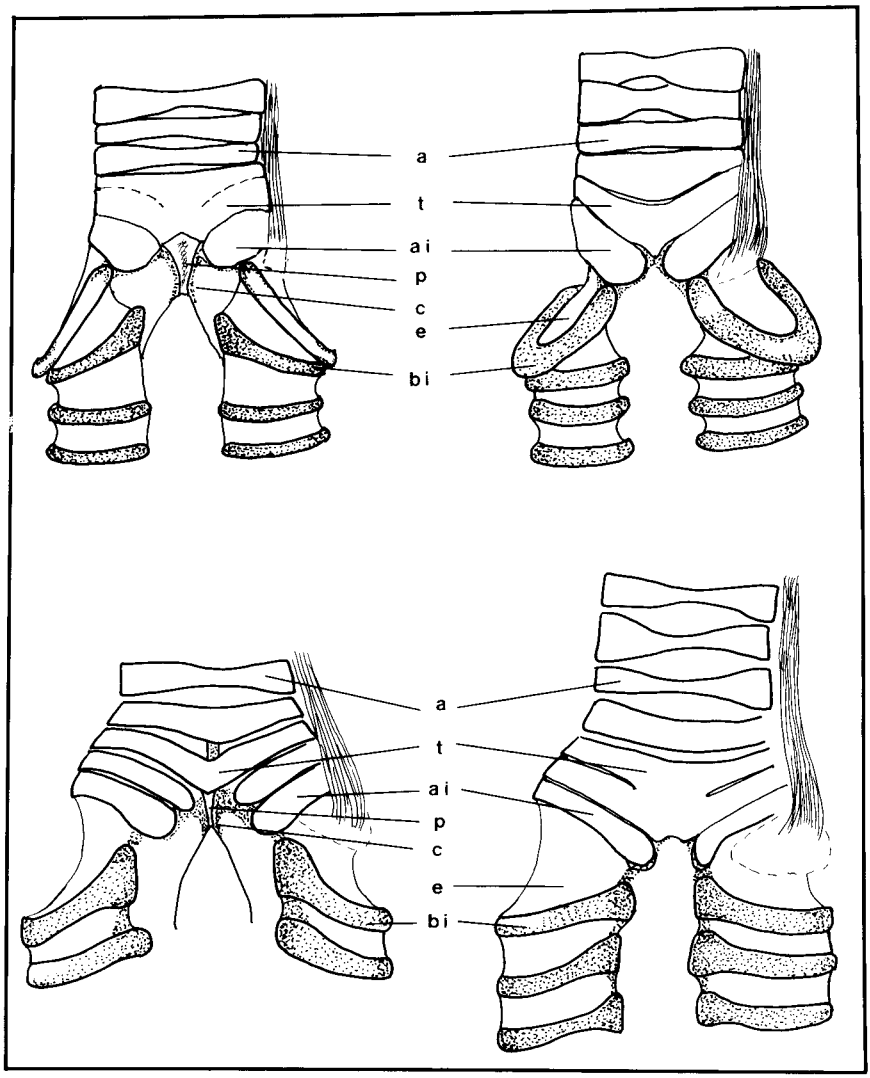

FIGURE 6. Syringes of the two *Polihierax* species. Top: *P. semitorquatus* (USNM 615218). Bottom: *P. insignis* (AMNH 8627). Left, dorsal view; right, ventral view. Abbreviations: a (A elements), ai (double A1 elements), bi (double B1 elements), c (cartilaginous border on internal membrane), e (external membrane), p (pessulus), t (tympanum).

laris (Bat Falcon), and *F. femoralis* (Aplomado Falcon) are ambiguous. In all trees, however, *F. rufigularis* and *F. femoralis* are sister taxa; both have A1 elements that are medially straight and not concave (character 13).

