

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 179

# **Phylogenetic Analysis of Avian Hindlimb Musculature**

by  
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## ABSTRACT

*McKittrick, M. C. Phylogenetic analysis of avian hindlimb musculature. Misc. Publ. Mus. Zool., Univ. Michigan 179:1-87, 3 figs.* Data from the literature on hindlimb muscle variation in birds were gathered with the following goals: 1) to attempt a phylogenetic analysis for all birds, and to tabulate the available data on hindlimb musculature and evaluate the limits of its resolution and its usefulness toward that phylogenetic end; 2) to create a data base that can serve as a guide to other anatomists wishing to use or generate myological data for phylogenetic or other comparative studies; 3) to assess the extent of information available on avian hindlimb musculature, review the work published since a compilation done more than two decades ago, and thereby identify which avian groups are most in need of study; 4) to make hindlimb muscle data available towards the formulation of phylogenetic hypotheses based on a large body of data from a variety of character systems, not just limb musculature. The data were evaluated for their utility in estimating phylogenetic relationships; interpretable variations were coded as character states and analyzed cladistically. Analysis of a 103-taxon by 68-character matrix yielded over 6,000 trees of 340 steps ( $ci = .300$ ). The data reflect homoplasy in these hindlimb muscle characters, but no more so than expected for a data set of this size. The characters are informative and corroborate numerous traditional groupings. The so-called "formula muscles" are no more informative phylogenetically than other muscle characters. Hypotheses of convergence have been proposed to explain the similarity of numerous avian taxa; some of these taxa, such as loons and grebes, and hawks and owls, are clustered in the present analyses. Such hypotheses of relationship must be tested by additional data from anatomical systems not directly associated with the hindlimb.

*Key words: Hindlimb musculature, birds, phylogeny, cladistics, homoplasy.*

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## INTRODUCTION

The higher level classifications of birds in widest use today (e.g., The Peters' Check-list; Wetmore, 1960) are still largely the legacy of two German anatomists, Maximilian Fürbringer (1888) and Hans Gadow (1892). In the last two decades, attempts have been made to bring more rigor to these classifications by testing the legitimacy of the characters on which they are based, and by seeking additional data with which old hypotheses of relationship may be tested or new hypotheses generated. In 1981, Cracraft published a phylogenetic taxonomy of birds that served to evaluate the data on which knowledge of avian relationships is based. This data base was surprisingly scanty. An increasing number of phylogenetic analyses have been performed during the last decade, using a variety of types of data (see Cracraft, 1988 for a review). Osteological data are available for some pelecyaniforms (Cracraft, 1985), Phalacrocoracidae (Siegel-Causey, 1988), Piciformes (Simpson and Cracraft, 1981), and some of the major groupings of Aves (Cracraft, 1988; Cracraft and Mindell, 1989); data on hindlimb musculature are available for hummingbirds (Zusi and Bentz, 1984), Coraciiformes (Maurer and Raikow, 1981), Piciformes (Swierczewski and Raikow, 1981), Old World suboscines (Raikow, 1987), Tyrannidae (McKittrick, 1985b), corvines (Borecky, 1977), and New World nine-primaried oscines (Raikow, 1978); data on forelimb musculature are available for some nonpasserines (McKittrick, 1991), some Tyrannidae (McKittrick, 1985a), and New World nine-primaried oscines (Raikow, 1978). Siegel-Causey's (1988) study is probably the most in-depth phylogenetic analysis of any group of birds (36 taxa, 137 characters). Such extensive data are not the norm: McKittrick (1991) reviewed the literature on wing musculature of non-passerine birds and found that relatively complete data were available for fewer than two dozen species. To date, the most taxonomically comprehensive classification of birds available is based on a single type of data, DNA hybridization (Sibley et al., 1988). Ideally, phylogenetic analyses should include as many data as possible from as many sources as possible; there is still much work to be done to achieve such a goal for any group of birds.

The following review of the hindlimb musculature of birds was undertaken for several reasons. One reason was to attempt a phylogenetic analysis for all birds, and to tabulate the available data on hindlimb musculature and evaluate the limits of its resolution and its usefulness toward that phylogenetic end. This effort was attempted specifically to test whether Charadriiformes is monophyletic, as a preliminary step in a planned, in-depth analysis of hindlimb musculature and syrinx morphology of members of that group. The second reason was to create a data base that could serve as a guide to other anatomists wishing to use or generate myological data for phylogenetic or other comparative studies. The character data summarized here should encourage other workers to evaluate the same characters in the avian groups they are studying; thus the data base can

increase in size and in its value for comparative analyses. The third reason was to assess the extent of information available on avian hindlimb musculature, review the work done since George and Berger's (1966) compilation, and thereby identify which avian groups are most in need of study. The final reason was to make hindlimb muscle data available towards the formulation of phylogenetic hypotheses based on a large body of data from a variety of character systems, not just limb musculature. It is hoped that other workers will use this data base as a taxonomic guide, and plan their studies of other character systems to complement this one.

The first part of this study consists of descriptive summaries of published reports on variation in avian hindlimb musculature, supplemented by data on *Merops* (Meropidae) and *Eurystomus* (Coraciidae) (McKitrick, ms.), and an evaluation of the utility of this variation for phylogenetic analysis. The resulting matrix of taxa and characters forms the basis for the phylogenetic analyses that constitute the second part of the study.

## MATERIALS AND METHODS

### MUSCLE AND CHARACTER DESCRIPTIONS

I gathered data on hindlimb muscle variation by studying all published reports on hindlimb musculature of birds. I included only a few studies of passerines because their monophyly has been well corroborated (Raikow, 1982) and I did not feel it necessary to slow the analysis with the addition of more than a few token groups. I restricted the survey by including only studies with complete descriptions, and to those that appeared thorough and accurate; this limited the scope of the project primarily to Hudson (1937), who set the standard for studies of limb musculature in birds, and to papers published since Hudson. Descriptions of each of the 46 muscles of the hindlimb were assessed, and from one to eight characters were extracted for each muscle; these are discussed below. Some of these characters could not be evaluated for all taxa or were difficult to interpret and thus to code, and were not included in the final matrix although they are described in the text. Therefore, there are many more characters described than are actually numbered and incorporated into the final matrix. It is hoped that additional study of these characters will elucidate patterns of variation so that they may be incorporated into future analyses.

In addition, where information was lacking for Coraciiformes (Maurer and Raikow, 1981), I added information from my own observations of muscle variation in *Merops* and *Eurystomus* (McKitrick, ms.).

The resulting matrix included over 200 taxa and 66 characters, to which I added one character (67: presence of feathers) to reflect monophyly of birds, and another (68: "neognath monophyly") to reflect monophyly of the ingroup. Neognath monophyly is supported by eight osteological characters (Cracraft, 1986); numerous molecular characters support this clade



as well (Cracraft and Mindell, 1989). I reduced this to 103 taxa by eliminating redundant taxa or those differing from others only by autapomorphies. A list of the characters used is given in Appendix 1. The complete matrix of taxa and characters is given in Appendix 2, with the 103 taxa used in the analysis in boldface type.

#### PHYLOGENETIC ANALYSIS

Selecting an appropriate outgroup for this analysis is problematical. The closest living relatives of birds are the crocodylians (Gauthier, 1986); if one were to use crocodylians as the outgroup, and even if homologous structures in the hindlimb musculature could be consistently identified, such an analysis might not be meaningful because crocodylians are rather distantly related to birds compared with non-avian dinosaurs (Gauthier, 1986). At present, however, the primary reason for not using a crocodylian outgroup is the lack of comparative data on the limb muscles of crocodylians; very little has been published other than the studies of Romer (1923) and Rowe (1986) which dealt only with thigh muscles. Some work has been done by Müller as well (pers. comm.; see also Müller, 1989). Despite these difficulties, I use an outgroup based on crocodylians (see below).

In 1979, Baumel et al. published a comprehensive atlas of avian anatomical nomenclature. The nomenclature was updated to reflect uniquely avian features; e.g. the name *M. iliofibularis* replaced *M. biceps femoris* because the muscle in birds does not attach on the femur nor is it bicipital. This effort skirted the issue of homology with anatomical features of other tetrapods, and it would be difficult for someone using this nomenclature to compare bird muscles with muscles of crocodylians. What is needed is a thorough comparative study of the morphology and development of limb muscles of crocodylians and birds. For the present, I use the nomenclature from Baumel et al. (1979) and in the Results section (below) I also present in parentheses the name in use prior to that publication if different from that of Baumel et al. Where anything is known about homology with crocodylian muscles, I note this.

For the moment it is appropriate to seek an avian outgroup, but this is also problematical due to the paucity of phylogenetic hypotheses that include all birds. Sibley et al. (1988) showed a group including paleognaths (ostriches, rheas, cassowaries, emus, tinamous), gallinaceous birds (guans, pheasants, quail), and anseriforms (geese, swans, ducks) as the sister group to the remainder of birds. Cracraft's (1981) classification differs from that of Sibley et al. (1988); however, the information content of his classification is limited because the largest subgroupings of Recent birds are Divisions, of which there are nine. In the first Division of Recent birds Cracraft includes loons, grebes, peleciforms, and procellariiforms (albatrosses, shearwaters, petrels); paleognaths are included in a different Division and anseriforms and gallinaceous birds in another. In the Peters' Check-list (Mayr and Cottrell, 1979), the first subdivision of Recent birds includes the

paleognaths. The first taxon of Recent birds in Wetmore's (1960) classification is the Superorder Impennes (penguins), followed by the Superorder Neognathae. In the latter, the first taxa are the "paleognath" orders, followed by loons, grebes, procellariiforms, and pelecaniforms. The first taxa in Storer's (1971) classification of Recent birds are also paleognaths.

The majority of these classifications concur in the placement of ratites and tinamous at the beginning; therefore for purposes of this analysis I will use paleognaths as the sister group to the remainder of birds. Monophyly of paleognaths is supported by DNA hybridization (Sibley and Ahlquist, 1985; Sibley et al., 1988), as well as osteological characters (Cracraft, 1986; Cracraft and Mindell, 1989).

Generally, it is not enough simply to have an ingroup and an outgroup. Usually one selects a monophyletic ingroup and an outgroup that is closely related to the ingroup (preferably the sister group). Within the ingroup is a less inclusive group whose monophyly one wishes to test. The ingroup is the smallest monophyletic group that includes this hypothesized monophyletic group. For polarity determinations one therefore has two levels at which to compare character states with those of the hypothesized monophyletic group (i.e., two "outgroups"). In the present case, however, I wish to assume as little phylogenetic structure as possible, because there is little evidence on which to base such assumptions—i.e., few detailed phylogenetic hypotheses have been presented for birds that also include the evidence on which the hypotheses are based. Therefore I am maintaining one large ingroup (neognaths), whose monophyly is fairly well corroborated (character 67), and within which I assume no structure; one small sister group (paleognaths); and a crocodylian outgroup (see below).

Characters in the ingroup were polarized with reference to the paleognaths. The one paleognath taxon used in the analysis presented here is *Tinamus*, which emerged as a primitive paleognath in preliminary analyses. I also included in the analysis a semi-hypothetical, non-avian "ancestor" (listed as Ancestor in the matrix and figures) with most characters coded as zero; this was treated as the outgroup. There were eight characters that were non-zero for *Tinamus*; four of these are coded as zero for the hypothetical ancestor and four as missing. The justification for this is as follows: Character state 1 for character 6 occurs only in tinamous (*Tinamus*, *Tinamotis*, *Crypturellus*, *Eudromia*, *Nothoprocta*), and 0 is likely to be the primitive condition. For Character 8 state 0 is the presence of a distal head in *M. femorotibialis externus*; this seems to be the condition present in crocodylians (Romer, 1923) and is therefore probably primitive for birds. Characters 52, 53, 54, and 66 are coded as missing (?) for the hypothetical ancestor because there are numerous states in birds and no particular justification is presently available for polarizing the states. Character 67 represents avian monophyly, and is coded as 0 for the hypothetical ancestor.

Some authors, principally Hudson et al. (1969), noted variation in a number of hindlimb muscles. Usually I coded characters showing such

variation based on the most common condition found; if no choice could be made, I coded the character as polymorphic.

I coded all multi-state characters as unordered (characters 2, 3, 11, 15, 16, 21, 24, 30, 38, 40, 41, 43, 46, 52, 53, 55, 58, 63–66). In other words, character transformations can take any sequence; for example with a 4-state character the transformation to state 3 can be achieved by any of several pathways, such as 0→1→2→3, 0→3, etc. The other characters were treated as ordered. All characters were given a weight of one. I analyzed the data using the computer program PAUP 3.0q (Swofford, 1991), employing the heuristic branch-swapping routine with random addition and tree bisection branch-swapping options. I enforced topological constraints to ensure that the ingroup remained monophyletic, that *Tinamus* was the sister group to the ingroup, and that Ancestor was the outgroup. The data were analyzed on a Macintosh IIfx. Initially, I performed 10 replications allowing 50 trees per replication in order to find the shortest tree; I then used one of these shortest trees as a "seed" and allowed 6,000 trees to be sought.

I also analyzed the data using Hennig86 (Farris, 1988), with the "Hennig" and branch-breaking routines.

## RESULTS

### MUSCLE AND CHARACTER DESCRIPTIONS

**M. iliotalibialis cranialis (ICR), origin** (sartorius; evidently not differentiated in crocodylians [see Romer, 1923:551]). The origin is from the synsacrum and ilium in tinamous (Hudson et al., 1972); from the trunk vertebrae and from the cranial half of the ventrolateral margin of the ilium in *Gavia immer* (Wilcox, 1952); from the vertebrae and the ilium in ciconiiforms (Vanden Berge, 1970), *Grus americana* (Fisher and Goodman, 1955), *Corvus* (Hudson, 1937), and *Tyrannus* (McKittrick, 1985b); and from the last two trunk vertebrae in Old World suboscines (Raikow, 1987). It is from the dorsal ridge of the synsacrum in *Sula brewsteri* (Hudson, 1937) and in *Colinus* (Berman and Raikow, 1982); from the cranial edge of the ilium only, in Oxyurini and *Anas* (Raikow, 1970), *Fregata magnificens*, *Pedioncetes phasianellus*, *Colinus virginianus* and some *Buteo* and *Falco*; ventral edge of ilium in *Bubo virginianus* and *Otus asio*; iliac crest in anhingas and cormorants (Owre, 1967); ilium in cathartids (Fisher, 1946); by an aponeurosis shared with *M. latissimus dorsi caudalis* from the last trunk vertebra and the cranial 5 cm of the dorsal ridge of the synsacrum in *Grus canadensis* (Berger, 1956b); from the synsacrum and the tendons of the *M. spinalis thoracis* in *Coua* (Berger, 1953) and many other cuckoos; from the craniodorsal end of the ilium in *Tauraco leucotis* (Berger, 1960); from the thoracic vertebrae and the craniodorsal tip of the preacetabular ilium in some but not all specimens of *Diomedea immutabilis* observed (origin is only

from thoracic vertebrae in *D. nigripes*), and in eight species of *Puffinus*; the occurrence of this type of origin in procellariiforms is unclear from Klemm's (1969) descriptions. The origin is from the thoracic vertebrae, the cranial margin of the ilium, and the cranial part of the synsacrum in hummingbirds (Zusi and Bentz, 1984), and from the thoracic vertebrae and the synsacrum in *Amazona albifrons* (Berman, 1984).

**M. iliotibialis cranialis, number of parts.** *Colius* has no deep head (Berman and Raikow, 1982). Old World suboscines have only one origin, from the dorsal vertebrae, none from the ilium (Raikow, 1987). This character is not explicitly discussed by most authors.

**M. iliotibialis cranialis, insertion.** Hudson (1937) noted that in *Gavia* and *Podiceps nigricollis* the insertion is fleshy directly onto the tibiotarsus.

**M. iliotibialis medialis (IM), presence (Character 1).** This is present only in *Phoenicopterus*, *Phoenicoparrus* (Vanden Berge, 1970; 1976), and *Cladorhynchus* (Olson and Feduccia, 1980).

**M. iliotibialis lateralis (IL) (Character 2: presence of pars preacetabularis; Character 3: presence of pars acetabularis; Character 4: presence of pars postacetabularis)** (iliotibialis). Pars postacetabularis is absent in penguins, but the acetabular and evidently the preacetabular portions are present (Schreiweis, 1982). The postacetabular part is absent in *Sagittarius*, Accipitridae, *Pandion*, and *Falco* (Hudson, 1948); *Polihierax* (Berger, 1956a); *Podargus*, *Chaetura pelagica*, *Sula*, *Uria*, *Buteo*, *Bubo*, *Otus*, *Buceros* (see Gadow and Selenka, 1891:154; Hudson, 1937; Berger, 1956a; Hoff, 1966), and *Tyrannus* (McKitrick, 1985b); it is apparently absent in *Anhinga* and *Phalacrocorax* (Owre, 1967 and fig. 28), in Lari and Alcae (Hudson et al., 1969 and fig. 5), *Diomedea immutabilis* (Klemm, 1969, figs. 29 and 49), and in all other procellariiforms except *Oceanites* (Klemm, 1969, fig. 49B). Both the acetabular and the postacetabular parts are absent in *Eugenes* and other hummingbirds (Zusi and Bentz, 1984), *Pharomachrus mocino* and *Chloroceryle americana* (George and Berger, 1966), *Colius* (Berman and Raikow, 1982), and *Amazona albifrons* (Berman, 1984). The preacetabular and acetabular parts are absent in *Chordeiles minor* (Hudson, 1937). The acetabular part is absent in *Podiceps* (Hudson, 1937) and Old World suboscines except Acanthisittidae (Raikow, 1987). The muscle is vestigial in *Fregata magnificens*, with fibers from only the acetabular part remaining (Hudson, 1937). Among coraciiforms, the acetabular and postacetabular parts are absent in Trogonidae, Todidae, Momotidae, Meropidae, Alcedinidae, and *Eurystomus*; all others possess all three parts. In all Coracii except *Eurystomus* the acetabular part is aponeurotic (Maurer and Raikow, 1981). In Caprimulgidae the preacetabular part is vestigial, the acetabular part present, and the postacetabular part well developed (Hoff, 1966). The pre- and

postacetabular parts are present in *Colaptes* and *Picoides* but the acetabular part is aponeurotic (Hudson, 1937).

All parts are present in *Apteryx australis mantelli* (McGowan, 1979), tinamous (Hudson, 1972), *Gavia immer* (Hudson, 1937; Wilcox, 1952), Oxyurini and *Anas* (Raikow, 1970), cathartids (Fisher, 1946), galliforms (Hudson et al., 1959), *Cladorhynchus* (Olson and Feduccia, 1980), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), Caprimulgidae (Hoff, 1966), *Columba* (George and Berger, 1966), *Totanus*, *Zenaida*, and *Corvus* (Hudson, 1937). In most ciconiiforms all three parts are present, except in Ciconiidae in which only the preacetabular portion is present; the pre- and postacetabular parts are present in flamingos, but the acetabular part is absent (Vanden Berge, 1970).

**M. ilirotibialis lateralis, number of heads.** Hudson (1948) reported two bellies in *Sagittarius*.

**M. ilirotrochantericus caudalis (ITCA), extent (Character 5)** (homologous to crocodilian *iliofemoralis, part* [see Rowe, 1986]). In *Daption capensis*, *Fulmarus glacialis*, *Pachyptila forsteri*, *P. desolata*, *Adamastor cinereus*, *Procellaria aequinoctialis*, and *Puffinus*, the origin on the ilium is considerably reduced in extent; in the rest of procellariiforms the muscle appears typical of most other birds (Klemm, 1969, fig. 4).

**M. ilirotrochantericus cranialis (ITCR), presence** (homologous to crocodilian *pubo-ischio-femoralis internus pars dorsalis* [see Rowe, 1986]). The muscle has been found in all birds except *Sula* (Hudson, 1937).

**M. ilirotrochantericus cranialis, relationship to M. ilirotrochantericus caudalis (Character 6).** The muscle is partially fused with M. ITCA (or has failed to separate from it) in *Pterodroma leucoptera*, strongly so in tinamous (Hudson et al., 1972).

**M. ilirotrochantericus cranialis, miscellaneous.** Klemm (1969) describes other variations within procellariiforms, but from these and the illustrations it does not appear that the variation is significant. McGowan (1979) reported the muscle absent in one of two specimens of *Apteryx australis mantelli*.

**M. ilirotrochantericus medius (ITM), presence** (homologous to crocodilian *pubo-ischio-femoralis internus pars dorsalis* [see Rowe, 1986; see M. ilirotrochantericus cranialis, above]). The muscle is present in *Apteryx* (McGowan, 1979), tinamous (Hudson et al., 1972), procellariiforms (Klemm, 1969), penguins (Schreiweis, 1982), *Gavia immer* (Wilcox, 1952), *Struthio*, *Rhea*, *Casuarinus*, and *Podiceps* (George and Berger, 1966); procellariiforms

(Klemm, 1969), anhingas and cormorants (Owre, 1967), ciconiiforms (Vanden Berge, 1970), cathartids (Fisher, 1946), falconiforms (Hudson, 1948), *Chauna*, Galliformes (except *Opisthocomus*), *Pediocetes*, *Colinus*, *Larus*, *Zenaida*, and *Colaptes* (Hudson, 1937); the three scolopacid species studied by Fleming (1966), *Fulica americana* (Rosser et al., 1982) (although George and Berger [1966] reported it absent in that species), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Amazona albifrons* (Berman, 1984), *Colius* (Berman and Raikow, 1982), *Columba*, *Goura*, *Gallicolumba*, *Eugenes* (but see below), *Pharomachrus*, *Chloroceryle*, *Coracias*, *Upupa*, *Aceros* (Bucerotinae), and *Indicator* (George and Berger, 1966); and *Corvus* (Hudson, 1937), and vestigial in *Philepitta* and *Neodrepanis* (Raikow, 1987). The muscle was reported by Hudson (1937) to be absent in a number of species, but Hudson contradicted himself in later publications. These errors were perpetuated by George and Berger (1966), who listed some of the same species as lacking the muscle, but without citing their source. George and Berger also reported the muscle absent in *Tauraco* and Cuculidae. The muscle is absent in *Eulampis* and other hummingbirds (Zusi and Bentz, 1984) and in *Eugenes* (Cohn, 1968), *contra* George and Berger (1966).

**M. iliostrochantericus medius accessorius.** This was present in some specimens of *Diomedea nigripes* (Klemm, 1969).

**Mm. iliostrochantericus cranialis and iliostrochantericus medius, fusion.** The two muscles are fused distally in *Grus canadensis* (Berger, 1956b), and either closely associated or fused in *Fulica americana* (Rosser et al., 1982). They are fused in anhingas and cormorants (Owre, 1967), *Colius* (Berman and Raikow, 1982), and Oxyurini and *Anas*, except for some specimens of *Oxyura* (Raikow, 1970). There is no fusion in *Gavia immer* (Wilcox, 1952), cathartids (Fisher, 1946), *Grus americana* (Fisher and Goodman, 1955), *Amazona albifrons* (Berman, 1984), or *Corvus* (Hudson, 1937). In hummingbirds M. ITM is absent (Zusi and Bentz, 1984), so fusion of ITCR and ITM is moot. In *Tinamus* and *Crypturellus* the two are completely fused, but they are distinct in *Eudromia*, *Nothura*, *Nothoprocta*, and on one side of the one specimen of *Tinamotis* examined (Hudson et al., 1972). The two are only partially separable in ciconiiforms (Vanden Berge, 1970). In penguins the two muscles insert in common, except in *Eudyptula* in which the insertions are separate (Schreiweis, 1982). Among galliforms, the two muscles are independent in all forms examined by Hudson et al. (1959) except *Opisthocomus*, in which they are fused.

The two muscles are separate, or fused only at insertion, in Stercorariidae, *Rissa*, *Sterna*, some *Uria*, and *Cepphus*, and fused in *Chlidonias*, *Gelochelidon*, *Thalasseus*, and most Alcae (Hudson et al., 1969).

The condition is not specified for *Apteryx australis mantelli* (McGowan, 1979).

In eurylaimids except *Pseudocalyptomena* the two muscles are separate

with a common tendon of insertion; in *Pseudocalyptomena* the muscles are separate to the point of insertion, where they fuse (Raikow, 1987). The muscles are entirely separate in *Acanthisitta*, *Xenicus*, *Pitta versicolor*, and *P. brachyura*, but the tendons are fused in *P. erythrogaster*. In *Philepitta* and *Neodrepanis* M. ITM is vestigial and fuses with the distal end of M. ITCR.

**M. iliofemoralis externus (IFE), presence (Character 7)** (gluteus medius et minimus; homologous to crocodylian *iliofemoralis* [see Rowe, 1986; see M. iliostrochantericus caudalis, above]). This is absent in *Podiceps*, *Zenaida*, *Coccyzus*, *Geococcyx*, *Chordeiles*, *Chaetura*, *Colaptes*, and *Picoides* (Hudson, 1937); *Columba*, *Goura*, *Gallicolumba*, *Didunculus*, Cuculidae, *Apus*, *Eugenes*, *Pharomachrus*, *Chloroceryle*, *Momotus*, *Coracias*, *Eurystomus*, *Upupa*, *Aceros*, and *Indicator* (George and Berger, 1966); all caprimulgiforms (Hoff, 1966), *Eulampis* and other hummingbirds (Zusi and Bentz, 1984; Cohn, 1968), all Coraciiformes (including Trogoniformes) (Maurer and Raikow, 1981), *Corvus* (Hudson, 1937), *Tyrannus* (Hudson, 1937; McKittrick, 1985b), and Old World suboscines (Raikow, 1987). It is present in *Apteryx australis mantelli* (McGowan, 1979), tinamous (Hudson et al., 1972), *Gavia immer* (Wilcox, 1952) in which it is fused with M. ITCA (Hudson, 1937), anhingas and cormorants (Owre, 1967), ciconiiforms (Vanden Berge, 1970), Oxyurini and *Anas* (Raikow, 1970), *Polihierax* (Berger, 1956a), falconiforms (Fisher, 1946; Hudson, 1948), galliforms (Hudson et al., 1959), *Grus americana* and *G. canadensis* (Fisher and Goodman, 1955; Berger 1956b), *Fulica americana* (Rosser et al., 1982), *Sula*, *Fregata*, *Ardea*, *Chen*, *Butorides*, *Buteo*, *Falco*, *Pediocetes*, *Colinus*, *Fulica*, *Totanus*, *Larus*, *Uria*, *Otus*, and *Bubo* (Hudson, 1937); *Lari* and *Alcae* (Hudson et al., 1969), *Tauraco* (George and Berger, 1966), *Tryngites subruficollis*, *Limnodromus griseus* and *Gallinago gallinago* (Fleming, 1966, figs. 1–3); *Colius* (Berman and Raikow, 1982), and *Amazona albifrons* (Berman, 1984). It is present, but small and weak, in cathartids (Fisher, 1946).

This muscle was noted by George and Berger (1966) to be absent in *Spheniscus*, but Schreiweis (1982) reported it to be present in penguins (including *Spheniscus*) although weakly developed. The belly was separate from ITCA in only one specimen (*Megadyptes antipodes*), but the insertions were separate in all.

Klemm (1969) does not report the muscle as absent in any procelariiform, but rather as fused with ITCA in most taxa, with variation in some taxa in the degree of fusion. In *Diomedea* and *Pelecanoides* the muscle is partly fused with ITCA. It is present and reduced in *Hydrobates*. In most other taxa the muscle is completely fused: *Pterodroma*, *Halobaena*, *Pachyptila*, *Adamastor*, *Procellaria*, *Puffinus*, *Oceanodroma*.

The muscle is unusually large in *Colius* (Berman and Raikow, 1982).

**M. femorotibialis externus (FTE), distal head (Character 8)**. This is present in *Apteryx australis mantelli* (McGowan, 1979), ciconiiforms (Vanden Berge, 1970), *Lari* and *Alcae* (Hudson et al., 1969), the three scolopacids

studied by Fleming (1966), numerous gruiforms including *Fulica americana* (Rosser et al., 1982), *Grus americana* and *G. canadensis* (Berger, 1956b; the proximal head was described by Fisher and Goodman [1955] as *M. vastus lateralis*, the distal head as *M. femorotibialis externus*); *Columba*, *Goura victoria*, *Gallicolumba luzonica*, *Coua caerulea*, and *Indicator variegatus* (George and Berger, 1966); *Amazona albifrons* (Berman, 1984), strigiforms and caprimulgiforms (Hoff, 1966), *Colinus* (Berman and Raikow, 1982), woodpeckers (Swierczewski and Raikow, 1981), *Tyrannus* (McKitrick, 1985b), and Old World suboscines (Raikow, 1987). It is evidently present in procelariiforms, in which Klemm (1969) referred to it as a "deep" part. It is not mentioned for *Gavia immer* (Wilcox, 1952), cathartids (Fisher, 1946), cuckoos (Berger, 1952), nor hummingbirds (Zusi and Bentz, 1984), and is presumed absent. It is presumed absent in tinamous (Hudson et al., 1972), aningas and cormorants (Owre, 1967), and Oxyurini and *Anas* (Raikow, 1970). It is not mentioned by Maurer and Raikow (1981) for coraciiforms and no inference can be made about its occurrence in that group; however it is present in *Eurystomus* (McKitrick, ms.).

Schreiweis (1982) reported that in penguins the *M. femorotibialis externus* is very small, limited to the distal one-third of the femur; in *Eudyptula* it is not evident, and it is absent or amorphous in *Aptenodytes* and *Pygoscelis*. This is a non-standard interpretation. According to the illustrations, this small FTE is actually the distal head of FTE, and what Schreiweis is calling *M. femorotibialis medialis* is in fact the complex formed by the FTE proximal head and FTM. Hudson et al. (1959) made the same error; pars distalis is present in all galliforms examined by them. Pars distalis is present (although not so named) in *Ardea*, *Fulica*, *Larus*, *Totanus*, and *Zenaida*, and absent in the other species examined by Hudson (1937).

