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Hindlimb Myology and Evolution of the Old World Suboscine Passerine Birds (Acanthisittidae, Pittidae, Philepittidae, Eurylaimidae)

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INTRODUCTION

The purpose of this study is to increase our understanding of the evolutionary history of the passerine birds by adding to our knowledge of their morphology, reconstructing their phylogeny, and using the information thus obtained to improve existing classifications. To do this, I will provide detailed descriptions of the hindlimb musculature of the Old World suboscines (Acanthisittidae, Pittidae, Philepittidae, and Eurylaimidae), and will use this information to infer the phylogenetic relationships among these taxa.

The relationships of birds are reasonably well established at the species level, but are progressively less satisfactory at higher levels. The fact that a fairly stable classification has existed for several decades is misleading if it suggests that the relationships among most avian families and orders are well understood: many ambiguities and disagreements concerning these relationships exist (Stresemann 1959; Cracraft 1972, 1981). An especially serious problem occurs with the largest order of birds, the Passeriformes. Although 25–30 orders of living birds are generally recognized, the Passeriformes alone contain more than half of all species. These are divided into about 70 families (Wetmore 1960), most of them in the suborder Passeres (oscines or true songbirds). The relationships among the Passeriformes have long been poorly understood. Many families might prove to be monophyletic, but this possibility must be tested and not assumed. The relationships of the families to each other, and of the genera within families, are very obscure. Some families have been erected for one genus or a few genera simply because their relationships are not understood. To a considerable extent existing classifications reflect more the procedures and philosophy of traditional taxonomy than they do the patterns of corroborated phylogenetic hypotheses (Raikow 1985a).

The basic problem to be investigated is the phylogenetic history of the Passeriformes; this must be approached, for practical reasons, through subordinate problems of manageable size. Previous studies in this program emphasized relationships between various oscine groups (Bentz 1979; Borecky 1977, 1978; Raikow 1973, 1976, 1977a, b, 1978, 1985d; Raikow et al., 1980; Urik 1983), of nonpasserine orders suspected of close relationship to the Passeriformes (Berman and Raikow 1982; Maurer and Raikow 1981; Swierczewski and Raikow 1981), and the demarcation of the Passeriformes as a monophyletic group (Raikow 1982). The present consideration of suboscines thus forms a link between the separate approaches previously pursued.

A detailed history of passerine classification is beyond the scope of this work, but is thoroughly covered by Sibley (1970:23–31) and Ames (1971:127–129, 153–164). Thus, only a brief review of the groups studied will be offered here. The major problems deal with the arrangement of the suboscines within a phylogenetic framework. Are the Eurylaimidae the most primitive passerines as often suggested? Are they closely related to the Cotingidae? Are the Acanthisittidae suboscine or oscine? Are the Old World suboscines linked with the New World Tyrannoidea as traditional interpretations of syringeal anatomy have suggested? Answers will be offered to such questions in the form of a corroborated phylogenetic hypothesis.

In this work I will consider as monophyletic a group that appears from its characteristics to include all of the known descendants of a single common ances-

tor. This ancestor is hypothetical, but would be included in the group if known. Paraphyletic groups, which contain only some of these descendants, are, therefore, not considered monophyletic. Wiley (1981:82–92, 255–260) reviews these concepts. This definition of "monophyletic" corresponds to Ashlock's (1984) term "holophyletic," but not to his usage of "monophyletic," which means "holophyletic *or* paraphyletic."

Despite considerable work in recent years, our knowledge of the comparative anatomy of birds is still very incomplete. Berger (1966:229) considered "descriptions of the complete appendicular myology of all genera in different families of birds . . ." to be a major area of needed research, and later (Berger 1969) commented on the limited information available about passerine myology. With few exceptions (Hudson 1937; McKitrick 1985b) there appear to be no comprehensive descriptions of the hindlimb musculature of any suboscines. The present study will, therefore, fill a large gap in our knowledge of avian morphology.

EURYLAIMIDAE

The broadbills comprise a family of eight genera and fourteen species in the Old World tropics (Peters 1951:4–13). *Smithornis* and *Pseudocalyptomena* are African, whereas *Corydon, Cymbirhynchus, Eurylaimus, Serilophus, Psarisomus,* and *Calyptomena* range variously from India and China through Indochina, the Malay peninsula, Sumatra, Java, and Borneo to the Philippines. Broadbills inhabit forests and forest edges, where they feed on insects, small vertebrates, and sometimes fruits and seeds. The head is broad, the eyes large, and the bill typically large, broad, flattened, hooked, and with a wide gape. The legs are short, strong, and to different degrees, the toes are syndactyl. Wing and tail proportions vary. The different genera tend to have distinctly colored and patterned plumages. Brief reviews of the characteristics of the Eurylaimidae are given by Gilliard (1958: 260–261), Clench and Austin (1974), Van Tyne and Berger (1976:704), Olson (1978), and Bock (1982:997).

The early history of eurylaimid classification was reviewed by Olson (1971). The passerine relationships of the Eurylaimidae were not at first recognized, and the species were allied with various caprimulgiform or coraciiform groups. Using different lines of evidence Nitzsch (1867), Sclater (1872), Garrod (1877, 1878), Forbes (1880a), and Pycraft (1905) demonstrated that the broadbills are passerine, and Olson (1971) confirmed this with osteological investigations. My own studies of hindlimb myology reported previously (Raikow 1982) and developed further below also confirm this point. The eurylaimids have M. pubo-ischio-femoralis divided into Pars cranialis and Pars caudalis, and show the loss of most of the intrinsic muscles of the foot; both of these are diagnostic passeriform characters. Doubtless, the Eurylaimidae belong within the order Passeriformes.

It was assumed that the Eurylaimidae are restricted to the Oriental region until Bates (1914) reported that the African genus *Smithornis,* then placed in the Muscicapidae, lacks the syringeal muscles of oscines and possesses a plantar vinculum. Lowe (1924) made further anatomical studies and concluded that *Smithornis* is a eurylaimid. Subsequently Lowe (1931) showed that the rare African form *Pseudocalyptomena graueri* is likewise a broadbill.

For many years the broadbills have occupied a rather special place in passerine systematics. Because they possess certain characters thought to be primitive within

the Passeriformes, they have been regarded as being the most primitive of passerine birds, and have usually been classified apart for this reason. The idea that they are primitive has permeated the literature and has been accepted uncritically by those who classify and write about birds. In fact, this idea is based upon very little concrete evidence. It began with Garrod (1876:508), whose technical definition of the Passeriformes included a point first noted by Sundevall (see Nicholson 1889), namely that the deep plantar tendons, the tendons of M. flexor hallucis longus (FHL) and M. flexor digitorum longus (FDL), are not connected by a vinculum. These tendons are interconnected in various ways among birds (Raikow 1985c) and the formal recognition of various types by Gadow (1893–96) led to their being given an exaggerated importance as taxonomic characters (Sibley and Ahlquist 1972:17–20; Raikow 1985c). Shortly after thus defining the Passeriformes Garrod (1877) withdrew this character from the diagnosis after finding a vinculum in three species of broadbills. He believed that ". . . either Sundevall's character no longer holds, or the Eurylaemidae are not Passeres" and chose the former alternative on the basis of other evidence. Garrod believed that the vinculum was a retained primitive character and suggested informally that it provided a basis for separating the Eurylaimidae from the other passerines. Forbes (1880b) formalized this idea by dividing the order into the Desmodactyli, containing only the broadbills, and the Eleutherodactyli, with all other passerines. The Desmodactyli were defined as having retained the plantar vinculum and having the manubrium sterni unforked, the Eleutherodactyli as having lost the vinculum and having the manubrium generally strongly forked. Ridgway (1901:14) retained these taxa and characters, but added to them. He suggested that in the Desmodactyli the hallux is weak, whereas in the Eleutherodactyli it is the strongest toe. In association with the plantar tendons he characterized the eurylaimid foot as being "syndactyle," and that of other passerines as being "eleutherodactyle" or "schizopelmous." Finally, he claimed that the Desmodactyli have 15 cervical vertebrae, and the Eleutherodactyli 14. Lowe (1931) made a distinction between the form of the joint between the quadrato-jugal and the quadrate in eurylaimids and at least some other passerines.

This subordinal division, under various names, has been retained in most classifications until recently, in association with the idea that the eurylaimids are morphologically distinctive and primitive. These ideas were widely accepted until Olson (1971) reexamined them. Olson found that the spina externa is forked in *Smithornis,* as Bates (1914) and Lowe (1924) had previously reported, and that an unforked spina externa occurs in the Philepittidae (Ames 1971) and in some species of *Procnias* (Cotingidae). *Smithornis* has 14 cervical vertebrae as earlier noted by Lowe (1931). Olson (1971) could not detect the "weakness" of the hallux referred to by Ridgway (1901), and neither can I. Olson also found the "eurylaimid-type" quadrato-jugal/quadrate articulation in a variety of suboscines. He concluded that only the plantar vinculum definitively sets the Eurylaimidae apart from other passerine birds. Considering this to be an inadequate basis for subordinal separation, Olson (1971) placed the Eurylaimidae next to the Philepittidae within a suborder Tyranni containing all passerine birds except the Oscines and Menurae. He suggested further that they might be closely related to the Cotingidae, an idea also explored by Pycraft (1905).

Recent workers have similarly demoted the broadbills in classifications reflect-

ing their phylogenetic ideas. Cracraft (1981) grouped the Eurylaimidae and Phil-
epittidae as an infraorder Eurylaimi at the same level as the Pitti, Furnarii, and
Tyrannomorpha. Sibley et al. (1982) regarded them as the sister group of the
Pittidae, with a provisional relationship to the Philepittidae, which they did not
study.

Following Sclater (1888), the family Eurylaimidae is often divided into subfam-
ilies Calyptomeninae for *Calyptomena* and Eurylaiminae for the rest. Among
recent workers, Ames (1971) supported this view but Olson (1971) did not.

<center>PHILEPITTIDAE</center>

This family, endemic to Madagascar, is composed of two genera, *Philepitta* (the
asities) and *Neodrepanis* (the false sunbirds), each containing two species (Amadon
1979). Philepittids are rather quiet and often solitary birds of the forest, feeding
on fruit and insects; *Neodrepanis,* with its long bill and tubular tongue, also takes
nectar. Accounts of the biology and characteristics of the Philepittidae are given
by Salomonsen (1934), Rand (1936), Gilliard (1958:290–291), Clench and Austin
(1974:1059), Van Tyne and Berger (1976:716), and Bock (1982:997).

The two genera were not originally classified together. *Philepitta* was at first
considered an oscine and affinities were suggested, for example, with the Sturnidae
(Bonaparte 1850), Pittidae (Gray 1869), and Paradisaeidae (Sharpe 1870). Sun-
devall (Nicholson 1889) included *Philepitta* (which he called *Paictes*) in a heter-
ogeneous family Paictidae next to the Thamnophilinae and including even *Me-
nura*. Milne-Edwards and Grandidier (1879) placed *Philepitta* next to the
Nectariniidae, apparently, as Forbes (1880b) suggests, because the eye wattles and
bifid tongue resemble those of *Neodrepanis,* which at that time was considered
to be a sunbird.

Forbes (1880b) studied the internal anatomy of *Philepitta*. He found that the
syrinx is not of the oscine type, but mesomyodian and haploophone in nature,
and more specifically, similar to that of the Eurylaimidae. He noted that the
manubrium sterni, being only slightly bifid, resembles that of the broadbills, and
also that the pterylosis is more like that of the Eurylaimidae than that of the
Pittidae. He stated (Forbes 1880b:388) that *Philepitta* differs from the Eurylai-
midae in lacking a plantar vinculum, but as reported below, this is incorrect.

The suboscine nature of *Philepitta* was affirmed by Pycraft (1907), who included
it along with the Eurylaimidae, Cotingidae, and Pipridae in a suborder Eurylaimi
based on a primarily osteological investigation of those groups.

Neodrepanis was described by Sharpe (1875) and considered by Milne-Edwards
and Grandidier (1879) to be a sunbird, Nectariniidae, although as noted above
they had detected a resemblance to *Philepitta*. Shelley (1900), also impressed by
this similarity, suggested that *Neodrepanis* might form an oscine/suboscine link.
This dilemma was resolved by Amadon (1951), who showed that *Neodrepanis* is
neither a sunbird nor even an oscine. The tenth (outermost) primary is long,
whereas in sunbirds (and oscines generally) it is quite short. The hyporachis is
reduced as in *Philepitta,* but long in the sunbirds. The tarsus has a double row of
scutes on the posterior face, like *Philepitta* and unlike oscines. Most significantly,
the syrinx of *Neodrepanis* is mesomyodian, lacking intrinsic muscles, and with
large external membranes as in *Philepitta,* whereas sunbirds have the characteristic
oscine syrinx. Amadon (1951) reported further that the tongue of *Neodrepanis* is
tubular as befits its nectar-feeding habits, but that in structural details it is quite

different from that of the Nectariniidae. He concluded that *Neodrepanis* is not a sunbird, but is closely related to *Philepitta*. Amadon (1951) felt that there was no need to place the two genera in separate subfamilies, but later (Amadon 1979) he did so separate them. Wolters (1975–82:168) went further, placing *Neodrepanis* and *Philepitta* in separate families.

Ames (1971) found that the syringes of *Neodrepanis* and *Philepitta* are similar but not identical both as regards their cartilaginous elements and their musculature, confirming that both lack intrinsic muscles. He combined the Philepittidae with the Eurylaimidae in a suborder Eurylaimi (Ames 1971:153), but recognized that their syringeal similarities were due in part to the absence of what we would now call derived states characterizing other passerine groups.