DISCUSSION

SYRINGEAL VARIATION

In order to resolve phylogeny, the patterns of variation of characters must be informative at the level of the question asked. Thus, characters varying among individuals within a species will not generally be able to resolve generic relationships. Systematists must choose characters with rates of evolution consistent with the taxonomic level of the group in question. However, rates of change of characters may vary among taxa. For example, osteological characters have been used successfully in genus-level analyses in Anseriformes (Livezey 1986), but in the Cathartidae they were useful only at the familial and ordinal level (Emslie 1988). This study examined the levels of usefulness of syringeal data for the Falconidae.

Intraspecific variation was examined in nine specimens of *F. sparverius* (American Kestrel). There was variation among adults only in the number of rings fused in the tympanum. Six specimens (including both males and females) had three rings fused, whereas two (one male and one female) had four. There was additional variation between adult and juvenile specimens. In all adult falconid specimens examined, the A rings were completely ossified. However, the juvenile kestrel had cartilaginous medial sections, both dorsally and ventrally. Similar ontogenetic variation in A element ossification has been observed in passerines (Ames 1971) as well as in the Accipitridae and the Tytonidae (Griffiths, in press). Neither of these two morphological variations was used in this analysis.

Syringeal morphology is relatively conservative within genera and there may not be enough variation within speciose genera to resolve relationships. Thus, among the nine species of *Falco* examined, there was slight variation in the fusion of the tympanum, in the appearance of a ridge over the dorsal attachment of the pessulus to the tympanum, and in the method of insertion of the M. tracheolateralis. While this variation may be useful in identifying major clades or some small groups of sister taxa, it is not enough to infer the phylogeny of 38 species.

MULTISTATE CHARACTERS

Although multistate characters are used extensively in phylogenetic analysis, there is a lack of consensus as to the best method for describing the transformation between the different character states. The most commonly used transformations are ordered and unordered characters, both of which entail assumptions about character evolution. Unordered character states assume that any state can transform directly into any other, while ordering states implies a (usually linear) relationship among the character states (Swofford and Olsen 1990).

Currently, the use of ordered characters is being questioned. There may be three possible reasons for the trend towards unordered characters: (1) the prevalence of molecular phylogenetic studies which use unordered characters, (2) the conviction that ordering entails a risk that the wrong order may be chosen (Slowinski 1993), and (3) the possible constraining effect that ordering may have on the number of most parsimonious trees found in an analysis (Hauser and Presch 1991). There have been, however, no definitive studies about the effect of these assumptions on phylogenetic analyses and results that have been reported are contradictory. For example, ordering characters may result in phylogenies with greater resolution (Mickevich and Weller 1990, Slowinski 1993) or may have no effect on resolution (Hauser and Presch 1991). Ordering characters may or may not constrain the number of most parsimonious trees found in an analysis; the effects may, in fact, be data-set specific (Hauser and Presch 1991).

The decision to order a multistate character should be made on a character by character basis. If there is evidence for relationships of the states in a multistate character, then to treat that character as unordered is discarding information (Lipscomb 1992, Maddison and Maddison 1992). In this study, similarity of states was the criterion used to hypothesize character state order. For characters 3, 4 and 18 (increases in amount of ossification or fusion of various elements), the ordering patterns were also observed in ontogenetic sequences and are in agreement with general developmental processes. In addition, similar patterns were observed in syringes from juveniles and adults in species within the Strigiformes, Ciconiiformes, Cathartidae, Falconidae and Accipitridae, and through descriptions in the literature for the Passeriformes (Ames 1971).

MONOPHYLY OF GENERA

There were no discrete characters distinguishing the two *Milvago* species from *Phalcoboenus*. The species composition of caracara genera and the relationships among these genera have always been ambiguous. For example, Sharpe (1874) placed *Daptrius, Phalcoboenus* and *Milvago* in one genus, *Ibycter*. *Milvago* was separated first (Swann 1922) and then all four were recognized as separate genera (Peters 1931). Brown and Amadon (1968) proposed a close relationship of *Polyborus, Phalcoboenus* and *Milvago,* and Vuilleumier (1970) recommended that the three be placed in one genus. This analysis suggests the need for additional study of these genera.