In *Sagittarius* the FTE is a separate head; in cathartids and some other falconiforms the muscle is fused with FTM (i.e., pars distalis is absent) (Hudson, 1948).

Romer (1923:538) notes that in the Crocodylia, "an additional external head is found." It is not illustrated, but this could be homologous with the distal head of FTE in birds.

**M. femorotibialis medius (FTM).** In tinamous FTM has a lateral and a medial head (Hudson et al., 1972).

**M. femorotibialis internus (FTI), longitudinal division (Character 9).** The muscle has a longitudinal division in *Buteo* (Hudson, 1937). In *Fregata* the tendon of insertion bifurcates, with one part inserting with the patellar tendon, the other on the tibia (Hudson, 1937).

Klemm (1969) described this muscle as having two parts in procelariiforms, a main head and an accessory head, with the main head being divided into proximal and distal parts. He reported the accessory head to be absent in *Hydrobates* and in the Oceanitinae (see Klemm, 1969), and perhaps in *Pterodroma cooki*. Hudson et al. (1972) reported that distally, the



cranial and caudal edges of the belly were “more or less separate” in tinamous. The muscle has two heads, caput cranialis and caput caudalis, in *Fulica americana* (Rosser et al., 1982). The two heads insert together. This is also true of *Aramus guarauna* (Allen, 1962).

Raikow (1987) noted that whereas the muscle is not divisible in Old World suboscines, the tendon is separable into superficial and deep layers.

**M. iliofibularis (IF)** (biceps femoris). There are two heads of origin in *Metallura*, *Thalurania*, *Calliphlox*, and possibly *Eulampis* (Zusi and Bentz, 1984), and in *Aceros undulatus* and *Ceratogymna elata* (George and Berger, 1966). Beddard (1898) reported a separate slip of the tendon inserting on the surface of *M. gastrocnemius* in *Struthio*, Anatidae, some Rallidae, and Alcidae. He also reported three points of insertion in *Podica*. In some Caprimulgiformes (*Podargus* and *Batrachostomus*) a small, fleshy slip arises on the femoral shaft (Hoff, 1966 and fig. 8). Raikow (1987) noted two heads present in *Eurylaimus*, *Pseudocalyptomena*, and “faintly” so in *Cymbirhynchus*, but not in other Old World suboscines.

The IF is limited to the acetabular and postacetabular ilium in *Gavia*, *Podiceps nigricollis*, *Chen*, *Buteo*, *Falco*, *Coccyzus*, *Bubo*, *Otus*, *Colaptes*, and *Picoides* (Hudson, 1937).

**M. iliofibularis, ansa iliofibularis.** This has three arms in *Gavia immer* (Wilcox, 1952), *Fulica americana* (Rosser et al., 1982), *Colinus* (Berman and Raikow, 1982), *Amazona albifrons* (Berman, 1984), hummingbirds (Zusi and Bentz, 1984), all the species examined by Hudson (1937), and Old World suboscines (Raikow, 1987). Beddard (1898) reported it to be absent in *Phaethon* and some swifts. In Oceanitinae (Klemm, 1969:10) and *Hydrobates* the biceps loop is formed of a single ligament open at the distal end (**Character 10**), rather than two arms (Klemm, 1969). There are two arms in *Grus americana*, with the third being reduced to a vinculum passing to several shank flexors (Fisher and Goodman, 1955). There appear to be three arms in cathartids (Fisher, 1946), although this is not stated. The condition is not noted for tinamous by Hudson et al. (1972).

**M. iliofibularis, length of ansa iliofibularis (Character 11).** In *Gavia immer* and *Podiceps nigricollis* the arms are very long, because the muscle inserts at about mid-shank. The arms are moderately long in penguins, *vide* illustrations in Schreiweis (1982).

**M. flexor cruris lateralis (FCRL) pars pelvica, origin** (semitendinosus). The origin is from the ischium as well as the ilium in *Gavia*, *Podiceps nigricollis*, *Sula*, *Chen*, *Uria*, and *Picoides* (Hudson, 1937), and from the pubis as well as the ilium in *Grus americana* (Fisher and Goodman, 1955), *Chauna* (George and Berger, 1966), and cathartids (Fisher, 1946). It is from the ilium and the first free caudal vertebrae in penguins (Schreiweis, 1982), tinamous (Hudson et al., 1972), anhingas and cormorants (Owre, 1967),

Oxyurini and *Anas* (Raikow, 1970), *Colius* (Berman and Raikow, 1982), and Old World suboscines (Raikow, 1987). The origin is from the ilium alone in ciconiiforms (Vanden Berge, 1970), *Gavia*, *Podiceps*, *Opisthocomus*, *Grus*, *Fulica*, *Goura*, *Tauraco*, *Geococcyx*, *Coua*, and *Aceros* (George and Berger, 1966); and in *Amazona albifrons* (Berman, 1984), among others. It is from the ilium and by fascia from the vertebrae in *Corvus* (Hudson, 1937).

**M. flexor cruris lateralis pars accessoria, presence (Character 12).** The accessory part is present in *Apteryx australis mantelli* (McGowan, 1979), tinamous (Hudson et al., 1972), Struthionidae, Rheidae, Casuariidae, Dromiceidae, *Phaethon*, *Ardea*, *Butorides*, *Phoenicopterus*, and *Anhima cornuta* (George and Berger, 1966); cathartids (Fisher, 1946; Hudson, 1948), *Sagittarius* (Hudson, 1948), galliforms (in which it is well developed; Hudson et al., 1959), Turnicidae (George and Berger, 1966), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Fulica*, Otididae, *Totanus*, *Larus*, Columbidae, Psittacidae (except see Beddard, 1898:261), and Cuculidae (Berger, 1952); *Tauraco*, *Steatornis*, *Chordeiles*, Coliidae, Momotidae, Meropidae, *Coracias*, *Upupa*, *Aceros*, *Galbula*, *Indicator*, *Colaptes*, *Dryocopus*, and *Melanerpes* (George and Berger, 1966); *Amazona albifrons* (Berman, 1966), *Colius* (Berman and Raikow, 1982), *Corvus* (Hudson, 1937), *Tyrannus* (Hudson, 1937; McKitrick, 1985b), and Old World suboscines (Raikow, 1987). Among procellariiforms, it is present in *Oceanites oceanicus*, *Pelagodroma marina*, *Fregatta grallaria*, *Nesofregatta*, and *Garrodia* and absent in all the others (Klemm, 1969). It is present in the three scolopacid species studied by Fleming (1966).

The accessory part is absent in penguins (Schreiweis, 1982), *Gavia immer* (Wilcox, 1952), *Pelecanus* and *Chauna torquata* (George and Berger, 1966), anhingas and cormorants (Owre, 1967), accipitrids and falconids (Hudson, 1948), Oxyurini and *Anas* (Raikow, 1970), owls (Hoff, 1966), and in *Podica*, *Heliornis*, *Alca*, Trogonidae, *Chloroceryle*, and *Sphyrapius* (George and Berger, 1966). Hudson (1937) reported pars accessoria absent in *Gavia*, *Podiceps nigricollis*, *Fregata*, *Sula*, *Chen*, *Uria*, and *Picoides*. He reported both parts present in *Ardea*, *Butorides*, *Cathartes*, *Pediocetes*, *Colinus*, *Grus*, *Fulica*, and *Zenaida*. Maurer and Raikow (1981) reported pars accessoria present in all coraciiforms except Trogonidae and Alcedinoidea (includes *Merops*); however McKitrick (ms.) found FCRLA to be variably present in *Merops*.

The accessory part is present in all ciconiiforms examined by Vanden Berge (1970), with the possible exception of Ciconiidae in which it is only "suggested by a small bundle of fleshy fibers, closely grown together with the P. med. M. gas., which fuse with the lateral surface of the distal end of the Add. long. [= M. pubo-ischio-femoralis]. There is no insertion on the femur in any [ciconiid] specimen I have examined" (p. 338).

Pars accessoria is present in all Lari but "greatly reduced" in most: "It is best developed in *Larus*, terns and *Rynchops*; apparently absent in some Stercorariidae and *Rissa*" (Hudson et al., 1969:472). Pars accessoria is absent in all Alcae (Hudson et al., 1969). The latter authors note that in Lari

there is a strong connection between FCRL and *M. gastrocnemius pars medialis*; no such connection exists in Alcae. I therefore code this character as 0 for all Lari but character 14 (see below) is coded as 1 (FCRL pars accessoria reduced) for this group. FCRL pars accessoria is not completely absent unless this connection is gone (pers. obs.).

**M. flexor cruris lateralis pars pelvica, presence (Character 13).** Both parts of the muscle are reported absent in most procellariiforms (Klemm, 1969), *Fregata*, *Buteo*, *Falco*, *Chaetura*, *Bubo*, and *Otus* (Hudson, 1937); in all falconiforms studied by Hudson (1948) except *Sagittarius* and cathartids, and in hummingbirds (Zusi and Bentz, 1984). My own observations (McKitrick, ms.) indicate that pars pelvica is present in *Chaetura* but is fused with *M. flexor cruris medialis*. The combined muscle is very broad, and the caudal fiber mass inserts on the tendon of origin about 4 mm distal to the cranial mass. It is possible that the two muscles failed to divide in hummingbirds as well: Zusi and Bentz (1984) report that the tendon of insertion of FCRM is divided. Character 13 is coded as ? for hummingbirds.

**M. flexor cruris lateralis pars accessoria, number of heads.** According to George and Berger (1966), Fisher and Goodman (1955) report that the accessory part has two heads in *Grus americana*. From the description by Fisher and Goodman (1955) it is not clear that they are not simply referring to the two points of insertion, i.e., in the popliteal region of the femur and on *M. gastrocnemius*, as occurs in most other birds. They refer to distal and proximal accessory heads (p. 83), but they do not illustrate them. Berger (1956b) states that *Grus canadensis* has two distinct parts as well. Fisher (1946) reports "two fairly distinct parts" in cathartids. In *Amazona albifrons*, pars accessoria has one head and appears to be reduced distally (Berman, 1984, fig. 3). In *Colinus* it has one head and has an extensive insertion on the femoral shaft (Berman and Raikow, 1982). It has one head in *Corvus* (Hudson, 1937) and Old World suboscines (Raikow, 1987); the condition is variable in *Tyrannus* (McKitrick, 1985b).

**M. flexor cruris lateralis pars accessoria, development (Character 14).** In tinamous the muscle is very strongly developed, inserting on 46% of the femur in *Nothoprocta* (Hudson et al., 1972). Pars accessoria is moderately well developed in the three scolopacid species studied by Fleming (1966) and in Old World suboscines (Raikow, 1987). It is reduced in *Apteryx australis mantelli* (McGowan, 1979), and greatly reduced in Ciconiidae so that no fibers insert on the femoral shaft (Vanden Berge, 1970).

Pars accessoria is reduced in Alcae and in some Lari (Hudson et al., 1969), *Amazona* (Berman, 1984, fig. 4), *Steatornis* and possibly other caprimulgiforms (Hoff, 1966), *Eurystomus* (McKitrick, ms.), and in some specimens of *Tyrannus* (McKitrick, 1985b).

**Insertion of *M. flexor cruris lateralis pars accessoria* on *M. gastrocnemius*.** In *Cathartes* and *Gymnogyphs* FCRL pars accessoria (FCRLA) does not insert on pars intermedia of *M. gastrocnemius* but rather on the common tendon of pars medialis and pars lateralis. In *Vultur* there is no connection between FCRLA and gastrocnemius (Fisher, 1946). In *Grus americana* the insertion is on the common tendon of insertion of *M. gastrocnemius* (Fisher and Goodman, 1955), but FCRLA does not insert on gastrocnemius in *G. canadensis* (Berger, 1956b). In *Fulica americana* it inserts on *M. gastrocnemius* pars intermedia, as well as in the popliteal region of the femur (Rosser et al., 1982). In tinamous (Hudson et al., 1972), *Corvus* (Hudson, 1937), and *Tyrannus* (McKitrick, 1985b) it has a strong connection with *M. gastrocnemius* pars intermedia. Hudson (1937) noted that there was no connection between FCRL and gastrocnemius in *Gavia*, *Podiceps nigricollis*, *Sula*, *Uria*, *Chen*, and *Picoides*. In Old World suboscines there is partial fusion in some species and in others only the tendon from FCRL attaches to *M. gastrocnemius* (Raikow, 1987).

**Insertion of *M. flexor cruris lateralis* on the tibiotarsus.** In ciconiiforms the tendon from the raphe to the tibiotarsus, when present, inserts with the tendon of *M. flexor cruris medialis*. The raphe is present but weak in *Leucophoyx*, *Nycticorax*, *Mycteria*, *Leptoptilos*, *Phoenicopterus*, and *Phoenicoparus*, and somewhat stronger in *Balaeniceps*, *Ciconia*, *Eudocimus*, and *Ajaia*. It is absent in *Ardea*, *Butorides*, *Florida*, *Dichromanassa*, *Leucophoyx*, *Hydranassa*, *Agamia*, *Nycticorax*, *Nyctanassa*, *Heterocnus*, *Ixobrychus*, *Botaurus*, *Cochlearius*, and *Plegadis* (Vanden Berge, 1970).

The insertion of *M. flexor cruris lateralis* pars pelvica is "very long and slender" in *Gavia immer* and "somewhat similar" in *Podiceps nigricollis*, both of which lack pars accessoria. In most birds this tendon is wider (Hudson, 1937).

***M. caudofemoralis* (CF), presence (Character 15)** (piriformis pars caudofemoralis). The muscle is reportedly absent in *Sagittarius* but present in other falconiforms (Hudson, 1948), absent in *Meleagris* but present in all other galliforms examined by Hudson et al. (1959), absent in *Rhea*, *Dromiceius*, *Cariama cristata*, *Chunga burmeisteri*, *Psophia*, *Otis*, and *Burhinus* (George and Berger, 1966); absent in *Balearica* (Beddard, 1898:367), and absent in *Steatornis* (Hoff, 1966). It is present in *Apteryx australis mantelli* (McGowan, 1979). It is present in most cathartids, but absent in *Gymnogyphs*, *Sarcoramphus*, and *Vultur* (Fisher, 1946). It is present in procellariiforms (Klemm, 1969), penguins (Schreiweis, 1982), tinamous except *Eudromia* (Hudson et al., 1972), *Gavia immer* (Wilcox, 1952), anhingas and cormorants (Owre, 1967), *Polihierax* (Berger, 1956a), Oxyurini and *Anas* (Raikow, 1970), *Fulica americana* (Rosser et al., 1982), two out of three specimens of *Grus americana* (Fisher and Goodman, 1955), three specimens of *G. canadensis* (Berger, 1956b), all Lari and Alcae (Hudson et al., 1969), the three scolopacids studied by Fleming (1966), *Columba* (George and Berger,

1966), owls and caprimulgiforms (except *Steatornis*; Hoff 1966), *Amazona albifrons* (Berman, 1984), *Colinus* (Berman and Raikow, 1982), *Eurystomus* (McKittrick, ms.), hummingbirds (Zusi and Bentz, 1984), *Corvus* (Hudson, 1937), *Tyrannus* (Hudson, 1937; McKittrick, 1985b), and Old World suboscines (Raikow, 1987).

Hudson (1937) reported that caudofemoralis is present in all the forms he examined except for *Podiceps nigricollis*. It was therefore present in *Gavia*, *Chen*, *Pediocetes*, *Colinus*, *Grus*, *Fulica*, *Uria*, *Zenaidra*, *Fregata*, *Sula*, *Ardea*, *Cathartes*, *Buteo*, *Falco*, *Totanus*, *Larus*, *Bubo*, *Otus*, *Coccyzus*, *Chordeiles*, *Chaetura*, *Colaptes*, and *Picoides*. He noted that the muscle was very weakly developed in *Fregata*, *Ardea*, *Grus*, *Larus* (not so noted by Hudson et al., 1969, and not so coded here), *Bubo* and *Otus*. It is present in the cuckoos studied by Berger (1952), weakly so in *Geococcyx*.

Within ciconiiforms, caudofemoralis is absent in *Nyctanassa*, *Heterocnus*, *Cochlearius*, *Leptoptilos*, *Phoenicopterus*, *Phoenicoparrus*, and one of two legs of *Agamia*; it is present in *Mycteria*, *Ciconia*, *Butorides*, *Dichromanassa*, *Hydranassa*, and one leg of *Agamia* (Vanden Berge, 1970). Vanden Berge (1970) did not give a complete list of the species in which the muscle was present or absent, but in his Table 4 (p. 357) he noted the muscle was present in nine genera of Ardeidae and absent in three genera; it was present in Balaenicipitidae, present in two genera of Ciconiidae and absent in one genus, present in Threskiornithidae and absent in Phoenicopteridae. He noted that when present the muscle was fairly weak.

**M. caudofemoralis, width.** The muscle is fairly broad in *Tryngites subruficollis* and *Limnodromus griseus*, and considerably narrower in *Capella* (= *Gallinago*), 2 mm at the widest; the origin is also weak in *Gallinago* (see figs. 1 and 2 in Fleming, 1966).

**M. caudofemoralis, insertion.** In *Fregata*, *Sula*, and *Chaetura* the insertion is long and slender.

**M. caudofemoralis, relationship to M. ischiofemoralis.** Owre (1967) noted that Wilcox (1952) described a fusion of the tendons of insertion of *M. caudofemoralis* and *M. flexor ischiofemoralis* (= *M. ischiofemoralis*). This is erroneous; Wilcox (1952) reported fusion of *M. caudofemoralis* and *M. iliofemoralis*, not ischiofemoralis.

**M. iliofemoralis (ILF), presence (Character 16)** (piriformis pars iliofemoralis). The muscle is present in *Apteryx australis mantelli* (McGowan, 1979). It is present in penguins (Schreiweis, 1982), and well developed in tinamous (Hudson et al., 1972) and in *Gavia immer* (Wilcox, 1952). It is present in *Sagittarius* but absent in other falconiforms (Hudson, 1948). The muscle is reportedly present in Struthionidae, Rheidae, Casuariidae, Dromiceidae, Tinamidae, Gaviidae, Podicipedidae (but see Hudson, 1937) (George and Berger, 1966); most procellariiforms (Klemm, 1969); variably

present in *Phalacrocorax* and present in some Anhimidae (George and Berger, 1966), in Oxyurini and *Anas* (Raikow, 1970), *Chen* and *Zenaida* (Hudson, 1937), galliforms (Hudson et al., 1959), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), some Charadriiformes (Jacanidae, Haematopodidae, Recurvirostridae, Dromadidae, Glareolidae, Thinocoridae, Chionididae, some terns, Rynchopidae, *Uria*), Pteroclididae, Columbidae (not *Lopho-laemus*—Beddard, 1898:310), *Tauraco leucotis*, (George and Berger, 1966); and in *Geococcyx* and *Crotophaga* (Berger, 1952). It was present in one of four specimens of *Anhinga* but not in cormorants (Owre, 1967). Among the ciconiiforms examined by Vanden Berge (1970), the muscle is present only in Threskiornithidae and Phoenicopteridae; it is absent in Ardeidae, Ciconiidae, and Balaenicipitidae. Hudson (1937) reported it absent in *Fregata*, *Sula*, *Ardea*, *Cathartes*, *Buteo*, *Falco*, *Totanus*, *Larus*, *Bubo*, *Otus*, *Coccyzus*, *Chordeiles*, *Chaetura*, *Colaptes*, and *Picoides*.

It is absent in *Phaethon* and *Pelecanus* (George and Berger, 1966), cathartids (Fisher, 1946), *Polihierax* (Berger, 1956a), *Turnix* and *Grus leucogeranus* (George and Berger, 1966), *Balearica regulorum* (Beddard, 1898:367), the three scolopacids studied by Fleming (1966), owls and caprimulgidiforms (Hoff, 1966), *Eurystomus* (McKitrick, ms.), and in *Totanus*, *Stercorarius*, *Larus*, parrots, *Chordeiles minor*, *Chaetura pelagica*, *Eugenes fulgens*, *Colius striatus*, *Pharomachrus mocino*, *Chloroceryle americana*, *Coracias abyssinica*, *Upupa epops*, *Aceros undulatus*, *Indicator variegatus*, and woodpeckers (George and Berger, 1966). It is absent in *Amazona albifrons* (Berman, 1984), *Colius* (Berman and Raikow, 1982), *Corvus* (Hudson, 1937), *Tyrannus* (Hudson, 1937; McKitrick, 1985b), and Old World suboscines (Raikow, 1987). It was not mentioned for hummingbirds by Zusi and Bentz (1984), and is presumed absent.

Among Lari and Alcae, iliofemoralis is present in all Sterninae, *Uria*, *Cepphus*, *Brachyramphus*, and *Synthliboramphus*; it is variable in *Stercorarius*, *Larus*, *Rynchops*, and *Alca* and very weak or vestigial in those individuals possessing it; it is absent in *Catharacta*, *Rissa*, *Ptychoramphus*, *Cerorhinca*, *Fratercula*, and *Lunda* (Hudson et al., 1969).

Presence and absence of Mm. caudofemoralis and iliofemoralis is variable in cuckoos, with some genera having formula AB and some A (Berger, 1960).

**M. iliofemoralis, origin.** The origin is from the ilium in most birds in which the muscle is present, including *Apteryx australis mantelli* (McGowan, 1979), tinamous (Hudson et al., 1972), *Gavia immer* (Wilcox, 1952), threskiornithids and phoenicopterids (Vanden Berge, 1970), *Grus americana* (Fisher and Goodman, 1955), and *G. canadensis* (Berger, 1956b), but is limited to the ischium in *Uria*. It arises from the pelvis where the ilium and ischium fuse in Oxyurini and *Anas* (Raikow, 1970).

The origin varies in penguins in being fleshy in *Spheniscus*, mostly so in *Aptenodytes*, primarily tendinous in *Eudyptes*, and entirely so in *Pygoscelis*, *Eudyptula*, and *Megadyptes* (Schreiweis, 1982).

**M. iliofemoralis, size relative to M. caudofemoralis.** The muscle is bulkier than *M. caudofemoralis* in most birds (George and Berger, 1966), but is a thin sheet in *Crax*, *Grus*, and *Goura*. Fisher and Goodman (1955) reported that it is "by far the larger" of the two in *Grus americana*, however (p. 85).

**M. iliofemoralis, insertion relative to M. caudofemoralis.** *M. iliofemoralis* is separate from *M. caudofemoralis* for most of its length in *Pachyptila* (both species) and in *Halobaena*, but the two muscles insert together. In *Puffinus carneipes* *M. iliofemoralis* is completely separate from *M. caudofemoralis*. The insertions are separate in *Grus americana* (Fisher and Goodman, 1955) and *G. canadensis* (Berger, 1956b). The two are fused in *Gavia immer* (Wilcox, 1952). In threskiornithids and phoenicopterids the two insert together (Vanden Berge, 1970).

**M. iliofemoralis, number of heads.** In tinamous there is a small cranial head in addition to the main belly (Hudson et al., 1972).

**M. ischiofemoralis (ISF).** It arises by two heads in *Colinus* (Berman and Raikow, 1982), but only one in *Amazona albifrons* (Berman, 1984) and probably most birds.

**M. flexor cruris medialis (FCRM), number of parts (Character 17)** (semimembranosus). This muscle has "two distinct parts which originate and insert together" in *Falco* (Hudson, 1937). There are two such parts in *Polihierax semitorquatus* also, but they originate and insert independently (Berger, 1956a).

The muscle is very wide in Phoenicopteridae; in Ardeidae it is narrow and arises primarily from the ischium rather than the pubis (Vanden Berge, 1970).

FCRM is absent in *Podiceps nigricollis*, and weakly developed in *Sula* and *Colinus* (Hudson, 1937).

**M. flexor cruris medialis tendon, fusion with tendon of M. flexor cruris lateralis (Character 18).** In most birds the tendons of insertion of these two muscles are connected distally and may insert together, as in tinamous (Hudson et al., 1972), penguins (Schreiweis, 1982), *Gavia immer* (Wilcox, 1952), ciconiiforms (Vanden Berge, 1970), cathartids (Fisher, 1946), falconiforms (Hudson, 1937; 1948), Oxyurini and *Anas* (Raikow, 1970), galliforms (Hudson et al., 1959), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Fulica americana* (Rosser et al., 1982), Lari and Alcae (Hudson et al., 1969), *Columba* (George and Berger, 1966), *Corvus* (Hudson, 1937), and Old World suboscines except some species of *Pitta* (Raikow, 1987). They are independent in *Aegotheles insignis* and *Chordeiles* (Hoff, 1966), in *Tauraco leucotis* and *Coccyzus erythrophthalmus* (George and Berger, 1966), and in *Geococcyx* and *Crotophaga* (Berger, 1952). The

tendons of Mm. flexor cruris lateralis and flexor cruris medialis are fused distally for a common insertion in most procellariiforms; in all *Puffinus* except *griseus* the two tendons are separate (Klemm, 1969). In aningas the two insertions are separate; in cormorants the two muscles insert in common (Owre, 1967). Within caprimulgiforms the tendons insert together in *Steatornis*, *Nyctidromus*, *Phalaenoptilus*, and *Caprimulgus*; they are separate in *Aegothales* and *Chordeiles* (Hoff, 1966). They are separate in *Colius* (Berman and Raikow, 1982). In *Amazona albifrons* FCRM has its own tendon of insertion; FCRL pars pelvica inserts by tendinous fibers on the surface of FCRM (Berman, 1984). The tendons are independent in *Podiceps nigricollis* and *Picoides*; in the other species examined by Hudson (1937) they insert together. The condition was not mentioned for *Apteryx australis mantelli* (McGowan, 1979), nor for coraciiforms (Maurer and Raikow, 1981), but the tendons insert together in *Eurystomus* (McKitrick, ms.).

**M. pubo-ischio-femoralis (PIF)** (adductor longus et brevis; probably homologous with *adductor femoris* in crocodylians; see Romer [1923]). This is apparently a single muscle mass in *Gavia immer* (Hudson, 1937; Wilcox, 1952), falconiforms (Hudson, 1948), *Larus*, *Uria*, *Zenaidra*, *Chaetura*, *Colaptes*, and *Picoides* (Hudson, 1937); and *Goura*, *Gallicolumba*, *Eugenes*, and *Chloroceryle* (George and Berger, 1966). The descriptions of hummingbirds by Zusi and Bentz (1984) agree with those of George and Berger (1966), except that the former authors note that there are two insertions. In most other birds the muscle is divided into a superficial and a deep part or, in passerines, a cranial and a caudal portion. Pars externa generally inserts on a fraction of the femoral shaft (e.g., distal one-fifth in *Anas*, distal one-half in *Goura*, distal two-thirds in *Crotophaga*, distal two-thirds to three-fourths in *Grus*), but it inserts on almost the entire length in *Uria*. Usually pars externa is larger than interna, but it is smaller in *Fregata*, *Pediocetes*, and *Tympanuchus*, among others. In *Oxyura* and *Biziura*, but not *Heteronetta* and *Anas*, pars interna is considerably expanded as well, with its origin extending far caudad on the pubis (Raikow, 1970). In *Aceros* pars interna has two to three points of insertion.

This muscle is partially separable into deep and superficial layers in *Apteryx australis mantelli* (McGowan, 1979) and in *Diomedea immutabilis*, and mostly or completely so in *D. nigripes*; in *Puffinus* it is slightly separable; it is not separable in *Pterodroma* and *Bulweria* (Klemm, 1969). This varies in tinamous as well; the division is "slight to none" in *Nothura* and *Nothoprocta*, limited to the distal portion in *Tinamotis*, and limited to the proximal portion in others (Hudson et al., 1972).

Both parts are present and separable in the three scolopacid species studied by Fleming (1966), and in aningas and cormorants (Owre, 1967) and *Fulica americana* (Rosser et al., 1982).

In *Amazona albifrons* (Berman, 1984) the two parts (lateral and medial) are fused at the origin but otherwise separable and distinct.



In *Colinus*, this muscle has three bellies including a pars accessoria (Ber- man and Raikow, 1982); this is not known to occur in other birds.

In Ardeidae and *Balaeniceps* and evidently Phoenicopteridae the two parts are mostly separate (Vanden Berge, 1970). In ciconiids and thres- kiornithids the parts are mostly fused proximally. In penguins the muscle is separable into a lateral and medial part (Schreiweis, 1982).

Among Lari and Alcae (Hudson et al., 1969), the muscle is separable into two parts cranially but fused caudally in *Stercorarius*, Larinae, *Thalas- seus*, *Rynchops*, *Alca* (one of six legs), *Uria*, and *Cepphus columba* (two of four legs); it is divided all the way in *Cepphus columba* (one of four legs) and *Synthliboramphus* (two of three legs), and undivided in the remainder of the group, except possibly terns in which a vague cranial division is suggested.

**M. pubo-ischio-femoralis, division into pars cranialis and pars caudalis (Character 19).** A cranio-caudal division, rather than a latero- medial division, is present in *Corvus* (Hudson, 1937), *Tyrannus* (Hudson, 1937; McKittrick, 1985b), and Old World suboscines (Raikow, 1987).

**M. pubo-ischio-femoralis, muscular slip (Character 20).** A small muscu- lar slip arising from one or both parts and attaching to the femur is present in *Diomedea*, *Pterodroma*, and all Oceanitinae.

**M. pubo-ischio-femoralis, origin of pars superficialis.** Among the Hy- drobatidae, the origin of pars superficialis is considerably reduced in *Oceanites*, *Pelagodroma*, *Fregatta*, *Nesofregatta*, and *Oceanodroma*, but not in *Hydrobates* or *Halocyptena*. It arises on the ischium in ciconiiforms, and there is no origin from the pubis (Vanden Berge, 1970). It arises from the pubis in the three scolopacid species studied by Fleming (1966).