The treatment of the Philepittidae in other recent classifications reflects the ideas that the family is valid, that it is suboscine, and that it is related to the Eurylaimidae. This connection, however, is sometimes obscured by the tendency to separate the Eurylaimidae at the subordinal level because of their supposed primitiveness, as discussed above. Thus, Mayr and Amadon (1951), Wetmore (1960), and Clench and Austin (1974) included them in a suborder Tyranni apart from the broadbills. Storer (1971) and Amadon (1979) considered their subordinal position to be uncertain. Olson (1971) eliminated the separate suborder Eurylaimi, and placed the Philepittidae next to the Eurylaimidae in one of two superfamilies of the suborder Tyranni. The intent of these classifications is further obscured by the unclear relationship between ideas of phylogeny and taxonomy that characterize many traditional classifications (Raikow 1985a).

PITTIDAE

The pittas form a family of largely terrestrial forest and scrubland birds of the Old World tropics, ranging from Africa across Asia to Australia. In plumage they show a variety of colorful patterns. The bill is fairly stout, the wings rounded, and the tail short. The tarsi are long in association with the pittas' ground-dwelling habits, and these birds feed mainly on arthropods and other small animals. About two dozen species are recognized, although the exact number varies among authors. Most workers have considered the pittas to be sufficiently similar to be placed in a single genus *Pitta* (e.g., Mayr 1979a), but Wolters (1975–82:168–169) recognized six genera. The characteristics of the pittas are discussed by Gilliard (1958:272, 289), Clench and Austin (1974:1059), Van Tyne and Berger (1976: 714), Ginn (1978), and Bock (1982:997–998).

Although the pittas form a clearly bounded group, their relationships to other birds have remained obscure. Modern ideas derive from the work of Garrod (1876) who showed that they are not oscine, and that they possess the "haploophone" type of mesomyodian syrinx. On this basis they, and the Acanthisittidae and Philepittidae, have been grouped with several New World families in a superfamily Tyrannoidea apart from the "tracheophone" passerines or Furnarioidea (e.g., Mayr and Amadon 1951; Wetmore 1960; Clench and Austin 1974). Other workers have been more cautious about grouping the pittas with New World suboscines, and have listed them as being of uncertain subordinal position (Ames 1971; Olson 1971; Storer 1971; Mayr 1979a) or as a separate infraorder (Cracraft 1981). Sibley (1970), who studied egg-white proteins, also failed to support an alliance of the pittas with New World suboscines, and suggested a possible oscine relationship. However, in recent DNA hybridization studies, Sibley et al. (1982)

considered the Pittidae to be the sister group of the Eurylaimidae, with this cluster in turn being the sister group of the New World suboscines.

ACANTHISITTIDAE

This family, also known as the Xenicidae, contains four recent species endemic to New Zealand (Mayr 1979b). They are insectivorous birds of forest and scrub habitats. Acanthisittids are small birds with a slender, straight, and pointed bill, short wings and tail, and long legs. *Acanthisitta chloris,* a diminutive species with arboreal foraging habits, is still fairly common. *Xenicus longipes,* which might be extinct, and *X. gilviventris,* feed somewhat more on the ground. *X. lyelli,* which might have been flightless, became extinct nearly a century ago. The Acanthisittidae probably represent the remnants of a once more extensive New Zealand radiation. For general information see Oliver (1955:447–457), Gilliard (1958: 290–291), Van Tyne and Berger (1976:715), Dawson (1978), and Bock (1982: 998).

The taxonomic history of the New Zealand wrens was recently reviewed by Sibley et al. (1982), so only a few highlights need be mentioned here. Acanthisittids were first classified in various oscine genera. Forbes (1882) discovered that they have a suboscine syrinx, lacking intrinsic muscles, and proposed affinities to various Old and New World suboscine families. Subsequent studies by various workers resulted in suggested alignments with such varied groups as the neotropical tyrannoids and furnarioids, and the pittas and broadbills. Sibley (1970) found that the egg-white proteins of *Acanthisitta* differ from those of New World suboscines, and suggested a possible oscine relationship. Ames (1971) examined the syrinx and failed to find useful information linking the Acanthisittidae to any other group. Feduccia (1974) showed that the stapes (middle ear ossicle) of suboscines has a derived morphology, whereas oscines retain a primitive form. Subsequently, he showed that *Acanthisitta* has a slightly modified oscine-type stapes and is thus excluded from the main suboscine assemblage (Feduccia 1975a, b). On this basis he suggested possible oscine affinities for the Acanthisittidae.

Thus, in recent years the Acanthisittidae (or Xenicidae) have either been listed along with other Old World suboscines and non-tracheophone New World suboscines in a superfamily Tyrannoidea (Mayr and Amadon 1951; Wetmore 1960; Clench and Austin 1974), or they have been listed in a more tentative manner reflecting their uncertain relationships (Ames 1971; Storer 1971). Cracraft (1981) listed them *incertae sedis* within the oscines.

Based on a study of DNA-DNA hybridization Sibley et al. (1982) and Sibley and Ahlquist (1985b) proposed a phylogeny of the major passerine groups in which the order is divided into two suborders, the Passeres or Polymyodi (=oscines) and the Oligomyodi. Within the latter assemblage the Acanthisittidae form the sister group of the remaining suboscines.

MATERIALS AND METHODS

DISSECTION

Preserved specimens of birds borrowed from museum collections were studied by dissection. For most species only one specimen was dissected. The specimens were provided by the American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), Carnegie Museum of Natural History (CM),

Delaware Museum of Natural History (DEL), National Museum of Natural History (NMNH), and Peabody Museum, Yale University (YPM). The following species were studied: EURYLAIMIDAE: *Eurylaimus ochromalus* (DEL 60888), *E. steeri* (USNM 510277), *Smithornis capensis* (USNM 227138), *Pseudocalyptomena graueri* (AMNH 2233), *Cymbirhynchus macrorhynchus* (DEL 61632), *Serilophus lunatus* (USNM 505628), *Psarisomus dalhousiae* (USNM 509482), *Calyptomena whiteheadi* (USNM 429241), *C. viridis* (YPM 7812); PHILEPITTIDAE: *Philepitta castanea* (AMNH 2230), *Neodrepanis coruscans* (USNM 512779); PITTIDAE: *Pitta versicolor* (AMNH 4376), *P. guajana* (CM 1728, 1729), *P. brachyura* (YPM 8023), *P. erythrogaster* (YPM 8700); ACANTHISITTIDAE: *Acanthisitta chloris* (BMNH 1904.8.2.3), *Xenicus longipes* (USNM 559447).

Because of their small size, the birds were dissected with the aid of a stereomicroscope, using magnifications of $6\times{-}25\times$. Specimens were stained with an iodine solution (Bock and Shear 1972), which makes muscle fibers clearly visible in contrast to other tissues, so that details of muscle architecture and the presence of very small muscles are easily determined.

DATA

The primary data are descriptions of the limb muscles, including the location and nature of the origin and insertion (fleshy, tendinous); muscle shape (e.g., fan-shaped, spindle-shaped); fiber architecture (e.g., parallel-fibered, unipennate); position and size relative to adjacent structures; and any additional details. In the text a description is first given for the reference species, *Eurylaimus ochromalus,* and then comparisons are made with the other species. Drawings were made directly from the specimens with the aid of a drawing tube attached to the microscope. Anatomical nomenclature follows the Nomina Anatomica Avium (Baumel et al. 1979). The abbreviations in the figures (Appendix I) mostly follow Zusi and Bentz (1984).

ANALYSIS

Phylogeny was inferred by the construction of cladograms; groups of species hypothesized to represent monophyletic groups were clustered by their shared possession of derived character states. The primitive/derived polarity of characters was determined by the method of *outgroup comparison.* Because this method, although widely used, is still sometimes misunderstood, a brief explanation is warranted. The *primitive state* of a variable character is that which is found in some members of a monophyletic group (the ingroup) as well as in species outside of that group (the outgroup). The corresponding *derived state* is that which is restricted to the remaining species within the ingroup. For example, suppose we have previously determined that the order Passeriformes is monophyletic, i.e., that all passerine species share a more recent common ancestor with each other than they do with any nonpasserine species. The passerines now constitute an ingroup for which the nonpasserine birds might serve as an outgroup. We might now use the outgroup comparison to recognize derived character states within the ingroup. For instance, we might note that some species have a structurally complex syrinx with certain features in the supporting elements and four pairs of intrinsic muscles, whereas other species do not have this attribute. Looking at the outgroup we see that none of the nonpasserines has a syrinx anything like this.

We might, therefore, conclude that this syringeal specialization evolved after the origin of the passerines, and is, therefore, a derived condition within the passerines. Thus, the species possessing this characteristic form a monophyletic subgroup (clade) within the larger passerine group. In studies of this sort it is sometimes found that groups previously recognized as taxa in formal classifications are monophyletic, and have a real historical existence, like the Oscines in the above example. Sometime, however, traditional taxa cannot be shown to be monophyletic, and it is important that no prior assumptions of this sort be made. A potential problem of logical circularity in the use of the outgroup comparison method was circumvented by avoiding such ad hoc assumptions of ingroup monophyly (Raikow 1982).

The polarities of the character states were determined by outgroup comparisons as described in a general way above. More specifically, this was done in a progressive way as the following example illustrates. Initially the nonpasserine birds were used as an outgroup for the Passeriformes, which is a valid ingroup because of its monophyly (Raikow 1982). Comparisons were made with published information about many orders of birds (especially from George and Berger 1966), with emphasis on groups considered close to the passerines (Coraciiformes: Maurer 1977; Maurer and Raikow 1981; Piciformes: Swierczewski 1977; Swierczewski and Raikow 1981). Data from numerous oscine and suboscine groups were compiled from our previous studies, as listed in the Introduction. When a clade within the Passeriformes was thus established it could then become an ingroup for which the excluded passerines (in addition to the nonpasserines) served as outgroup. For example, accepting passerine monophyly, outgroup comparison shows that the derived suboscine stapes defines a clade consisting of the traditional suboscines, but excluding the Acanthisittidae. Once established, this clade can in turn be treated as an ingroup, and outgroup comparison to the remaining passerines shows, for example, that the attenuate form of M. gastrocnemius pars medialis is derived, and defines a still smaller clade. In many cases the order Passeriformes is the ingroup used, and nonpasserines form the outgroup. In some cases the clade of suboscines based on the derived stapes (Feduccia 1975b) is used as the ingroup, with other passerines as the outgroup. Specific comments are provided below to explain the polarity determinations of the characters individually.

A phylogeny is a hypothesis about the genealogical relationships within a group of species, and it takes the form of a dendrogram with nested clusters of taxa united by a pattern of hypothesized common ancestors. The method for hypothesizing a phylogeny in this study was first to construct a cladogram as just described. A cladogram is not identical to a phylogeny because one cladogram can generate more than one phylogeny if ancestor-descendant relationships are proposed among the species studied. This problem did not arise in the present work because only extant species were studied, so that only sister-group relationships are hypothesized. Thus, a cladogram postulates only a single phylogeny, and both have the same shape. In the cladogram the nodes represent the clustering of groups by shared possession of derived states (synapomorphies), whereas in the corresponding phylogeny they represent the hypothetical common ancestor of the group, which possessed those character states. Thus, my use of the cladogram for organizing data has the purpose of generating a phylogeny, and not, as with some workers, the purpose of mapping character state distributions without reference to their evolutionary origins.

In constructing cladograms I accepted the use of the parsimony principle, that is, I searched for the cladogram consistent with the data that required the smallest number of ad hoc hypotheses about the multiple origin of derived states. Kluge (1984) has distinguished two concepts of parsimony in phylogenetic studies. "Evolutionary parsimony" is the idea that the simplest hypothesis (shortest tree) is most likely to represent the true historical phylogeny. "Methodological parsimony" is the position that, given character conflict, the shortest tree is philosophically the least objectionable. My use of parsimony is in the latter sense. This approach confers consistency on a procedure whose goal is the creation of testable hypotheses. The limitations of this approach will be discussed below, and my phylogenetic hypotheses will be tested by comparison with the results of other studies.

Numerical cladistic analyses were performed with two different computer programs, PENNY (part of the PHYLIP package of Joseph Felsenstein, University of Washington), and the PAUP program of David L. Swofford (University of Illinois, Illinois Natural History Survey). This analysis used the MULPARS option with global branch-swapping to generate cladograms. Data were analyzed, ordered and unordered, with the same results. The CONTREE program was used to generate the consensus tree. Both PHYLIP and PAUP assumed the conditions of Wagner parsimony, namely that the multiple origin of derived states and evolutionary reversal are both permitted. They seek the parsimonious solution as discussed above. All characters were given equal weight.

MUSCLES OF THE THIGH

M. ILIOTIBIALIS CRANIALIS (ICR)
(Figs. 1, 6, 14, 15, 17–24, 27, 31)

Eurylaimus. — This muscle forms the cranial border of the thigh. It is strap-shaped and nearly parallel-fibered, but slightly wider at its origin than at its insertion. It lies cranial to M. iliotibialis lateralis, and its caudal edge lies deep to the cranial margin of the latter. The origin is by fleshy and short tendinous fibers from the spinous processes of the last two dorsal vertebrae. Only the one head of origin is evident; there is no origin from the pelvic girdle. Distally the belly passes to the craniomedial surface of the thigh and a fleshy insertion on the head of the tibiotarsus, where it is overlain by the origin of M. gastrocnemius pars supramedialis.

Comparison. — Some species dissected in this study appear to show a partial area of origin from the craniodorsal edge of the ilium. However, this is highly variable and difficult to discern accurately, and, therefore, is not a reliable character.

M. ILIOTIBIALIS LATERALIS (IL)
(Figs. 1, 6, 14, 15, 17–24, 26, 27)

Eurylaimus. — This muscle has two separate bellies on the lateral surface of the thigh. The *preacetabular belly* lies cranial to the femur and the *postacetabular belly* lies caudal to the femur. There is no central or *acetabular* portion, so the proximal end of M. femorotibialis externus and the insertion of M. iliotrochantericus caudalis upon the femur are exposed after skinning. This opening in M. iliotibialis lateralis is the *acetabular gap.*

The preacetabular belly is a flat sheet of muscle which overlies the caudal two-thirds of M. iliotrochantericus caudalis. It arises by a broad aponeurosis from the dorsal iliac crest (*Crista iliaca dorsalis*), and is continuous caudally with that contributing to the origin of the cranial end of M. iliofibularis. Distally the pre-acetabular belly passes to the lateral surface of M. femorotibialis externus, where it inserts as the *lateral aponeurosis* applied tightly to the surface of the muscle. The most cranial fibers extend farthest distally.