Daptrius was found to be polyphyletic. The two *Daptrius* species have traditionally been united by plumage color and by tarsal and toe characters (Friedmann 1950). Brown and Amadon (1968), however, noted that habitat and be-

havioral differences suggest that these two should be separated generically and that the genus name *Ibycter* be used again for *D. americanus.* Syringeal data, by demonstrating that *D. americanus* and *Polyborus plancus* are sister taxa, support that conclusion.

The two species of *Polihierax* are not sister taxa. *P. semitorquatus* is in the falconet clade, sister taxon to *Falco. P. insignis,* on the other hand, is basal to *Falco* and the other falconet species. Morphological differences (tail length and shape, and 2nd primary length) between the two *Polihierax* species have also been recognized previously, leading to *P. insignis* being placed in a monotypic genus, *Neohierax* (Swann 1922). Brown and Amadon (1968) proposed that generic status be accorded to these species; this is also supported by syringeal data.

PHYLOGENETIC RELATIONSHIPS OF THE FALCONIDAE

Previous designations of falconid subfamilies have been based on combinations of characters, many of which may be plesiomorphic. Cladistic analysis of syringeal data (Fig. 3) results in a division of the family into three comprehensive clades; (1) the genus *Micrastur* basal to the other two clades, (2) the Polyborinae (including only the four caracara genera), and (3) the Falconinae (consisting of *Falco,* the pygmy falcons and falconets, and *Herpetotheres*). It does not support the following currently accepted (Stresemann and Amadon 1979) designations:

(1) The division of the Falconidae into two subfamilies,

(2) The position of three genera (*Spiziapteryx, Herpetotheres* and *Micrastur*) in the Polyborinae,

(3) The clade of pygmy falcons and falconets (based on similarity of tarsal and nostril characters, Friedmann 1950).

Syringeal data also indicate that two genera are not monophyletic, suggesting that more detailed investigations of species relationships in this family must be performed using all extant taxa.

Congruence of these conclusions with the two previous cladistic analyses of the family (Fig. 1) cannot be assessed with rigor since neither of these examined all the species analyzed in this paper. Nevertheless, some comparisons can be made. Becker's (1987) hypothesis based on osteology (Fig. 1B) agrees generally with the syringeal hypothesis; in both, *Micrastur* is basal and *Spiziapteryx* is related to *Falco* and the falconets, rather than to the caracaras. Only the position of *Herpetotheres* and *Polihierax insignis* differs between the two. The topology derived from allozyme data (Fig. 1A, Boyce 1989) differs from the syringeal and osteological phylogenies. However, if the allozyme hypothesis were rooted at *Micrastur* rather than at the falconets, there would be substantial congruence among all three.

This study has demonstrated that syringeal data can be used to resolve phylogenetic questions at the generic and family levels of the Falconidae. The value of syringeal morphology for systematics has been known for at least one hundred years (Beddard 1898). Avian systematists, however, have not used syringeal characters to develop phylogenies for orders of birds other than the Passeriformes, and avian biologists, in general, have ignored the syrinx. In 1960, Andrew Berger observed, "There are few anatomical structures throughout the families of birds that need study as badly as the syrinx" (King 1989, page 106). By reinforcing the value of syringeal morphology as a systematic tool, this analysis should encourage systematists to explore little known morphological structures as sources of information for phylogenetic reconstruction.

ACKNOWLEDGMENTS

I am indebted to Drs. G. Barrowclough and R. Rockwell for their insight, support and advice throughout the course of this study. I thank Drs. R. Prum and P. Cannell for early guidance on syringeal morphology, and the following curators for lending me specimens in their collections: Dr. G. Barrowclough, Dr. R. Zusi, and Dr. V. Remsen. Helpful comments on earlier versions of this manuscript and much-needed moral support were provided by E. Griffiths, J. Groth, S. Hackett, S. Ratner, and P. Sweet. Final versions were improved by reviews from D. Amadon, J. Cracraft, C. Farquahr, F. Gill, L. Marcus, M. Novacek, R. Zusi and two anonymous reviewers. This research was supported by grants from the Frank M. Chapman Memorial Fund of the American Museum of Natural History, a Frank M. Chapman Pre-doctoral Fellowship, and a City University of New York Dissertation Improvement Grant.