**M. pubo-ischio-femoralis pars profundus, aponeurosis.** In *Grus ameri- cana* and *G. canadensis* pars profundus is covered on its medial surface with a dense aponeurosis (Fisher and Goodman, 1955). Berger (1956b) did not find such an aponeurosis in his three specimens of *G. canadensis*. An apo- neurosis is present also in ciconiiforms (Vanden Berge, 1970).

**M. pubo-ischio-femoralis pars profundus, division (Character 21).** In some cathartids this is divided proximally into two parts (Fisher, 1946). A partial division occurs in *Nycticorax* and most other Ciconiiformes; the divi- sion is strong in Ardeidae and *Balaeniceps* (Vanden Berge, 1970). A division occurs in Bucorvinae and Bucerotinae (Maurer and Raikow, 1981).

**M. pubo-ischio-femoralis, insertion.** In *Uria* the insertion is on the cau- dal surface of nearly the whole length of the femoral shaft. In *Gavia immer* the insertion is by a narrow tendon and is limited to the medial condyle. It is one-half to three-fifths the length of the femur in *Fulica americana* (Rosser et al., 1982).

**M. pubo-ischio-femoralis, relation to gastrocnemius.** In the forms examined by Hudson (1937), pars interna was fused with *M. gastrocnemius* pars intermedia in all except *Coccyzus* and *Chordeiles*, in which there was "little or no connection" (p. 29). In passerines, it is pars caudalis that connects with *M. gastrocnemius* (Hudson, 1937; McKitrick, 1985b; Raikow, 1987).

**M. pubo-ischio-femoralis, passage of femoral vein.** The femoral vein passes through the insertion of the muscle in auks except *Alca* and possibly *Synthliboramphus*, but not in *Lari* except for *Gelochelidon* and *Rynchops* (one of seven legs) (Hudson et al., 1969).

**M. obturatorius lateralis (OL), number of heads** (obturator externus). The muscle has one head of origin in *Apteryx australis mantelli* (McGowan, 1979), tinamous (Hudson et al., 1972), *Gavia immer* (Wilcox, 1952), Anatidae, *Columba*, *Goura*, *Gallicolumba*, *Tauraco*, *Eugenes*, *Upupa*, *Aceros*, and *Indicator* (George and Berger, 1966); *Lari* and *Alcae* (Hudson et al., 1969—a contradiction of Hudson, 1937), and, apparently, *Pandion* (Hudson, 1948). In galliforms there is one head except in *Gennaesus*, *Pavo*, and *Meleagris*; in these there are two slips each inserting separately (Hudson, 1959). Zusi and Bentz (1984) found only the ventral head in *Eulampis* (they evidently did not study it in other species), as did Berman (1984) in *Amazona albifrons* and Berman and Raikow (1982) in *Colius*. It appears to have one head in penguins (see fig. 12 in Schreiweis, 1982). It has two independent (dorsal and ventral) heads in *Fulica americana* (Rosser et al., 1982), and in *Pharomachus*, *Chloroceryle*, and *Coracias* (George and Berger, 1966). Hudson (1937) reported two heads for *Grus canadensis*, but Fisher and Goodman (1955) stated (p. 90) that this was only a superficial separation in *G. canadensis* as well as *G. americana*; this was confirmed by Berger (1956b) for *G. canadensis*. Fisher and Goodman (1955) noted that the description was the same as for vultures described by Fisher (1946); however the latter author does report two distinct parts externally. Two distinct parts were reported for *Fulica*, *Larus*, *Uria*, *Corvus*, and *Tyrannus* (Hudson, 1937) and Old World suboscines except *Cymbirhynchus*, *Serilophus*, *Philepitta*, *Neodrepanis* and *Pitta*, in which pars dorsalis is absent (Raikow, 1987) (**Character 22**). Variation in this muscle in procellariiforms was not interpretable by Klemm (1969).

In anhingas and cormorants the tendon of *M. obturatorius medialis* separates this muscle into ventral and dorsal bellies (Owre, 1967).

**M. obturatorius medialis (OM), number of heads (Character 23)** (obturator internus). In most birds this muscle has one head; there are two heads in *Fulica*, *Porzana*, and *Colinus* (Hudson, 1937) and in galliforms except *Opisthocomus* (Hudson et al., 1959:13–14 and fig. 6); there are two heads in *Tauraco*, *Coua*, *Geococcyx*, *Coccyzus*, and *Coccyx* (George and Berger, 1966; Berger, 1952). Hudson (1937) noted that *Fulica* and *Porzana* differ

from *Colinus* in that the two parts are more or less separate muscles with separate tendons of insertion.

**M. obturatorius medialis, number of tendons of insertion (Character 24).** Hudson (1937) reported two tendons of insertion in *Fulica* and *Porzana*, but Rosser et al. (1982) reported three tendons of insertion for *Fulica americana*. There are two tendons of insertion in some cathartids (Fisher, 1946), and three tendons in *Coua*, *Geococcyx*, *Crotophaga*, *Coccyzus*, and *Coccyx* (Berger, 1952; 1953). These fuse to form a single point of insertion. The muscle is unremarkable in *Apteryx australis mantelli* (McGowan, 1979), procellariiforms (Klemm, 1969), *Amazona albifrons* (Berman, 1984), Oxyurini and *Anas* (Raikow, 1970), hummingbirds (Zusi and Bentz, 1984), and passerines (Hudson, 1937; McKittrick, 1985b; Raikow, 1987).

**M. obturatorius medialis enlarged in width (Character 25).** In *Colinus* (Berman and Raikow, 1982) and in ardeids including *Nycticorax* the muscle is enlarged in width; in *Balaeniceps*, Ciconiidae, Threskiornithidae, and Phoenicopteridae it is confined to the interosseal space (Vanden Berge, 1970).

**Mm. obturatorius medialis and obturatorius lateralis, independence (Character 26).** Whereas in most birds the insertion of obturatorius medialis is connected with M. obturatorius lateralis, the two are independent in cathartids (Fisher, 1946) and apparently so in falconiforms (Hudson, 1948) and Oxyurini and *Anas* (Raikow, 1970), independent in *Totanus* (Hudson, 1937), *Fulica* (Rosser et al., 1982), *Amazona* (Berman, 1984), *Colinus* (Berman and Raikow, 1982), hummingbirds (Zusi and Bentz, 1984), Old World suboscines (Raikow, 1987), *Tyrannus* (McKittrick, 1985b), and *Corvus* (Hudson, 1937). They are independent in Lari, but somewhat fused in some Alcae, particularly *Uria* and *Brachyramphus*. In ciconiiforms this muscle is evidently fused with M. obturatorius medialis, except in Ardeidae (Vanden Berge, 1970).

**M. iliofemoralis internus (IFI), presence (Character 27)** (iliacus). This muscle is present in *Apteryx australis mantelli* (McGowan, 1979), tinamous (Hudson et al., 1972), procellariiforms (Klemm, 1969), penguins (Schreiweis, 1982), *Gavia immer* (Wilcox, 1952), Oxyurini and *Anas* (Raikow, 1970), galliforms (Hudson et al., 1959), ciconiiforms (Vanden Berge, 1970), vultures (Fisher, 1946), falconiforms (Hudson, 1948), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), Lari and Alcae (Hudson et al., 1969), *Amazona albifrons* (Berman, 1984), and *Colinus* (Berman and Raikow, 1982). It is very small in anhingas and cormorants (Owre, 1967). Hudson (1937:14) reported that this muscle is present in "all the forms examined," and that it was particularly weak in *Dryobates* (= *Picoides*). It is present in Old World suboscines (Raikow, 1987) and *Tyrannus* (McKittrick, 1985b).

The muscle is absent in *Tauraco leucotis*, *Coua*, *Carpococcyx*, *Centropus*, *Chrysococcyx*, *Cuculus*, *Upupa epops*, *Indicator variegatus*, and *Eugenes fulgens* (George and Berger, 1966). Zusi and Bentz (1984) reported it absent in hummingbirds.

**M. iliofemoralis internus, development (Character 28).** Hudson (1937) noted that iliofemoralis internus was unusually short and broad in *Podiceps nigricollis* and *Gavia immer*, and strongly developed in *Fulica* and *Chordeiles*. Hoff (1966) reported it to be "short and stout" in *Nyctibius* and Caprimulgidae.

**M. ambiens (AM), presence (Character 29).** The muscle is present in *Apteryx australis mantelli* (McGowan, 1979), tinamous (Hudson et al., 1972), procellariiforms (except *Fregetta*, *Nesofregetta*, and *Pelecanoides*; Klemm, 1969), *Gavia immer* (Hudson, 1937; Wilcox, 1952), *Struthio*, *Rhea*, *Casuarius*, *Apteryx*, *Sula*, *Phalacrocorax*, *Anhinga*, *Fregata*, and Anhimidae (George and Berger, 1966); Oxyurini and *Anas* (Raikow, 1970), galliforms (Hudson et al., 1959), cathartids (Fisher, 1946), falconiforms (Hudson, 1948), *Polihi-erax* (Berger, 1956a), *Buteo*, *Falco*, *Chen*, *Pediocetes*, *Colinus*, *Totanus*, *Larus*, *Uria*, and *Zenaida* (Hudson, 1937); *Fulica americana* (Hudson, 1937; Rosser et al., 1982), *Grus americana* and *G. canadensis* (Fisher and Goodman, 1955; Berger, 1956b), Charadriiformes (except *Rynchops* and *Cerorhinca*), Pteroclididae, most columbids, some psittacids, Musophagidae, and Cuculidae (George and Berger, 1966). It is present in the three scolopacid species studied by Fleming (1966) and in aningas and cormorants (Owre, 1967). It is present and large in penguins (Schreiweis, 1982). It is absent in *Dromiceius*, *Podiceps*, Pelecanidae, *Rynchops*, most aluids, some columbids (*Goura*, *Treron*, *Geopelia*), most psittacids, Coliiformes, Trogoniformes, Coraciiformes, Piciformes, and Passeriformes, and questionable in *Phaethon* and Scopidae (George and Berger, 1966); absent in *Podiceps nigricollis*, *Ardea*, *Butorides*, *Bubo*, *Otus*, *Chordeiles*, *Chaetura*, *Colaptes*, *Picoides*, and *Corvus* (Hudson, 1937); absent in *Tyrannus* (Hudson, 1937; McKitrick, 1985b) and Old World suboscines (Raikow, 1987). Maurer and Raikow (1981) confirmed that it is absent in all Coraciiformes they examined (including Trogoniformes). It is absent in *Amazona albifrons* (Berman, 1984), owls and caprimulgiforms (Hoff, 1966). Zusi and Bentz (1984) do not mention it for hummingbirds nor Berman and Raikow (1982) for *Colius*; it is presumed absent in these species.

In Ciconiiformes, *M. ambiens* is present in *Mycteria*, *Ciconia*, *Leptoptilos*, *Eudocimus*, *Plegadis*, *Ajaia*, and *Phoenicopterus*; it is absent in *Ardea*, *Butorides*, *Leucophoyx*, *Nycticorax*, *Ixobrychus*, *Botaurus*, *Agamia*, *Heterocnus*, *Cochlearius*, and *Balaeniceps* (Vanden Berge, 1970). The muscle is present in Lari except *Chlidonias* (1 specimen), *Sterna albifrons*, and *Rynchops*. It is well developed in Stercorariidae and Larinae, less so in Sterninae. It is absent in Alcae except *Cerorhinca*, *Fraterecula*, and *Lunda* (Hudson et al., 1969). Hudson et al. (1969) note that they found no trace of the muscle in any specimen of

*Uria*, although Hudson (1937) had found a minute ambiens in one specimen of *Uria aalge*.

**M. ambiens, origin (Character 30).** This muscle arises from the pectineal process in many birds, e.g., in *Apteryx australis mantelli* (McGowan, 1979), and anhingas and cormorants (Owre, 1967). In penguins (Schreiweis, 1982), procellariiforms (Klemm, 1969), *Chen* (Hudson, 1937), and *Gavia immer* (Wilcox, 1952) the origin extends to the pubis. In Oxyurini and *Anas*, the origin is by two heads, one from the pectineal process and one from the pubis (Raikow, 1970). There are two heads in *Fulica americana* as well, a cranial and a caudal one that fuse distally (Rosser et al., 1982).

**M. ambiens, tendon of insertion.** In most birds in which the ambiens is present, the tendon gives rise to one or more of the digital flexors, e.g., in *Apteryx australis mantelli* (McGowan, 1979), *Gavia immer* (Wilcox, 1952), anhingas and cormorants (Owre, 1967), Oxyurini and *Anas* (Raikow, 1970), cathartids (Fisher, 1946), *Grus americana* (Fisher and Goodman, 1955), and *G. canadensis* (Berger, 1956b); this is not the case in *Opisthocomus* (Hudson et al., 1959), *Rhea* (variable), *Casuarius*, *Uria*, *Strigops*, *Burhinus*, *Phaethon*, and some procellariiforms (George and Berger, 1966).

**M. ambiens, insertion.** In most procellariiforms, the tendon of insertion passes down the lateral surface of the tibiotarsus, but in *Oceanites* and *Pelagodroma* the tendon ends on the tibial crest (Klemm, 1969). In one *Grus americana* the tendon gave off a branch to the tibiotarsus (Fisher and Goodman, 1955).

**M. ambiens, relation to M. iliofibularis.** In *Polihierax* the tendon passes medial to the insertion of M. IF (Berger, 1956a); Hudson (1937) noted that in *Falco* the tendon passes lateral to the insertion of IF. He remarked (1948) that this was apparently unique among birds.

**M. ambiens, relation to M. iliotibialis lateralis.** Hudson (1937) noted that the ambiens passes lateral to the insertion of M. IL in *Gavia*.

**M. ambiens, longitudinal division (Character 31).** The muscle is divided into two parts longitudinally in *Anas* and Oxyurini (Raikow, 1970), and in *Fulica* and *Porzana carolina* (Hudson, 1937).

**M. ambiens, length.** Hudson (1937) noted that the muscle is very short and broad in *Colinus*, and passes only halfway down the thigh.

**M. gastrocnemius pars lateralis (G), origin (pars externa).** In most birds, pars lateralis arises from a tubercle at the distal end of the femur; in *Gavia* it arises from the femoral shaft (Hudson, 1937; Wilcox, 1952).

**M. gastrocnemius pars lateralis, number of heads (Character 32).** Pars lateralis has a medial head in *Halobaena*, *Pachyptila forsteri*, *P. desolata*, all Hydrobatidae, *Pterodroma*, *Bulweria* (variable), *Diomedea immutabilis* and *D. nigripes* (variable and vestigial in both), and Oceanitinae (Klemm, 1969).

Pars lateralis has an extra head arising tendinously in the intercondylar region in *Larus* (19 legs, six species), *Chlidonias* (one leg), *Gelochelidon*, *Sterna* (12 legs), *Thalasseus*, and *Rynchops* (two legs?); this is absent in the Stercorariidae, *Larus* (five legs), *Rissa* (two legs, and possibly a third), *Chlidonias* (five legs), *Sterna* (three legs), *Rynchops* (six legs), and Alcae (Hudson et al., 1969). Pars lateralis is double in cuckoos.

**M. gastrocnemius pars intermedia, accessory head (pars media)** An accessory head is present in *Grus canadensis* (Berger, 1956b) and *Aceros undulatus* (George and Berger, 1966). Pars intermedia is present in *Daption*, *Fulmarus*, *Adamastor*, *Procellaria*, and *Puffinus griseus*. Possible vestiges of pars intermedia are present in *Pelecanoides garnoti* (uncertain in *P. exsul* and in non-*griseus* *Puffinus*) and some specimens of *Bulweria* and *Diomedea*. Rosser et al. (1982) questioned whether pars intermedia was really absent in some procellariiforms or whether the supposed distal head of FCRLA might not be M. G pars intermedia. *Heteronetta* lacked pars intermedia (Raikow, 1970). The muscle is present in cathartids (Fisher, 1946), and Hudson (1948) noted that it was double in *Cathartes*. The muscle is present in *Amazona albifrons* (Berman, 1984). It is present in all the forms examined by Hudson (1937). In *Gavia immer* the origin is from the distal half of the femur (Hudson, 1937).

**M. gastrocnemius pars medialis, patellar band (Character 33)** (pars interna). A patellar band of fibers occurs as part of pars medialis in *Apteryx australis mantelli* (McGowan, 1979), tinamous (Hudson et al., 1972), procellariiforms (Klemm, 1969), aningas and cormorants evidently (see Owre, 1967), ciconiiforms (Vanden Berge, 1970); *Oxyura* and *Biziura* (but not *Heteronetta* or *Anas*) (Raikow, 1970), cathartids (Fisher, 1946; Hudson, 1948), *Sagittarius* (Hudson, 1948), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Chen*, *Pediacetes*, *Colinus*, *Fulica*, *Totanus*, *Larus*, and *Uria* (but not the others examined by Hudson, 1937); and *Coua* (Berger, 1953). A patellar band is present in all galliforms examined by Hudson et al. (1959) except *Opisthocomus*. Among Lari and Alcae (Hudson et al., 1969), a patellar band is present in Stercorariidae, Larinae, *Chlidonias*, *Sterna paradisaea*, *Gelochelidon*, *Thalasseus* (one specimen), *Rynchops* (three legs), *Cerorhinca*, *Fratercula*, and *Lunda*; there is a small slip in *Rynchops* (five legs), *Uria* (four legs), and *Cephus* (one leg), and no band at all in *Sterna albifrons*, *S. forsteri*, *Thalasseus* (one specimen), *Alca*, *Uria* (12 legs), *Cephus* (nine legs), *Brachyramphus*, *Synthliboramphus*, and *Ptychoramphus*. A patellar band was present in *Batrachostomus*, *Aegotheles*, and Caprimulgidae (*Chordeiles*, *Nyctidromus*, *Phalaenoptilus*, *Caprimulgus*) (Hoff, 1966). A poorly developed patellar band

was present in some specimens of *Glaucis* but otherwise absent in hummingbirds (Zusi and Bentz, 1984).

Penguins appear to lack the patellar band (see figures in Schreiweis, 1982). In *Gavia* the medial head arises on the femur (Wilcox, 1952), but it is not known whether this implies a patellar band as such. There is no patellar band in accipitrids, *Pandion*, or *Falco* (Hudson, 1948), *Amazona albifrons* or *Colius* (Berman and Raikow, 1982), nor in the species examined by Hudson (1937) except as noted above. *Corvus* (Hudson, 1937) and *Tyrannus* (Hudson, 1937; McKittrick, 1985b) lack a patellar band. There is apparently none in *Columba* (George and Berger, 1966), cuckoos (Berger, 1952), and owls (Hoff, 1966). Among Old World suboscines, a patellar band is present in *Pitta*, *Acanthisitta* and *Xenicus*, and absent in the other forms examined by Raikow (1987).

**M. gastrocnemius pars medialis, number of heads (Character 34).**

There is a cranial and a caudal head in Oxyurini and *Anas* (Raikow, 1970). Pars medialis is double in *Gavia*, *Podiceps nigricollis*, *Uria*, and *Chaetura* (Hudson, 1937).

Among Lari and Alcae (Hudson et al., 1969), pars medialis has an extra head in *Alca*, *Uria* (10 legs), *Cepphus*, *Synthliboramphus*, and *Lunda* (minute in one specimen). There is no extra head in Lari, *Uria* (one leg), *Brachyramphus*, *Ptychoramphus*, *Cerorhinca*, *Fratercula*, and *Lunda* (two specimens).

In *Fulica americana* there is a superficial longitudinal division in pars medialis (Rosser et al., 1982).

Pars medialis is divided into superficial and deep heads in *Pitta*, *Acanthisitta*, and *Xenicus*, but not in the eurylaimids and philepittids examined by Raikow (1987).

**M. gastrocnemius pars medialis, origin.** In *Gavia immer* and *Podiceps nigricollis* this muscle arises from the proximal half of the tibiotarsus (Hudson, 1937).

**M. gastrocnemius, fourth head (Character 35).** This is present in Ciconiidae, Threskiornithidae, and Phoenicopteridae (Vanden Berge, 1970).

**M. gastrocnemius pars supramedialis.** This was described by Raikow (1987) in *Eurylaimus*, *Psarisomus*, *Cymbirhynchus*, and *Philepitta*; it was absent in the other Old World suboscines examined. The description indicates that the muscle is not comparable to the fourth head described by Vanden Berge (1970) in some ciconiiforms nor to the extra head of *M. gastrocnemius pars medialis* of some Alcae (Hudson et al., 1969).

**M. gastrocnemius, insertion.** The insertion is by two tendons, one from pars lateralis and the other from pars medialis and pars intermedia, in *Gavia*, *Podiceps nigricollis*, *Chen*, *Fulica*, *Totanus*, *Larus*, *Uria*, and *Chaetura*

(Hudson, 1937). In *Fregata*, the tendon divides after passing over the tibial-tarsometatarsal (ankle) joint (Hudson, 1937).

**M. gastrocnemius, insertion and hypotarsus (Character 36).** In Ardeidae and *Balaeniceps* the tendon of insertion of *M. gastrocnemius* contributes to the ossification of the hypotarsus (Vanden Berge, 1970).

**M. tibialis cranialis (TCR), relative size of heads.** The muscle has a tibial and a femoral head, and in most birds the femoral head is the smaller one (e.g., tinamous, Hudson et al., 1972; hummingbirds, Zusi and Bentz, 1984; *Amazona albifrons*, Berman, 1984; ciconiiforms, Vanden Berge, 1970; anhingas and cormorants, Owre, 1967; *Corvus*, Hudson, 1937; *Tyrannus*, McKitrick, 1985b; Old World suboscines, Raikow, 1987). The two heads are nearly equal in *Uria* (Hudson, 1937) and in *Grus canadensis* (Berger, 1956b). Fisher and Goodman (1955:93) note that the femoral head is "unusually well developed proximally" in *G. americana*. In ciconiiforms the (main) tendon is perforated by a nerve in all but Ardeidae and *Cochlearius* (Vanden Berge, 1970). The origin of the tibial head is extensive in *Buteo* and *Falco* (Hudson, 1937).

In *Apteryx australis mantelli* (McGowan, 1979) there is a cranial and a caudal slip which remain separate for most of the length of the belly.

**M. tibialis cranialis, accessory tendon.** This is present in all Ardeidae except *Ixobrychus*; it is present in *Nycticorax*. It is absent in *Balaeniceps*, *Phoenicopterus chilensis*, and *Phoenicoparrus jamesi* (Vanden Berge, 1970). The accipitrid species examined by Hudson (1948) had a small accessory tendon of insertion; *Falco* had two accessory tendons and *Sagittarius*, *Pandion*, and cathartids had none. An accessory tendon of insertion was noted by Hudson et al. (1969) as being comparable to that noted by Hudson (1937). This was found in *Rissa*, some *Sterna* and *Thalasseus*, *Cepphus*, some *Ptychoramphus*, *Cerorhinca*, *Fratercula*, and *Lunda* (Hudson et al., 1969).

An accessory tendon is present in *Fulica americana*; it widens and inserts on the tarsometatarsus (Rosser et al., 1982).

**M. tibialis cranialis, number of tendons of insertion (Character 37).** In most birds the insertion is single, but in *Bubo* and *Otus* there are two distinct tendons that may correspond to the two heads of origin (Hudson, 1937). The tendon bifurcates in procellariiforms (Klemm, 1969).

**M. tibialis cranialis, small tendon in addition to main branch.** This occurs in *Gavia*, *Podiceps*, *Fregata*, *Chen*, *Ardea*, *Buteo*, *Falco*, *Fulica*, *Totanus*, *Coccyzus*, and *Chordeiles* (Hudson, 1937) and in most Caprimulgiformes examined by Hoff (1966).



**M. tibialis cranialis, relation to M. extensor brevis digiti IV.** In *Fregata* the tendon of insertion gives rise to a strong lateral branch that gives rise to part of M. extensor brevis digiti IV.

**M. tibialis cranialis, perforation by M. extensor proprius digiti III.** This occurs in *Apteryx australis mantelli* (McGowan, 1979).

**M. extensor digitorum longus (EDL), miscellaneous.** Within Procellariiformes (Klemm, 1969), there is usually a medial branch of the tendon to digit IV; this is absent in all Hydrobatidae. The muscle is "typical" in Oxyurini and *Anas* (Raikow, 1970). In hummingbirds the branch to digit III bifurcates for a multiple insertion on that digit (Zusi and Bentz, 1984). Cormorants have a patellar origin, anhingas do not (Owre, 1967).

**M. extensor digitorum longus, loops through which tendon passes.** The tendon of insertion passes through two loops. The first is bony in all forms examined by Hudson (1937) except for *Bubo* and *Otus*, in which it is fibrous; the second is fibrous in all except *Fulica*, *Zenaida*, *Chaetura*, *Bubo*, *Otus*, *Colaptes*, *Picoides*, *Tyrannus*, and *Corvus*. Raikow (1987) noted that the tendon passes through a fibrous loop, the Retinaculum extensorium tarsometatarsi, in Old World suboscines.

**M. extensor digitorum longus, origin (Character 38).** In most birds the origin is from the tibia; in *Bubo* and *Otus* there is a fibular origin as well (Hudson, 1937). A fibular origin occurs in *Steatornis*, *Nyctibius*, and *Aegotheles* but not Podargidae or Caprimulgidae (Hoff, 1966). A femoral origin is present in hummingbirds (Zusi and Bentz, 1984).

**M. extensor digitorum longus, hallucal tendon (Character 39).** In *Amazona albifrons* (Berman, 1984) and *Colius* (Berman and Raikow, 1982) M. EDL sends a branch to the hallux.

**M. extensor digitorum longus, accessory tendons.** In *Amazona albifrons* three accessory tendons arise from a tendinous sheath "formed by an extension from digit IV" (Berman, 1984). Two of these fuse with the main tendon to digit III to insert on the distal phalanx of that digit; the third attaches on the third phalanx. There are evidently two accessory tendons to digit IV as well, but the description is unclear. In *Colius* there are two tendons to digit IV, one from the main tendon and one from the union of part of the branch to digit III and an extension of the main tendon on the distal end of the tarsometatarsus (Berman and Raikow, 1982). The tendon so constructed forms a sheath around the other, evidently.

**M. extensor digitorum longus, insertions.** Hudson (1937) summarized the insertion of this muscle according to the forms in which the insertion was clearly by one tendon to each of toes 2-4, and those in which it was

clearly by two to each. Those with one tendon are *Sula*, *Ardea*, *Pediocetes*, *Colinus*, *Uria*, and *Chordeiles*. Those with two are *Gavia*, *Fregata*, *Cathartes*, *Fulica*, *Zenaida*, *Coccyzus*, *Tyrannus*, and *Corvus*. The insertions are not clearly assignable to either category in *Podiceps nigricollis*, *Grus*, *Larus*, and *Totanus*. Among most galliforms examined by Hudson et al. (1959), the tendon bifurcates halfway down the tarsometatarsus; in *Opisthocomus* the tendon does not bifurcate, but rather sends a branch to each foretoe at the distal end of the tarsometatarsus. Raikow (1987) noted one branch to each of the three forward toes in Old World suboscines, and secondary branches that he did not describe.

**M. fibularis longus (FL), presence (Character 40)** (peroneus longus). This is present in most birds, including *Apteryx australis mantelli* (McGowan, 1979), procellariiforms except *Pterodroma leucoptera*, *P. cooki*, *Bulweria* (absent in one of three specimens), Hydrobatinae, and *Pelecanoides* (Klemm, 1969); penguins (Schreiweis, 1982), tinamous (Hudson et al., 1972), *Gavia immer* (Wilcox, 1952), anhingas and cormorants (Owre, 1967), *Camptorhynchus* (Zusi and Bentz, 1978), Oxyurini and *Anas* (Raikow, 1970), cathartids (Fisher, 1946), falconiforms (Hudson, 1948), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Colinus* (Berman and Raikow, 1982), *Corvus* (Hudson, 1937), *Tyrannus* (McKittrick, 1985b), and Old World suboscines (Raikow, 1987). It is absent in *Pandion* (Hudson, 1948), owls, *Steatornis*, *Aegotheles* (Hoff, 1966); *Chaetura* (Hudson, 1937), Bucorvinae, Bucerotinae, Phoeniculidae, Upupidae, and Meropidae (Maurer and Raikow, 1981); and hummingbirds (Zusi and Bentz, 1984). It is extremely reduced in *Nesofregatta* and is aponeurotic in *Puffinus assimilis* (Klemm, 1969). It is poorly developed in *Polihierax* (Berger, 1956a), *Amazona* (Berman, 1984), and *Columba* (George and Berger, 1966). It is present in ciconiiforms, but fairly weakly developed in Ardeidae (Vanden Berge, 1970).

**M. fibularis longus, origin (Character 41)**. In *Falco* the origin is limited to the fibula; in *Gavia* it is "from the underlying muscles only" (Hudson, 1937). Wilcox (1952) reported a more typical origin for *Gavia*, from the tibia. The origin is from the tibia and underlying muscles in galliforms (Hudson et al., 1948), *Grus americana* (Fisher and Goodman, 1955), *Amazona* (Berman, 1984), *Columba* (George and Berger, 1966), and *Colinus* (Berman and Raikow, 1982).