The postacetabular belly is very well developed, being both wide and thick. It arises mostly fleshy from the dorsolateral iliac crest and adjacent surface of the postacetabular iliac wing (*Ala postacetabularis ilii*) from a point slightly caudal to the antitrochanter caudally to a point just cranial to the terminal iliac process (*Processus terminalis ilii*). Thus, it lies superficial to Mm. iliofibularis and flexor cruris lateralis pars pelvica. The muscle extends craniodistally to insert by fleshy and tendinous fibers onto the caudolateral surface of M. femorotibialis externus, contributing in the process to the lateral aponeurosis.

Comparison. — In *Smithornis* the postacetabular belly is greatly reduced both in thickness and width; it is less than one-third as wide as in *Eurylaimus* (Fig. 14). Reduction has occurred on both the cranial and caudal margins, so that the muscle remains only as a narrow, strap-shaped belly. Cranially it arises over the midpoint of the underlying M. iliofibularis. The caudal margin arises near the caudal end of the origin of the latter muscle, and slightly cranial to the cranial margin of M. flexor cruris lateralis pars pelvica. The reduced postacetabular belly inserts at a more proximal level on M. femorotibialis externus, failing to reach the distal end of that muscle because of the loss of its more caudal portion.

In *Calyptomena* the postacetabular belly is slightly reduced as compared to *Eurylaimus,* but less than in *Smithornis* (Fig. 15). The cranial border shows a slight reduction, its point of origin lying farther caudad so that more of the cranial end of M. iliofibularis is exposed. The caudal margin shows greater reduction, so that it overlies only the cranial edge of M. flexor cruris lateralis pars pelvica, and its insertion ends somewhat more proximally than in *Eurylaimus*. This description applies to both species of *Calyptomena* dissected.

In *Pitta* the postacetabular belly is wide, but originates somewhat farther caudad than in *Eurylaimus* so that the acetabular gap is wider (Fig. 23). Distally the postacetabular belly divides into separate superficial and deep layers (Fig. 26). Each of these inserts separately by a flat tendon, contributing respectively to the superficial and deep layers of the patellar tendon. The deep layer inserts, specifically, along the caudal margin of M. femorotibialis externus pars distalis.

In the Acanthisittidae M. iliotibialis lateralis is complete, including preacetab-ular, acetabular, and postacetabular portions arising by a broad, continuous apo-neurosis from the dorsal iliac crest and the dorsolateral iliac crest (Fig. 27). There is no acetabular gap as in the other groups studied. The origin of the postacetabular part shows no reduction, but extends caudally nearly to the terminal iliac process. The distal end of the postacetabular portion is not divided as in *Pitta.*

<div style="text-align:center">

M. ILIOFIBULARIS (IF)
(Figs. 1–4, 14, 15, 17, 19, 21, 23, 28)

</div>

Eurylaimus. — This muscle lies in the caudolateral region of the thigh deep to M. iliotibialis lateralis. It is shaped like an elongated triangle with the origin forming the narrow base, and the tendon of insertion arising at the apex, within

the distal one-fourth of the muscle. The belly is divided into two separate heads. The cranial head arises by an aponeurosis from the caudal end of the cranial iliac crest, overlying the caudal part of M. iliotrochantericus caudalis, and from the cranial end of the caudolateral iliac crest, overlying the antitrochanter. The caudal head arises by mixed tendinous and fleshy fibers from the caudolateral iliac crest caudal to the cranial head. The two heads are separated by a narrow gap extending nearly three-fourths the length of the belly. The two heads converge on the tendon of insertion. This tendon passes distad through the biceps loop (*Ansa M. iliofibularis*) and then medial to the lateral head of M. flexor hallucis longus and lateral to M. flexor digitorum longus before inserting on the caudolateral surface of the fibular shaft.

The biceps loop has the usual three arms. The *proximal femoral arm* arises on the lateral surface of the femoral shaft proximal to the origin of M. gastrocnemius pars lateralis and lateral to the insertion of M. flexor cruris lateralis pars accessoria. The *distal femoral arm* arises farther distally in common with M. gastrocnemius pars lateralis. The *fibular arm* arises from the lateral surface of the fibular shaft just distal to the head of the fibula. It is fused with the tendon of origin of the lateral head of M. flexor hallucis longus.

Comparison. —A gap separating the cranial and caudal heads was also seen in *Pseudocalyptomena,* and faintly in *Cymbirhynchus.* In the other forms, including *Eurylaimus steeri,* there was either no discernable gap or a faint trace of one. This condition is a trivial structural modification of the usual condition in which the same two heads are present but without a gap. It is variable, difficult to define, and probably of no significance.

<div align="center">M. ILIOTROCHANTERICUS CAUDALIS (ITCA)
(Figs. 1, 2, 14, 19, 29)</div>

Eurylaimus. —This large muscle lies on the laterodorsal surface of the preacetabular iliac wing (*Ala preacetabularis ilii*) and is roughly oval in shape. It arises fleshy from the surface of the dorsal iliac fossa (*Fossa iliaca dorsalis*) and the dorsal iliac crest, and from the cranioventral margin of the ilium by a narrow aponeurosis shared with M. iliotrochantericus cranialis. The muscle is asymmetrically fan-shaped, its fibers converging on a wide, flat tendon. This inserts on the lateral surface of the proximal end of the femur just distal to the trochanter. This muscle completely overlies Mm. iliotrochantericus cranialis and iliotrochantericus medius.

Comparison. —M. iliotrochantericus caudalis does not overlie M. iliotrochantericus cranialis in *Smithornis, Pseudocalyptomena, Philepitta, Neodrepanis, Pitta, Acanthisitta,* or *Xenicus.* This variation depends on the relative sizes of the muscles and is highly variable in passerines, so that polarity cannot be determined. In *Calyptomena* the superficial fascicles on the ventral half of the muscle end more proximally than on the dorsal part, so that the tendon, which arises deep in the belly, is exposed superficially (Fig. 16).

<div align="center">MM. ILIOTROCHANTERICUS CRANIALIS AND ILIOTROCHANTERICUS MEDIUS
(ITCR, ITM)
(Figs. 5, 9, 16, 18, 20, 22, 24, 28, 29, 31)</div>

Eurylaimus. —M. iliotrochantericus cranialis arises fleshy from the cranioventral margin of the preacetabular ilium; M. iliotrochantericus medius arises

similarly from the same element immediately caudal to the origin of the former muscle. Although their bellies are separate, the two muscles converge onto a single tendon of insertion. This tendon narrows as it passes to its insertion on the craniolateral surface of the proximal end of the femur.

Comparison.—Several variations were noted (Fig. 9). In all the eurylaimids except *Pseudocalyptomena* the two muscle bellies are separate but have a common tendon of insertion (character 5 in Tables 1 and 2). In *Pseudocalyptomena,* however, the two muscles are separate, including their tendons, which are separate except just at the insertion.

In *Eurylaimus ochromalus* a small, very narrowly fan-shaped muscle was observed arising fleshy adjacent to the caudal end of the origin of M. iliotrochantericus medius and passing to a fleshy insertion on the femur just proximal to the combined insertion of Mm. iliotrochantericus cranialis and iliotrochantericus medius. It is not a misplaced M. iliofemoralis internus, which is present normally. It is absent in the other (right) limb of the specimen and in all other forms dissected. Apparently it is an anomalous muscle and of no phylogenetic significance.

In *Philepitta* and *Neodrepanis* a different kind of muscle fusion occurs. M. iliotrochantericus medius is very small, actually reduced to a vestige, and joins the distal end of the belly of M. iliotrochantericus cranialis, which alone appears to give rise to the tendon. This is structurally quite different from the eurylaimid condition, and is character 6 in Tables 1 and 2.

In *Pitta versicolor* and *P. brachyura* the two muscles are entirely separate, including their tendons of insertion. In *P. erythrogaster* they were also separate but their tendons are more or less fused together. In one specimen of *P. guajana* the separate bellies inserted via a common, broad tendon (bilaterally), whereas in another specimen the tendons were separate on the left side but partially fused on the right.

In *Acanthisitta* and *Xenicus* the two muscles are entirely separate, including their insertions.

M. ILIOFEMORALIS INTERNUS (IFI)
(Figs. 5, 6, 8, 9, 18, 20–22, 24, 31, 32)

Eurylaimus.—This small, strap-shaped muscle arises fleshy from the ventro-lateral margin of the preacetabular ilium at a point just caudal to the origin of M. iliotrochantericus medius. It inserts fleshy on the medial surface of the proximal end of the femur. It is nearly parallel-fibered, but fans out slightly at its insertion.

Comparison.—In *Psarisomus* and *Calyptomena* the origin slightly overlaps that of M. iliotrochantericus medius, whereas in the Acanthisittidae it is at about the same level as the latter muscle. In *Calyptomena* the muscle is more distinctly fan-shaped, being about twice as wide at its insertion as at its origin.

MM. FEMOROTIBIALIS EXTERNUS AND FEMOROTIBIALIS MEDIUS (FTE, FTM)
(Figs. 1, 2, 6, 8, 14, 15, 17, 18, 20, 22–24, 26, 28, 31, 32)

Eurylaimus.—M. femorotibialis externus lies on the lateral surface of the thigh deep to the central portion of M. iliotibialis lateralis, and overlying the lateral aspect of the femoral shaft. There are two parts. *Pars proximalis* (FTEP) arises fleshy from the shaft of the femur beginning just proximal to the level of the insertion of M. ischiofemoralis. This muscle is completely fused along its cranial

margin with M. femorotibialis medius, so recognition of these as separate muscles is arbitrary. Distally the muscle gives rise to the lateral superficial portion of the patellar tendon. *Pars distalis* (FTED) is an elongate, asymmetrically fan-shaped belly that arises fleshy from the caudolateral surface of the femoral shaft, beginning proximally at about the level of the M. caudofemoralis insertion. Distally it forms a flat tendon that becomes the deep, caudal portion of the patellar tendon. The patellar tendon inserts on the head of the tibiotarsus, specifically the lateral cnemial crest and the patellar crest.

M. femorotibialis medius arises fleshy on the cranial surface of the femoral shaft between M. femorotibialis externus laterally and M. femorotibialis internus medially. It is fused with the former as indicated above, but separate from the latter. It inserts on the proximal face of the patella, which then is connected via the patellar tendon to the head of the tibiotarsus.

Comparison. — No variations from these patterns were noted in these muscles.

M. FEMOROTIBIALIS INTERNUS (FTI)
(Figs. 6, 8, 18, 20, 22, 24, 31, 32)

Eurylaimus. — This elongate muscle arises fleshy for most of the length of the mediocaudal surface of the femoral shaft. The fibers converge on a tendon that arises on the surface of the distal half of the belly. The flat tendon inserts on the medial side of the head of the tibiotarsus. Although the muscle appears somewhat fan-shaped at its distal end, the overall fiber arrangement is basically unipennate. There is no indication of a division into two heads, or of two separate tendons of insertion as in some birds, but the tendon can be split easily into superficial and deep layers.

Comparison. — No variations from these patterns were noted in this muscle.

M. FLEXOR CRURIS LATERALIS (FCRLA, FCRLP)
(Figs. 1, 2, 5, 6, 8, 14, 15, 17–23, 25, 27–29)

Eurylaimus. — This muscle consists of a proximal portion (*Pars pelvica*) separated by a raphe from the distal *Pars accessoria.* Pars pelvica (FCRLP) arises fleshy from the caudal end of the dorsolateral iliac crest and the surface of the ilium just ventral to this on the terminal iliac process; the caudal end of the origin extends beyond the ilium, arising from the connective tissue associated with the first one or two caudal vertebrae. The nearly parallel-fibered belly passes distad, ending at the raphe that separates it from Pars accessoria.

Pars accessoria (FCRLA) is a parallel-fibered muscle arising from the raphe as a continuation of Pars pelvica. It passes craniodistally to insert fleshy on the caudolateral surface of the distal third of the femoral shaft and in the popliteal fossa, extending medially at its distal end to insert also on the proximal margin of the medial femoral condyle adjacent to the origin of M. gastrocnemius pars intermedia. The most distal fascicles arise not from the raphe itself, but from its extension as tendon G (see below). The ventral margin of the muscle lies adjacent to the dorsal surface of M. gastrocnemius pars intermedia, and when the crus is flexed the two lie together, fibers parallel, and appear fused. However, there is a definite space between them, as becomes apparent when the crus is extended, and it can be seen that there is a section of tendon G from which no fascicles arise, i.e., there is a gap between the attachments of the two muscles.

Two tendinous extensions arise from the raphe: these have been noted in earlier studies, but not described in detail. *Tendon G* is a narrow, rather stout tendon that arises as a continuation of the raphe on the ventrolateral side of the muscle. It turns distad and merges into the dorsal margin of the distal third of the belly of M. gastrocnemius pars intermedia, contributing to the formation of that muscle's tendon of insertion. *Tendon M* is a wide, flat tendon that arises from the distal half of the raphe on the medial side of M. flexor cruris lateralis; it passes distad with its caudal part lying lateral to the cranial part of the M. flexor cruris medialis tendon, and its cranial part cranial to the latter (e.g., the two tendons overlap partially). Distally tendon M fuses with the M. flexor cruris medialis tendon more or less completely, so that the two insert together.

Comparison. — In *Smithornis* tendon M lies entirely lateral to the M. flexor cruris medialis tendon; there is no overlap. It joins the latter tendon at its origin; the two fuse and insert as a single, wide tendon.