Finally, as a raptor systematist, I would like to acknowledge the debt we all owe to Dr. D. Amadon, whose work provides the basis for research on raptor biology and systematics.

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APPENDIX I. List of specimens examined. Abbreviations for the institutions are given in the Materials and Specimens section.

Falconidae	
Daptrius americanus	AMNH 8667, unnum 24/7/90
Daptrius ater	KUMNH 041874, AMNH 10128
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 8413, 8430, 8688, 15808, 15931, 16307, CSG21, CSG9210
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 unnum 8/9/90
Outgroups	
Pelecanus roseus	AMNH 8619
Gampsonyx swainsonii	AMNH 8529
Otus asio	AMNH 8310
Mycteria americanus	AMNH 8513
Sula bassanus	AMNH 8618
Buteo jamaicensis	AMNH 18764
Aegypius tracheliotus	AMNH 81668
Accipiter striatus	AMNH 18761
Cathartes aura	AMNH 20933

APPENDIX II. DESCRIPTIONS OF 25 SYRINGEAL CHARACTERS

The characters for the syringeal analysis are divided into the following categories:

1. Tympanum (characters 1–9)
2. A and B elements (characters 10–18)
3. Membranes and muscles (characters 19–25)

Characters 3, 4, 8 and 18 are ordered multistate characters. Character 21 is an unordered multistate character. The plesiomorphic or primitive state for each character is described either as state [0] for the character, or in the general description for a group of characters.

TYMPANUM

(1) Presence of a tympanum or tracheal drum.

[0] There is no tracheal drum.

[1] The first A elements are ossified totally and more extensively than more craniad A elements. The first A elements are fused medially and may be partially or completely fused to each other along their margins, dorsally, laterally and ventrally forming a tracheal drum to which the pessulus is attached. The tracheal drum is always formed from elements A1 and A2, which are double elements. A3, which is usually single, and single elements from A4 to A8 may also be fused to the tympanum (see below).

The following 8 characters describe variations in the tympanum within the Falconidae. The tympanum is either primitively: (a) absent (within the species of Galliformes, Pelecaniformes, Strigiformes and Ciconiiformes examined) or (b) has a different pattern of fusion and different shape (within the Accipitridae).

Degree of dorsal fusion of tympanum (2–4)

(2) The first 2 single A elements are fused medially only, by an ossified bar which is an extension of the pessulus.

(3) The first 3 or 4 A elements are fused lightly but entirely along their margins. This is an ordered character:

(3.1) Margins are apparent along the edges of each ring.
(3.2) Margins are somewhat obliterated and only light sutures are apparent medially.

(4) At least 5 A elements are fused entirely along their margins. This is an ordered character:

(4.1) Sutures are apparent along the margins of all 5 A elements except medially.
(4.2) Sutures are always obliterated between the first two A single elements (usually A3 and A4).

Degree of ventral fusion of tympanum (5–7)

(5) The first three or four A elements (both double, usually A1 and A2, and single A elements) are fused along their margins. Spaces are apparent between the elements.

(6) The first three or four A elements are fused lightly but entirely along their margins.

(7) At least five A elements are fused entirely along their margins with some sutures apparent along the margins, except medially.

Tympanum shape (8–9)

(8) The shape of the fused A elements forming the tympanum varies from cylindrical (the most caudal and cranial elements having the same diameter) to a graduated A shape (the most caudal element wider in diameter than the most cranial). This is a partially ordered character: the transformations between states 0, 1, and 2 are treated as unordered; the transformation from state 2 to 3 is ordered.