**M. fibularis longus, branch to M. flexor perforatus digiti III (Character 42)**. Typically there is a branch to M. flexor perforatus digiti III, e.g. in *Fulica americana* (Rosser et al., 1982), penguins (Schreiweis, 1982), Oxyurini and *Anas* (Raikow, 1970), ciconiiforms (Vanden Berge, 1970), anhingas and cormorants (Owre, 1967), cathartids (Fisher, 1946), *Corvus* and *Tyrannus* (Hudson, 1937), and Old World suboscines (Raikow, 1987). This branch is absent in *Podiceps nigricollis*, *Indicator*, *Colaptes*, *Picoides*, *Melanerpes*

*erythrocephalus*, and *Sphyrapicus varius* (Hudson, 1937); *Amazona albifrons* (Berman, 1984), Coraciidae, Todidae, and Alcedinidae (Maurer and Raikow, 1981); and *Colinus* (Berman and Raikow, 1982). Hudson (1937) noted that in *Gavia immer* the branch is present but leads nowhere; Wilcox (1952) reported no such branch for *Gavia*.

The branch to *M. flexor perforatus digiti III* is present in tinamous (Hudson et al., 1972), *Campylorhynchus* (Zusi and Bentz, 1978), and *Grus americana* (Fisher and Goodman, 1955) and said to be similar in *G. canadensis* (Berger, 1956b). Apparently there is only one tendon in *Polihierax* (Berger, 1956a), viz., to *M. flexor perforatus digiti III*.

The tendon of insertion bifurcates in one specimen of *Apteryx australis mantelli* and trifurcates in the other, with the third branch attaching to the tibiotarsus (McGowan, 1979).

**M. fibularis brevis (FB), presence (Character 43)** (peroneus brevis). This is reportedly absent in ratites (except *Apteryx*; McGowan, 1979), in *Scopus*, *Aramus*, Otididae, *Burhinus*, *Pterocles*, *Nyctidromus*, and *Caprimulgus* (George and Berger, 1966); and in *Podiceps nigricollis*, *Sula*, and *Chordeiles* (Hudson, 1937). It is reduced or absent in *Recurvirostra*, *Haematopus*, and *Vanellus*; it is absent in *Tinamotis* but present in other tinamous (Hudson et al., 1972). It is absent in Ciconiidae and Phoenicopteridae, vestigial in *Balaeniceps* and threskiornithids, well developed in Ardeidae (Vanden Berge, 1970) and *Fulica americana* (Rosser et al., 1982). It is absent in caprimulgiforms (Hoff, 1966). It is present in procellariiforms (Klemm, 1969), in anhingas and cormorants (Owre, 1967), *Gavia* (Wilcox, 1952), *Campylorhynchus* (Zusi and Bentz, 1978), *Corvus* (Hudson, 1937), owls (Hoff, 1966), *Tyrannus* (Hudson, 1937; McKittrick, 1985b), and Old World suboscines (Raikow, 1987). It is weak in penguins (Schreiweis, 1982) and in *Totanus*, *Larus*, and *Uria* (Hudson, 1937).

Among Lari and Alcae (Hudson et al., 1969) the muscle is present in Stercorariidae, Larinae, and Alcae; the muscle is absent in most Sterninae and in most specimens of *Rynchops*. It is weak in *Chlidonias* (one leg), *Gelochelidon* (one specimen), *Sterna albifrons* (four legs), *Sterna forsteri* (two legs); vestigial in *Chlidonias* (two legs?), *Sterna albifrons* (one leg), *Thalasseus* (three legs), and *Rynchops* (one leg). It was not reported to be weak in *Larus* and *Uria* by Hudson et al. (1969) and is not so coded.

**M. fibularis brevis, size relative to M. fibularis longus.** In most birds it is smaller than *M. fibularis longus*, but it is the larger of the two in *Pterodroma heraldica* and *Puffinus creatopus* (Klemm, 1969), falconids and vulturids (Mitchell, 1913), some psittacids, *Podargus*, and some coraciiforms and piciforms (George and Berger, 1966); and *Amazona albifrons* (Berman, 1984). The two are about equal in size *Halobaena*, *Pachyptila desolata*, *Pterodroma phaeopygia*, and *P. mollis*; in the other procellariiforms *M. fibularis longus* is the larger of the two (Klemm, 1969). *M. fibularis longus* is also larger in cathartids (Fisher, 1946), *Grus americana* (Fisher and Goodman,

1955), *G. canadensis* (Berger, 1956b), and *Colinus* (Berman and Raikow, 1982).

**M. fibularis brevis, number of heads of origin.** There are two heads of origin in *Amazona albifrons* (Berman, 1984), but one in *Colinus* (Berman and Raikow, 1982). There is one head in tinamous (Hudson et al., 1972), *Gavia immer* (Wilcox, 1952), cathartids (Fisher, 1946), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), and *G. canadensis* (Berger, 1956b). In *Apteryx australis mantelli* (McGowan, 1979) and in anhingas and cormorants (Owre, 1967) there is a tibial and a fibular origin. Old World suboscines have a fibular head only (Raikow, 1987).

**M. flexor perforans et perforatus digiti III (FPPD3), vinculum (Character 44).** A vinculum has been found between the tendons of Mm. flexor perforans et perforatus digiti III and flexor perforatus digiti III in tinamous (Hudson et al., 1972), cathartids (Fisher, 1946), Galliformes (except *Opisthocomus*) (Hudson et al., 1959), *Fulica americana* (Rosser et al., 1982), *Grus canadensis* (Berger, 1956b), *Gavia*, *Sula*, *Chen*, *Cathartes*, *Pediocetes*, *Colinus*, *Grus*, *Fulica*, *Totanus*, *Larus*, and *Zenaida* (Hudson, 1937); *Sagittarius* and cathartids (Hudson, 1948), *Pterocles*, *Columba*, *Goura*, *Gallicolumba*, and *Tauraco* (George and Berger, 1966). It is absent in *Apteryx australis mantelli* (McGowan, 1979), procellariiforms (Klemm, 1969, fig. 7a), penguins (Schreiweis, 1982), *Pandion* and accipitrids (Hudson, 1948), *Podiceps nigricollis*, *Fregata*, *Ardea*, *Buteo*, *Falco*, *Uria*, *Chordeiles*, *Chaetura*, *Bubo*, *Otus*, *Colaptes*, *Picoides*, *Tyrannus*, and *Corvus* (Hudson, 1937); *Crotophaga*, *Geococcyx*, and *Coccyzus* (Berger, 1952); and, evidently, Old World suboscines (Raikow, 1987). Hoff (1966) reported it present in *Steatornis*, *Nyctidromus*, *Phalaenoptilus*, and *Caprimulgus* but absent in all other Caprimulgiformes (and Strigiformes) examined. Vanden Berge (1970) reported it absent in ardeids but present in all other ciconiiforms examined. A vinculum may have been present in the extinct *Camptorhynchus*; Zusi and Bentz (1978:414) referred to it as a "tendinous branch" but were uncertain of its homology to the vinculum described by Hudson (1937). It has not been found in *Polihierax*, Cuculidae, *Pharomachrus*, *Chloroceryle*, *Coracias*, *Upupa*, *Aceros*, or *Indicator*. No vinculum was mentioned for Oxyurini or *Anas* (Raikow, 1970), *Amazona albifrons* (Berman, 1984), or hummingbirds (Zusi and Bentz, 1984), and I code these taxa as lacking the vinculum. Fleming (1966) did not note the condition in the three scolopacid species he studied, nor did Owre (1967) for anhingas and cormorants, and I code these taxa as ?.

A vinculum is present in all Lari except: one abnormal leg of *Catharacta*, in *Sterna albifrons*, *Thalasseus* (one leg), and *Rynchops* (two legs) in which the two tendons were fused. In Alcae the vinculum is usually absent, except that in *Alca* it was present in three legs and absent in three (Hudson et al., 1969).

**M. flexor perforans et perforatus digiti III, vinculum to M. flexor perforatus digiti IV.** Fisher (1946) reported a vinculum between these two muscles in *Vultur*.

**M. flexor perforans et perforatus digiti III, length.** It is very short in *Pelagodroma*, *Fregetta*, and *Nesofregetta* (Klemm, 1969).

**M. flexor perforans et perforatus digiti III, fiber architecture.** The muscle is bipinnate in *Grus americana* (Fisher and Goodman, 1955), anhingas and cormorants (Owre, 1967), and procellariiforms other than *Pelecanoides exsul* and Oceanitinae (except *Oceanites*, in which it is bipinnate). It is bipinnate in Oxyurini and *Anas* (Raikow, 1970) and Old World suboscines (Raikow, 1987).

**M. flexor perforans et perforatus digiti III, number of heads.** The muscle has two heads in *Oceanodroma tethys* (Klemm, 1969), and in *Amazona albifrons* in which the two fuse 4 mm distal to their insertion (Berman, 1984). It arises by two tendons in *Colinus* (Berman and Raikow, 1982). Evidently there is only one head in penguins (Schreiweis, 1982) and *Gavia immer* (Wilcox, 1952). In *Apteryx australis mantelli* (McGowan, 1979), one specimen evidently had one head, and the other had two origins, proximal to the lateral condyle of the femur. In most ciconiiforms there is one head, which arises from the tibial crest and the fibula; in flamingos, however, there are two heads but no fibular attachment (Vanden Berge, 1970). There is evidently one head in anhingas and cormorants (Owre, 1967).

Hudson (1948) reported the origin as partly from the fibular shaft in cathartids and *Falco*, but not in *Sagittarius*, *Pandion*, or accipitrids. It is from the lateral condyle of the femur, the lateral side of the tibial crest, the fibular head, and the lateral surface of the fibula in *Corvus* (Hudson, 1937). The muscle has two heads in Old World suboscines (Raikow, 1987).

**M. flexor perforans et perforatus digiti II (FPPD2), relationship to M. flexor perforans et perforatus digiti III (Character 45).** FPPD2 overlaps and completely conceals the proximal part of FPPD3 in *Larus*, which is an unusual pattern (Hudson, 1937). This is apparently true of all Lari and Alcae (Hudson et al., 1969). This is also true of Ardeidae and *Balaeniceps* but not Ciconiidae, Phoenicopteridae, or Threskiornithidae (Vanden Berge, 1970). The condition occurs in *Anas* and Oxyurini (Raikow, 1970, fig. 15), *Fulica americana* (Rosser, 1982), *Grus canadensis* (Berger, 1956b), and *G. americana* (Fisher and Goodman, 1955; Berger, 1956b).

**M. flexor perforans et perforatus digiti II, number of heads (Character 46).** Many birds have a single head, e.g., tinamous (Hudson et al., 1972), penguins (Schreiweis, 1982), hummingbirds (Zusi and Bentz, 1984), Old World suboscines (Raikow, 1987), *Tyrannus* (McKittrick, 1985b), and all the forms examined by Hudson (1937) except *Gavia*. Some galliforms have

two: *Megapodius* (questionable), *Alectoris*, *Perdix*, *Gennaesus*, *Gallus*, *Phasianus*, *Pavo*, *Numida*, and *Meleagris*; other galliforms have one: *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus*, *Bonasa*, *Tympanuchus*, and *Opisthocomus*; and others are intermediate: *Lagopus*, *Canachites*, *Pediocetes*, *Centrocercus*, *Oreortyx*, *Lophortyx*, and *Colinus* (Hudson et al., 1959). In ciconiiforms there is one head only, from the lateral condyle of the femur, except in flamingos in which there are two heads, one from the lateral condyle and one from the head of the fibula and the tibial crest (Vanden Berge, 1970). *Anas* has two heads, as do Oxyurini (except *Oxyura* which lacks the lateral head) (Raikow, 1970). *Gavia immer* has three (Hudson, 1937; Wilcox, 1952), as do Procellariiformes (Klemm, 1969), but it is not clear whether these are homologous.

The origin of FPPD2 is typically from the lateral condyle of the femur and from the patellar ligament; it has a tibial origin as well in *Ardea*, *Falco*, *Fulica*, and *Larus*. In *Fregata* the origin is primarily fibular (Hudson, 1937); in anhingas and cormorants it is femoral (Owre, 1967). The muscle is relatively large in *Gavia*, *Podiceps nigricollis*, *Pediocetes*, *Fulica*, *Bubo*, and *Otus* (Hudson, 1937). George and Berger (1966) noted that this is true of many galliforms as well.

**M. flexor perforans et perforatus digiti II, origin from ansa iliofibularis (Character 47).** The muscle arises from the ansa iliofibularis as well as the femur and fibula in *Casuaris* and *Rhea* (Gadow, 1880 in McGowan, 1979), penguins (Schreiweis, 1982), *Gavia* (Wilcox, 1952), ardeids and *Balaeniceps* (Vanden Berge, 1970), vultures (Fisher, 1946), galliforms, including *Opisthocomus* (Hudson et al., 1959), *Amazona albifrons* (Berman, 1984), *Coccyzus*, *Geococcyx*, and *Crotophaga* (Berger, 1952).

**M. flexor perforans et perforatus digiti II, perforation.** In *Vultur* the tendon of this muscle is not perforated by the deep flexor tendons (Fisher, 1946). It is perforated in *Apteryx australis mantelli* (McGowan, 1979), *Gavia immer* (Wilcox, 1952), *Fulica americana* (Rosser et al., 1982), and *Tyrannus* and *Corvus* (Hudson, 1937), among others. Schreiweis (1982) does not mention the condition for penguins. The description for anhingas and cormorants by Owre (1967) is confused: the tendon is said to be perforated by *M. flexor hallucis longus* in anhingas and therefore divided; not perforated by *M. flexor digitorum longus* in cormorants and therefore not divided. Hudson (1937) noted that a slender branch of the tendon of insertion is attached to phalanx 2 and is unperforated by FDL in *Colaptes*, *Picoides villosus*, *Melanerpes erythrocephalus*, and *Sphyrapicus varius*; the insertion is similar in *Chaetura*. The condition is not mentioned for Old World suboscines by Raikow (1987).

**M. flexor perforans et perforatus digiti II, fusion with M. flexor perforatus digiti II.** The tendon of insertion is completely fused with that of FPD2 in *Pandion* (Hudson, 1948).

**M. flexor perforatus digiti IV (FPD4) origin.** The literature descriptions of this origin are difficult to interpret. Typically this muscle has two heads of origin, e.g. in tinamous (Hudson et al., 1972), *Ardea*, *Chen*, *Buteo*, *Pediocetes*, *Colinus*, *Grus*, *Totanus*, *Larus*, *Bubo*, *Otus*, *Zenaida*, *Coccyzus*, *Chordeiles*, *Colaptes*, *Picoides*, and *Tyrannus* (Hudson, 1937); *Sagittarius* and accipitrids (Hudson, 1948), Oxyurini and *Anas* (Raikow, 1970), Lari and Alcae (Hudson et al., 1969), *Fulica americana* (Hudson, 1937; Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Amazona albifrons* (Berman, 1984), and *Colius* (Berman and Raikow, 1982). There is a single head in *Gavia*, *Podiceps nigricollis*, *Fregata*, *Sula*, and *Corvus*, arising either from the lateral condyle or from the intercondylar region, in *Falco* (lateral condyle and head of fibula), and in *Uria* and *Chaetura* (lateral condyle) (Hudson, 1937). Hudson (1948) reported it to be single headed in cathartids, *Pandion*, and *Falco*; in cathartids the single head arises from the lateral condyle and intercondylar region. In *Polihierax* the single head arises from the lateral condyle of the femur and from the head of the fibula (George and Berger, 1966). The single head arises from the intercondylar region, lateral condyle, and head of the fibula in penguins (Schreiweis, 1982). The muscle has a single origin in hummingbirds, from the lateral femoral condyle (Zusi and Bentz, 1984). In ciconiiforms only the Ardeidae have a fibular attachment, all the rest lack it; in *Leptoptilos* there is a double fibrous attachment like that for FPD3 (see p. 35) (Vanden Berge, 1970).

The muscle is divided into three parts in procellariiforms (Klemm, 1969).

In one specimen of *Apteryx australis mantelli* (McGowan, 1979) the muscle has two heads of origin, one from the common aponeurotic origin of Mm. FDL, FPD2, and FPD3 (= intercondylar region), the other from the ambiens tendon. In the other specimen there was only one head of origin (from the intercondylar region).

In tyrannids the muscle has a proximal head arising from the intercondylar region of the femur, and a distal head arising by an aponeurosis from the surface of Mm. flexor perforatus digiti II, flexor perforans et perforatus digiti II, flexor perforans et perforatus digiti III, and flexor hallucis longus, all of which arise from the lateral condyle of the femur (McKittrick, 1985b). Raikow (1987) described a similar origin for Old World suboscines, but did not mention the involvement of Mm. FPPD2 or FPPD3.

In galliforms, there are three heads, one arising from the intercondylar region, one from the head of the fibula, the lateral condyle of the femur, and the lateral arm of the biceps loop; and one from the common tendon of origin of Mm. FPD2 and FPD3 (Hudson et al., 1959).

**M. flexor perforatus digiti IV, relationship to M. iliofibularis.** The tendon of M. iliofibularis passes between the two heads of FPD4 in *Fulica americana* (Hudson, 1937; Rosser et al., 1982), *Ardea*, *Buteo*, *Pediocetes*, *Colinus*, *Grus*, *Totanus*, *Larus*, *Bubo*, *Otus*, and *Tyrannus*; lateral to the two

heads in *Chen*, *Zenaida*, *Coccyzus*, *Chordeiles*, *Colaptes*, and *Picoides* (Hudson, 1937).

**M. flexor perforatus digiti IV, relationship to M. flexor perforatus digiti III.** In *Grus americana* the tendon of FPD3 encloses the tendon of FPD4 craniolaterally and the two pass through the same hypotarsal canal; FPD4 is fleshily connected proximally with FPD3 (Fisher and Goodman, 1955). This is not mentioned for *G. canadensis* by Berger (1956b) nor for *Fulica americana* by Rosser et al. (1982). The tendon of FPD3 encases the tendon of FPD4 in tinamous (Hudson et al., 1972), anhingas and cormorants (Owre, 1967), cathartids (Fisher, 1946), *Corvus* (Hudson, 1937), and Old World suboscines (Raikow, 1987) as well. In penguins the tendon of FPD3 ensheathes that of FPD4 and attaches to the FPD4 belly. The two are intimately connected in ciconiiforms (Vanden Berge, 1970). In *Apteryx australis mantelli* (McGowan, 1979) the two are ensheathed by the tibial cartilage.

**M. flexor perforatus digiti IV, insertion.** In tinamous the tendon splits into four branches to insert on the four phalanges of digit IV (Hudson et al., 1972). In ciconiiforms there are three branches, one to phalanges 1 and 2, one to phalanges 2 and 3, and one to phalanges 3 and 4. In penguins there are four branches; branches 1 and 4 fuse and insert on phalanx 2, branches 2 and 3 fuse and insert on phalanx 3 (Schreiweis, 1982).

**M. flexor perforatus digiti IV, perforation.** *M. flexor digitorum longus* perforates the two branches of the FPD4 tendon separately in *Zenaida*; in woodpeckers (*Picoides villosus*, *Melanerpes erythrocephalus*, *Sphyrapicus varius*) neither branch is perforated and the two branches pass lateral to the deep flexor tendon (Hudson, 1937).

**M. flexor perforatus digiti III (FPD3), origin.** The origin of this muscle is variable. It has a single head arising in the intercondylar region in Old World suboscines (Raikow, 1987), *Fregata*, *Sula*, *Cathartes* (but see below), and *Tyrannus*; *Ardea* has a second, distal head arising on the lateral condyle (Hudson, 1937; but see below). In the other forms studied by Hudson (1937) there are two heads. *Falco* and accipitrids have two heads, *Sagittarius* and *Pandion* have one, and *Cathartes* and *Coragyps* have a division by the vagus nerve into two heads (Hudson, 1948). Wilcox (1952) noted that the muscle arises in the intercondylar region of the femur in *Gavia immer*, but not the fibula, although Hudson (1937) noted a distal head arising from the ambiens tendon and the Caput fibulae in this species. In *Fulica americana* there is a femoral head from the intercondylar region and a distal head arising fleshy from the ambiens tendon and by a long tendon from the head of the fibula (Rosser et al., 1982). The distal head arises from the lateral condyle in *Chaetura*, *Colaptes*, and *Picoides villosus* (Hudson, 1937); from the lateral condyle and fibula in anhingas and cormorants (Owre,



1967); from the ambiens tendon and M. FPD4 in *Columba*, and from the ambiens tendon and fibula in *Colinus*, *Fulica*, *Totanus*, *Larus*, *Zenaidra*, and *Coccyzus* (George and Berger, 1966); from the head of the fibula in *Chordeiles*, from the shaft of the fibula in *Podiceps* and *Uria*, and from other flexor muscles in *Chen*, *Buteo*, *Falco*, *Pediocetes*, *Bubo*, and *Otus* (Hudson, 1937). The origin of FPD3 is from the lateral condyle of the femur in hummingbirds, and there is only one head (Zusi and Bentz, 1984). In *Amazona albifrons* a large proximal head arises from the intercondylar region of the femur and the fibula, and a smaller distal head from the fibula. The large proximal head in *Colinus* arises in the intercondylar region and the small, distal belly in common with the distal head of M. FPD4 on the fibula (Berman and Raikow, 1982); the condition is similar in *Corvus* (Hudson, 1937). In *Grus americana* and *G. canadensis* the lateral head arises with M. ambiens and tendinously from the fibular head; the posterior (caudal) head arises from the popliteal region of the femur (Fisher and Goodman, 1955; Berger, 1956b). In cathartids the main head arises from the popliteal region of the femur while the accessory head arises from the surface of Mm. FHL and FPD4 half way down the tibiotarsus (Fisher, 1946); in *Cathartes* the accessory head arises with the main head and from the tendon of M. ambiens. In *Gymnogyps* the accessory head arises from FDL, while in *Sarcoramphus* it arises with the main head and is fused to it. In tinamous a large medial head arises in the intercondylar region and a small lateral head arises "from a common tendon of the three perforated flexors" (Hudson et al., 1972:243).

In ciconiiforms there is one head only, *contra* Hudson (1937), arising in the intercondylar region and, in the Ardeidae only, from the fibula (Vanden Berge, 1970). *Leptoptilos* has a "double fibrous connection," presumably on the fibula or tibiotarsus, "lateral and medial to the biceps tendon" (Vanden Berge, 1970:348).

Schreiweis (1982) noted that in penguins FPD3 arises from the intercondylar region by a broad, flat tendon, and in common with FPD2 and FPD4 on the head of the fibula and lateral condyle of the femur by a short tendon. He did not refer to these as separate heads, but it seems clear that they are.

In *Falco* the femoral head arises as a long tendon rather than being fleshy and attached to the underlying muscles; the condition is similar in *Coccyzus* and in *Chaetura* (Hudson, 1937).

**M. flexor perforatus digiti III, accessory head.** An accessory head (arising from the tendon of M. ambiens) occurs in Procellariiformes except that it is indistinct in *Halobaena* (Klemm, 1969). An accessory head occurs in cathartids (Fisher, 1946); this may be simply one of the two heads of origin that many birds have.

**M. flexor perforatus digiti III, small fan-shaped branch.** This is present in all tinamous (Hudson et al., 1972).

**M. flexor perforatus digiti III, insertion.** When two heads are present, they unite to form a single tendon in *Gavia*, *Podiceps nigricollis*, *Chen*, *Buteo*, *Falco*, *Grus*, *Totanus*, *Larus*, *Zenaida*, *Coccyzus*, *Chordeiles*, *Bubo*, *Otus*, *Picoides*, and *Corvus* (Hudson, 1937); and in *Megapodius*, *Leipoa*, *Crax*, *Ortalis*, *Pipile*, *Alectoris*, *Gallus*, *Pavo*, *Numida*, *Meleagris*, and *Opisthocomus* (one specimen) (Hudson et al., 1959). There are two separate tendons in *Pediocetes*, *Colinus*, *Fulica*, *Uria*, and *Colaptes* (Hudson, 1937) and in *Penelope*, *Dendragapus*, *Canachites*, *Centrocercus*, *Perdix*, *Gennaeus*, *Phasianus*, *Opisthocomus* (two specimens), *Lagopus*, *Bonasa*, *Tympanuchus*, *Oreortyx*, and *Lophortyx* (Hudson et al., 1959). Rosser et al. (1982:1248–1249) reported that the two tendons unite to form a single tendon, which bifurcates to allow passage of the tendons of Mm. FPPD3 and FDL. The two resulting branches insert separately.

Among Lari and Alcae (Hudson et al., 1969), the two heads form one tendon in *Catharacta* (one leg), *Gelochelidon* (one leg), *Sterna* (two legs), *Rynchops* (three legs), *Cepphus* (three legs), *Synthliboramphus* (one specimen). There are two tendons that fuse in *Catharacta* (one leg), *Stercorarius* (three legs), *Larus* (10 legs), *Rissa*, *Chlidonias* (three legs), *Sterna* (five legs), *Thalasseus*, *Uria*, *Cepphus* (four legs), *Brachyramphus* (three legs), *Synthliboramphus* (one specimen), *Ptychoramphus*, *Cerorhinca*, *Fratercula*, and *Lunda*. There is one tendon, but with a division evident, in *Catharacta* (four legs), *Stercorarius* (two legs), *Larus* (two legs), *Chlidonias* (three legs), *Sterna* (six legs), *Rynchops* (four legs), *Cepphus* (two legs), and *Brachyramphus* (one leg).

**M. flexor perforatus digiti II (FPD2), origin.** This muscle typically arises in the intercondylar region of the femur (as in penguins, Schreiweis, 1982; anhingas and cormorants, Owre, 1967; cathartids, Fisher, 1946; *Corvus*, Hudson, 1937) but in *Uria* and *Ardea* it has a fibular origin as well (Hudson, 1937). It arises from the FPD3 femoral tendon of origin and from the patellar tendon, rather than from the intercondylar region, in *Grus americana* (Fisher and Goodman, 1955) and *G. canadensis* (Berger, 1956b). It has two heads in *Fulica americana*; the proximal head arises on the lateral condyle of the femur, the distal head from the ambiens tendon and the tendon of origin of the distal belly of M. FPD3 (Rosser et al., 1982). In *Bubo* and *Otus* there are two heads of origin, one from the intercondylar region and one from the lateral condyle, with the insertion of M. iliofibularis passing in between (Hudson, 1937). A strong branch of the muscle arises below the hypotarsus and inserts on the hallux in *Fregata* (Hudson, 1937). There is no femoral origin in *Amazona albifrons*; the muscle is poorly developed in this species (Berman, 1984). In Ardeidae and *Balaeniceps* there is a strong fibular origin as well; in Ciconiidae, Threskiornithidae, and Phoenicopteridae there is no fibular origin (Vanden Berge, 1970).

Hudson (1937) noted that in many birds the tendon of M. ambiens ends on M. FPD2 or is the point of origin for the lateral head of FPD2. This is true of *Gavia immer* (Wilcox, 1952), Ciconiidae, Threskiornithidae, and

Phoenicopteridae (Vanden Berge, 1970); Oxyurini and *Anas* (Raikow, 1970), and cathartids (Fisher, 1946), but not true of most procellariiforms (Klemm, 1969). In Old World suboscines the origin is by a tendon from the lateral condyle, and by a branch tendon from the fibula (Raikow, 1987).

**M. flexor perforatus digiti II, position (Character 48).** In most birds this muscle is deeply situated on the shank, above FDL; Hudson (1937 and fig. 1) reported it to be primarily superficial in *Tyrannus* and *Corvus*. It appears to be similar in Old World suboscines (Raikow, 1987: fig. 27).

**M. flexor perforatus digiti II, perforation.** The tendon of insertion is not perforated by the two deep flexor tendons (FHL and FDL) in *Camp-torhynchus* (Zusi and Bentz, 1978), Oxyurini or *Anas* (Raikow, 1970), *Polihierax*, *Aceros*, or *Paradisaea* (George and Berger, 1966); or in *Amazona albifrons* (Berman, 1984). It is perforated by FPPD2 in penguins (Schreiweis, 1982), anhingas and cormorants (Owre, 1967), and in hummingbirds (Zusi and Bentz, 1984), and by FPPD2 or FDL in cathartids (Fisher, 1946). It is not perforated by Mm. FPPD2 or FDL in *Colinus* (Berman and Raikow, 1982). It is barely perforated by Mm. FDL and FPPD3 in *Grus americana* and *G. canadensis* in that the medial branch thus formed is very small (Fisher and Goodman, 1955; Berger, 1956b). In *Fulica americana* it is perforated by FPPD2 and FDL (Rosser et al., 1982). Vanden Berge (1970) makes no mention of perforation by the deep flexor tendons in Ciconiiformes, nor does Owre (1967) mention this for anhingas and cormorants. It is perforated in *Sagittarius*, not so clearly in *Cathartes* and *Coragyps*, and not perforated in *Pandion*, *Falco*, or accipitrids (Hudson, 1948).

Hudson (1937) reported that FPD2 is not perforated at all (whether he meant by FPD3 and FPD4 or by any other tendon is not clear) in *Chen*, *Cathartes*, *Buteo*, *Falco*, or *Uria*. It is not perforated by FDL or FPPD2 in Old World suboscines (Raikow, 1987).

**M. flexor perforatus digiti II, accessory head.** An accessory head occurs in *Daption* (Klemm, 1969). A distal head occurs in *Colinus*, arising from the fibular arm of ansa iliofibularis (Berman and Raikow, 1982). A small, deep head arises from the tendon of origin of the lateral head of M. FPD3 in *Grus americana* (Fisher and Goodman, 1955) and *G. canadensis* (Berger, 1956b), but not in cathartids (Fisher, 1946). Vanden Berge (1970) mentions a tendon in *Cochlearius* and *Balaeniceps* arising from the head of the fibula and from the ansa iliofibularis.

**Intermediate muscle complex.** In *Apteryx australis mantelli* (McGowan, 1979), the Mm. FPD4, FPD3, FPD2, and FDL form a complex of intimately related muscles.