In *Cymbirhynchus* Pars accessoria extends well down tendon G, so that it and M. gastrocnemius pars intermedia are approaching fusion, and are not as easy to separate as in *Eurylaimus*.

In *Serilophus* the cranial edge of tendon M is joined by an extension from the insertion of M. pubo-ischio-femoralis pars caudalis. This could well be an individual variation.

In *Calyptomena* Pars accessoria has grown so far down tendon G as nearly to obliterate the gap between it and M. gastrocnemius pars intermedia. Superficially the two muscles appear to be fused together, especially on the lateral side, but in fact they are still separate, if only barely so. Tendon M fuses with the tendon of M. flexor cruris medialis; it does not overlap the latter cranially.

In *Pitta guajana, P. erythrogaster,* and *P. versicolor* tendon M arises as a broad, flat tendon from the raphe and from the belly of Pars pelvica. It passes distad to an insertion on the tibiotarsus proximal to that of M. flexor cruris medialis, whose insertion by a tendon of similar proportions is entirely separate, there being a small gap between the two. In *P. brachyura,* however, tendon M fuses with the deep, cranial surface of the flexor cruris medialis tendon (Fig. 25). Pars accessoria and M. gastrocnemius pars intermedia are directly adjacent but not quite fused together.

In the Acanthisittidae tendon M is wide and is fused with the flexor cruris medialis tendon at the latter's origination; thus the two muscles insert by one combined tendon without overlap.

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M. FLEXOR CRURIS MEDIALIS (FCRM)

(Figs. 1, 2, 5, 6, 8, 14, 15, 18–25, 29, 31, 32)

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Eurylaimus. — This muscle lies deep in the caudal region of the thigh. The origin is fleshy from the lateral surface of the ischium along the caudal half of the dorsal rim of the ischiopubic fenestra. The belly is wide and flat, and narrows slightly toward the insertion, so that it is slightly fan-shaped, although more nearly parallel-fibered. As it approaches the crus deep to M. flexor cruris lateralis, and at the level of the dorsal margin of M. gastrocnemius pars intermedia, the belly of M. flexor cruris medialis gives rise to a wide, flat tendon. This passes distad medial to the former muscle and to Mm. plantaris and flexor digitorum longus, but medial to M. gastrocnemius pars medialis, to insert on the dorsomedial margin of the

proximal end of the shaft of the tibiotarsus. Before its insertion the tendon is joined by tendon M from M. flexor cruris lateralis as described under that muscle.

Comparison. —In some *Pitta* species the tendon of insertion is separate from that of tendon M, as described above under M. flexor cruris lateralis.

M. CAUDOFEMORALIS (CF)
(Figs. 1, 2, 5, 6, 8, 14, 15, 17–24, 29)

Eurylaimus. —This is a flat, spindle-shaped muscle passing from the pygostyle to the femur. The origin is by a short tendon from the undersurface of the pygostyle and associated cruciate ligament. The belly passes craniad between Mm. flexor cruris lateralis and flexor cruris medialis to insert by a flat tendon on the caudolateral surface of the femoral shaft distal to the insertion of M. ischiofemoralis.

Comparison. —In *Smithornis* the tendon of origin is relatively longer and narrower than in *Eurylaimus*. In *Pitta* the muscle has a more discrete origin from the pygostyle than shown by the diffuse origin via the cruciate ligament as in the others. In *Neodrepanis* the tendon of insertion is slightly shorter than in the other species, whereas in *Pitta* the belly is relatively narrower. These variations do not appear to be of any particular significance. This muscle is sometimes grouped with M. iliofemoralis as parts of a common M. caudo-ilio-femoralis (Baumel et al. 1979:183). M. iliofemoralis was absent in all the species studied herein, as expected in the Passeriformes.

M. ISCHIOFEMORALIS (ISF)
(Figs. 2, 5, 6, 28, 29, 31)

Eurylaimus. —This large, fan-shaped muscle arises fleshy from the lateral surface (*Lamina ischiadica*) of the ilium dorsal and caudal to the ilioischiadic foramen, and from the *Ala ischii* caudal and ventral to that opening. The caudal margin of the muscle arises from a membrane passing across the caudal end of the pelvis from the *Processus terminalis ilii* to the *Processus terminalis ischii*. The tendon of insertion arises on the craniolateral surface of the muscle as it narrows cranially. The stout tendon inserts on the lateral surface near the proximal end of the femur, caudal to the insertion of Mm. iliotrochantericus cranialis and iliotrochantericus medius, and distal to the insertion of M. obturatorius medialis.

Comparison. —The muscle arises slightly farther caudad in the Eurylaimidae, Philepittidae, and Acanthisittidae than in the Pittidae.

M. OBTURATORIUS LATERALIS (OLD, OLV)
(Figs. 30, 31)

Eurylaimus. —This small muscle lies deep in the hip at the caudal aspect of the proximal end of the femur. *Pars dorsalis* (OLD) is a tiny, narrowly fan-shaped muscle that arises fleshy from the cranial end of the ischium (*Corpus ischii*) at the craniodorsal margin of the obturator foramen. The belly extends craniad to insert fleshy on the caudal margin of the head of the femur deep to the insertion of M. obturatorius medialis at the dorsal edge of Pars ventralis. Pars dorsalis is minute compared to its size in many birds, almost vestigial. Following the system of Raikow (1978:18) it is classified as small.

Pars ventralis (OLV) is much larger than Pars dorsalis. It arises fleshy at the cranioventral margin of the obturator foramen, at the ill-defined juncture of is-

chium and pubis, and passes craniodorsally to insert on the caudal surface of the proximal end of the femur just distal to the insertions of Pars dorsalis and of M. obturatorius medialis. A few of the most dorsal fascicles insert on the deep ventral surface of the tendon of insertion of the latter muscle.

Comparison. —In *Psarisomus* and *Calyptomena* the muscle is as in *Eurylaimus.* In *Smithornis* and *Pseudocalyptomena* Pars dorsalis is slightly larger. Its origin begins just caudal to the level of the caudal margin of the obturator foramen, so it is considered medium in size. Pars dorsalis is absent in *Cymbirhynchus, Serilophus, Philepitta, Neodrepanis,* and *Pitta.*

In *Acanthisitta* and *Xenicus* Pars dorsalis is extremely large, arising from the caudoventral margin of the ilio-ischiadic fenestra and inserting on the femur over the insertion of the obturatorius medialis tendon (Fig. 30).

Variations in the size and presence of Pars dorsalis have in the past been used as taxonomic characters, but are of uncertain value. Because of the small size and deep position of the muscle, it is extremely subject to deterioration because of poor fixation, as well as to dissection artifacts.

M. OBTURATORIUS MEDIALIS (OM)
(Figs. 5, 6, 8, 18, 20, 22, 24, 30, 31)

Eurylaimus. —This flat, bipennate muscle occupies the ischiopubic fenestra on the medial surface of the pelvic girdle, arising fleshy from the medial surfaces of the ischium and pubis that form the rim of the fenestra. It is situated medial to the ischiopubic membrane, which spans the fenestra. The tendon of insertion passes craniolaterally through the obturator foramen to insert on the caudolateral corner of the trochanter of the femur. In shape the belly is elongate and narrow, and extends farther caudad at its ventral margin than at its more rounded dorsal margin.

Comparison. —In *Calyptomena* the caudal margin is more rounded than in *Eurylaimus,* especially on the ventral side. In *Philepitta* and *Neodrepanis* the muscle is distinctly different in shape, being nearly triangular with a long, rounded caudal margin (Figs. 20 and 22). In the Acanthisittidae the muscle is rather elliptical (Fig. 31). Such shapes occur widely among passerines, so a polarity determination is not possible.

M. PUBO-ISCHIO-FEMORALIS (PIFCA, PIFCR)
(Figs. 5, 6, 8, 20, 22, 24, 29, 31, 32)

Eurylaimus. —This muscle consists of two separate bellies. *Pars cranialis* (PIFCR) is a wide, parallel-fibered muscle. It arises fleshy from the ventral margin of the Ala ischii just dorsal to the ischiopubic fenestra, and at its cranial end, from the cranial extremity of the pubis just ventral to the obturator foramen and M. obturatorius lateralis pars ventralis. The origin is separated from that of M. flexor cruris medialis by the intervening origin of Pars caudalis. The muscle passes craniodistally to fleshy insertion along the caudal face of the femoral shaft beginning proximally at the level of the M. ischiofemoralis insertion and continuing distally to the proximal edge of the medial femoral condyle. Along its caudal border the muscle slightly overlaps the cranial edge of Pars caudalis.

Pars caudalis (PIFCA) is a parallel-fibered muscle lying caudal to Pars cranialis and entirely separate from it. It arises from the ventral margin of the Ala ischii

just caudal to the origin of Pars cranialis. The origin is mainly fleshy. The belly passes distad to fuse into the dorsomedial surface of M. gastrocnemius pars intermedia, its more cranial fibers contributing to the tendinous origin of the latter.

Comparison. —In the other eurylamids the origin of Pars cranialis begins slightly farther caudally, at the caudal edge of M. obturatorius lateralis pars ventralis rather than ventral to it. The same is true in *Philepitta, Neodrepanis, Acanthisitta,* and *Xenicus.*

The origin of Pars caudalis is by a wide, flat tendon, rather than mainly fleshy, in the other eurylaimids, the philepittids, and the acanthisittids. There is some variation in the level at which the fleshy belly arises from this tendon. In *Pseudocalyptomena* the tendon is relatively long, the belly arising distal to the pubis. In *Psarisomus* it is shorter, the belly arising proximal to the pubis. In the others the belly arises at about the level of the pubis.

MUSCLES OF THE CRUS

M. TIBIALIS CRANIALIS (TCR)
(Figs. 2, 3, 6, 8, 20, 22, 24, 27, 28, 31, 32)

Eurylaimus. —This muscle lies on the cranial surface of the crus deep to M. fibularis longus, arising by two heads which remain separate for most of the muscle's length. The tibial head (*Caput tibiale*) arises fleshy from the lateral and cranial cnemial crests and the intervening patellar crest of the head of the tibiotarsus. The femoral head (*Caput femorale*) arises by a short, stout tendon from the apex of the lateral femoral condyle. The two heads converge on a common tendon of insertion, fusing near the distal end of the tibiotarsus. The tendon passes beneath the transverse ligament (*Ligamentum transversum*), crosses the intertarsal joint, and inserts on the proximocranial surface of the tarsometatarsus.

Comparison. —In *Neodrepanis* the muscle is less robust than in most species studied. The fleshy belly does not extend the full distance to the Ligamentum transversum, but gives rise to the tendon a short distance before it. In *Pitta* the belly extends only about two-thirds the length of the crus, whereas in *Acanthisitta* and *Xenicus* it extends only a little more than one-half the length of the crus.

M. EXTENSOR DIGITORUM LONGUS (EDL)
(Figs. 4–6, 8, 10, 20, 22, 24, 25, 29, 32)

Eurylaimus. —This is the deepest muscle on the cranial surface of the crus, lying deep to M. tibialis cranialis. It arises fleshy from the lateral surface of the medial cnemial crest, the patellar crest, and the distal end of the lateral cnemial crest. The belly is asymmetrically bipennate at the origin, changing to unipennate for most of its length. The belly extends along the tendon of insertion for most of the length of the tibiotarsus, ending just proximal to the transverse ligament. The tendon continues under the transverse ligament and then beneath the supratendinal bridge (*Pons supratendineus*) at the distal end of the tibiotarsus, and from there crosses the intertarsal joint. At the dorsoproximal end of the tarsometatarsus the tendon is held in place by a fibrous loop, the tarsometatarsal extensor retinaculum (*Retinaculum extensorium tarsometatarsi*). Then, it continues distad along the dorsal surface of the tarsometatarsus, initially between the origin of M. extensor hallucis longus and the insertion of M. iliotibialis cranialis, and beyond the latter

dorsolaterally to the former muscle. Near the distal end of the tarsometatarsus the tendon divides into three branches, one to each of the three forward toes. Each branch passes along the dorsal surface of its respective digit to insert at the base of the ungual phalanx. There are also secondary insertions more proximally by branches of the main tendons, but these will not be described.

Comparison. — The belly is slightly shortened in *Neodrepanis,* a condition which is probably a reflection of this species small size. The belly is quite short in *Pitta* as well. In the Acanthisittidae the belly extends only one-half the length of the crus.

In the Eurylaimidae and Philepittidae the belly is highly asymmetrical, approaching a unipennate condition for much of its length as the fleshy belly extends much farther distad along the medial side of the tendon than the lateral side. This is also true in the Acanthisittidae, although the belly is more slender. In *Pitta,* by contrast, this extension is hardly evident, the muscle being nearly symmetrical (Fig. 10).

M. FIBULARIS LONGUS (FL)
(Figs. 1, 6, 7, 11, 14, 17–24, 26, 27)

Eurylaimus. — This well-developed muscle occupies the craniolateral surface of the crus, cranial to M. flexor perforans et perforatus digiti III and superficial to M. tibialis cranialis. It has a fleshy origin from the cranial and lateral cnemial crests, and from the patellar crest. In addition there is an aponeurotic origin from the medial surface of the cranial cnemial crest; this aponeurosis overlies M. tibialis cranialis adjacent to the tibiotarsus on the medial side of the crus. The muscle is bipennate, the fibers converging on a central tendon. The belly extends nearly the full length of the crus. The tendon continues distad and divides into two branches. The fleshy belly extends right up to the bifurcation of the tendon, some fibers even inserting onto its shorter branch. The shorter branch of the tendon fuses with the proximolateral corner of the tibial cartilage. The larger branch continues distad, passes beneath a retinaculum, then superficial to the M. fibularis brevis tendon. It crosses the intertarsal joint to the proximolateral surface of the tarsometatarsus, passes beneath another retinaculum, and enters the bundle of tendons exiting the hypotarsus, where it fuses with the tendon of M. flexor perforatus digiti III.