(8.1) Tympanum shape is graduated and widens caudally.
(8.2) Tympanum is cylindrical.
(8.3) Tympanum is cylindrical; in addition, A1 lat-

erally is flattened causing a 'pinching in' of the most caudal element.

(9) Dorsal tympanum shape, medially, at pessulus ascent.

[1] A ridge of ossified tissue forms a medial bridge or connection between the dorsal A1 element ends and covers the dorsal ascent of the pessulus.

A AND B ELEMENTS

In all Falconidae genera, A1 and B1 dorsal and ventral ends are fused (A1 left to B1 left, A1 right to B1 right).

A1 elements (10–13)

In all Falconidae genera, A1 is a double element; both rings are incomplete medially, and A1 ends border the internal membranes.

(10) Separation of dorsal A1 element ends.

[0] A1 dorsal ends are separated.

[1] The dorsal ends of A1 are close medially and are fused together by ossified tissue.

(11) Size of A1 ends.

[0] A1 is a single element or the width of the A1 ends is proportionally similar to the width of A1 medially.

[1] The dorsal ends of A1 are very flattened and very enlarged.

(12) Flattening of the paired A1 elements.

[0] A1 is a single element or each half is rounded and forms a C shaped ring.

[1] Each A1 is flattened dorso-ventrally into a parenthetical shape. When viewed laterally, the A1 dorsal and ventral ends protrude out.

(13) Appearance of A1 on lateral view.

[0] A1 is concave up medially.

[1] Al is flattened medially.

B1 elements (14–17)

The following 4 characters describe modifications of the dorsal ends of the first B element and subsequent variations in the fusion of A1 and B1. The primitive state for these characters is hypothesized to be B1 ends which are rounded and end at the medial membrane without fusing to A1.

(14) B1 ends are very thick and wide and ascend sharply in an L shape to fuse with A1 ends.

(15) B1 ends are thin and ascend gradually to fuse with A1.

(16) There is a knobbing of B1 craniad edges; the craniad extension or knob fuses with A1.

(17) B1 ends are thick and rounded and ascend gradually to fuse with A1.

Fusion of A and B ventral ends

(18) Fusion of additional B elements ends to form a ridge bordering the internal membrane. This is an ordered character:

(18.0) There is no fusion of B element ends.
(18.1) B2 ends are fused to B1/A1.
(18.2) B3 ends are also fused.

MEMBRANES AND MUSCLES

(19) Existence of external (lateral) membrane on bronchi.

[0] There is no membrane, or, if one exists, the membrane lies between B1–4 elements.

[1] An external membrane is located between A1 which is concave up and B1 which is concave down.

M. tracheolateralis (20–22)

Within the Falconidae the M. tracheolateralis always inserts on the external (lateral) membrane. The following 3 characters describe variations in this derived character; the primitive state is hypothesized to be absence of the insertion on the membrane.

(20) A cartilaginous bar exists on the lateral membrane onto which the M. tracheolateralis inserts.

(21) M. tracheolateralis inserts on a membranous extension of the external membrane.

(21.1) There is a thick, bulbous membrane on the dorsal half of the external membrane. The M. tracheolateralis inserts on the bulbous extension and on the external membrane.
(21.2) The bulbous membrane covers the entire width of the external membrane.

(22) The M. tracheolateralis inserts on the dorsal half of the lateral membrane.

Cartilaginous border on internal membrane (23–25)

(23) Appearance of the internal (medial) membrane.

[0] There is no membrane, or, if one exists, the membrane is thin and has no cranial border.

[1] The internal (medial) membrane has a thickened cartilaginous cranial border.

The following 2 characters describe the appearance of the cartilaginous border, which is primitively hypothesized to be absent.

(24) The cartilaginous border is thick and even, and concave up from A1 dorsal to A1 ventral ends.

(25) Additional thin, amorphous cartilage edges the border, forming a straight caudal edge from A1 dorsal to A1 ventral ends.