**M. plantaris (PL), presence (Character 49).** The muscle is present in most birds. It is absent in the Hydrobatidae except for *Oceanites oceanicus*

and *Hydrobates pelagicus* (Klemm, 1969). It is absent in Accipitridae, *Sagittarius*, and *Pandion* (Hudson, 1948); Pteroclididae and Psittacidae (including *Amazona albifrons*; Berman, 1984), *Eugenes* and *Aceros* (George and Berger, 1966); and in *Buteo*, *Bubo*, *Otus*, and *Chaetura* (Hudson, 1937); but it is present in all the other species examined by Hudson (1937). Zusi and Bentz (1984) report it absent in hummingbirds. It is not mentioned for *Colinus* (Berman and Raikow, 1982) and is presumed absent. It is present in tinamous (Hudson et al., 1972), penguins (Schreiweis, 1982), *Gavia immer* (Wilcox, 1952), aningas and cormorants (Owre, 1967), ciconiiforms (Vanden Berge, 1970), cathartids (Fisher, 1946), *Polihierax* (Berger, 1956a), Oxyurini and *Anas* (Raikow, 1970), galliforms (Hudson et al., 1959), *Grus americana* (Fisher and Goodman, 1955), *Fulica americana* (Rosser et al., 1982), Lari and Alcae (except *Brachyramphus*) (Hudson et al., 1969), caprimulgiforms (Hoff, 1966), and coraciiforms (Maurer and Raikow, 1981). The muscle was absent in one specimen of *Apteryx australis mantelli* but well developed in the other (McGowan, 1979).

**M. plantaris, development (Character 50).** It is very powerfully developed in *Polihierax* (Berger, 1956a), *Falco peregrinus anatum*, *F. mexicanus* and *F. sparverius* (Hudson, 1948).

**M. flexor hallucis longus (FHL), branch to hallux (Character 51).** In *Uria* and *Picoides* (George and Berger, 1966), and in birds lacking a hallux, such as *Eudromia* and *Tinamotus* (Hudson et al., 1972), the tendon of this muscle fuses with that of *M. flexor digitorum longus*. This fusion also occurs in *Casuarinus*, *Dromiceius*, *Rhea*, *Podiceps*, some anhimids, *Phoenicopterus*, Turnicidae, *Hydrophasianus*, *Cariama*, and *Larus* (George and Berger, 1966); some Procellariiformes (Klemm, 1969), and *Gavia immer* (Wilcox, 1952), all of which possess a hallux. Fusion occurs in Oxyurini and *Anas* as well, but there is also a fine tendinous connection with the hallux (Raikow, 1970). A branch to the hallux was not found in *Camptorhynchus* (Zusi and Bentz, 1978).

Some specimens of *Diomedea immutabilis* and *D. nigripes* have a weak hallux, but it receives no tendon from *M. FHL* or other muscle (Klemm, 1969). The belly of *FHL* is bipartite in all procellariiforms except *Diomedea*. Klemm (1969) does not indicate which procellariiforms have a well developed hallux and whether the hallux in those forms receives a tendon from *FHL*. He does mention that the hallux is well developed in most Fulmarinae and Puffininae, and weak in Hydrobatidae.

Vanden Berge (1970:350) notes that there is no branch to the hallux in *Phoenicopterus* and *Phoenicoparrus jamesi*. This notation is made under the description for *FDL* and is worded in a confusing manner. It actually sounds as if he might be referring to *FDL*, except that there is never a hallucal branch of *FDL*. *Phoenicoparrus* has no hallux, so there cannot be a branch of *FHL* to it.

In penguins, in which the hallux is weak, the *FHL* belly is large for the

size of the hallux. The three branches to digits II-IV fuse with the branches of M. FDL; there is a fourth, weak branch to the hallux (Schreiweis, 1982).

Among Lari and Alcae, most species of terns (unspecified) possess a branch to the hallux (Hudson et al., 1969); in the other Lari and Alcae this branch is absent.

The muscle is absent in *Apteryx australis mantelli* (McGowan, 1979), although the hallux is present.

FHL does not supply the hallux in Alcedinidea except in Trogonidae (Maurer and Raikow, 1981).

**Arrangement of the deep plantar tendons, Mm. flexor digitorum longus (FDL) and flexor hallucis longus (Character 52).** See George and Berger (1966:447 ff.) for description of the eight types of arrangements of the deep plantar tendons. See Raikow (1985:113-116) for a summary of the distribution of arrangement types.

Typically the deep plantar tendons (FHL and FDL) are connected by a vinculum (e.g., galliforms, Hudson et al., 1959). George and Berger (1966) indicate that *Apteryx* has the Type II arrangement in which most of the FHL tendon becomes a vinculum; however McGowan (1979) reported that the FHL was lacking in *Apteryx*. Procellariiforms have the Type IV arrangement (Klemm, 1969), as do *Podiceps* (Hudson, 1937) and Phoenicopteridae (Vanden Berge, 1970). Penguins have the Type II arrangement (see Schreiweis, 1982); so evidently do anhingas and cormorants (see George and Berger, 1966 and Owre, 1967). *Fregata* has Type V (Hudson, 1937). *Gavia immer* has the Type IV arrangement; Wilcox (1952) does not mention a vinculum for this species. In ciconiiforms there is a weak vinculum in Ardeidae, *Balaeniceps*, Ciconiidae, and Threskiornithidae; they have the Type I arrangement. *Polihierax* (Berger, 1956a) has Type III (fusion, with vinculum). *Sagittarius*, accipitrids, and *Falco* have the Type III arrangement while cathartids and *Pandion* have Type V (Hudson, 1948). Raikow (1970) does not mention a vinculum in Oxyurini and *Anas*, but these birds seem to have the Type II arrangement (George and Berger, 1966) as do *Chen* (Hudson, 1937), *Nothoprocta*, and *Nothura* with a strong vinculum; other tinamous have the Type I arrangement except for *Eudromia* and *Tinamotus*, which lack a hallux (Hudson et al., 1972). Galliforms have the Type I arrangement (Hudson et al., 1959) as does *Grus americana*; some specimens of the latter have a vinculum (Fisher and Goodman, 1955). *Fulica americana* has a vinculum and the Type I arrangement (Rosser et al., 1982).

In the Lari and Alcae there is no vinculum (Hudson et al., 1969). The tendinal arrangement appears generally to be Type IV (see George and Berger, 1966:447), but a branch to the hallux is found variably in some terns (Hudson et al., 1969); however I code them as Type IV for present purposes. *Totanus* has the Type I arrangement (Hudson, 1937). *Amazona albifrons* has a Type X arrangement (described in Berman, 1984 and coded as 9 in Appendix 2) and a vinculum between Mm. FHL and FDL.

Owls have Type I, caprimulgiforms Type V (Hoff, 1966). In hummingbirds FHL supplies digits I-IV and FDL supplies digits II-IV. Hummingbirds are coded as 0 in Appendix 2. *Colinus* has the Type V arrangement (Berman and Raikow, 1982).

Woodpeckers and their allies (Piciformes) have the Type VI arrangement, in which FHL sends tendinous branches to digits I, II, and IV, and FDL supplies digit III only (Swierczewski and Raikow, 1981). Maurer and Raikow (1981) report the Type V arrangement in coraciiforms; Trogonidae has Type VIII (George and Berger, 1966). Most Passeriformes have the Type VII arrangement, e.g. *Procnias* (George and Berger, 1966), *Tyrannus* (McKittrick, 1985b), and *Corvus* (Hudson, 1937). Eurylaimids and *Philepitta* have the "Type I" arrangement, but the vinculum is not homologous to that found in nonpasserines (Raikow, 1987), and I code them as Type VII to ensure that Old World suboscines emerge with the rest of passerines as indicated by characters 19 and 48.

Hudson (1937) reported a vinculum in *Sula* (Type I), *Ardea*, *Buteo*, *Falco*, *Pediocetes*, *Colinus*, *Grus*, *Fulica*, *Totanus*, *Zenaida*, *Coccyzus*, *Bubo*, *Otus*, *Colaptes*, and *Picoides*; and in *Sagittarius*, accipitrids, and *Falco* (Hudson, 1948).

**M. flexor hallucis longus, number of heads (Character 53).** There may be some error in the characterizations below, as not all authors have presented clear statements about the number of heads of this muscle.

There appears to be only one head in *Apteryx* (McGowan, 1979), tinamous (Hudson et al. 1972), procellariiforms (except *Pterodroma leucoptera* and *Diomedea immutabilis*, which have two; Klemm, 1969:104), penguins (Schreiweis, 1982), *Gavia immer* (Wilcox, 1952), *Podiceps*, *Fregata*, *Sula*, *Chen*, *Fulica*, *Totanus*, *Zenaida*, *Chordeiles*, *Chaetura*, *Picoides*, and *Colaptes* (Hudson, 1937); ciconiiforms (Vanden Berge, 1970), Oxyurini and *Anas* (Raikow, 1970), galliforms (Hudson et al., 1959), Lari and Alcae (Hudson et al., 1969), *Fulica* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Columba* (George and Berger, 1966), *Amazona* (Berman, 1984), *Coccyzus*, *Geococcyx*, and *Crotophaga* (Berger, 1952), caprimulgiforms (Hoff, 1966), hummingbirds (Zusi and Bentz, 1984), and *Mereops* (McKittrick, ms.).

There are two heads in *Phalacrocorax* and *Anhinga* (Owre, 1967), vultures (Fisher, 1946) and other falconiforms (Hudson, 1948), *Bubo* and *Otus* (Hudson, 1937), *Colinus* (Berman and Raikow, 1982), and *Eurystomus* (McKittrick, ms.).

Many species of tyrannids have three to four heads (McKittrick, 1985b), as do Old World suboscines except *Philepitta*, which has two (Raikow, 1987). Hudson (1937) reports two heads of origin for *Corvus*.

**M. flexor hallucis longus, size of proximal [or only] head.** This is very large in *Colinus* (Berman and Raikow, 1982). Within ciconiiforms, FHL is most strongly developed in Ardeidae and *Balaeniceps*, less so in Threskior-

nithidae, and weak and short in Ciconiidae and Phoenicopteridae (Vanden Berge, 1970). FHL is very powerful in *Bubo* and *Otus* (Hudson, 1937) and in *Sagittarius*, accipitrids, *Pandion*, and *Falco*; it is "weak and typical" in cathartids (Hudson, 1948:107). The lateral head is small in most galliforms, but much larger in *Leipoa*; it is tiny in *Ortalis canicollis* and *Crax* (Hudson et al., 1959).

**M. flexor digitorum longus, number of heads (Character 54).** FDL has two heads of origin in most birds, although there is some confusion in the literature about this. Hudson (1937) reported one head for all the birds he examined except for *Corvus* and *Tyrannus*; however it is clear from other studies of these same taxa that the usual condition is two heads. Furthermore, McKitrick (1985b) reported three heads for *Tyrannus*. I have coded all taxa as having two heads, with a few exceptions: *Gavia* (Wilcox, 1952), *Columba* (George and Berger, 1966), and passerines (*Eurylaimus* through *Corvus*, except *Philepitta*) are coded as having a third, femoral head.

**M. flexor digitorum longus, fusion with M. fibularis brevis.** McGowan (1979:65–66) states that the tendon of insertion of FDL is fused with that of *M. fibularis brevis* in *Apteryx* and other paleognaths; this remains to be substantiated (Vanden Berge, 1982). It was not mentioned by Hudson et al. (1972).

**M. flexor digitorum longus, size (Character 55).** The muscle is "extremely large and powerful" in *Bubo* and *Otus* (Hudson, 1937:47) and in *Chaetura pelagica* (McKitrick, ms.). In hummingbirds (Zusi and Bentz, 1984) and *Tyrannus* (McKitrick, 1985b), the muscle is of intermediate size.

**M. flexor digitorum longus, position (Character 56).** In *Pandion* and accipitrids the muscle is visible superficially on the lateral side of the shank, whereas in most birds it is deeply situated (Hudson, 1948).

**M. popliteus (POP), presence (Character 57).** The muscle is present in most nonpasserines, including penguins (Schreiweis, 1982), tinamous (Hudson et al., 1972), *Gavia immer* (Wilcox, 1952), Procellariiformes (Klemm, 1969), anhingas and cormorants, in which it is very small (Owre, 1967); Oxyurini and *Anas* (Raikow, 1970), galliforms (Hudson et al., 1959), ciconiiforms (Vanden Berge, 1970), cathartids (Fisher, 1946), falconiforms (Hudson, 1948), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), and *G. canadensis* (Berger, 1956b).

It was not mentioned for *Apteryx australis mantelli* by McGowan (1979) and is presumed absent in that species. It is absent in *Chaetura*, *Picoides*, and *Colaptes* (Hudson, 1937); *Amazona albifrons* (Berman, 1984), *Colius* (Berman and Raikow, 1982), *Psittacus*, *Eugenes fulgens*, *Pharomachrus mocino*, *Chloroceryle americana*, *Upupa epops*, *Aceros undulatus*, and *Indicator variegatus* (George and Berger, 1966); *Aegothales* (Hoff, 1966), hummingbirds (Zusi

and Bentz, 1984), Coraciiformes except Coraciidae, Brachypteraciidae, and Leptosomidae (Maurer and Raikow, 1981); it is absent in Piciformes except Galbulidae (Swierczewski and Raikow, 1981). It is absent in *Corvus* (Hudson, 1937), *Tyrannus* (Hudson, 1937; McKitrick, 1985b), and Old World suboscines (Raikow, 1987).

**M. flexor hallucis brevis (FHB), presence (Character 58).** The muscle is present in tinamous, except for *Tinamotis* and *Eudromia*, which lack a hallux. FHB is absent in *Phoebetria*, *Pterodroma phaeopygia*, *Pelagodroma*, *Fregetta*, *Oceanodroma melania*, *Halocyptena*, *Pelecanoides garnoti*, and vestigial in *Oceanodroma tethys*. It is present in *Diomedea* and *Procellaria*; the condition could not be determined for *Daption*, *Pachyptila forsteri*, *P. desolata*, *Pterodroma mollis*, *P. cooki*, *Nesofregetta*, or *Oceanodroma leucorhoa* (Klemm, 1969). It is present in anhingas and cormorants and is considerably bigger in the former (Owre, 1967); it is present in ciconiiforms (but vestigial in Phoenicopteridae) (Vanden Berge, 1970), falconiformes (Hudson, 1948), *Polihierax* (Berger, 1956a), cathartids (Fisher, 1946), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Amazona albifrons* (Berman, 1984), *Colinus* (Berman and Raikow, 1982), hummingbirds (Zusi and Bentz, 1984), *Corvus* (Hudson, 1937), tyrannids (McKitrick, 1985b), and Old World suboscines except *Acanthisitta* and *Xenicus* (Raikow, 1987). It is present in galliforms—weak in *Lagopus*, powerful in *Opisthocomus* (Hudson et al., 1959).

In the Alcae, which lack a hallux, the muscle is present in *Alca* (two legs), *Uria* (four legs), *Cepphus* (one leg), *Brachyramphus* (one leg), *Ptychoramphus* (two legs), *Fratercula* (four legs), and *Lunda* (four legs). The muscle is absent in *Alca* (four legs), *Uria* (14 legs), *Cepphus* (six legs), *Brachyramphus* (three legs), *Synthliboramphus* (four legs), *Ptychoramphus* (four legs), *Cerorhinca* (six legs), *Fratercula* (two legs), and *Lunda* (two legs) (Hudson et al., 1969).

The muscle was not mentioned for *Apteryx australis mantelli* by McGowan (1979) and is presumed absent in that species. It was reported absent in *Uria* and *Gavia* by Hudson (1937), although Wilcox (1952) found it to be present tendinously in *Gavia*. It is absent in some penguins (Schreiweis, 1982) and in *Cygnus* (George and Berger, 1966).

**M. flexor hallucis brevis, number of tendons (Character 59).** The muscle has two independent tendons in *Fulica americana* (Hudson, 1937; Rosser et al., 1982), *Totanus*, *Larus*, *Bubo*, and *Otus*, and in addition *Ardea* and *Buteo* show some division of the tendon (Hudson, 1937). All the accipitrids examined by Hudson (1948) have a double tendon of insertion that fuses to a single tendon distally; the other falconiforms had one tendon. Vanden Berge (1970) reports that the tendon is divided in Ardeidae, but single in *Balaeniceps*, Ciconiidae, and Threskiornithidae. In Caprimulgidae (*Nyctidromus*, *Caprimulgus*, *Chordeiles*), the distal end of the tendon is double; in all other Caprimulgiformes the tendon is single (Hoff, 1966). Two ten-



dons occur in *Eurystomus* and *Merops* (McKittrick, ms.). The muscle is single throughout in Oxyurini and *Anas* (Raikow, 1970), cathartids (Fisher, 1946), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Corvus* (Hudson, 1937), *Tyrannus* (McKittrick, 1985b), and Old World suboscines (Raikow, 1987).

Among Lari (Hudson et al., 1969), the belly and tendon are single in *Stercorarius*, *Sterna albifrons*, *Rynchops*, and *Catharacta*. They are double in *Chlidonias*, *Sterna forsteri*, *Thalasseus*, and *Rissa*; in *Larus* they are variable, with the belly divided (nine legs) or single (three legs), and the tendon double (five legs) or single (six legs). The belly may be either double or single in *Sterna paradisaea*. It is single in the Alcae that possess the muscle.

**M. flexor hallucis brevis, ensheathement of M. flexor hallucis longus.**

The tendon of insertion typically ensheathes that of M. flexor hallucis longus, as in *Fregata*, *Sula*, *Ardea*, *Cathartes*, *Pediocetes*, *Colinus*, *Zenaida*, *Coccyzus*, *Colaptes*, *Picoides villosus*, and *Corvus* (Hudson, 1937), and evidently in all Old World suboscines that possess the muscle (Raikow, 1987). This is not the case in *Polihierax* (Berger, 1956a), *Buteo*, *Falco*, *Grus*, *Fulica*, *Totanus*, *Larus*, *Bubo*, *Otus*, *Chordeiles*, or *Chaetura* (Hudson, 1937); *Amazona albifrons* (Berman, 1984), nor *Colius* (Berman and Raikow, 1982). Klemm (1969) makes no mention of ensheathement of M. FHL in procellariiforms, nor does Raikow (1970) for Oxyurini and *Anas*, nor Zusi and Bentz (1984) for hummingbirds, nor Schreiweis (1982) for penguins. Fisher (1946) does not mention this for cathartids, except that in *Gymnogyps* the tendon to digit I from FHL is ensheathed by the FHB tendon; Fisher and Goodman (1955) report that the condition for *Grus* is the same as that reported by Fisher (1946) for cathartids. Wilcox (1952) notes that FHB is not in contact with any other muscle in *Gavia immer*.

**M. flexor hallucis brevis, perforation by M. flexor digitorum longus.**

In most birds, M. FHB is perforated by M. FDL. This perforation does not occur in any of the falconiform birds examined by Hudson (1948) except cathartids.

**M. extensor hallucis longus (EHL), presence (Character 60).** The muscle is absent in *Podiceps nigricollis* and *Uria* (Hudson, 1937); Hudson (1937) also reported it absent in *Gavia immer* but Wilcox (1952) found it in that species although it was very small. It is vestigial or absent in procellariiforms (Klemm, 1969). It is very small in penguins (Schreiweis, 1982) and short and weak in *Chen* and *Totanus* (Hudson, 1937). It is present in *Apteryx australis mantelli* (McGowan, 1979), although small, and in tinamous except for *Eudromia* and *Tinamotis*, which lack a hallux (Hudson et al., 1972). It is present in *Polihierax* (Berger, 1956a), Oxyurini and *Anas* (Raikow, 1970), cathartids (Fisher, 1946), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), *Amazona albifrons* (Berman, 1984), *Colius* (Berman and Raikow,

1982), and hummingbirds (Zusi and Bentz, 1984). It was present in *Campylorhynchus* (Zusi and Bentz, 1978). It is present in ciconiiforms except *Phoenicoparrus*; it is vestigial in *Phoenicopterus* (Vanden Berge, 1970). It is very powerful in *Buteo* and presumably in *Falco* as well (see Hudson, 1937).

The muscle is present in Lari, absent in most Alcae, except for *Cerorhinca* (three legs) and *Lunda* (five legs) in which it is minute, and possibly *Cepphus* in which there may be a trace of the muscle (Hudson et al., 1969). It is present in *Corvus* (Hudson, 1937), tyrannids (McKitrick, 1985b), and Old World suboscines but is vestigial in *Acanthisitta* and *Xenicus* (Raikow, 1987).

**M. extensor hallucis longus, number of heads (Character 61).** There is one head in *Apteryx* (McGowan, 1979). Two heads occur in tinamous except for *Crypturellus* and those lacking the muscle (Hudson et al., 1972), in *Pandion*, *Falco*, and accipitrids (Hudson, 1948); *Polihierax* (Berger, 1956a), *Buteo*, *Larus*, *Sterna antillarum*, *Zenaidra*, *Columba*, *Bubo*, and *Otus* (Hudson, 1937); *Fulica americana* (Rosser et al., 1982), and *Aceros*, (George and Berger, 1966). EHL has one head in *Gavia immer* (Wilcox, 1952), *Phalacrocorax* and *Anhinga* (Owre, 1967), Oxyurini and *Anas* (Raikow, 1970), *Chen*, *Fregata*, *Sula*, *Totanus*, *Chordeiles*, *Chaetura*, *Colaptes*, and *Picoides* (Hudson (1937); and in *Coccyzus*, *Geococcyx*, and *Crotophaga* (Berger, 1952). Within ciconiiforms, the muscle consists of one well developed head in Ardeidae, *Ciconia*, and threskiornithids. There are two distinct heads in *Mycteria* and *Leptoptilos*, and a very well developed proximal head and small distal head in *Balaeniceps*. The muscle is vestigial in *Phoenicopterus* and absent in *Phoenicoparrus* (Vanden Berge, 1970). It is single in *Sagittarius* (Hudson, 1948) and cathartids (Fisher, 1946; Hudson, 1948), and variable in galliforms (Hudson et al., 1959). There is evidently only one head in *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), and penguins (Schreiweis, 1982). There are two parts in *Amazona albifrons* but Berman (1984) questioned their homology with pars proximalis and distalis. Hoff (1966) reported two heads in owls and in *Steatornis*, one in other caprimulgiforms. Hummingbirds have two heads, a proximal and a much smaller distal one; in *Glaucis* the distal head is "barely discernible" (Zusi and Bentz, 1984:40). Pars distalis is present in *Colius*, pars proximalis having been lost (Berman and Raikow, 1982); it is coded in Appendix 2 as having two parts.

In the Lari (Hudson et al., 1969) there are usually two widely separated bellies; the proximal head was absent in *Larus* (four legs), *Gelochelidon* (one leg), *Sterna albifrons* (?), and *Thalasseus* (two legs). The proximal belly was absent in *Rynchops* also but the distal belly was well developed. In Alcae (Hudson et al., 1969) there is one head, except in *Lunda* and *Cerorhinca*, which are variable. The muscle is single in *Eurystomus* (McKitrick, ms.), *Corvus* and *Tyrannus* (Hudson, 1937), and in Old World suboscines (Raikow, 1987).

**M. extensor hallucis longus, accessory (Character 62).** This is present in *Amazona albifrons*; it is very small and consists of a few fibers (Berman, 1984). It is present in *Colius* (Berman and Raikow, 1982), *Columba* (George and Berger, 1966), and *Zenaida* (Hudson, 1937). It may also be present in *Tyto* (see Hoff, 1966).

**M. extensor hallucis longus, condition of medial head.** This is very powerful and forms a fleshy sheath around the tendon of M. EDL in accipitrids; in *Pandion* and *Falco* this head is not so well developed and does not form a sheath (Hudson, 1948).

**M. abductor digiti II (ABD2), presence (Character 63).** The muscle is absent in the Alcedinomorphae (Phoeniculidae through Cerylini in Appendix 2) (Maurer and Raikow, 1981), *Colaptes*, *Picoides villosus*, and *Corvus* (Hudson, 1937); *Tyrannus* (Hudson, 1937; McKittrick, 1985b), and in Old World suboscines (Raikow, 1987). The muscle is present in penguins (Schreiweis, 1982), anhingas and cormorants (Owre, 1967), *Gavia immer* (Wilcox, 1952), Oxyurini and *Anas* (Raikow, 1970), *Camptorhynchus* (Zusi and Bentz, 1978), galliforms (Hudson et al., 1959), and in procellariiforms except for *Puffinus assimilis*; the condition could not be determined in seven species (Klemm, 1969). It is present in *Polihierax* (Berger, 1956a), Lari and Alcae (Hudson et al., 1969), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), ciconiiforms (Vanden Berge, 1970), and cathartids (Fisher, 1946). It is absent in *Amazona albifrons* (Berman, 1984), and was not mentioned for *Colius* (Berman and Raikow, 1982) or hummingbirds (Zusi and Bentz, 1984) and is presumed absent. Hudson (1937) reported that the muscle is "reduced to a tendinous sheet and is probably incapable of contraction" in *Gavia immer* and *Podiceps nigricollis*. It is short and stout in *Sagittarius*, short in cathartids and *Pandion*, weak in *Falco*, and extends the length of the tarsometatarsus in accipitrids (Hudson, 1948).

In *Apteryx australis mantelli* (McGowan, 1979:70) a "poorly differentiated and thin strip of muscle tissue" is situated on the tarsometatarsus and divides to send vague tendons to digits II-IV. These were identified by McGowan as Mm. abductor digiti II, extensor brevis digiti III, and extensor brevis digiti IV.

**M. adductor digiti II (ADD2), presence (Character 64).** The muscle is very weak in *Sagittarius*, *Falco*, and accipitrids, stronger in cathartids, and stronger still in *Pandion* (Hudson, 1948). The muscle is absent in *Tinamotis* (but present in other tinamous; Hudson et al., 1972), penguins (Schreiweis, 1982), *Amazona albifrons* (Berman, 1984), presumably in *Colius* (Berman and Raikow, 1982), absent in *Pediocetes*, *Colaptes*, *Picoides villosus*, *Tyrannus*, and *Corvus* but present in the other species examined by Hudson (1937), absent in Upupidae, Momotidae, Trogonidae, Alcedinidae (Maurer and

Raikow, 1981), and Old World suboscines (Raikow, 1987). Among procellariiforms, the muscle is separate in *Phoebastria*, weakly developed in *Puffinus pacificus* and *Oceanodroma tethys*, and absent in *Pterodroma phaeopygia*, *Pelagodroma*, *Fregatta*, *Hydrobates*, *Oceanodroma melania*, *Halocyptena*, and *Pelecanoides garnoti*; the condition could not be determined for seven species (Klemm, 1969). It is present in aningas and cormorants, larger in the former (Owre, 1967). The muscle is present in *Gavia immer* (Wilcox, 1952), *Polihierax* (Berger, 1956a), Oxyurini and *Anas* (Raikow, 1970), *Camptorhynchus* (Zusi and Bentz, 1978), ciconiiforms (Vanden Berge, 1970), Lari and Alcae (Hudson et al., 1969), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), cuckoos (Berger, 1952), caprimulgiforms (Hoff, 1966), and hummingbirds (Zusi and Bentz, 1984). The muscle is present in galliforms except tetraonids (*Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pediocetes*, *Tympanuchus*, *Centrocercus*). In *Gennaues* and *Pavo* there was no connection to the second toe (Hudson et al., 1959).

This muscle was not mentioned for *Apteryx australis mantelli* by McGowan (1979) and is presumed absent in that species.

**M. adductor digiti II, length.** The belly extends almost the length of the tarsometatarsus in *Fulica americana* (Rosser et al., 1982), *Fregata*, *Sula*, *Zenaida*, *Chordeiles*, and *Chaetura* (Hudson, 1937); and in *Columba* (George and Berger, 1966). The belly is restricted to the distal half or less in Oxyurini and *Anas* (Raikow, 1970), and in *Ardea*, *Chen*, and various galliforms (George and Berger, 1966). In *Podiceps*, *Opisthocomus*, *Bubo*, and some cuckoos the belly is limited to the proximal half of the bone and the tendon of insertion is long (George and Berger, 1966). The belly extends the length of the tarsometatarsus in hummingbirds except for *Heliodoxa*, in which it extends only half the length of that bone (Zusi and Bentz, 1984). The muscle is almost entirely tendinous in *Gavia immer* (Wilcox, 1952).

**M. extensor proprius digiti III (EPD3), presence.** The muscle is "very short and weak" in *Sula*, *Chen*, *Falco*, *Pediocetes*, *Colinus*, *Fulica*, *Totanus*, and *Uria* (Hudson, 1937); Rosser et al. (1982) did not find the muscle in *Fulica americana*. It is vestigial in *Polihierax* (Berger, 1956a), cathartids (Fisher, 1946), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (Berger, 1956b), and *Chaetura* (George and Berger, 1966). It is present in galliforms, very powerful in *Opisthocomus*, but almost vestigial in *Alectoris* (Hudson et al., 1959). It is vestigial in most procellariiforms; it is distinct only in *Phoebastria*, *Puffinus pacificus*, and *P. assimilis* (Klemm, 1969). It was present in *Camptorhynchus* (Zusi and Bentz, 1978) and is present in Oxyurini and *Anas* (Raikow, 1970). Schreiweis (1982) does not mention the muscle for penguins, nor do Zusi and Bentz (1984) for hummingbirds. It is conspicuous in *Amazona albifrons* (Berman, 1984). It is present in tinamous (Hudson et al., 1972) and *Colius* (Berman and Raikow, 1982). It is very small in *Gavia immer* (Wilcox, 1952). It is absent in aningas and

cormorants (Owre, 1967); Hudson (1937) reported it absent in *Fregata*, *Grus*, *Tyrannus*, and *Corvus* and well developed in *Ardea*, *Butorides*, *Zenaida*, *Coccyzus*, *Bubo*, *Otus*, *Colaptes*, and *Picoides villosus*. It is absent in Old World suboscines (Raikow, 1987).