Comparison. — There is variation in the relative length of the fleshy belly, but this is variable, size-related, and difficult to characterize.

M. FIBULARIS BREVIS (FB)
(Figs. 1–3, 14, 17, 23, 27–29)

Eurylaimus. — This long, narrow, asymmetrically bipennate muscle lies deep on the lateral surface of the crus. It arises fleshy from the craniolateral surface of the fibular shaft caudal to the M. iliofibularis insertion, and from the craniolateral surface of the shaft of the tibiotarsus for most of its length. This corresponds to the "fibular head" described by Raikow (1976:785); there is no "tibial head" as in the Drepanididae. The belly terminates distally in a tendon that passes beneath the fibularis retinaculum *(Retinaculum m. fibularis)* just proximal to the lateral condyle, crosses the intertarsal joint, and inserts on the proximolateral corner of the tarsometatarsus.

Comparison. — In *Neodrepanis* the muscle is less robust, the belly extending about three-fourths the length of the crus instead of reaching to the retinaculum. In *Pitta* the muscle is slender and reaches about two-thirds the length of the crus, and in the Acanthisittidae only about half that length.

M. GASTROCNEMIUS (GI, GL, GM, GS)
(Figs. 1, 6–8, 11, 14, 17–27, 31, 32)

Eurylaimus. — This muscle consists of four separate bellies that contribute to a common tendon of insertion. *Pars lateralis* (GL) is a large, fusiform or spindle-shaped muscle on the caudolateral surface of the crus. It arises by a flat tendon from the distolateral surface of the femoral shaft proximal to the lateral condyle and deep to M. femorotibialis externus pars distalis. The lateral arm of the biceps loop fuses with this tendinous origin. The muscle is unusually well-developed in *Eurylaimus,* its cranial border overlying the distal portion of M. flexor perforans et perforatus digiti III and nearly all of M. flexor perforatus digiti IV, so that its margin reaches and slightly overlaps M. fibularis longus. In most forms the two flexor muscles are visible between the gastrocnemius and fibularis longus (cf. Figs. 1 and 14). The tendon of origin spreads over the medial surface of the belly. The tendon of insertion arises over the lateral surface of the belly as it narrows distally, and joins with the tendons of the other bellies to form the common tendon of insertion of M. gastrocnemius.

Pars intermedia (GI) is the smallest and most deeply situated of the four bellies comprising M. gastrocnemius. It arises partly fleshy and partly by short tendinous fibers from the proximocaudal margin of the medial femoral condyle just medial to the insertion of M. flexor cruris lateralis pars accessorius, and in close association with the insertion of M. pubo-ischio-femoralis pars caudalis. The narrow, elongated belly is essentially parallel-fibered. It extends less than half the length of the crus, then gives rise to a tendon that joins with those of the other bellies in forming the common gastrocnemius tendon of insertion. Tendon G from M. flexor cruris lateralis joins the dorsal margin of the distal one-fourth of the belly, and also contributes to the tendon of insertion.

Pars medialis (GM) lies on the medial surface of the crus deep to Pars supramedialis. It arises fleshy from the head of the tibiotarsus, i.e., the medial surface of the cranial cnemial crest, starting just distal to the origin of Pars supramedialis. It passes distad, giving rise to a tendon over its medial surface, which continues distad to join the tendons of the other bellies in forming the common tendon of the muscle. This belly is not typical of its form in passerines, in which it is typically broad, with a convex cranial margin. Instead it is relatively narrow, attenuate, and its cranial margin is slightly concave proximally, all of which give it a distinctive appearance (Fig. 7).

Pars supramedialis (GS) lies on the medial surface of the crus, medial (superficial) to Pars medialis (Fig. 6). It is a fourth separate belly of M. gastrocnemius, and to my knowledge has never been described before. It arises by fleshy fibers and a few tendinous fibers from the medial surface of the head of the tibiotarsus, and slightly also from the patellar ligament. The belly passes distad superficial to Pars medialis. It narrows to form a narrow tendon that continues distad superficial to the distal end of the belly of Pars medialis and to the proximal end of the tendon of the latter. It fuses into the common tendon of M. gastrocnemius slightly

proximal to the tibial cartilage. The belly is sufficiently wide as to cover all but the barest edge of the underlying Pars medialis.

The common tendon of insertion of M. gastrocnemius passes over the tibial cartilage and over the hypotarsus, to whose lateral and medial edges it has loose connections. Beyond the hypotarsus it turns laterally and spreads out to an insertion on the low lateral plantar crest (*Crista plantaris lateralis*) on the caudolateral surface of the tarsometatarsus.

Comparison.—There is variation in the size of M. gastrocnemius pars lateralis. In *Psarisomus* it is as large as in *Eurylaimus,* also reaching contact with M. fibularis longus. In *Pseudocalyptomena* (Fig. 17), *Cymbirhynchus,* and *Serilophus* it is less enlarged, so that M. flexor perforans et perforatus digiti III is exposed but M. flexor perforatus digiti IV is more or less covered. In the remaining forms it is still smaller, so that both flexors are exposed.

Pars supramedialis is present in *Psarisomus* in a similar size to that in *Eurylaimus,* is somewhat smaller in *Cymbirhynchus* and *Philepitta* (Fig. 20), is rather small in *Serilophus,* and is lacking in the remaining forms dissected (Figs. 18, 22, 24, 31).

The unusual attenuate form of Pars medialis occurs in all of the eurylaimids and philepittids dissected. In *Pitta* Pars medialis is large and its cranial margin extends around to the craniomedial surface of the crus and is convex rather than concave; in this it is of typical passerine form. The muscle arises fleshy from the medial surface of the head of the tibiotarsus by superficial and deep heads. The superficial head arises in part as a patellar band from about one-half the length of the patellar ligament. In *Acanthisitta* and *Xenicus* Pars medialis does not have the attenuate form described in *Eurylaimus.* It is large, with a convex cranial margin as in most passerines, and arises from the head of the tibiotarsus by superficial and deep heads (Fig. 31). The superficial head arises in part from the patellar tendon, where its origin (patellar band) spans the full length of the tendon in *Acanthisitta,* and half that length in *Xenicus.*

In the Pittidae and Acanthisittidae the tendon of insertion of M. gastrocnemius has a dense connection with the connective tissue covering the flexor tendon bundle on the plantar surface of the pes, merging with it so that essentially it inserts on both lateral and medial plantar crests. It lacks the clear distinction from that connective tissue, and the consequent restriction of insertion to the lateral plantar crest only, which is found in the eurylaimids and philepittids (Fig. 11).

M. PLANTARIS (PL)
(Figs. 5, 8, 25, 32, 33)

Eurylaimus.—This muscle lies in the caudomedial region of the crus. It arises fleshy from the caudomedial surface of the head of the tibiotarsus medial to the origin of the medial head of M. flexor digitorum longus, and just lateral to the medial collateral ligament (*Ligamentum collaterale mediale*). It has an elongated triangular shape, flattened mediolaterally. The narrowly fan-shaped belly approaches a unipennate arrangement as the deeper fibers pass to the tendon of insertion, which arises as a superficial sheet over the distal part of the medial side of the belly. The belly extends distad approximately one-third the length of the crus, and the tendon proceeds to its insertion at the proximomedial corner of the tibial cartilage.

Comparison. —In *Neodrepanis* the belly extends only one-fifth the length of the crus, and about one-fourth in the Acanthisittidae.

M. FLEXOR PERFORANS ET PERFORATUS DIGITI II (FPPD2)
(Figs. 2, 14, 17, 19, 21, 23, 28)

Eurylaimus. —This muscle lies on the proximolateral surface of the crus, caudal to M. flexor perforans et perforatus digiti III, and mostly deep to M. gastrocnemius pars lateralis. The origin is fleshy from the proximocaudal margin of the lateral femoral condyle in close association with the tendon of origin of the lateral head of M. flexor hallucis longus, and distal to the origin of M. gastrocnemius pars lateralis. The belly is flattened and spindle-shaped, extending about one-fourth the length of the crus. The fine tendon of insertion arises on the lateral surface of the belly and proceeds distad. It passes through the medial regions of the tibial cartilage and hypotarsus, and continues along the plantar surface of the tarsus to the base of digit II, where it inserts on the medial side of the proximal end of the second phalanx. An elastic vinculum arises from the deep surface of the tendon just before the latter's insertion and inserts on the distoplantar surface of the first phalanx.

Comparison. —No significant variations were noted in this muscle.

M. FLEXOR PERFORANS ET PERFORATUS DIGITI III (FPPD3)
(Figs. 1, 14, 17, 19, 21, 23, 26, 27)

Eurylaimus. —This muscle lies on the lateral surface of the crus cranial and partly deep to M. gastrocnemius pars lateralis and caudal to M. fibularis longus. The proximal part of the long, slender belly is bipennate, the distal part becoming unipennate. The origin is by two heads. The cranial head is more superficial, arising fleshy from the lateral cnemial crest and adjacent patellar tendon. The deeper caudal head arises by an aponeurosis from the lateral femoral condyle in association with M. flexor perforatus digiti II and M. flexor perforans et perforatus digiti II. The tendon of insertion arises over the lateral surface of the belly. It passes distad through the tibial cartilage and hypotarsus. At the distal end of the tarsometatarsus it ensheathes the branch tendon of M. flexor digitorum longus; these then perforate the tendon of M. flexor perforatus digiti III on the plantar surface of the third digit. The tendon then bifurcates, that of M. flexor digitorum longus continuing distad. The two branches of the tendon of M. flexor perforans et perforatus digiti III insert on the lateral and medial sides of the proximoplantar end of phalanx 3.

Comparison. —In *Pitta* (Fig. 23) the belly is relatively short, extending about two-thirds the length of the crus, rather than most of its length as in the other species. In *Acanthisitta* (Fig. 27) and *Xenicus* the belly extends only about one-half the length of the crus.

M. FLEXOR PERFORATUS DIGITI II (FPD2)
(Figs. 2-4, 27, 28)

Eurylaimus. —This elongate, spindle-shaped muscle lies on the lateral side of the crus deep to the lateral head of M. flexor perforatus digiti IV and cranial to the lateral head of M. flexor digitorum longus. It originates by a wide tendon from the caudal edge of the lateral femoral condyle; a branch tendon arises from

the fibula. This tendon of origin is shared with the lateral head of M. flexor hallucis longus. The belly ends about two-thirds of the way down the crus, giving rise to a fine tendon. This passes through the tibial cartilage and hypotarsus and down the plantar surface of the tarsometatarsus. It passes through a canal in the cartilaginous pad at the base of digit II and inserts on the proximomedial corner of the first phalanx of digit II. It is not perforated here by the tendons of Mm. flexor perforans et perforatus digiti II or flexor digitorum longus.

Comparison.—The belly is relatively shorter, extending only about half the length of the crus in *Pseudocalyptomena, Serilophus, Calyptomena, Neodrepanis, Pitta, Acanthisitta,* and *Xenicus.*

M. FLEXOR PERFORATUS DIGITI III (FPD3)
(Figs. 2–4, 8, 29, 31–33)

Eurylaimus.—This elongate, spindle-shaped muscle lies deep in the caudal region of the crus, medial and (distally) partly superficial to M. flexor hallucis longus. It arises by a tendon from the intercondyloid region of the femur in common with the medial head of M. flexor hallucis longus, and in association with M. flexor perforatus digiti IV. The tendon of insertion arises over the medial surface, so the muscle is unipennate. The belly extends nearly to the tibial cartilage, and gives rise to a tendon that passes through the tibial cartilage and then the hypotarsus, during which it ensheathes the tendon of M. flexor perforatus digiti IV loosely. Beyond the hypotarsus the tendon is joined by the long branch tendon of M. fibularis longus, and continues distad to the base of digit III. On the plantar surface of the first phalanx the tendon bifurcates, permitting passage of the more deeply-lying tendons of Mm. flexor perforans et perforatus digiti III and flexor digitorum longus. The branches of the M. flexor perforatus digiti III tendon insert on either side of the base of the second phalanx and the cartilaginous pad underlying the joint between the first and second phalanges.

Comparison.—In *Pitta* the belly is relatively shorter, extending about three-fourths the length of the crus, whereas in *Acanthisitta* (Fig. 31) and *Xenicus* it extends only one-half this distance.

M. FLEXOR PERFORATUS DIGITI IV (FPD4)
(Figs. 2, 3, 12, 14, 19, 21, 23, 28, 29, 31–33)

Eurylaimus.—There are two heads. The *proximal head* arises fleshy from the intercondyloid region of the femur in common with M. flexor perforatus digiti III, and also from a tendinous inscription along its medial border shared with the latter muscle. Distally more fascicles also arise from the caudolateral surface of M. flexor hallucis longus. The *distal head* arises aponeurotically from the surface of M. flexor perforatus digiti II, and in part also from the surface of M. flexor hallucis longus. Here the origin is close to part of that of the medial head, and the two heads are indistinctly separated. Distally, however, the distal head extends farther caudally. The two parts of the muscle give rise to a single tendon of insertion; there are not two tendons as in many other birds. The tendon passes through the tibial cartilage and hypotarsus, and continues down the lateroplantar surface of the tarsometatarsus to the base of digit IV. Here it ensheathes the branch tendon of M. flexor digitorum longus to digit IV, passes distad on the plantar surface of digit IV, and divides into two branches. The small lateral branch

inserts at the base of the second phalanx. The main branch continues distad deep to the M. flexor digitorum longus tendon to insert at the base of the third phalanx.

   Comparison. — This muscle shows four distinct variations in the forms studied (Fig. 12). *Type 1* (Fig. 12A): In *Calyptomena, Philepitta, Neodrepanis,* and *Pitta* the muscle has two entirely separate bellies. The proximal belly arises in the intercondyloid region of the femur and by a common origin with the adjacent M. flexor perforatus digiti III. The distal belly arises over M. flexor perforatus digiti II, starting cranially at or a short distance caudal to the level of the M. iliofibularis tendon. Each belly gives rise to a separate tendon of insertion; these pass distad to join into a single tendon shortly proximal to the tibial cartilage.