Hudson (1948) reported that *Sagittarius* lacks any short extensor to the third toe. A rudimentary extensor occurs in *Cathartes*, *Coragyps*, and *Falco*. A single flexor was found in accipitrids, well developed in *Aquila* and *Buteo*, weaker in *Circus* and *Accipiter*. *Pandion* has two well developed extensors, of which this is one; the other is probably *M. extensor brevis digiti III*.

For *Lari* and *Alcae* see description for *M. extensor brevis digiti III*, below.

The muscle is very small in *Apteryx australis mantelli* (McGowan, 1979); it was reported to insert on the terminal phalanx of digit IV, which is presumably a misprint.

**M. extensor proprius digiti III, length.** The belly of this muscle is weak and limited to the distal end of the tarsometatarsus in some galliforms (Hudson et al., 1959), in Oxyurini and *Anas* (Raikow, 1970), in *Sula*, *Chen*, *Falco*, *Pediocetes*, *Colinus*, *Fulica*, *Totanus*, *Uria* (Hudson, 1937), and in *Geococcyx* (Berger, 1952). It extends half the length of the tarsometatarsus in *Amazona albifrons* (Berman, 1984) and the entire length of that bone in *Colius* (Berman and Raikow, 1982). It is represented by a tendon in cathartids, when present (Fisher, 1946). The length is variable in tinamous (Hudson et al., 1972). The muscle is mostly tendinous in *Gavia immer* and arises at the distal end of the tarsometatarsus (Wilcox, 1952).

**M. extensor proprius digiti III, accessory.** This was described by Berman (1984) in *Amazona albifrons*. It is not present in *Colius* (Berman and Raikow, 1982).

**M. extensor brevis digiti III (EBD3), presence.** See description under *M. abductor digiti II* for *Apteryx australis mantelli* (p. 45). This muscle is absent in many birds including aningas and cormorants (Owre, 1967), *Amazona albifrons* (Berman, 1984), and *Colius* (Berman and Raikow, 1982); it is present in penguins (Schreiweis, 1982), tinamous (Hudson et al., 1972), and *Pandion* (Hudson, 1948). It is present in procellariiforms, although absent in some specimens of *Diomedea* (Klemm, 1969). It was not mentioned for Oxyurini and *Anas* (Raikow, 1970), nor *Gavia immer* (Wilcox, 1952), nor hummingbirds (Zusi and Bentz, 1984), and is presumed absent. It is tiny in *Fulica americana* (Rosser et al., 1982). It is present but very small in cathartids (Fisher, 1946) and in *Grus americana* (Fisher and Goodman, 1955). It is not mentioned by Berger (1956b) for *G. canadensis*. Vanden Berge (1970:352) states that he is referring to *M. extensor proprius digiti III* and *M. extensor brevis digiti III* as the same muscle, and notes that the muscle is present in all ciconiiforms.

Hudson (1937) found only one extensor to the third toe in the species

he studied, and referred to it as *M. extensor proprius digiti III*. By 1969 he was referring to the muscle as *M. extensor brevis digiti III* and noted (Hudson et al.) that it was present in Lari and Alcae, but poorly developed to vestigial.

**M. extensor brevis digiti IV (EBD4), presence (Character 65).** See description for *Apteryx australis mantelli* (p. 45) under *M. abductor digiti II*. It is coded as vestigial (1) for *Apteryx*.

Among procellariiforms, the muscle was absent or vestigial in half the specimens of *Diomedea* examined by Klemm (1969), and present in the others. It was present in the remainder of the group, except for six species (see Klemm, 1969) in which the condition could not be determined. The muscle is reduced to connective tissue in *Podiceps nigricollis* (Hudson, 1937). It is present in penguins (Schreiweis, 1982), *Sagittarius* (short and stout) (Hudson, 1948), galliforms (Hudson et al., 1959), cathartids and *Pandion* (well developed) and accipitrids and *Falco* (short belly) (Hudson, 1948); present and stout in anhingas, less stout in cormorants (Owre, 1967); and present but mostly tendinous in *Gavia immer* (Wilcox, 1952). It is present in tinamous (Hudson et al., 1972), *Camptorhynchus* (Zusi and Bentz, 1978), Oxyurini and *Anas* (Raikow, 1970), Lari and Alcae (Hudson et al., 1969), *Fulica americana* (Rosser et al., 1982), *Grus americana* (Fisher and Goodman, 1955), *G. canadensis* (although rudimentary; Berger, 1956b), cuckoos (Berger, 1952), caprimulgiforms (Hoff, 1966), and *Colius* (Berman and Raikow, 1982); it is very small in *Amazona albifrons* (Berman, 1984). It is absent in Todidae, Momotidae, and Meropidae (Maurer and Raikow, 1981); *Colaptes*, *Picoides villosus*, and *Corvus* (but present in the other species examined) (Hudson, 1937); *Tyrannus* (Hudson, 1937; McKittrick, 1985b), and Old World suboscines (Raikow, 1987). Zusi and Bentz (1984) do not mention it for hummingbirds, and it is presumed absent. It is poorly developed in *Polihierax* (Berger, 1956a). In ciconiiforms it is well developed (Vanden Berge, 1970).

**M. extensor brevis digiti IV, number of heads.** In *Fregata* it has two heads of origin (Hudson, 1937).

**M. extensor proprius digiti IV (EPD4).** This was described and named by Berman and Raikow (1982) for *Colius*.

**M. abductor digiti IV (ABD4), presence and development.** The muscle is present in *Apteryx australis mantelli* (present in one of two specimens; McGowan, 1979), penguins (Schreiweis, 1982), and galliforms (Hudson et al., 1959). It is weakly developed in *Polihierax* (Berger, 1956a), *Podiceps*, woodpeckers, and passerines, and relatively weakly developed in *Columba* (George and Berger, 1966). It is present in all falconiforms examined by Hudson (1948), although variably developed. It is present in tinamous

(Hudson et al., 1972), cormorants and anhingas (larger in anhingas than cormorants; Owre, 1967), *Gavia immer* (Wilcox, 1952), procellariiforms (Klemm, 1969), *Camptorhynchus* (Zusi and Bentz, 1978), and Oxyurini and *Anas* (Raikow, 1970), and is well developed in *Amazona albifrons* (Berman, 1984). It is present in *Colius* (Berman and Raikow, 1982). Hudson (1937) found it to be very stout in *Fregata* and *Sula*, and very weakly developed in *Gavia*, *Podiceps nigricollis*, *Colaptes*, *Picooides villosus*, *Tyrannus*, and *Corvus*. Among Old World suboscines it is very small in *Eurylaimus*, vestigial in *Xenicus*, and absent or vestigial in *Acanthisitta*; it was not found in *Pitta* (Raikow, 1987). Zusi and Bentz (1984) do not mention it for hummingbirds. It has an upper and a distal belly in cathartids, on the same tendon (Fisher, 1946); Fisher and Goodman (1955) note that the condition in *Grus americana* is the same as that described in Fisher's (1946) paper on cathartids. It is minute in *G. canadensis* (Berger, 1956b). It extends about half the length of the tarsometatarsus in *Fulica americana* (Rosser et al., 1982). It is present in ciconiiforms, and in *Ixobrychus* and *Botaurus* the muscle has two heads (Vanden Berge, 1970). It is well developed in Lari and Alcae (Hudson et al., 1969).

**M. adductor digiti IV (ADD4), presence.** Little information is available. The muscle is absent in penguins (Schreiweis, 1982), and in all falconiforms examined by Hudson (1948). Wilcox (1952) found the muscle in *Gavia immer*; Hudson (1937) found it well developed only in *Phasianus colchicus*, and absent in the other forms he studied. Hudson et al. (1959) did not find it in any of the galliforms they studied. It was not mentioned for procellariiforms (Klemm, 1969), Oxyurini and *Anas* (Raikow, 1970), *Amazona albifrons* (Berman, 1984), *Colius* (Berman and Raikow, 1982), nor hummingbirds (Zusi and Bentz, 1984) and it is presumed absent. It is absent in tinamous (Hudson et al., 1972), cathartids (Fisher, 1946), and *Grus americana* and *G. canadensis* (Fisher and Goodman, 1955; Berger, 1956b). It was reported to be reduced to a ligament in *Chen hyperborea*, *Grus canadensis*, and *Fulica americana* (Rosser et al., 1982). It was present and well developed in the gruiform species studied by Allen (1962). It is not mentioned by Vanden Berge (1970) for ciconiiforms nor Owre (1967) for anhingas and cormorants and is presumed absent. It is absent in Lari and Alcae (Hudson et al., 1969).

**M. lumbricalis (L), presence (Character 66).** The muscle is well developed in *Pandion* (Hudson, 1948), *Ardea*, *Butorides*, *Zenaida*, *Coccyzus*, *Chordeiles*, and *Chaetura* (but not in the other species examined) (Hudson, 1937); *Gallicolumba*, many cuckoos, *Goura*, *Opisthocomus*, *Columba*, and *Aceros* (George and Berger, 1966). It is very weak in all falconiforms examined by Hudson (1948) except for *Pandion* (see above). It is weak in most galliforms, evidently absent in *Pavo*, but strongly developed in *Opisthocomus* (Hudson et al., 1959). It is present, although vestigial, in procellariiforms

except *Pelagodroma* in which it is apparently absent (Klemm, 1969). It is vestigial in penguins (Schreiweis, 1982). It is present and with two bellies in Oxyurini and *Anas* (Raikow, 1970), although very small indeed. It is present with two bellies in tinamous (Hudson et al., 1972); in *Nothoprocta* and *Nothura* the lateral head arises out of the tendon of insertion of FHL. It is present though poorly developed in *Amazona albifrons* (Berman, 1984), but well developed in *Colinus* (Berman and Raikow, 1982). Fisher and Goodman (1955) do not mention it for *Grus* nor Wilcox (1952) for *Gavia immer* nor Zusi and Bentz (1984) for hummingbirds, and it is presumed absent. It is almost entirely tendinous in cathartids (Fisher, 1946). Berger (1956b) found it in some specimens of *G. canadensis* but termed it poorly developed. It is "extremely tiny" in *Fulica americana* (Rosser et al., 1982). Hoff (1966) found it to be weak in owls, indistinct in *Nyctibius*, and present in all other Caprimulgiformes. It is present in *Coccyzus*, *Geococcyx*, and *Crotophaga* (Berger, 1952). It is very small in Old World suboscines (Raikow, 1987).

The muscle is very weak to vestigial in ibises, storks, flamingos, *Ajaia*, and *Balaeniceps*; it is better developed and has two heads in Ardeidae (Vanden Berge, 1970). Owre (1967) was unable to find fleshy fibers of the muscle in anhingas and cormorants; the muscle could be vestigial in these forms. It is weak to vestigial in *Lari*, stronger in *Alcae* (Hudson et al., 1969).

The muscle is present in *Apteryx australis mantelli* but appears to be weak (McGowan, 1979). It is absent in *Tyrannus* (McKitrick, 1985b), and apparently in *Corvus* (Hudson, 1937).

#### PHYLOGENETIC ANALYSIS

The analysis performed using Hennig86 (Farris, 1988) was unable to find more than 884 trees due to memory constraints of the program. The PAUP analysis was terminated at 6,000 trees. The trees obtained using PAUP were 340 steps (consistency index [ci] = .300 excluding uninformative characters). The 75% majority-rule consensus tree is shown in Figure 1. This tree shows all groups occurring in at least 75% of all 6,000 trees. This kind of consensus tree is presented because it is more informative about the results of the analysis than the strict consensus. The strict consensus tree can be inferred from the groups occurring 100% of the time; all groups collapse that occur in less than 100% of the trees. Figure 2 shows the same tree but with node numbers instead of group percentages. Figure 3 shows Tree #1 of 6,000. Character changes for Tree #1, based on ACCTRAN optimization, are listed in Appendix 3. An apomorphy list based on that tree is presented in Appendix 4.



## DISCUSSION

## COMPARISON WITH PREVIOUS HYPOTHESIS

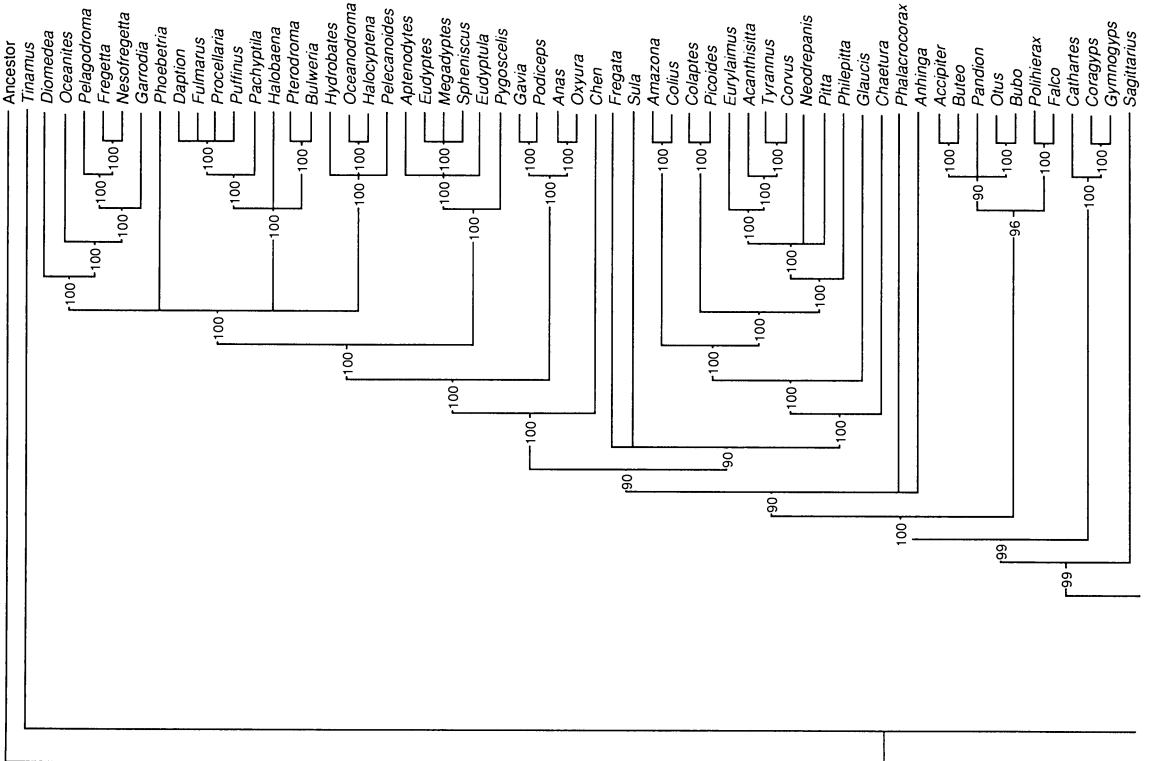
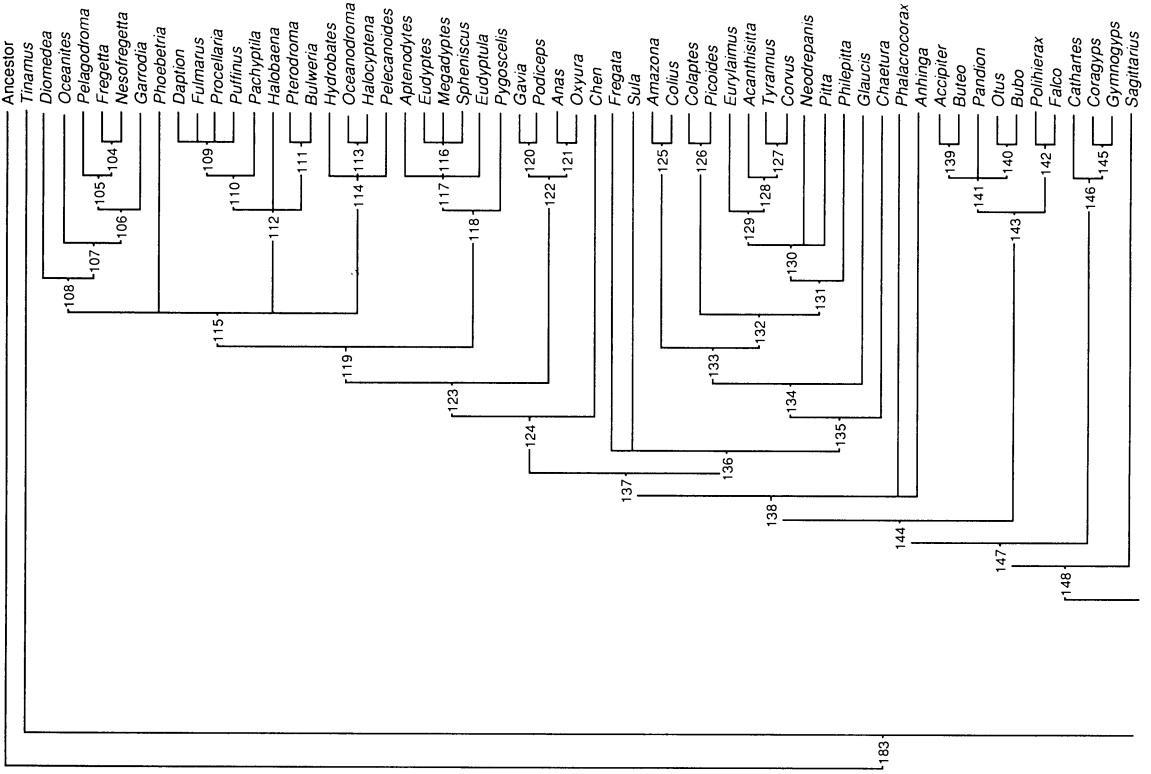
The trees support a number of traditional groupings but fail to corroborate others. Monophyly of Procellariiformes (node 115: *Diomedea* through *Pelecanoides*) is supported in 100% of all trees, and penguins (node 118: *Aptenodytes* through *Pygoscelis*) are the sister group to the procellariiform clade in all trees. Loons and grebes (node 120: *Gavia* and *Podiceps*) are always a clade and ducks (node 121: *Anas* and *Oxyura*) are their sister group. The loon-grebe-duck clade are the sister group to the procellariiform-penguin group in all trees. The goose (*Chen*) emerges not with ducks but rather as the sister group to all the preceding taxa.

Passeriformes (node 131: *Eurylaimus* through *Philepitta*) are monophyletic in all trees. Old World suboscines do not emerge monophyletic because of an artifact of character coding (see description for Character 52, above); the arrangement of the deep flexor tendons in Old World suboscines is derived (Raikow, 1987), but because PAUP can accommodate only 10 states per character I coded Old World suboscines the same as the other passerines. Woodpeckers (node 126: *Colaptes* and *Picoides*) are the sister group to passeriforms. Parrots and mousebirds (node 125: *Amazona* and *Colius*) are always a clade and are the sister group to the woodpecker-passeriform group. Hummingbirds (*Glaucis*) are the sister group to the preceding three groups (node 133), and swifts (*Chaetura*) are the sister group to that large clade in all trees.

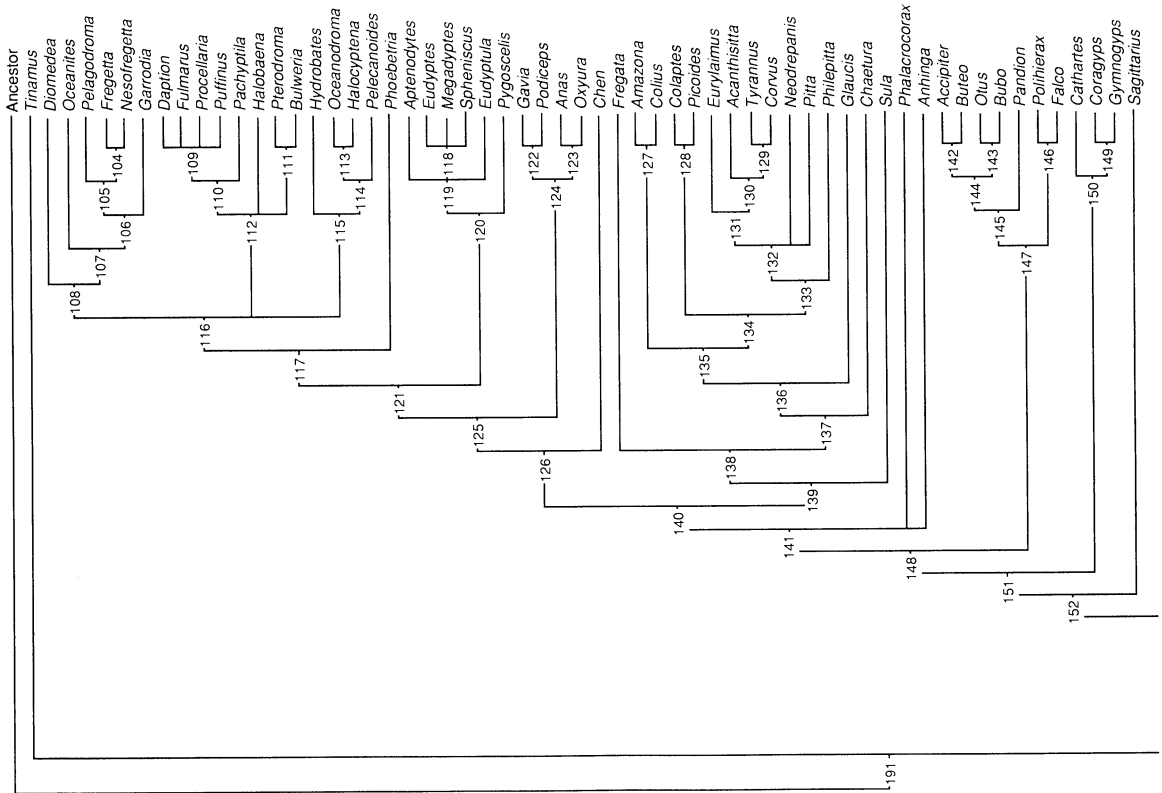
Monophyly of Pelecaniformes is not supported in this analysis, whereas it was highly supported by Cracraft (1985). *Fregata* and *Sula* float unresolved outside of the passerine-swift clade. The other two pelecaniiform taxa, *Phalacrocorax* and *Anhinga*, emerge unresolved outside of all the preceding taxa (*Diomedea* through *Chaetura*). The whale-headed stork (*Balaeniceps*) is sister to the herons and there is no link between herons and any pelecaniiforms (compare Cracraft [1985] and Sibley et al. [1988]).

Falconiformes is also broken apart in this analysis. Accipitrids (node 139: *Accipiter* and *Buteo*) are always monophyletic; owls (node 140: *Bubo* and *Otus*) are always a clade; and accipitrids, owls, and osprey (*Pandion*) emerge as a trichotomy in 90% of all trees. Their sister group is the falcons (node 142: *Polihierax* and *Falco*) in 96% of all trees. This hawk-owl clade is the sister group of all the preceding taxa (*Diomedea* through *Anhinga*) in 90% of all trees. The sister group to this large group is the vultures (node 146: *Cathartes* through *Gymnogyps*) in 99% of all trees, with the secretary-bird (*Sagittarius*) outside that group in all trees.

Charadriiformes is not monophyletic in this analysis, in that the one sandpiper (*Totanus*) never emerges with the auks, gulls, and terns. The latter group, however, (node 158: *Rynchops* through *Thalasseus*) is a clade in 100% of all trees, but there is little resolution within that group other than within the auk clade (node 153: *Alca* through *Cerorhinca*). Coots







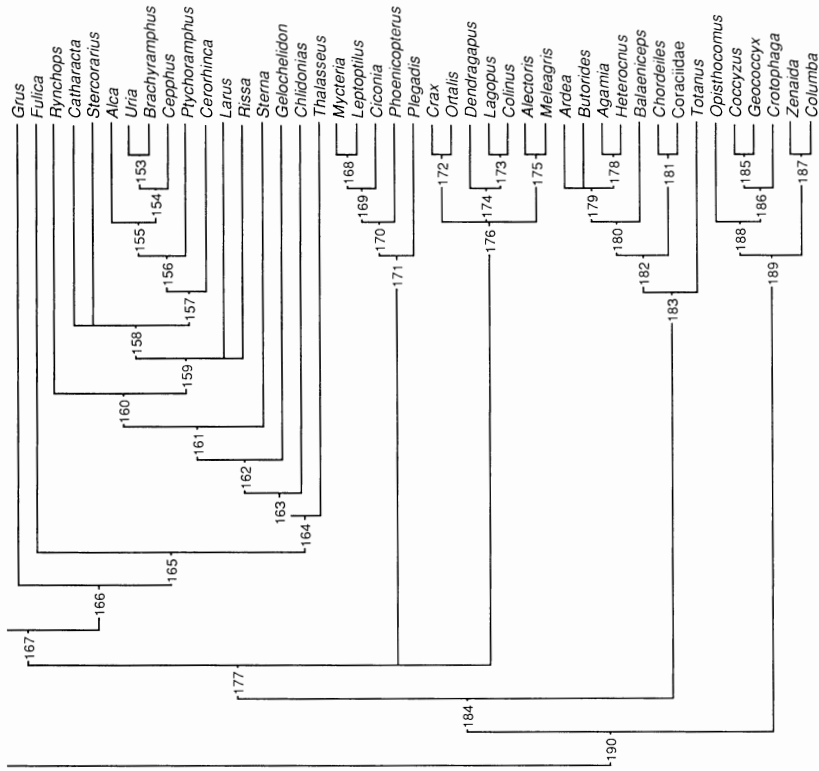


Fig. 3. Tree #1 of 6,000.

(*Fulica*) are the sister group to this restricted charadriiform clade, and sandhill crane (*Grus*) is the sister to the coot-auk-gull clade. That entire group (node 160) is the sister group to all the preceding taxa in 99% of all trees. Contra the suggestion by Feduccia (1976) and Olson and Feduccia (1980) that flamingos are shorebirds (Charadriiformes), flamingos emerge with ibises and storks as in traditional groupings.

Ciconiiformes is not monophyletic here. Storks, flamingos, and ibis (node 165: *Mycteria* through *Plegadis*) are always a fully resolved clade, and they emerge as a polytomy with all the preceding taxa (node 161) and with Galliformes (node 168: *Crax* through *Meleagris*), which are also monophyletic in all trees. The sister group to all of the preceding groups in 99% of all trees is a clade comprising the following: herons (node 171: *Ardea* through *Heterocnux*) and the whale-headed stork (*Balaeniceps*), their sister group the nighthawk-coraciid clade (*Chordeiles* and Coraciidae); the sandpiper (*Totanus*) is the sister group to the heron-coraciid clade. The sister group to all the preceding (node 169: *Diomedea* through *Totanus*) is the hoatzin-dove clade (node 181). The hoatzin (*Opisthocomus*) is the sister group to cuckoos in all trees, and their sister group is doves (node 180: *Zenaida* and *Columba*).

The tree topologies within some of the major groups of this analysis may differ from traditional and in some cases from more recent proposals, as well. For example, gulls have been regarded as monophyletic, as have terns, based on osteological characters (e.g. Strauch, 1978; Mickevich and Parenti, 1980) as well as general appearance. In the present analysis there is little if any resolution among gulls and terns in most trees.

The alliance of loons and grebes (*Gavia*, *Podiceps*) was not accepted by Storer (1971) on the grounds that the similarities are due to convergence, although Cracraft (1982) argued in favor of the grouping on the basis of skeletal characters. In the present analysis they are linked in 100% of all trees.

*Chordeiles* (Caprimulgiformes) does not emerge with swifts or hummingbirds (Apodiformes) in this analysis, whereas in Cracraft (1981, 1988) they are sister groups; in Wetmore (1960), Storer (1971), and Peters (1940, 1945) these taxa are also classified together. In Sibley et al. (1988), caprimulgiforms and owls are sister groups (as implied also by traditional arrangements), with Musophagidae being their sister group and swifts and hummingbirds the sister group to the entire assemblage. In the present analysis, owls are related to hawks as suggested by Cracraft (1981). The alliance indicated here among herons, caprimulgiforms, and coraciiforms is completely non-traditional and has not been suggested by any other analyses. With additional data it will most likely disappear.

Galliformes and Anseriformes do not come out together in this analysis *contra* Cracraft (1981, 1988) and Sibley et al. (1988). Monophyly of suboscines is supported by a derived morphology of the stapes (Feduccia, 1979), but not by the hindlimb muscle characters presented herein (*Tyrannus* and *Corvus* are closer than *Tyrannus* and Old World suboscines).

The results of this analysis differ from the phylograms presented in Sibley et al. (1988) in numerous other ways. Parrots and mousebirds are sister groups in my analysis, whereas in Sibley et al., mousebirds are the sister group to a large group containing cuckoos, parrots, swifts, hummingbirds, owls, doves, gruiforms, ciconiiforms, and passeriforms. Gruiforms (*Grus* and *Fulica*) are not monophyletic here; in Sibley et al. they are.

In Sibley et al., New World vultures form a clade with ciconiiforms, a surprising hypothesis that was first suggested by Ligon (1967) on the basis of morphology. In the present analysis, however, vultures are the sister group to a large clade including *Diomedea* through *Falco* (node 144), an arrangement that differs from traditional ones in which vultures are falconiforms.

Sibley et al. do not depict the grebes as closely related to loons, whereas they are sister groups in the present analysis. Furthermore, loons and ducks are not close, either in Sibley et al. or in Cracraft's (1981) classification. In both these classification schemes, ducks and geese are the sister group to galliforms. Sibley et al. place loons and procellariiforms together as sister groups, with penguins as their closest relatives. The present analysis does not exactly corroborate this finding. Procellariiforms and penguins are a clade, with the loon-duck clade being their sister group. In an analysis based on wing musculature (McKittrick, 1991), procellariiforms (represented only by *Pelecanoides*) are grouped with penguins, but loons do not emerge as particularly closely related to them.