   Type 2a (Fig. 12B): In *Smithornis* and *Pseudocalyptomena* the two parts are not in direct contact with each other, and so might be termed bellies. In *Smithornis* the proximal belly arises in the intercondyloid region and with M. flexor perforatus digiti III as in *Eurylaimus,* but no fascicles arise from M. flexor hallucis longus. The distal belly is relatively larger than in *Eurylaimus.* The two bellies do not have separate tendons, however, but insert onto a single common tendon.

   In *Pseudocalyptomena* the proximal belly arises by a short tendon from the distal femoral arm of the biceps loop. More distally it arises from a midline inscription with M. flexor perforatus digiti III. It has no femoral origin. This is so unusual that a developmental anomaly must be suspected. In any case it is autapomorphic and is not relevant to the problem of interspecific relationships. There is a single tendon as in *Smithornis.*

   Type 2b (Fig. 12C): *Cymbirhynchus, Serilophus,* and *Psarisomus* also share the condition described above for *Eurylaimus* in which the two bellies are in contact distally (hence, perhaps better termed "heads"), and insert on a common tendon. Compared to Types 1 and 2a, furthermore, the lateral portion is also reduced in size.

   Type 3 (Fig. 12E): In *Acanthisitta* and *Xenicus* only the proximal belly is present; the distal belly is completely lost.

M. FLEXOR HALLUCIS LONGUS (FHL)
(Figs. 2–4, 8, 13, 27–29, 33)

   Eurylaimus. — This muscle lies in the caudal region of the crus, deep to the individual flexors and superficial to M. flexor digitorum longus. It arises by several separate heads. The *lateral head* arises by a tendon from the caudolateral surface of the proximal end of the lateral condyle of the femur. It shares this origin with M. flexor perforatus digiti II, and the belly of the lateral head begins just at the distal edge of the M. iliofibularis tendon, which lies medial to it. The *intermediate head* typically passes medial to the iliofibularis tendon and merges with the tendon of origin on its medial side. In *Eurylaimus ochromalus* DEL 60888 there are two intermediate heads. The *lateral intermediate head* arises fleshy on the medial surface of the tendon of the lateral head just cranial to the M. iliofibularis tendon, passes medial to that tendon, and then merges into the medial side of the lateral head. The *medial intermediate head* arises separately from the tendon farther proximally, adjacent to the femur, and merges distally into the lateral surface of the medial head. The *medial head* is the largest part of the muscle. It arises fleshy from the intercondyloid region of the femur in common with M. flexor perforatus digiti III; many of its fibers also arise on its medial side from a broad tendon

shared with M. flexor perforatus digiti III. The belly of M. flexor hallucis longus extends distad nearly to the tibial cartilage, but is slightly shorter than the underlying M. flexor digitorum longus. In overall form it is bipennate. Fibers from the medial head and the medial intermediate head converge from the medial side, and fibers from the other heads from the lateral side, onto a central tendon of insertion. This passes through the tibial cartilage and hypotarsus and distad along the deep plantar surface of the tarsus. At about the midpoint of the tarsus a flat vinculum (branch tendon) arises on the lateroplantar surface of the tendon and passes distad to join the medioplantar surface of the M. flexor digitorum longus tendon a short distance proximal to the latter's trifurcation. This is the plantar vinculum, an important character in eurylaimid systematics. It is a single, discrete tendon, and is not divided into a group of parallel, more or less separate strands as is commonly the case in nonpasserines. The main tendon of M. flexor hallucis longus continues distad, lying just lateral to the tendon of M. flexor hallucis brevis. Together these tendons pass lateral to metatarsal I and curve around its trochlea. Here the tendon of M. flexor hallucis brevis expands and ensheathes the tendon of M. flexor hallucis longus. The flexor hallucis longus tendon proceeds distad along the plantar surface of digit I, inserting at the base of the ungual phalanx. An elastic vinculum arises from the deep surface of the M. flexor hallucis longus tendon near the distal end of the first phalanx. It divides into deep and superficial portions. The deep portion inserts on the plantar surface of the distal end of the shaft of the first phalanx. The superficial portion proceeds distad around the end of phalanx I and joins the connective tissue capsule of the joint deep to the insertion of the main tendon of M. flexor hallucis longus on the ungual phalanx.

Comparison. — Some variation is found in the origin of this muscle. The primitive condition in suboscines is an origin by three heads with the lateral head passing lateral to the M. iliofibularis tendon, the intermediate head arising in common with the lateral head but passing medial to the M. iliofibularis tendon, and the medial head arising from the intercondyloid region of the femur. This arrangement occurs commonly in both oscines and suboscines with occasional exceptions (Raikow 1976, 1978; Bentz 1979; Borecky 1977; Raikow et al. 1980). In the present study this condition occurred in most species. The division of the intermediate head into two parts in *Eurylaimus ochromalus* (Fig. 4) is exceptional and possibly anomalous. In most species, including *E. steeri,* the intermediate head is single, and arises fleshy from the medial surface of the proximal end of the tendon of the lateral head (and M. flexor perforatus digiti II) and from the adjacent femoral surface. In *Pitta* the intermediate head arises partly fleshy and partly by a tendon that spreads over its proximolateral surface. Also in *Pitta* the belly extends about three-fourths the length of the crus.

In *Philepitta* there are only two heads of origin. The lateral and medial heads arise in the usual way as described in *Eurylaimus,* but there is no intermediate head. Instead a femoral head of M. flexor digitorum longus occupies the space between the lateral and medial heads, a condition previously reported in *Lanius* (Raikow et al. 1980).

In *Acanthisitta* and *Xenicus* the muscle arises by the three typical passerine heads. The lateral head arises by a flat tendon (shared with M. flexor perforatus digiti II) from the lateral femoral condyle and adjacent fibular head. This passes lateral to the iliofibularis tendon before becoming fleshy. The intermediate head is also tendinous at its origin just medial to the lateral head, but passes medial

to the iliofibularis tendon. The medial head is the largest, having a fleshy origin from the popliteal region and closely associated with the intermediate head. The belly extends one-half the length of the crus.

A plantar vinculum, connecting the tendon of M. flexor hallucis longus to that of M. flexor digitorum longus, was found in all of the eurylaimids dissected (Fig. 13), but not in *Pitta* or *Neodrepanis* (in which both feet were carefully checked), nor in the Acanthisittidae. However, it was found in *Philepitta,* contrary to Forbes (1880b:390). This is apparently the first report of a plantar vinculum in any passerine species outside of the Eurylaimidae.

M. FLEXOR DIGITORUM LONGUS (FDL)
(Figs. 2–5, 8, 13, 25, 29, 32, 33)

Eurylaimus. —This is the deepest muscle on the caudal surface of the crus, lying deep to M. flexor hallucis longus. The smaller lateral (fibular) head arises fleshy from the caudal surface of the head and shaft of the fibula. The somewhat larger medial (tibiotarsal) head arises fleshy from the caudal surface of the head and proximal end of the shaft of the tibiotarsus just lateral to M. plantaris. There is no femoral head as in some passerine birds. The fibers from the two heads converge upon a central tendon, so that the muscle is bipennate in architecture. The belly extends nearly the full length of the crus. The tendon passes through the tibial cartilage and hypotarsus and proceeds distad along the plantar surface of the tarsometatarsus, emerging proximally from a position deep to the laterally expanded portion of M. flexor hallucis longus. Near the distal end of the tarsometatarsus M. lumbricalis arises from the deep surface of the tendon. The tendon then divides into three branches. The branch to digit II passes through a deep portion of the cartilaginous joint pulley at the base of the digit and proceeds distad along the plantar surface of the digit to insert at the base of the ungual phalanx. Near its termination it gives rise to an elastic vinculum which inserts on the plantar surface of the second phalanx. The branch to digit III inserts on the base of the ungual phalanx, and by means of elastic vinculae, onto the plantar surface of the distal end of phalanx 3 and on the cartilaginous pad at the proximal end of phalanx 3. The branch to digit IV is ensheathed at the base of the digit by the tendon of M. flexor perforatus digiti IV. It then continues distad to insert at the base of the ungual phalanx, giving off elastic vinculae to the proximal and distal ends of phalanx 4.

Comparison. —In *Smithornis* and *Serilophus* the branch tendon to digit IV has an additional vinculum to the proximal end of phalanx 3. In *Acanthisitta* and *Xenicus* the branch to digit III has a single vinculum to phalanx 3, and the branch to digit IV sends vinculae to the proximal ends of phalanges 2, 3, and 4.

In addition to the usual medial and lateral heads, this muscle in *Philepitta* also arises by a fairly well-developed femoral head that has a fleshy origin from the caudolateral surface of the distal end of the femoral shaft just proximal to the lateral condyle (character 19 in Tables 1 and 2). This passes distad to merge via a flat aponeurotic sheet into the dorsal surface of the main part of the muscle at the level at which the other heads also converge. All three heads thus contribute to the formation of the common central tendon. *Neodrepanis,* like the eurylaimids and pittids, lacks a femoral head. In *Pitta* the belly extends three-fourths the length of the crus.

MUSCLES OF THE PES

M. EXTENSOR HALLUCIS LONGUS (EHL)
(Figs. 13, 34)

Eurylaimus. —This muscle lies on the dorsomedial surface of the tarsometa-
tarsus. Its origin is fleshy from the proximal dorsal surface of the tarsometatarsus
beginning just distal to the medial cotyla, and medial to the tendons of Mm.
tibialis cranialis and extensor digitorum longus. Laterally the origin spreads over
the dorsal face of the tarsometatarsus deep and lateral to the M. extensor digitorum
longus tendon, having its most proximal margin just lateral and slightly proximal
to the tibialis cranialis insertion. The belly extends distally as far as the middle
of the first metatarsal. The tendon of insertion arises on the dorsomedial surface
of the muscle, whose fiber arrangement is basically unipennate. This constitutes
the portion called the proximal belly or head in those forms also having a separate
distal portion (Raikow 1976:789). No distal portion occurs in *Eurylaimus,* how-
ever. The belly ends near the distal medial margin of the first metatarsal. The
tendon of insertion passes across the ventromedial surface of the first metatarsal,
against which it is held by a retinaculum. It passes to the dorsal surface of the
hallux, against which it is pressed by another retinaculum from the joint capsule.
It then proceeds distad along the dorsal surface of phalanx I to insert at the base
of the second or ungual phalanx in association with an automatic extensor liga-
ment.

Comparison. —In *Pseudocalyptomena* the muscle is smaller. The origin is lim-
ited to the region medial to the extensor digitorum longus and tibialis cranialis
tendons, and does not spread deep and lateral to the extensor digitorum longus
tendon as in *Eurylaimus.* Also, the belly is shorter, extending only one-half the
length of the tarsometatarsus. In *Calyptomena* the belly is very robust. In *Pitta*
the belly is very slender and extends only one-half the length of the tarsometa-
tarsus.

In *Acanthisitta* (Fig. 34) and *Xenicus* this muscle is reduced to an apparently
vestigial state. It has a fleshy origin from the proximodorsal surface of the tar-
sometatarsus slightly medial and proximal to the point of emergence of the M.
extensor digitorum longus tendon. The belly is extremely narrow and passes distad
in the Sulcus extensorius just medial to the extensor digitorum longus tendon.
The belly extends less than one-third the length of the tarsometatarsus before
giving rise to a fine, hairlike tendon. There is no distal belly. The tendon passes
as usual over the first metatarsal and onto the dorsal surface of the first phalanx
of the hallux, where it becomes incorporated into an unusually well-developed
automatic extensor ligament. This latter structure is connected also to the first
metatarsal, and evidently serves to keep the whole hallux extended when the flexor
digitorum longus is relaxed. This automatic extensor mechanism has apparently
largely replaced M. extensor hallucis longus functionally.

M. FLEXOR HALLUCIS BREVIS (FHB)
(Figs. 11, 13, 34)

Eurylaimus. —This muscle lies on the proximomedial surface of the tarsometa-
tarsus. It arises from the medial surface of the hypotarsus, and also from the

distolateral hypotarsal surface on the plantar aspect of the tarsometatarsus. These two areas of origin are separated by a deep groove in the muscle's surface, in which several digital flexor tendons lie as they exit the hypotarsus. The condition approaches a bicipital arrangement, except that the two areas of origin are connected by continuity of muscle tissue in the floor of the groove.

The belly is fairly stout and extends about one-half the length of the tarsometatarsus. It gives rise to a tendon that passes distad beneath metatarsal I beside the tendon of M. flexor hallucis longus. The tendon passes over the trochlea of metatarsal I and expands to ensheathe the tendon of M. flexor hallucis longus, and merges into the joint capsule at the base of the hallux.

Comparison.—In *Calyptomena* this muscle is unusually stout (Fig. 34). In *Philepitta* and *Neodrepanis* the expanded part of the muscle only reaches to the distal hypotarsal surface; it does not reach as far laterally as in the Eurylaimidae. In *Neodrepanis* it is only about one-fourth the length of the tarsometatarsus.

In *Pitta versicolor* and *P. guajana* the muscle is relatively small and slender, reaching about one-third the length of the tarsometatarsus. It arises only from the medial part of the hypotarsus; there is no expansion laterally nor any groove as in the Eurylaimidae and Philepittidae. However, in *P. brachyura* and *P. erythrogaster* a comparable moderate expansion has occurred.

This muscle is apparently completely lacking in *Acanthisitta* and *Xenicus*; I could find no trace of it even with iodine staining.

M. ABDUCTOR DIGITI IV(ABD4)
(Fig. 13)

Eurylaimus.—This very small muscle lies on the caudolateral surface of the distal end of the tarsometatarsus, and is only about one-fifth the length of the tarsometatarsus. It arises fleshy and is asymmetrically bipennate. The tendon of insertion passes distad and merges into the joint capsule at the juncture of the trochlea for digit IV with the first phalanx of that digit. The insertion is thus onto the proximolateral corner of phalanx I of digit IV, but more as part of the joint capsule than as a discrete tendon.