The hoatzin (*Opisthocomus*) is placed with galliforms in traditional classifications; here it emerges with cuckoos, far from galliforms. This corroborates the findings of Sibley et al. (1988), who place the hoatzin with cuckoos which are also not closely related to galliforms in their analyses.

Such comparisons are useful only insofar as they draw attention to areas where DNA hybridization data, hindlimb muscle data and other character data lead to different phylogenetic interpretations. The task at hand is not to choose among phylogenies, but to continue to generate data that will contribute to our understanding of these hypotheses and of the characters on which they are based. Ideally, phylogenies founded on morphological data should be based on as much evidence as possible (see, e.g., Kluge, 1989). My hope in offering the data herein is that other avian anatomists will contribute data for the same taxa from their own area of expertise; as the matrix grows so will our confidence in the resulting phylogenetic hypotheses.

#### EVOLUTION OF HINDLIMB MUSCLES

I used Tree #1 (see Fig. 3) as a reflection of the degree of homoplasy in the muscle characters used herein. Of the 42 informative muscle characters (i.e., those that are not autapomorphies for terminal taxa) that do not show multiple states, nine had no homoplasy (characters 5, 17, 19, 35, 36, 39, 48, 50, 57).

The ten muscles used in traditional classifications, the so-called “formula muscles,” are the following: (A) caudofemoralis, character 15; (B) iliofemoralis, character 16; (C) iliotrochantericus medius (not used in this analysis); (D) iliofemoralis externus, character 7; (E) iliofemoralis internus, character 27; (F) plantaris, character 49; (G) popliteus, character 57; (X) flexor cruris lateralis pars pelvica, character 13; (Y) flexor cruris lateralis pars accessoria, character 12; (Am) ambiens, character 38; and (V) vinculum (between Mm. FPD3 and FPPD3), character 44. Table 1 shows the consistency index for each of these characters. This value ranges from 0.111 to 1.000 (mean = 0.365, SD = 0.363) (mean and standard deviation are based on nine of the 10 formula muscles, as character 27 was not informative for this data set); for all 63 informative muscle characters  $c_i$  ranges from 0.111 to 1.000 (mean = 0.46, SD = 0.32). Clearly, the formula muscle characters are no more informative than other hindlimb muscle characters.

A complete list of character changes using ACCTRAN (Accelerated Transformation), based on Tree #1, is given in Appendix 3. The ACCTRAN algorithm assumes that reversals ( $0 \rightarrow 1 \rightarrow 0$ ) are more common than independent origins of a character state ( $1 \leftarrow 0 \rightarrow 1$ ). Arrows with double lines represent unambiguous changes and are the large majority of all changes; these changes are the same for all three optimization routines offered by PAUP (ACCTRAN, DELTRAN, and MIN-F). It is of interest to examine the characters that group some of the clades represented in Figure 3, in particular those clades that are controversial. The characters supporting each node are listed in Appendix 4.

The link between *Gavia* and *Podiceps* (node 122) is interesting in light of Storer's (1971) argument that similarities between loons and grebes are due to convergence. That grouping is supported by 7 characters: 11 (state 1), the ansa iliofibularis (biceps loop) of M. iliofibularis is elongated (occurs once); 28 (1), M. iliofemoralis internus is unusually broad and short (occurs three times); 42 (1) absence of a tendinous branch between Mm. fibularis longus and flexor perforatus digiti III (occurs three times); 54 (1), three heads of origin of M. flexor digitorum longus (occurs three times); 65 (2), M. abductor digiti II is vestigial (occurs once); 65 (1), M. extensor brevis digit IV is vestigial (occurs five times). Again, the phylogeny presented here obviously supports the hypothesis that these characters reflect common ancestry of loons and grebes, and with seven characters supporting this node, this is one of the three best supported nodes in the phylogeny. If the characters really are convergent, this can only be demonstrated with additional data.

The grouping of ducks with loons and grebes (node 124) is non-traditional. It is based on two character states: 4 (0), M. iliotibialis lateralis, postacetabular part present (occurs four times); and 34 (1), M. gastrocnemius medialis, presence of two heads (occurs three times). The grouping of owls and accipitrids (node 144) is also of interest. It is based on one character state: 59 (1), M. flexor hallucis brevis, two tendons of insertion



TABLE 1  
CONSISTENCY OF CHARACTERS BASED ON FORMULA MUSCLES.

Formula Code	Muscle Name	Character	CI
A	caudofemoralis	15	.182
B	iliofemoralis	16	.231
C	iliotrochantericus medius	N/A	N/A
D	iliofemoralis externus	7	.167
E	iliofemoralis internus (uninformative)	27	1.000
F	plantaris	49	.143
G	popliteus	57	1.000
X	flexor cruris lateralis pars pelvica	13	.250
Y	flexor cruris lateralis pars accessoria	12	.200
Am	ambiens	38	1.000
V	vinculum	44	.111

(occurs four times). The entire grouping of owls with all hawks (node 147) is based on three character states: 13 (1), absence of *M. flexor cruris lateralis* pars pelvica (occurs three times); 33 (1), *M. gastrocnemius* pars medialis, patellar band absent (occurs six times); and 61 (0), *M. extensor hallucis longus*, two heads present (occurs six times).

The grouping of charadriiforms (except *Totanus*) (node 164), which this study initially sought to examine, is based on four characters: 4 (1), *M. iliotibialis* pars postacetabularis absent (occurs four times); 32 (1), *M. gastrocnemius* pars lateralis is double (occurs three times); 43 (1), *M. fibularis brevis* absent (occurs five times); and 52 (4), arrangement of the deep flexor tendons is Type IV (occurs four times).

Sanderson and Donoghue (1989) compared consistency indices (ci) for morphological and molecular data sets and found that ci is strongly correlated with number of taxa, but not with number of characters. They presented a formula for calculating expected ci for a given number of taxa below about 60; the present data set started with 103 taxa and is therefore above the limit of resolution possible for the formula. For 60 taxa the expected ci is .30. One may therefore conclude that the ci of .300 in the present analysis is at least as high as would be expected for 103 taxa and that the hindlimb muscle data presented here are at least as statistically consistent as would be expected for a data set of this size.

The hindlimb muscle data reported here demonstrate the phylogenetic information content of one set of characters, and as such they offer the basis both for a suite of phylogenetic hypotheses and for hypotheses about the evolution of hindlimb muscle characters. No single data set should be the exclusive basis for a phylogenetic analysis, however. All character systems are important and contain some degree of phylogenetic evidence, including those with a high degree of homoplasy at some taxonomic levels. Furthermore, the utility of any one kind of data cannot be predicted *a*

*priori*. Future phylogenetic studies of birds based on character data should attempt to integrate the evidence from many different systems in order to maximize the utility of each data set.

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### LITERATURE CITED

- Allen, T. T. 1962. Myology of the limpkin. Ph.D. thesis, Univ. of Florida, Gainesville.
- Baumel, J. J., A. S. King, A. M. Lucas, J. E. Breazile, and H. E. Evans (eds.). 1979. *Nomina Anatomica Avium*. Academic Press, London. 637 pp.
- Beddard, F. E. 1898. The structure and classification of birds. Longmans, Green & Co., New York. 548 pp.
- Berger, A. J. 1952. The comparative functional morphology of the pelvic appendage in three genera of Cuculidae. *Amer. Midl. Natur.* 47:513-605.
- Berger, A. J. 1953. On the locomotor anatomy of the blue coua, *Coua caerulea*. *Auk* 70:49-83.
- . 1956a. The appendicular myology of the pygmy falcon (*Polihierax semitorquatus*). *Amer. Midl. Natur.* 55:326-333.
- . 1956b. The appendicular myology of the sandhill crane with comparative remarks on the whooping crane. *Wilson Bull.* 68:282-304.
- . 1960. Some anatomical characters of the Cuculidae and the Musophagidae. *Wilson Bull.* 72:60-104.
- Berman, S. L. 1984. The hindlimb musculature of the white-fronted amazon (*Amazona albifrons*, Psittaciformes). *Auk* 101:74-92.
- , and R. J. Raikow. 1982. The hindlimb musculature of the mousebirds (Coliiformes). *Auk* 99:41-57.
- Borecky, S. J. 1977. The appendicular myology and phylogenetic relationships of the avian "corvid assemblage." Ph.D. thesis, Univ. of Pittsburgh.
- Cohn, J. M. W. 1968. The convergent flight mechanism of swifts (Apodi) and hummingbirds (Trochili) (Aves). Ph.D. thesis, Univ. of Michigan.
- Cracraft, J. 1981. Toward a phylogenetic classification of the Recent birds of the world (Class Aves). *Auk* 98:681-714.
- . 1982. Phylogenetic relationships and monophyly of loons, grebes, and hesperornithiform birds, with comments on the early history of birds. *Syst. Zool.* 31:35-56.
- . 1985. Monophyly and phylogenetic relationships of the Pelecaniformes: A numerical cladistic analysis. *Auk* 102:834-853.
- . 1986. The origin and early diversification of birds. *Paleobiology* 12:383-399.
- . 1988. The major clades of birds. In Benton, M. J. (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*. Systematics Association Special Volume No. 35A:339-361. Clarendon Press, Oxford.
- , and D. P. Mindell. 1989. The early history of modern birds: A comparison of molecular and morphological evidence. In Fernholm, B., K. Bremer, and H. Jörnvall (eds.), *The Hierarchy of Life*: 389-403. Elsevier Science Publishers B. V., Amsterdam.
- Farris, J. S. 1988. Hennig86, version 1.5. Stony Brook, New York.

- Feduccia, A. 1976. Osteological evidence for shorebird affinities of the flamingos. *Auk* 93:587-601.
- . 1979. Comments on the phylogeny of perching birds. *Proc. Biol. Soc. Wash.* 92:689-696.
- Fisher, H. I. 1946. Adaptations and comparative anatomy of the locomotor apparatus of New World vultures. *Amer. Midl. Natur.* 35:545-727.
- , and D. C. Goodman. 1955. The myology of the whooping crane, *Grus americana*. *Illinois Biol. Monogr.* 24(2):1-127.
- Fleming, T. H. 1966. The thigh musculature of three species of Scolopacidae. *Condor* 68:293-298.
- Fürbringer, M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel. II. Allgemeiner Teil. Van Holema, Amsterdam. 875 pp.
- Gadow, H. 1880. Zur vergleichenden Anatomie der Muskulatur des Beckens und der hinteren Gliedmassen der Raiten. Fischer, Jena. 56 pp.
- Gadow, H. 1892. On the classification of birds. *Proc. Zool. Soc. Lond.* 1892:229:256.
- Gadow, H. and E. Selenka. 1891. Aves. *In* Bronn's Klassen und Ordnungen des Thier-Reichs, in Wort und Bild, 2 vols., Anatomischer Theil, 1891, Systematischer Theil, 1893. C.F. Winter, Leipzig. 1008 pp.
- Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *Calif. Acad. Sci. Mem.* 8:1-56.
- George, J. C., and A. J. Berger. 1966. *Avian Myology*. Academic Press, New York. 500 pp.
- Hecht, M. K. 1976. Phylogenetic inference and methodology as applied to the vertebrate record. *In* M. K. Hecht, W. C. Steere, and B. Wallace (eds.), *Evolutionary Biology* 9:335-363. Plenum Press, London.
- Hoff, K. M. 1966. A comparative study of the appendicular muscles of Strigiformes and Caprimulgiformes. Ph.D. thesis, Washington State Univ.
- Hudson, G. E. 1937. Studies on the muscles of the pelvic appendage in birds. *Amer. Midl. Natur.* 18:1-108.
- . 1948. Studies on the muscles of the pelvic appendage in birds II: The heterogeneous order Falconiformes. *Amer. Midl. Natur.* 39:102-127.
- , K. M. Hoff, J. Vanden Berge, and E. C. Trivette. 1969. A numerical study of the wing and leg muscles of Lari and Alcae. *Ibis* 111:459-524.
- , P. J. Lanzillotti, and G. D. Edwards. 1959. Muscles of the pelvic limb in galliform birds. *Amer. Midl. Natur.* 61:1-67.
- , D. O. Schreiweis, and S. Y. C. Wang. 1972. A numerical study of the wing and leg muscles of tinamous (Tinamidae). *Northwest Science* 46:207-255.
- Klemm, R. D. 1969. Comparative myology of the hind limb of procellariiform birds. *Southern Illinois Univ. Monogr. in the Sciences, Social Sciences and Humanities, Sci. Ser. 2*, 269 pp.
- Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.* 38:7-25.
- Ligon, J. D. 1967. Relationships of the cathartid vultures. *Occ. Pap. Mus. Zool., Univ. Michigan* 651:1-26.
- Maurer, D. R., and R. J. Raikow. 1981. Appendicular myology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). *Ann. Carnegie Mus. Nat. Hist.* 50:417-434.
- Mayr, E., and G. W. Cottrell (eds.). 1979. *Check-list of Birds of the World*. Vol. 1, 2nd Ed. *Mus. Comp. Zool., Cambridge, MA*. 547 pp.
- McGowan, C. 1979. The hind limb musculature of the brown kiwi, *Apteryx australis mantelli*. *J. Morphol.* 160:33-74.
- McKittrick, M. C. 1985a. Myology of the pectoral appendage in kingbirds (*Tyrannus*) and their allies. *Condor* 87:402-417.
- . 1985b. Pelvic myology of the kingbirds and their allies (Aves: Tyrannidae). *Ann. Carnegie Mus. Nat. Hist.* 54:275-317.
- . 1991. Forelimb myology of loons (Gaviiformes), with comments on the relationship of loons and tubenoses (Procellariiformes). *Zool. J. Linn. Soc.* 102:115-152.

- McKittrick, M. C. ms. (submitted). Trends in the evolution of hindlimb musculature in aerial-foraging birds.
- Mickevich, M. F., and L. R. Parenti. 1980. [Review of] Strauch, J. G., Jr., The phylogeny of the Charadriiformes (Aves): A new estimate using the method of character compatibility analysis. *Syst. Zool.* 29:108–113.
- Mitchell, P. C. 1913. The peroneal muscles in birds. *Proc. Zool. Soc. Lond.* 1913:1039–1072.
- Müller, G. 1989. Ancestral patterns in bird limb development: A new look at Hampé's experiment. *J. Evol. Biol.* 2:31–47.
- Olson, S. L., and A. Feduccia. 1980. Relationships and evolution of flamingos (Aves: Phoenicopteridae). *Smiths. Contrib. Zool.* 316:1–73.
- Owre, O. T. 1967. Adaptations for locomotion and feeding in the anhinga and the double-crested cormorant. *Ornithol. Monogr.* 6:1–138.
- Peters, J. L. 1940. *Check-list of Birds of the World*. Vol. 4. Harvard University Press, Cambridge, MA. 291 pp.
- . 1945. *Check-list of Birds of the World*. Vol. 5. Harvard University Press, Cambridge, MA. 306 pp.
- Raikow, R. J. 1970. Evolution of diving adaptations in the stiff-tail ducks. *Univ. Calif. Publ. Zool.* 94:1–52.
- . 1978. Appendicular myology and relationships of the New World nine-primaryed oscines (Aves: Passeriformes). *Bull. Carnegie Mus. Nat. Hist.* 7:1–43.
- . 1982. Monophyly of the passeriformes: Test of a phylogenetic hypothesis. *Auk* 99:431–445.
- . 1985. Locomotor system. In King, A. S., and J. McClelland (eds.), *Form and Function in Birds*: 57–146. Academic Press, London.
- . 1987. Hindlimb myology and evolution of the Old World suboscine passerine birds (Acanthisittidae, Pittidae, Philepittidae, Eurylaimidae). *Ornithol. Monogr.* 41:1–81.
- Romer, A. S. 1923. Crocodylian pelvic muscles and their avian and reptilian homologues. *Bull. Amer. Mus. Nat. Hist.* 48:533–552.
- Rosser, B. W. C., D. M. Secoy, and P. W. Riegert. 1982. The leg muscles of the American coot (*Fulica americana* Gmelin). *Can. J. Zool.* 60:1236–1256.
- Rowe, T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other Reptilia. *J. Morphol.* 189:327–346.
- Sanderson, M. J., and M. J. Donoghue. 1989. Patterns of variation in levels of homoplasy. *Evolution* 43:1781–1795.
- Schreiweis, D. O. 1982. A comparative study of the appendicular musculature of the penguins (Aves: Sphenisciformes). *Smiths. Contrib. Zool.* 341:1–46.
- Sibley, C. G., and J. E. Ahlquist. 1985. The relationships of some groups of African birds, based on comparisons of the genetic material, DNA. *Proc. Intern. Symp. African Vertebr.*: 115–161. Bonn, W. Germany.
- , ———, and B. L. Monroe, Jr. 1988. A classification of the living birds of the world based on DNA-DNA hybridization studies. *Auk* 105:409–423.
- Siegel-Causey, D. 1988. Phylogeny of the Phalacrocoracidae. *Condor* 90:885–905.
- Simpson, S. F., and J. Cracraft. 1981. The phylogenetic relationships of the Piciformes. *Auk* 98:481–494.
- Storer, R. W. 1971. Classification of birds. In Farner, D. S., and J. R. King (eds.), *Avian Biology* 1:1–18. Academic Press, New York.
- Strauch, J. G., Jr. 1978. The phylogeny of the Charadriiformes (Aves): A new estimate using the method of character compatibility analysis. *Trans. Zool. Soc. Lond.* 34:263–345.
- Swierczewski, E. V., and R. J. Raikow. 1981. Hind limb morphology, phylogeny, and classification of the Piciformes. *Auk* 98:466–480.
- Swofford, D. L. 1989. *Phylogenetic Analysis Using Parsimony (PAUP)*, version 3.0n. Illinois Natural History Survey, Champaign, IL.
- Vanden Berge, J. C. 1970. A comparative study of the appendicular musculature of the order Ciconiiformes. *Amer. Midl. Natur.* 84:289–364.

- . 1976. *M. iliobtibialis medialis* and a review of the *M. iliobtibialis* complex in flamingos. *Auk* 93:429–433.
- . 1982. Notes on the myology of the pelvic limb in kiwi (*Apteryx*) and in other birds. *Auk* 99:309–315.
- Wetmore, A. 1960. A classification for the birds of the world. *Smiths. Misc. Coll.* 139(11):1–37.
- Wilcox, H. H. 1952. The pelvic musculature of the loon, *Gavia immer*. *Amer. Midl. Natur.* 48:513–573.
- Zusi, R. L., and G. D. Bentz. 1978. The appendicular myology of the Labrador duck (*Camporhynchus labradorius*). *Condor* 80:407–418.
- Zusi, R. L., and G. D. Bentz. 1984. Myology of the Purple-throated Carib (*Eulampis jugularis*) and other hummingbirds (Aves: Trochilidae). *Smiths. Contrib. Zool.* 385:1–70.

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#### APPENDIX 1.—Characters used in the analysis.

1. *M. iliobtibialis medialis*. Present = 1, absence = 0
2. *M. iliobtibialis lateralis*, pars preacetabularis. Presence = 0, absence = 1, vestigial = 2
3. *M. iliobtibialis lateralis*, pars acetabularis. Presence = 0, absence = 1, aponeurotic = 2, A = 01
4. *M. iliobtibialis lateralis*, pars postacetabularis. Presence = 0, absence = 1, A = 01
5. *M. iliotrochantericus caudalis* reduced. Reduced = 1, unreduced = 0
6. *M. iliotrochantericus cranialis*, strongly fused with *M. iliotrochantericus caudalis*. Fused = 1, unfused = 0
7. *M. iliofemoralis externus*. Presence = 0, absence = 1
8. *M. femorotibialis externus*, distal head. Presence = 0, absence = 1
9. *M. femorotibialis internus*, longitudinal division. Presence = 1, absence = 0
10. *M. iliofibularis*, ansa iliofibularis forms a single ligament. Presence = 1, absence = 0
11. *M. iliofibularis*, ansa iliofibularis arms elongated. Presence = 1, absence = 0, moderately elongate = 2
12. *M. flexor cruris lateralis*, pars accessoria. Presence = 0, absence = 1, A = 01
13. *M. flexor cruris lateralis*, pars pelvica. Presence = 0, absence = 1
14. *M. flexor cruris lateralis*, pars accessoria reduced. Reduced = 1, not reduced = 0, absence = ?
15. *M. caudofemoralis*. Presence = 0, absence = 1, poorly developed = 2
16. *M. iliofemoralis*. Presence = 0, absence = 1, poorly developed = 2, A = 01
17. *M. flexor cruris medialis*, two distinct parts. Presence = 1, absence = 0
18. *M. flexor cruris medialis* and *M. flexor cruris lateralis*, tendons fused. Fused = 0, unfused = 1
19. *M. pubo-ischio-femoralis*, division into pars cranialis and pars caudalis. Thus divided = 1, not thus divided = 0
20. *M. pubo-ischio-femoralis*, muscular slip. Presence = 1, absence = 0
21. *M. pubo-ischio-femoralis*, pars profundus divided into two parts. Undivided = 0, divided = 1, intermediate = 2
22. *M. obturatorius lateralis*, pars dorsalis. Present = 0, absent = 1
23. *M. obturatorius medialis*, two heads of origin. Presence = 1, absence = 0
24. *M. obturatorius medialis*, number of tendons of insertion. One tendon = 0, two tendons = 1, three tendons = 2
25. *M. obturatorius medialis*, enlarged in width. Presence = 1, absence = 0
26. *Mm. obturatorius medialis* and *obturatorius lateralis*, distal fusion. Fusion = 0, independence = 1
27. *M. iliofemoralis internus*. Presence = 0, absence = 1
28. *M. iliofemoralis internus*. "Unusually short and broad" = 1, "typical" = 0

29. *M. ambiens*. Presence = 0, absence = 1
30. *M. ambiens*, extent of origin. Limited to pectineal process = 0, extending from pectineal process to pubis = 1, one origin from pectineal process and one from pubis = 2
31. *M. ambiens*, longitudinal division. Undivided = 0, divided = 1
32. *M. gastrocnemius pars lateralis*, single = 0, double = 1, A = 01
33. *M. gastrocnemius pars medialis*, patellar band. Present = 0, 1 = absent, A = 01
34. *M. gastrocnemius pars medialis*, number of heads. One head = 0, two heads = 1, A = 01
35. *M. gastrocnemius*, fourth head. Presence = 1, absence = 0
36. *M. gastrocnemius*, tendon of insertion contributes to ossification of the hypotarsus. No = 0, yes = 1
37. *M. tibialis cranialis*, number of tendons of insertion. Bifurcated tendon = 0, one tendon = 1
38. *M. extensor digitorum longus*, number of heads of origin. One head (from tibia) = 0, two heads (from tibia and fibula) = 1, two heads (from tibia and femur) = 2
39. *M. extensor digitorum longus*, hallucal tendon. Presence = 1, absence = 0
40. *M. fibularis longus*, presence = 0, poorly developed = 1, absent = 2, B = 02
41. *M. fibularis longus*, tibial head. Presence = 0, fibular head only = 1, arising from underlying muscles and from tibia = 2
42. *M. fibularis longus*, branch to FPD3. Presence = 0, absence = 1
43. *M. fibularis brevis*. Presence = 0, weak = 1, absence = 2
44. *M. flexor perforans et perforatus digiti III*, vinculum. Presence = 0, absence = 1
45. *M. flexor perforans et perforatus digiti II*, relationship to *M. flexor perforans et perforatus digiti III*. Overlaps and conceals FPPD3 = 1, does not overlap = 0
46. *M. flexor perforans et perforatus digiti II*, number of heads. One head = 0, intermediate = 1, two = 2, three = 3
47. *M. flexor perforans et perforatus digiti II*, origin from ansa iliofibularis. Presence = 1, absence = 0
48. *M. flexor perforatus digiti II*, position. Deeply situated = 0, superficial = 1
49. *M. plantaris*. Presence = 0, absence = 1, A = 01
50. *M. plantaris*. "Typical" = 0, very powerfully developed = 1
51. *M. flexor hallucis longus*, tendon to hallux. Branch to hallux lacking or weak = 1, branch to hallux present = 0
52. *M. flexor hallucis longus* and *M. flexor digitorum longus*, type of flexor arrangement. See George and Berger (1966: 447) for description of Types I-VIII, and Berman (1984) for a description of Type X (coded 9 herein). The modification found in hummingbirds is designated Type 0.
53. *M. flexor hallucis longus*, number of heads. One head = 0, two heads = 1, three heads = 2
54. *M. flexor digitorum longus*, number of heads. Two heads = 0, three heads = 1
55. *M. flexor digitorum longus*, size. "Typical" = 0, very powerful = 1, intermediate = 2
56. *M. flexor digitorum longus*, location. Superficially situated = 1, deeply situated = 0
57. *M. popliteus*. Presence = 0, absence = 1
58. *M. flexor hallucis brevis*. Presence = 0, vestigial = 1, absence = 2, B = 02
59. *M. flexor hallucis brevis*, number of tendons of insertion. One = 0, two = 1
60. *M. extensor hallucis longus*. Presence = 0, absent or vestigial = 1
61. *M. extensor hallucis longus*, number of heads. Two heads = 0, one head = 1, A = 01
62. *M. extensor hallucis longus*, accessory. Presence = 1, absence = 0
63. *M. abductor digiti II*. Presence = 0, absence = 1, vestigial = 2
64. *M. adductor digiti II*. Presence = 0, weak = 1, absence = 2
65. *M. extensor brevis digiti IV*. Presence = 0, vestigial = 1, absence = 2, C = 12
66. *M. lumbricalis*. Presence = 1, absence = 0, weak or vestigial = 2
67. Feathers. Presence = 1, absence = 0 (for analytical purposes).
68. Neognath monophyly. Reflects monophyly of the ingroup (see Cracraft 1986; Cracraft and Mindell 1989).









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APPENDIX 3.—Character changes for tree #1 of 6000 (Fig. 3) based on ACCTRAN optimization. Each change is one step. Arrows with double lines indicate unambiguous changes, i.e., those occurring in all optimizations. Arrows with single lines indicate changes that do not occur in all optimizations.