Comparison.—This muscle was not found in *Pitta*. In *Xenicus* a tiny vestige was seen, comparable in position but even smaller than in *Eurylaimus*. It was stretchy and might be more of an elastic ligament than a muscle in this form. I could not detect this muscle with certainty in *Acanthisitta*, but because of the small size of the specimen it is possible that some faint vestige was undetected.

M. LUMBRICALIS (L)
(Fig. 13)

Eurylaimus.—This tiny strap-shaped structure arises on the deep (dorsal) surface of the tendon of insertion of M. flexor digitorum longus at its distal end, just at the point of trifurcation. It passes a short way distad to insert on the joint pulleys at the base of the forward toes. The tissue absorbs iodine stain less readily than do other muscles, and perhaps in this form M. lumbricalis consists more of connective tissue, perhaps elastic tissue, than of muscle.

Comparison.—No significant variations were noted in this muscle.

DISCUSSION OF MORPHOLOGICAL CHARACTERS

MYOLOGICAL CHARACTERS

Many of the variations described above consist of small differences in the relative size or proportions of muscles. The genetic basis for such variations must be minimal, and there is a suspicion that individual variation within a species might exceed variation between species. For these reasons such character states will not be used for the interpretation of phylogenetic relationships. In this section I will analyze the polarity and significance of those variations that are sufficiently distinct as to be of value in the generation of phylogenetic hypotheses.

M. iliotibialis lateralis. — An acetabular gap occurs in all of the Eurylaimidae, Philepittidae, and Pittidae dissected. This is considered to be a derived condition in birds, resulting from the loss of the central or acetabular part of the muscle, which is present in most, but not all, oscines and nonpasserines (George and Berger 1966:385–388). An acetabular part is commonly present in the Piciformes, although reductional trends also occur (Swierczewski 1977; Swierczewski and Raikow 1981), and a similar pattern is seen in the Coraciiformes (Maurer 1977; Maurer and Raikow 1981). *Colius* has only a preacetabular part (Berman and Raikow 1982). Thus, the preacetabular and postacetabular portions are separated as distinct muscles in the Eurylaimidae, Philepittidae, and Pittidae, and are here referred to as bellies of a single muscle somewhat arbitrarily on the basis of their historical derivation. This condition is also found (pers. obs.) in some species of the two New World suboscine assemblages, the Furnarii (*Thamnophilus doliatus*: Formicariidae; *Dendrocolaptes certhia*: Dendrocolaptidae) and the Tyranni (*Pachyramphus rufus*: Cotingidae). However, other species in each of those groups retain the primitive intact condition of the muscle (*Acropternis orthonyx*: Rhinocryptidae; *Certhiaxis cinnamomea*: Furnariidae; *Procnias nudicollis*: Cotingidae), indicating that an acetabular gap originated independently in those groups from its origin in the present assemblage. Thus, this character state serves as a synapomorphy for the Eurylaimidae, Philepittidae, and Pittidae, but because it has arisen in other groups, the possibility remains that it also arose more than once in the present assemblage. It is parsimonius to accept it as a synapomorphy of this group, but one must recognize that it is a relatively uncertain character state. The acetabular gap is listed as character state 1.1 in Tables 1 and 2.

The reduction in size of the postacetabular belly in *Smithornis* and *Calyptomena* is considered to be further derived relative to the origin of the acetabular gap (character state 2.1 in Tables 1 and 2), as it appears to be a stage in a directional trend.

The division of the postacetabular belly into two parts in *Pitta* has not been described in any other birds, passerine or nonpasserine, as far as I know. Given passerine monophyly, this distinct and apparently unique character state thus serves as a synapomorphy of the Pittidae (character state 3.1 in Tables 1 and 2).

M. iliotrochantericus caudalis. — The shortened superficial fascicles (Fig. 16) are a synapomorphy of the *Calyptomena* species dissected because they occur neither in other suboscines nor oscines, nor for that matter, in any nonpasserines that I know of. This is character state 4.1 in Tables 1 and 2.

Mm. iliotrochantericus cranialis and iliotrochantericus medius. — These two muscles are separate in most passerine and nonpasserine birds, so given passerine

TABLE 1
CHARACTER STATES USED IN PHYLOGENETIC ANALYSIS[a]

1. M. iliotibialis lateralis (IL) acetabular gap absent (1.0) or present (1.1).
2. M. iliotibialis lateralis (IL) postacetabular belly large (2.0) or reduced (2.1).
3. M. iliotibialis lateralis (IL) postacetabular belly insertion single (3.0) or double (3.1).
4. M. iliotrochantericus caudalis (ITCA) superficial fascicles end distally (4.0) or are shortened relative to deeper fascicles (4.1).
5. Mm. iliotrochantericus cranialis (ITCR) and iliotrochantericus medius (ITM) tendons of insertion separate (5.0) or fused (5.1).
6. Mm. iliotrochantericus cranialis (ITCR) and iliotrochantericus medius (ITM) separate (6.0) or fused with ITM reduced (6.1).
7. M. iliofemoralis internus (IFI) parallel-fibered (7.0) or fan-shaped (7.1).
8. Mm. flexor cruris lateralis (FCRL) and flexor cruris medialis (FCRM) tendons of insertion joined (8.0) or separate (8.1).
9. M. pubo-ischio-femoralis pars caudalis origin restricted cranially (9.0) or expanded caudally (9.1).
10. M. extensor digitorum longus (EDL) belly asymmetrical (10.0) or symmetrical (10.1).
11. M. gastrocnemius pars lateralis (GL) small and does not overlie lateral flexors (11.0), or large and does overlie lateral flexors (11.1).
12. M. gastrocnemius pars supramedialis (GS) absent (12.0) or present (12.1).
13. M. gastrocnemius pars medialis (GM) of normal shape (13.0) or attenuate, with concave cranial margin (13.1).
14. M. gastrocnemius (G) insertion expanded over flexor tendons (14.0) or restricted (14.1).
15. M. flexor perforatus digiti IV (FPD4) with two bellies and two tendons [Type 1] (15.0), two bellies and one tendon [Type 2a] (15.1), or two bellies in contact [Type 2b] (15.2).
16. M. flexor perforatus digiti IV (FPD4) with two bellies and two tendons [Type 1] (16.0), or one belly and tendon [Type 3] (16.1).
17. M. flexor hallucis longus (FHL) intermediate head present (17.0) or absent (17.1).
18. Plantar vinculum absent (18.0) or present (18.1).
19. M. flexor digitorum longus (FDL) femoral head absent (19.0) or present (19.1).
20. M. flexor hallucis brevis (FHB) origin lacking groove or lateral expansion (20.0), grooved and with moderate expansion (20.1), or grooved and with extreme expansion (20.2).
21. M. flexor hallucis brevis (FHB) present (21.0) or absent (21.1).
22. M. flexor hallucis longus (EHL) of normal size (22.0) or vestigial (22.1).
23. M. abductor digiti IV (ABD4) present (23.0) or absent (23.1).
24. Syndactyly of digits III/IV poorly developed (24.0) or well-developed (24.1).
25. Bill not enlarged in characteristic "broadbill" fashion (25.0) or so enlarged (25.1).
26. Eye wattles absent (26.0) or present (26.1).
27. Stapes unexpanded (27.0) or expanded (27.1).
28. Oscine syrinx absent (28.0) or present (28.1).

[a] Characters are numbered as in the text. Primitive states are indicated as (0), derived states as (1), and further derived states as (2).

monophyly the various types of fusion might be considered derived. Because two different patterns are seen in different groups, the conditions presumably arose separately (character states 5.1 and 6.1 in Tables 1 and 2).

M. iliofemoralis internus.—The fan-shaped belly in *Calyptomena* differs from the parallel-fibered form in the remaining species, as in most passerines both suboscine and oscine, and is, therefore, probably derived for this genus (character state 7.1 in Tables 1 and 2).

M. flexor cruris lateralis.—It is difficult to assess the polarity of character state variations in the relationship between tendon M and the tendon of M. flexor cruris medialis because earlier studies, including our own, have not described this region in sufficient detail. The complete division in most *Pitta* species is considered derived within passerines on the basis of outgroup comparison between the monophyletic assemblage of suboscines defined by the derived stapes studied by Feduccia (1975b) and the remaining passerines (character state 8.1 in Tables 1 and 2).

TABLE 2
DISTRIBUTION OF CHARACTER STATES AMONG TAXA ANALYZED[a]

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Eurylaimus steeri	1	0	0	0	1	0	0	0	0	0	1	1	1	1	2	0	0	1	0	2	0	0	0	1	1	0	1	0
E. ochromalus	1	0	0	0	1	0	0	0	0	0	1	1	1	1	2	0	0	1	0	2	0	0	0	1	1	0	1	0
Smithornis	1	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	0	0	0	1	0	0	1	0
Pseudocalyptomena	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	2	0	0	0	0	1	0	1	0
Cymbirhynchus	1	0	0	0	1	0	0	0	0	0	1	1	1	1	2	0	0	1	0	2	0	0	0	1	1	0	1	0
Serilophus	1	0	0	0	1	0	0	0	0	0	1	1	1	1	2	0	0	1	0	2	0	0	0	1	1	0	1	0
Psarisomus	1	0	0	0	1	0	0	0	0	0	1	1	1	1	2	0	0	1	0	2	0	0	0	1	1	0	1	0
Calyptomena viridis	1	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	2	0	0	0	0	0	1	1	0
C. whiteheadi	1	1	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	2	0	0	0	0	0	1	1	0
Philepitta	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	0
Neodrepanis	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0
Pitta versicolor	1	0	1	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0
P. guajana	1	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0
P. brachyura	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0
P. erythrogaster	1	0	0	0	1	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1
Acanthisitta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	1	0	0
Xenicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0
Oscines/Menurae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	0	0	?	0	0	0	1
Furnarii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	?	0	0	?	?	0	0	1	0
Tyranni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	0	0	0	1	0

[a] The characters are numbered as in the text and in Table 1. Character-states are coded 0, primitive; 1, 2, derived; ?, undetermined.

This probably arose from the overlapping condition by further separation of the two tendons, as suggested by the retention of a small connecting slip in one specimen (Fig. 25).

M. pubo-ischio-femoralis. — In *Pitta* (Fig. 24) the area of origin of Pars caudalis is extended caudally nearly to the caudal margin of M. flexor cruris medialis, which appears to be unique in the suboscine clade, and hence, a derived condition for the pittas (character state 9.1 in Tables 1 and 2).

M. extensor digitorum longus. — The symmetrical form of the belly in *Pitta* differs from the asymmetrical form in the remaining species dissected (Fig. 10). If we accept, as argued below, that the eurylaimid-philepittid-pittid group is monophyletic, then other suboscines constitute an outgroup. The muscle is long and asymmetrical in *Tyrannus, Pachyramphus, Procnias, Pipra, Thamnophilus, Certhiaxis, Dendrocolaptes,* and *Acropternis* (pers. obs.). Likewise, if we take the stapes-defined suboscine group as a clade, the oscines form an outgroup, again confirming the determination. It thus appears that the symmetrical condition in *Pitta* constitutes a reduction of the medial fleshy portion of the belly, and is synapomorphic for the *Pitta* species examined. This is character state 10.1 in Tables 1 and 2.

M. gastrocnemius. — The smaller area size of Pars lateralis is the usual condition in other suboscines and in oscines, and is therefore primitive within suboscines, enlargement being derived (character state 11.1 in Tables 1 and 2). Because Pars supramedialis is not known to occur elsewhere in the suboscine clade, or for that matter in passerines or any other birds, it is clearly a derived state (12.1 in Tables 1 and 2). A similar argument indicates tha the attenuate form of Pars medialis is likewise derived (character state 13.1 in Tables 1 and 2).

The restricted area of insertion of the gastrocnemius tendon in eurylaimids and philepittids appears to be unique to these two groups among passerines, and on the basis of suboscine monophyly might be considered derived within the passerine birds (character state 14.1 in Tables 1 and 2).

M. flexor perforatus digiti IV. — There is a morphocline or transformation series from Type 1 to 2a to 2b. Type 1 is the primitive condition in the Passeriformes. This arrangement, with two bellies, is common among nonpasserines (Hudson 1937:42–44; George and Berger 1966:435–437), including the Coliiformes (Berman and Raikow 1982), some Coraciiformes and Trogoniformes (Maurer 1977), and most Piciformes (Swierczewski 1977; Swierczewski and Raikow 1981). (It should be noted, however, that the descriptions of the two parts are sufficiently varied and often unclear that homology between them in different taxa is sometimes uncertain. Also, in some nonpasserines having only a single part to the muscle, it is not always apparent from the description which part this is.) There is another reason for considering Type 1 to be primitive among passerines. It is well known (see below) that oscines have the Type 3 condition, with a distal belly lacking. Once I found a fully developed Type 1 condition bilaterally in a specimen of *Serinus mozambicus* (pers. obs.). This is best explained as the atavistic reappearance of a lost structure, a phenomenon well documented for the avian limb musculature (Raikow 1975; Raikow et al. 1979; Hall 1984).

Type 2a appears to have evolved from Type 1 by the fusion of the separate tendons of insertion, with the two bellies retaining their distinctiveness (character state 15.1 in Tables 1 and 2). In a further step, Type 2b evolved from Type 2a

by the coalescence of the two bellies, with the obliteration of the intervening
exposed segment of tendon, and the reduction in size of the lateral component
(character state 15.2 in Tables 1 and 2). A condition similar to Type 2b also
occurs in the Tyrannidae and their relatives, but differs in detail and apparently
evolved separately. Whereas in the Eurylaimidae the two parts are largely separate,
with the distal belly lying mainly distal to the proximal belly and bordered medially
by tendon, in *Tyrannus tyrannus* the two bellies are largely fused together in a
quite different way (Fig. 12D). McKitrick (1985b) found additional variations in
the Tyrannidae.