Character	CI	Changes
1	1.000	node 170 0 $\Rightarrow$ 1 Phoenicopterus
2	1.000	node 138 0 $\Rightarrow$ 1 Fregata node 181 0 $\Rightarrow$ 2 Chordeiles
3	0.429	node 122 0 $\Rightarrow$ 1 Podiceps node 137 0 $\Rightarrow$ 1 node 136 node 134 1 $\Rightarrow$ 2 node 128 node 131 1 $\Rightarrow$ 0 node 130 node 171 0 $\Rightarrow$ 1 node 170 Coraciidae 0 $\rightarrow$ 01 = A (within terminal) node 185 0 $\Rightarrow$ 2 Coccyzus
4	0.222	node 167 0 $\rightarrow$ 1 node 152 node 107 1 $\Rightarrow$ 0 Oceanites node 125 1 $\Rightarrow$ 0 node 124 node 135 1 $\Rightarrow$ 0 node 134 node 129 0 $\Rightarrow$ 1 Tyrannus node 151 1 $\rightarrow$ 0 node 150 node 165 0 $\Rightarrow$ 1 node 164 node 170 0 $\Rightarrow$ 1 node 169 Coraciidae 0 $\rightarrow$ 01 = A (within terminal)
5	1.000	node 112 0 $\Rightarrow$ 1 node 110
6	1.000	node 191 0 $\Rightarrow$ 1 Tinamus
7	0.167	node 122 0 $\Rightarrow$ 1 Podiceps node 138 0 $\Rightarrow$ 1 node 137 node 135 1 $\Rightarrow$ 0 node 127 node 182 0 $\Rightarrow$ 1 node 181 node 190 0 $\rightarrow$ 1 node 189 node 187 1 $\rightarrow$ 0 Opisthocomus
8	0.143	node 191 0 $\Rightarrow$ 1 Tinamus node 152 0 $\Rightarrow$ 1 node 151 node 121 1 $\Rightarrow$ 0 node 117 node 119 1 $\Rightarrow$ 0 node 118 node 136 1 $\Rightarrow$ 0 node 135 node 144 1 $\Rightarrow$ 0 node 143 node 187 0 $\Rightarrow$ 1 node 186
9	0.333	node 121 0 $\Rightarrow$ 1 node 117 node 114 1 $\Rightarrow$ 0 Pelecanoides node 142 0 $\Rightarrow$ 1 Buteo
10	0.500	node 108 0 $\Rightarrow$ 1 node 107 node 115 0 $\Rightarrow$ 1 Hydrobates
11	1.000	node 121 0 $\Rightarrow$ 2 node 120 node 124 0 $\Rightarrow$ 1 node 122
12	0.200	node 151 0 $\Rightarrow$ 1 node 148 node 108 1 $\Rightarrow$ 0 node 107 node 136 1 $\Rightarrow$ 0 node 135 node 128 0 $\Rightarrow$ 1 Picoides node 158 0 $\Rightarrow$ 1 node 157

## APPENDIX 3.—Continued

Character	CI	Changes
13	0.250	node 121 0 $\Rightarrow$ 1 node 117 node 108 1 $\Rightarrow$ 0 node 107 node 138 0 $\Rightarrow$ 1 Fregata node 148 0 $\Rightarrow$ 1 node 147
14	0.200	node 127 0 $\Rightarrow$ 1 Amazona node 129 0 $\Rightarrow$ 1 Tyrannus node 164 0 $\Rightarrow$ 1 node 163 node 170 0 $\Rightarrow$ 1 node 169 node 182 0 $\rightarrow$ 1 node 181
15	0.182	node 122 0 $\Rightarrow$ 1 Podiceps node 138 0 $\Rightarrow$ 2 Fregata node 149 0 $\Rightarrow$ 1 Gymnogyps node 152 0 $\Rightarrow$ 1 Sagittarius node 177 0 $\Rightarrow$ 2 node 171 node 168 2 $\Rightarrow$ 1 Leptoptilos node 170 2 $\Rightarrow$ 1 Phoenicopterus node 175 0 $\Rightarrow$ 1 Meleagris node 182 0 $\Rightarrow$ 2 node 180 node 178 2 $\Rightarrow$ 1 Heterocnus node 185 0 $\Rightarrow$ 2 Geococcyx
16	0.231	node 152 0 $\Rightarrow$ 1 node 151 node 140 1 $\Rightarrow$ 0 node 126 node 104 0 $\Rightarrow$ 1 Nesofregatta node 112 0 $\Rightarrow$ 1 node 111 node 114 0 $\Rightarrow$ 1 Pelecanoides Anhinga 1 $\rightarrow$ 01 = A (within terminal) node 161 0 $\Rightarrow$ 1 node 160 node 155 1 $\Rightarrow$ 2 Alca node 155 1 $\Rightarrow$ 0 node 154 node 170 0 $\Rightarrow$ 1 node 169 node 184 0 $\Rightarrow$ 1 node 183 node 186 0 $\Rightarrow$ 1 node 185 node 185 1 $\Rightarrow$ 2 Geococcyx
17	1.000	node 147 0 $\Rightarrow$ 1 node 146
18	0.125	node 109 0 $\Rightarrow$ 1 Puffinus node 122 0 $\Rightarrow$ 1 Podiceps node 135 0 $\rightarrow$ 1 node 127 node 128 0 $\Rightarrow$ 1 Picoides node 132 0 $\Rightarrow$ 1 Pitta node 141 0 $\Rightarrow$ 1 Anhinga node 181 0 $\Rightarrow$ 1 Chordeiles node 187 0 $\Rightarrow$ 1 node 186
19	1.000	node 134 0 $\Rightarrow$ 1 node 133
20	0.500	node 116 0 $\Rightarrow$ 1 node 108 node 111 0 $\Rightarrow$ 1 Pterodroma
21	0.500	node 150 0 $\Rightarrow$ 1 node 149 node 177 0 $\Rightarrow$ 2 node 171 node 182 0 $\Rightarrow$ 1 node 180 node 179 1 $\Rightarrow$ 2 node 178

## APPENDIX 3.—Continued

Character	CI	Changes
22	0.333	node 136 0 → 1 node 135 node 127 1 → 0 Amazona node 132 1 ⇒ 0 node 131
23	0.333	node 165 0 ⇒ 1 Fulica node 177 0 ⇒ 1 node 176 node 187 0 → 1 node 186
24	0.667	node 165 0 ⇒ 2 Fulica node 164 0 ⇒ 1 Thalasseus node 187 0 ⇒ 2 node 186
25	0.500	node 127 0 ⇒ 1 Colius node 180 0 ⇒ 1 node 179
26	0.111	node 177 0 ⇒ 1 node 167 node 148 1 → 0 node 141 node 124 0 ⇒ 1 node 123 node 137 0 ⇒ 1 node 136 node 134 1 ⇒ 0 node 128 node 144 1 ⇒ 0 node 143 node 154 1 ⇒ 0 node 153 node 180 0 ⇒ 1 node 179 node 183 0 ⇒ 1 Totanus
27	1.000	node 136 0 ⇒ 1 Glaucis
28	0.333	node 124 0 ⇒ 1 node 122 node 165 0 ⇒ 1 Fulica node 181 0 ⇒ 1 Chordeiles
29	0.111	node 105 0 ⇒ 1 node 104 node 114 0 ⇒ 1 Pelecanoides node 122 0 ⇒ 1 Podiceps node 138 0 ⇒ 1 node 137 node 144 0 ⇒ 1 node 143 node 162 0 → 1 node 161 node 160 1 → 0 node 159 node 157 0 ⇒ 1 node 156 node 183 0 ⇒ 1 node 182
30	1.000	node 140 0 ⇒ 1 node 126 node 124 1 ⇒ 2 node 123 node 165 0 ⇒ 2 Fulica
31	0.500	node 124 0 ⇒ 1 node 123 node 165 0 ⇒ 1 Fulica
32	0.375	node 117 0 ⇒ 1 node 116 Diomedea 1 → 01 = A (within terminal) node 110 1 ⇒ 0 node 109 Bulweria 1 → 01 = A (within terminal) node 114 1 ⇒ 0 Pelecanoides node 165 0 ⇒ 1 node 164 node 159 1 ⇒ 0 node 158 node 187 0 ⇒ 1 node 186
33	0.273	node 121 0 ⇒ 1 node 120 node 123 0 ⇒ 1 Anas node 140 0 ⇒ 1 node 139 node 130 1 ⇒ 0 Acanthisitta

## APPENDIX 3.—Continued

Character	CI	Changes
		node 132 1 $\Rightarrow$ 0 Pitta Glaucis 1 $\rightarrow$ 01 = A (within terminal)
		node 148 0 $\Rightarrow$ 1 node 147 node 157 0 $\Rightarrow$ 1 node 156 node 161 0 $\Rightarrow$ 1 Sterna Thalasseus 0 $\rightarrow$ 01 = A (within terminal)
34	0.250	node 190 0 $\Rightarrow$ 1 node 189 node 125 0 $\Rightarrow$ 1 node 124 node 137 0 $\Rightarrow$ 1 Chaetura node 156 0 $\Rightarrow$ 1 node 155 node 153 1 $\Rightarrow$ 0 Brachyramphus
35	1.000	node 177 0 $\Rightarrow$ 1 node 171
36	1.000	node 182 0 $\Rightarrow$ 1 node 180
37	0.500	node 121 0 $\Rightarrow$ 1 node 117 node 144 0 $\Rightarrow$ 1 node 143
38	1.000	node 136 0 $\Rightarrow$ 2 Glaucis node 144 0 $\Rightarrow$ 1 node 143
39	1.000	node 135 0 $\Rightarrow$ 1 node 127
40	0.273	node 104 0 $\Rightarrow$ 2 Nesofregatta Bulweria 0 $\rightarrow$ 02 = B (within terminal) node 116 0 $\Rightarrow$ 2 node 115 node 138 0 $\rightarrow$ 2 node 137 node 136 2 $\rightarrow$ 0 node 135 node 127 0 $\Rightarrow$ 1 Amazona node 147 0 $\rightarrow$ 2 node 145 node 144 2 $\rightarrow$ 0 node 142 node 146 0 $\Rightarrow$ 1 Polihierax node 180 0 $\Rightarrow$ 1 node 179 node 188 0 $\Rightarrow$ 1 Columba
41	0.400	node 135 0 $\Rightarrow$ 2 node 127 node 146 0 $\Rightarrow$ 1 Falco node 177 0 $\Rightarrow$ 2 node 176 node 187 0 $\Rightarrow$ 2 Opisthocomus node 188 0 $\Rightarrow$ 2 Columba
42	0.250	node 124 0 $\Rightarrow$ 1 node 122 node 138 0 $\rightarrow$ 1 node 137 node 134 1 $\rightarrow$ 0 node 133 node 181 0 $\Rightarrow$ 1 Coraciidae
43	0.200	node 121 0 $\Rightarrow$ 1 node 120 node 122 0 $\Rightarrow$ 2 Podiceps node 139 0 $\Rightarrow$ 2 Sula node 165 0 $\Rightarrow$ 1 node 164 node 160 1 $\Rightarrow$ 0 node 159 node 177 0 $\rightarrow$ 1 node 171 node 171 1 $\rightarrow$ 2 node 170 node 180 0 $\Rightarrow$ 1 Balaeniceps node 181 0 $\Rightarrow$ 2 Chordeiles node 183 0 $\Rightarrow$ 1 Totanus
44	0.111	node 151 0 $\rightarrow$ 1 node 148 node 122 1 $\Rightarrow$ 0 Gavia



## APPENDIX 3.—Continued

Character	CI	Changes
		node 126 1 → 0 Chen
		node 139 1 → 0 Sula
		node 158 0 ⇒ 1 node 157
		node 161 0 ⇒ 1 Sterna
		node 183 0 → 1 node 182
		node 180 1 → 0 Balaeniceps
		node 189 0 ⇒ 1 node 187
45	0.333	node 124 0 ⇒ 1 node 123
		node 167 0 ⇒ 1 node 166
		node 182 0 ⇒ 1 node 180
46	0.429	node 121 0 ⇒ 3 node 117
		node 122 0 ⇒ 3 Gavia
		node 123 0 ⇒ 2 Anas
		node 170 0 ⇒ 2 Phoenicopterus
		node 174 0 ⇒ 1 node 173
		node 176 0 ⇒ 2 node 175
		node 181 0 ⇒ 1 Coraciidae
47	0.143	node 121 0 ⇒ 1 node 120
		node 122 0 ⇒ 1 Gavia
		node 127 0 ⇒ 1 Amazona
		node 151 0 ⇒ 1 node 150
		node 177 0 ⇒ 1 node 176
		node 182 0 ⇒ 1 node 180
		node 189 0 ⇒ 1 node 187
48	1.000	node 134 0 ⇒ 1 node 133
49	0.143	node 107 0 ⇒ 1 node 106
		node 114 0 ⇒ 1 node 113
		node 138 0 ⇒ 1 node 137
		node 135 1 ⇒ 0 node 134
		node 147 0 ⇒ 1 node 145
		node 152 0 ⇒ 1 Sagittarius
		node 153 0 ⇒ 1 Brachyramphus
50	1.000	node 147 0 ⇒ 1 node 146
51	0.200	node 126 0 ⇒ 1 node 125
		node 116 1 ⇒ 0 node 112
		node 128 0 ⇒ 1 Picoides
		node 161 0 ⇒ 1 node 160
		node 170 0 ⇒ 1 Phoenicopterus
52	0.500	node 167 1 ⇒ 3 node 152
		node 148 3 ⇒ 2 node 141
		node 121 2 ⇒ 4 node 117
		node 124 2 ⇒ 4 node 122
		node 140 2 → 1 node 139
		node 139 1 → 5 node 138
		node 127 5 ⇒ 9 Amazona
		node 135 5 → 6 node 134
		node 134 6 → 7 node 133
		node 136 5 ⇒ 0 Glaucis
		node 144 3 ⇒ 1 node 143
		node 145 3 ⇒ 5 Pandion

## APPENDIX 3.—Continued

Character	CI	Changes
		node 151 3 $\Rightarrow$ 5 node 150 node 165 1 $\Rightarrow$ 4 node 164 node 170 1 $\Rightarrow$ 4 Phoenicopterus
53	0.250	node 182 1 $\Rightarrow$ 5 node 181 node 167 0 $\Rightarrow$ 1 node 152 node 141 1 $\Rightarrow$ 0 node 140 node 108 0 $\Rightarrow$ 1 Diomedea node 127 0 $\Rightarrow$ 1 Colius node 134 0 $\rightarrow$ 1 node 133 node 133 1 $\rightarrow$ 2 node 132 node 129 2 $\Rightarrow$ 1 Corvus node 181 0 $\Rightarrow$ 1 Coraciidae
54	0.333	node 124 0 $\rightarrow$ 1 node 122 node 133 0 $\Rightarrow$ 1 node 132 node 189 0 $\rightarrow$ 1 node 188
55	0.400	node 122 0 $\Rightarrow$ 2 Gavia node 129 0 $\Rightarrow$ 2 Tyrannus node 136 0 $\Rightarrow$ 2 Glaucis node 137 0 $\Rightarrow$ 1 Chaetura node 144 0 $\Rightarrow$ 1 node 143
56	0.500	node 147 0 $\rightarrow$ 1 node 145 node 144 1 $\rightarrow$ 0 node 143
57	1.000	node 138 0 $\Rightarrow$ 1 node 137
58	0.222	node 106 0 $\Rightarrow$ 2 node 105 node 115 0 $\Rightarrow$ 2 node 114 node 113 2 $\Rightarrow$ 1 Oceanodroma node 117 0 $\Rightarrow$ 2 Phoebetria node 120 0 $\Rightarrow$ 2 node 119 node 122 0 $\Rightarrow$ 1 Gavia node 130 0 $\Rightarrow$ 2 Acanthisitta node 158 0 $\Rightarrow$ 2 node 157 node 170 0 $\Rightarrow$ 1 Phoenicopterus
59	0.167	node 145 0 $\Rightarrow$ 1 node 144 node 166 0 $\Rightarrow$ 1 node 165 node 163 1 $\rightarrow$ 0 node 162 node 159 0 $\Rightarrow$ 1 Rissa node 184 0 $\Rightarrow$ 1 node 183 node 180 1 $\Rightarrow$ 0 Balaeniceps
60	0.200	node 126 0 $\rightarrow$ 1 node 125 node 124 1 $\rightarrow$ 0 node 123 node 130 0 $\Rightarrow$ 1 Acanthisitta node 158 0 $\Rightarrow$ 1 node 157 node 170 0 $\Rightarrow$ 1 Phoenicopterus
61	0.357	node 190 0 $\Rightarrow$ 1 node 184 node 137 1 $\rightarrow$ 0 node 136 node 135 0 $\rightarrow$ 1 node 134 node 148 1 $\Rightarrow$ 0 node 147 node 166 1 $\Rightarrow$ 0 node 165 node 160 0 $\Rightarrow$ 1 Rynchops Thalasseus 0 $\rightarrow$ 01 = A (within terminal)

## APPENDIX 3.—Continued

Character	CI	Changes
		node 169 1 $\Rightarrow$ 0 node 168
		node 176 1 $\Rightarrow$ 0 node 172
		Dendragapus 1 $\rightarrow$ 01 = A (within terminal)
		Lagopus 1 $\rightarrow$ 01 = A (within terminal)
		Meleagris 1 $\rightarrow$ 01 = A (within terminal)
		node 180 1 $\Rightarrow$ 0 Balaeniceps
		node 187 0 $\Rightarrow$ 1 node 186
62	0.500	node 135 0 $\Rightarrow$ 1 node 127
		node 189 0 $\Rightarrow$ 1 node 188
63	1.000	node 124 0 $\Rightarrow$ 2 node 122
		node 137 0 $\Rightarrow$ 1 node 136
64	0.200	node 106 0 $\Rightarrow$ 2 node 105
		node 116 0 $\Rightarrow$ 2 node 115
		node 113 2 $\Rightarrow$ 1 Oceanodroma
		node 121 0 $\Rightarrow$ 2 node 120
		node 136 0 $\Rightarrow$ 2 node 135
		node 144 0 $\Rightarrow$ 1 node 142
		node 146 0 $\Rightarrow$ 1 Falco
		node 152 0 $\Rightarrow$ 1 Sagittarius
		node 176 0 $\rightarrow$ 2 node 174
		node 173 2 $\rightarrow$ 0 Colinus
65	0.375	node 108 0 $\Rightarrow$ 1 Diomedea
		Diomedea 1 $\rightarrow$ 12 = C (within terminal)
		node 124 0 $\Rightarrow$ 1 node 122
		node 137 0 $\rightarrow$ 2 node 136
		node 135 2 $\rightarrow$ 0 node 127
		node 127 0 $\rightarrow$ 1 Amazona
		node 146 0 $\Rightarrow$ 1 Polihierax
		node 166 0 $\Rightarrow$ 1 Grus
66	0.214	node 184 1 $\Rightarrow$ 2 node 177
		node 141 2 $\Rightarrow$ 0 node 140
		node 125 0 $\Rightarrow$ 2 node 121
		node 105 2 $\Rightarrow$ 0 Pelagodroma
		node 124 0 $\Rightarrow$ 1 node 123
		node 136 0 $\rightarrow$ 2 node 135
		node 127 2 $\rightarrow$ 1 Colius
		node 134 2 $\rightarrow$ 0 node 128
		node 130 2 $\Rightarrow$ 0 node 129
		Chaetura 0 $\rightarrow$ 01 = A (within terminal)
		node 145 2 $\Rightarrow$ 1 Pandion
		node 158 2 $\Rightarrow$ 1 node 157
		node 180 1 $\Rightarrow$ 2 Balaeniceps
		node 183 1 $\Rightarrow$ 0 Totanus
67	1.000	node 191 1 $\Leftrightarrow$ 0 Ancestor
68	1.000	node 191 0 $\Rightarrow$ 1 node 190



APPENDIX 4.—Apomorphy list for each branch in tree #1 of 6000 (Fig. 3). Each change is one step. Arrows with double lines indicate unambiguous changes, i.e., those occurring in all optimizations. Arrows with single lines indicate changes that do not occur in all optimizations.

Branch	Character	Change
Ancestor ↔ node 191	67	0 ↔ 1
node 191 → Tinamus	6	0 ⇨ 1
	8	0 ⇨ 1
node 191 → node 190	68	0 ⇨ 1
node 190 → node 184	61	0 ⇨ 1
node 184 → node 177	66	1 ⇨ 2
node 177 → node 167	26	0 ⇨ 1
node 167 → node 152	4	0 → 1
	52	1 ⇨ 3
	53	0 ⇨ 1
node 152 → node 151	8	0 ⇨ 1
	16	0 ⇨ 1
node 151 → node 148	12	0 ⇨ 1
	44	0 → 1
node 148 → node 141	26	1 → 0
	52	3 ⇨ 2
node 141 → node 140	53	1 ⇨ 0
	66	2 ⇨ 0
node 140 → node 126	16	1 ⇨ 0
	30	0 ⇨ 1
node 126 → node 125	51	0 ⇨ 1
	60	0 → 1
node 125 → node 121	66	0 ⇨ 2
node 121 → node 117	8	1 ⇨ 0
	9	0 ⇨ 1
	13	0 ⇨ 1
	37	0 ⇨ 1
	46	0 ⇨ 3
	52	2 ⇨ 4
node 117 → node 116	32	0 ⇨ 1
node 116 → node 108	20	0 ⇨ 1
node 108 → Diomedea	53	0 ⇨ 1
	65	0 ⇨ 12 = C
node 108 → node 107	10	0 ⇨ 1
	12	1 ⇨ 0
	13	1 ⇨ 0
node 107 → Oceanites	4	1 ⇨ 0
node 107 → node 106	49	0 ⇨ 1
node 106 → node 105	58	0 ⇨ 2
	64	0 ⇨ 2
node 105 → Pelagodroma	66	2 ⇨ 0
node 105 → node 104	29	0 ⇨ 1
node 104 → Nesofregatta	16	0 ⇨ 1
	40	0 ⇨ 2
node 116 → node 112	51	1 ⇨ 0
node 112 → node 110	5	0 ⇨ 1

## APPENDIX 4.—Continued

Branch	Character	Change
node 110 → node 109	32	1 ⇒ 0
node 109 → Puffinus	18	0 ⇒ 1
node 112 → node 111	16	0 ⇒ 1
node 111 → Pterodroma	20	0 ⇒ 1
node 116 → node 115	40	0 ⇒ 2
	64	0 ⇒ 2
node 115 → Hydrobates	10	0 ⇒ 1
node 115 → node 114	58	0 ⇒ 2
node 114 → node 113	49	0 ⇒ 1
node 113 → Oceanodroma	58	2 ⇒ 1
	64	2 ⇒ 1
node 114 → Pelecanoides	9	1 ⇒ 0
	16	0 ⇒ 1
	29	0 ⇒ 1
	32	1 ⇒ 0
node 117 → Phoebetria	58	0 ⇒ 2
node 121 → node 120	11	0 ⇒ 2
	33	0 ⇒ 1
	43	0 ⇒ 1
	47	0 ⇒ 1
	64	0 ⇒ 2
node 120 → node 119	58	0 ⇒ 2
node 119 → node 118	8	1 ⇒ 0
node 125 → node 124	4	1 ⇒ 0
	34	0 ⇒ 1
node 124 → node 122	11	0 ⇒ 1
	28	0 ⇒ 1
	42	0 ⇒ 1
	52	2 ⇒ 4
	54	0 → 1
	63	0 ⇒ 2
	65	0 ⇒ 1
node 122 → Gavia	44	1 ⇒ 0
	46	0 ⇒ 3
	47	0 ⇒ 1
	55	0 ⇒ 2
	58	0 ⇒ 1
node 122 → Podiceps	3	0 ⇒ 1
	7	0 ⇒ 1
	15	0 ⇒ 1
	18	0 ⇒ 1
	29	0 ⇒ 1
	43	0 ⇒ 2
node 124 → node 123	26	0 ⇒ 1
	30	1 ⇒ 2
	31	0 ⇒ 1
	45	0 ⇒ 1
	60	1 → 0
	66	0 ⇒ 1

## APPENDIX 4.—Continued

Branch	Character	Change
node 123 → Anas	33	0 → 1
	46	0 → 2
node 126 → Chen	44	1 → 0
node 140 → node 139	33	0 → 1
	52	2 → 1
node 139 → node 138	52	1 → 5
node 138 → Fregata	2	0 → 1
	13	0 → 1
	15	0 → 2
node 138 → node 137	7	0 → 1
	29	0 → 1
	40	0 → 2
	42	0 → 1
	49	0 → 1
node 137 → node 136	57	0 → 1
	3	0 → 1
	26	0 → 1
	61	1 → 0
	63	0 → 1
node 136 → node 135	65	0 → 2
	8	1 → 0
	12	1 → 0
	22	0 → 1
	40	2 → 0
node 135 → node 127	64	0 → 2
	66	0 → 2
	7	1 → 0
	18	0 → 1
	39	0 → 1
node 127 → Amazona	41	0 → 2
	62	0 → 1
	65	2 → 0
	14	0 → 1
	22	1 → 0
node 127 → Colius	40	0 → 1
	47	0 → 1
	52	5 → 9
	65	0 → 1
	25	0 → 1
node 127 → node 134	53	0 → 1
	66	2 → 1
	4	1 → 0
node 135 → node 134	49	1 → 0
	52	5 → 6
	61	0 → 1
node 134 → node 128	3	1 → 2
	26	1 → 0
	66	2 → 0

## APPENDIX 4.—Continued

Branch	Character	Change
node 128 → Picoides	12	0 ⇒ 1
	18	0 ⇒ 1
	51	0 ⇒ 1
node 134 → node 133	19	0 ⇒ 1
	42	1 → 0
	48	0 ⇒ 1
	52	6 → 7
	53	0 → 1
node 133 → node 132	53	1 → 2
	54	0 ⇒ 1
node 132 → node 131	22	1 ⇒ 0
node 131 → node 130	3	1 ⇒ 0
node 130 → Acanthisitta	33	1 ⇒ 0
	58	0 ⇒ 2
	60	0 ⇒ 1
node 130 → node 129	66	2 ⇒ 0
node 129 → Tyrannus	4	0 ⇒ 1
	14	0 ⇒ 1
	55	0 ⇒ 2
node 129 → Corvus	53	2 ⇒ 1
node 132 → Pitta	18	0 ⇒ 1
	33	1 ⇒ 0
node 136 → Glaucis	27	0 ⇒ 1
	38	0 ⇒ 2
	52	5 ⇒ 0
	55	0 ⇒ 2
node 137 → Chaetura	34	0 ⇒ 1
	55	0 ⇒ 1
node 139 → Sula	43	0 ⇒ 2
	44	1 → 0
node 141 → Anhinga	18	0 ⇒ 1
node 148 → node 147	13	0 ⇒ 1
	33	0 ⇒ 1
	61	1 ⇒ 0
node 147 → node 145	40	0 → 2
	49	0 ⇒ 1
	56	0 → 1
node 145 → node 144	59	0 ⇒ 1
node 144 → node 142	40	2 → 0
	64	0 ⇒ 1
node 142 → Buteo	9	0 ⇒ 1
node 144 → node 143	8	1 ⇒ 0
	26	1 ⇒ 0
	29	0 ⇒ 1
	37	0 ⇒ 1
	38	0 ⇒ 1
	52	3 ⇒ 1
	55	0 ⇒ 1
	56	1 → 0



## APPENDIX 4.—Continued

Branch	Character	Change
node 145 → Pandion	52	3 ⇨ 5
	66	2 ⇨ 1
node 147 → node 146	17	0 ⇨ 1
	50	0 ⇨ 1
node 146 → Polihierax	40	0 ⇨ 1
	65	0 ⇨ 1
node 146 → Falco	41	0 ⇨ 1
	64	0 ⇨ 1
node 151 → node 150	4	1 → 0
	47	0 ⇨ 1
	52	3 ⇨ 5
node 150 → node 149	21	0 ⇨ 1
node 149 → Gymnogyps	15	0 ⇨ 1
node 152 → Sagittarius	15	0 ⇨ 1
	49	0 ⇨ 1
	64	0 ⇨ 1
node 167 → node 166	45	0 ⇨ 1
node 166 → Grus	65	0 ⇨ 1
node 166 → node 165	59	0 ⇨ 1
	61	1 ⇨ 0
	23	0 ⇨ 1
node 165 → Fulica	24	0 ⇨ 2
	28	0 ⇨ 1
	30	0 ⇨ 2
	31	0 ⇨ 1
	4	0 ⇨ 1
node 165 → node 164	32	0 ⇨ 1
	43	0 ⇨ 1
	52	1 ⇨ 4
	14	0 ⇨ 1
node 164 → node 163	59	1 → 0
node 163 → node 162	29	0 → 1
node 162 → node 161	16	0 ⇨ 1
node 161 → node 160	51	0 ⇨ 1
node 160 → Rynchops	61	0 ⇨ 1
node 160 → node 159	29	1 → 0
	43	1 ⇨ 0
node 159 → node 158	32	1 ⇨ 0
node 158 → node 157	12	0 ⇨ 1
	44	0 ⇨ 1
	58	0 ⇨ 2
	60	0 ⇨ 1
	66	2 ⇨ 1
	29	0 ⇨ 1
node 157 → node 156	33	0 ⇨ 1
node 156 → node 155	34	0 ⇨ 1
node 155 → Alca	16	1 ⇨ 2
node 155 → node 154	16	1 ⇨ 0
node 154 → node 153	26	1 ⇨ 0

## APPENDIX 4.—Continued

Branch	Character	Change
node 153 → Brachyramphus	34	1 ⇒ 0
	49	0 ⇒ 1
node 159 → Rissa	59	0 ⇒ 1
node 161 → Sterna	33	0 ⇒ 1
	44	0 ⇒ 1
node 164 → Thalasseus	24	0 ⇒ 1
node 177 → node 171	15	0 ⇒ 2
	21	0 ⇒ 2
	35	0 ⇒ 1
	43	0 → 1
node 171 → node 170	3	0 ⇒ 1
	43	1 → 2
node 170 → node 169	4	0 ⇒ 1
	14	0 ⇒ 1
	16	0 ⇒ 1
node 169 → node 168	61	1 ⇒ 0
node 168 → Leptoptilus	15	2 ⇒ 1
node 170 → Phoenicopterus	1	0 ⇒ 1
	15	2 ⇒ 1
	46	0 ⇒ 2
	51	0 ⇒ 1
	52	1 ⇒ 4
	58	0 ⇒ 1
	60	0 ⇒ 1
	60	0 ⇒ 1
node 177 → node 176	23	0 ⇒ 1
	41	0 ⇒ 2
	47	0 ⇒ 1
node 176 → node 172	61	1 ⇒ 0
node 176 → node 174	64	0 → 2
node 174 → node 173	46	0 ⇒ 1
node 173 → Colinus	64	2 → 0
node 176 → node 175	46	0 ⇒ 2
node 175 → Meleagris	15	0 ⇒ 1
node 184 → node 183	16	0 ⇒ 1
	59	0 ⇒ 1
	29	0 ⇒ 1
node 183 → node 182	44	0 → 1
	15	0 ⇒ 2
node 182 → node 180	21	0 ⇒ 1
	36	0 ⇒ 1
	45	0 ⇒ 1
	47	0 ⇒ 1
	47	0 ⇒ 1
node 180 → node 179	25	0 ⇒ 1
	26	0 ⇒ 1
	40	0 ⇒ 1
node 179 → node 178	21	1 ⇒ 2
node 178 → Heterocnus	15	2 ⇒ 1

## APPENDIX 4.—Continued

Branch	Character	Change
node 180 → Balaeniceps	43	0 ⇒ 1
	44	1 → 0
	59	1 ⇒ 0
	61	1 ⇒ 0
	66	1 ⇒ 2
node 182 → node 181	7	0 ⇒ 1
	14	0 → 1
	52	1 ⇒ 5
node 181 → Chordeiles	2	0 ⇒ 2
	18	0 ⇒ 1
	28	0 ⇒ 1
node 181 → Coraciidae	43	0 ⇒ 2
	42	0 ⇒ 1
	46	0 ⇒ 1
	53	0 ⇒ 1
node 183 → Totanus	26	0 ⇒ 1
	43	0 ⇒ 1
	66	1 ⇒ 0
node 190 → node 189	7	0 → 1
	33	0 ⇒ 1
node 189 → node 187	44	0 ⇒ 1
	47	0 ⇒ 1
node 187 → Opisthocomus	7	1 → 0
	41	0 ⇒ 2
node 187 → node 186	8	0 ⇒ 1
	18	0 ⇒ 1
	23	0 → 1
	24	0 ⇒ 2
	32	0 ⇒ 1
	61	0 ⇒ 1
	61	0 ⇒ 1
node 186 → node 185	16	0 ⇒ 1
node 185 → Coccozyus	3	0 ⇒ 2
node 185 → Geococcyx	15	0 ⇒ 2
	16	1 ⇒ 2
node 189 → node 188	54	0 → 1
	62	0 ⇒ 1
node 188 → Columba	40	0 ⇒ 1
	41	0 ⇒ 2



