The loss of the distal belly (Type 3) is also clearly derived on the basis of
outgroup comparison to nonpasserines, although there is no way to know whether
it arose via transitional states like those of Type 2. Type 3 occurs not only in the
Acanthisittidae but also in the oscines (Raikow 1976, 1978; Borecky 1977; Bentz
1979; Raikow et al. 1980; Urik 1983), including the Atrichornithidae and Me-
nuridae (Raikow 1985d). The presence of Type 3 is character state 16.1 in
Tables 1 and 2.

M. flexor hallucis longus. — The absence of the intermediate head in *Philepitta*
is evidently a derived state within the suboscines as determined by outgroup
comparison to oscines; most forms in both groups possess this structure. This is
character state 17.1 in Tables 1 and 2.

Plantar vinculum. — This connection between the tendons of Mm. flexor hallucis
longus and flexor digitorum longus has been an important taxonomic character
since Garrod (1877) reported that it set the Eurylaimidae apart from all other
passerines. Its presence has been considered a primitive character state, a holdover
from passerine ancestry, and thus a reason to consider the Eurylaimidae to be the
most primitive of living passerines. The discovery of the vinculum in *Philepitta*
is also of interest because it deprives the Eurylaimidae of their last remaining
unique traditional character state (Olson 1971).

The assumption that the plantar vinculum is primitive within the passerines
was developed from a casual outgroup comparison based on the observation that
most nonpasserine birds have connections of one kind or another between the
deep plantar tendons. This was unconsciously simplified in the literature to imply
a simple two-state condition: birds either have a connection or lack one. However,
the reality is much more complex. Birds show a bewildering variety of different
structural relationships between the deep plantar tendons, from complete sepa-
ration, to virtual separation except for a simple vinculum, through various degrees
and patterns of fusion and interconnection in association with different functional
and adaptive specializations of the feet (see Raikow 1985c for a review). It is
evident that the plantar tendons of birds are readily modified in various ways in
the course of evolution. There is no reason to believe that evolution leads only
to a loss of connections between the tendons; the establishment of new connections
must often occur as well. The evolution of the passerine plantar vinculum must
be examined in this context.

As I pointed out previously (Raikow 1982:439–440), the traditional belief that
the eurylaimid vinculum is primitive conflicts with other characters, including
the derived suboscine stapes studied by Feduccia (1975b). If the eurylaimid vin-
culum is primitive, then the Eurylaimidae and Philepittidae are excluded from
the monophyletic group defined by the stapes, and their derived stapes must have

evolved convergently with that of other suboscines. It is also in conflict with the acetabular gap of M. iliotibialis lateralis described above.

Although the origin of the Passeriformes is still a mystery, they are usually thought to be related to the Coraciiformes or Piciformes. In the former group a great variety of different plantar tendon arrangements occur (Maurer 1977), most of which involve extensive fusion or other specialized conditions that appear unlikely to be ancestral to the eurylaimid condition. The Upupidae do approach the passerine condition closely but apparently lack the plantar vinculum (Maurer 1977), despite an earlier report to the contrary (Gadow 1893–96). The Piciformes possess a plantar vinculum, but it is part of a complex reorganization of the foot associated with their form of zygodactyly (Swierczewski 1977; Swierczewski and Raikow 1981; Raikow and Cracraft 1983). At least in some species this vinculum is structurally different from that of passerines, being wide, short, and multiple rather than narrow and single (Raikow unpubl. data). Altogether there is no compelling evidence that the plantar vinculum of the Eurylaimidae is a primitive condition in the Passeriformes, and considerable evidence instead to regard it as a derived state. This is character 18.1 in Tables 1 and 2.

M. flexor digitorum longus. — The presence of a femoral head (character state 19.1 in Tables 1 and 2) appears to be a derived state in *Philepitta,* based on the idea that the development of this structure is correlated with the loss of the adjacent intermediate head of M. flexor hallucis longus, a correlation that also occurs in *Lanius* (Raikow et al. 1980). However, the two occur together in some birds, such as the Tyrannidae (McKitrick 1985b). Furthermore, a femoral head occurs sporadically in oscines as well, weakening any outgroup comparison between suboscines and oscines. Fortunately, this character state is found in only the one species among the forms studied, so it is not being used to suggest any relationships.

M. flexor hallucis brevis. — The laterally expanded and grooved condition is evidently derived because it does not occur in the suboscines outside the present group that we have dissected, nor as far as I know, in the oscines. Given monophyly of the suboscines (based on the stapes) and also that of the study group (based on the acetabular gap), this condition is reasonably considered a synapomorphy of the Eurylaimidae plus Philepittidae (character state 20.1 in Tables 1 and 2), and probably separately in some pittas. The lateral expansion is more extensive in the eurylaimids, and thus an additional synapomorphy of this family (character state 20.2).

The absence of M. flexor hallucis brevis in the Acanthisittidae is clearly a derived state because the muscle is commonly present in both passerine and nonpasserine birds. This is character state 21.1 in Tables 1 and 2.

M. extensor hallucis longus. — This muscle is so small in the Acanthisittidae that it is questionable whether it functions to a significant degree. The presence of an unusually well-developed automatic extensor ligament suggests its functional augmentation or replacement, thus supporting the idea that the small size of the muscle is due to reduction (hence, derived). Also, outgroup comparison supports this view; whatever ingroup is chosen the muscle is generally well-developed and functionally capable. This is character state 22.1 in Tables 1 and 2.

M. abductor digiti IV. — Given passerine monophyly, the absence of this muscle in pittas must be a derived state because it is present in many passerine and

nonpasserine birds, and is part of the intrinsic musculature of the pes found also in other tetrapod classes. Its absence is character state 23.1 in Tables 1 and 2. In an earlier paper (Raikow 1982, Table 1) I incorrectly reported this muscle as being absent in passerine birds.

NONMYOLOGICAL CHARACTERS

In addition to the myological characters that are original contributions of the present study, I will comment briefly on the phylogenetic significance of several previously known morphological variations that are included in the analysis.

Syndactyly. — Many groups, including oscine, suboscine, and nonpasserine birds have independently developed syndactyly in association with perching habits, so this is a weak character state, and is accepted as synapomorphous within the pittid-philepittid-eurylaimid group largely on the basis of parsimony. This is character state 24.1 in Tables 1 and 2.

Broad bill. — If we accept monophyly of the pittid-philepittid-eurylaimid group, which I consider to be well-founded, then outgroup comparison to the remaining passerines suggests that this characteristic bill shape is a derived specialization of the more advanced eurylaimids. Nevertheless, it must be remembered that bill shape is highly adaptable in birds and has often misled students of avian relationships. This is character state 25.1 in Tables 1 and 2.

Eye wattles. — Again, accepting the monophyly of the pittid-philepittid-eurylaimid group, the distinctive eye wattles of the philepittids are clearly derived by outgroup comparison. Somewhat similar adornments occur in some other groups, such as the Sturnidae, but they are so distantly related that there can be no question of common origin. This is character state 26.1 in Tables 1 and 2.

Stapes. — Feduccia (1974, 1975a, b) found that the stapes (middle ear ossicle) has a distinctive, expanded form in most suboscine groups, a derived condition within the Passeriformes. This is character state 27.1 in Tables 1 and 2.

Oscine syrinx. — The complex syringeal structure of oscines, long recognized as a diagnostic characteristic of the group, is not present in either suboscine passerines or in nonpasserines, and is, therefore, derived. The syrinx of the Menurae varies in minor respects from the typical condition but is clearly of the oscine type. This is character state 28.1 in Tables 1 and 2.

PHYLOGENY OF THE OLD WORLD SUBOSCINES

The evolutionary relationships of the Old World suboscines will now be considered within the larger context of passeriform phylogeny, as diagrammed in Figures 35 and 36. The analysis with the computer program PENNY found two equally parsimonious solutions. The analysis with PAUP found four, including the two found by PENNY. The differences in the four cladograms are minor, consisting of two combinations of two variations. One variation is in the position of *Pitta guajana,* which may cluster either with *P. erythrogaster* or *P. versicolor.* The second variation is in the position of *Smithornis,* which may cluster either with *Calyptomena* or with the terminal group of species. These variations have no effect on the general phylogenetic conclusions of the study. A representative cladogram with character-state positions is shown in Figure 35. A strict consensus tree for the four variants is shown in Figure 36, and represents the basic phylogenetic hypothesis of the present investigation.

Before analyzing the phylogeny of a group it should be determined that the

group itself is monophyletic; otherwise it will lack a unique history and any genealogical hypothesis will be incomplete at the very least. It is incorrect to assume that the taxa of earlier classifications are monophyletic; such concepts must be taken as hypotheses to be tested. I previously examined this question for the Passeriformes by analyzing 18 characters used by earlier workers to define the order phenetically (Raikow 1982). Each character was examined to see whether it was uniquely or independently evolved by the Passeriformes, and thus synapomorphous for the group. None of these characters refuted monophyly, which they could have done by clustering some passerines with some nonpasserines, whereas 13 were either not derived for passerines or could not be shown to be so. Five characters, however, were found to support passerine monophyly: the aegithognathous palate, the structure of M. tensor propatagialis brevis, the bundled spermatozoa with coiled head and large acrosome, the enlarged hallux, and the Type VII deep plantar tendons. To these characters I added information from the hindlimb musculature: the division of M. pubo-ischio-femoralis into Pars cranialis and Pars caudalis, and the loss of several intrinsic muscles of the forward toes. On the basis of this diversity of characters, the hypothesis of passeriform monophyly is considered strongly corroborated.

The oscines and Acanthisittidae share the derived Type 3 M. flexor perforatus digiti IV (character state 16.1). The oscines have a complex syrinx with four pairs of intrinsic muscles and other specializations (28.1) (Ames 1971). The Menurae (Atrichornithidae and Menuridae) have been classified as a suborder apart from the oscines largely because their syrinx, although basically oscine, is rather distinctive (e.g., Wetmore 1960), following the treatment by Garrod (1876). Sibley (1974) on the basis of egg-white protein electrophoresis, supported the idea that the two families are sister taxa. Sibley and Ahlquist (1985a), on the basis of DNA hybridization, again supported this idea, and concluded also that they form the sister group of the Ptilonorhynchidae. In contrast Feduccia and Olson (1982) found that the osteology of the Menurae is unlike that of the Ptilonorhynchidae but has similarities with the furnarioid family Rhinocryptidae. My study of the limb musculature of the Atrichornithidae and Menuridae (Raikow 1985d) shows that they possess the Type 3 flexor perforatus digiti IV (character state 16.1), thus supporting their placement with the oscines. However, their limb muscles are distinctively different from those of the Ptilonorhynchidae (as described by Borecky 1977) so that Sibley and Ahlquist's hypothesis is neither corroborated nor refuted. I consider that the available morphological evidence favors the grouping of the Atrichornithidae and Menuridae with the oscines, but does not clarify their position within that group.

The Acanthisittidae possess two derived conditions that are unique within the group studied: the reduction to a vestigial state of M. extensor hallucis longus and the apparent loss of M. flexor hallucis brevis (character states 21.1 and 22.1). These are functionally connected as parts of a reduction of the muscular mechanism of the hallux, although the adaptive basis for this change is not readily evident. The New Zealand wrens lack various derived specializations of the pittids, philepittids, and eurylaimids, as well as others that have been found (pers. obs.) in some New World suboscines, groups with which they have previously been taxonomically associated.

Except for the Acanthisittidae, the suboscines share a derived form of the stapes (Feduccia 1975a, b). No myological characters were found to corroborate the

clade defined by character state 27.1, but it is confirmed by the DNA hybridization studies of Sibley et al. (1982).

The Furnarii, including the Rhinocryptidae, Formicariidae, Furnariidae, and Dendrocolaptidae, has been considered a "natural" taxon by many workers based on its traditional defining characteristic, the "tracheophone" syrinx, with its tracheal location, lack of a pessulus, and such unique features as the Membrana trachealis and Processus vocalis (Ames 1971). This morphologically complex design is absent both in other passerines and in nonpasserines. Given the monophyly of the Passeriformes, the tracheophone syrinx is clearly derived within the order, defining the Furnarii as monophyletic. Sibley and Ahlquist (1985b) confirm the monophyly of this group on the basis of DNA hybridization.

The Tyranni includes the Tyrannidae, Cotingidae, Pipridae, Phytotomidae, and Oxyruncidae. This group was recognized as a taxon by Storer (1971), but other workers combined these families with the Pittidae, Acanthisittidae, and Philepittidae as a superfamily Tyrannoidea (e.g., Wetmore 1960; Clench and Austin 1974). Ames (1971) also recognized this group, but stressed the diversity of syringeal structures. Some tyrannid, cotingid, and piprid species have been dissected (unpubl. data) and share a derived form of M. flexor perforatus digiti IV (Fig. 12D), thus providing tentative corroboration that this group is monophyletic, a view also supported by the DNA studies of Sibley and Ahlquist (1985b).

The Pittidae, Philepittidae, and Eurylaimidae are clustered as a monophyletic group by the shared possession of an acetabular gap in M. iliotibialis lateralis (character state 1.1). A similar condition also occurs in some members of both the Furnarii and the Tyranni. I believe that it evolved independently in these three groups, because the primitive state also occurs among them. DNA hybridization studies by Sibley et al. (1982) show the Pittidae as the sister group of the Eurylaimidae and separate from the New World groups; they did not study the Philepittidae.

The pittas are clearly monophyletic on the basis of current data, although more species need to be studied before it is possible to generalize with confidence about the whole family. They share several derived characters not found in other birds.

The close relationship between the Philepittidae and Eurylaimidae, previously suggested on the basis of syringeal morphology (Ames 1971), is strongly supported by the present study. All of these forms share the distinctive attenuate form of M. gastrocnemius pars medialis (character state 13.1), and the restricted insertion of M. gastrocnemius (character state 14.1). They also share the plantar vinculum (character state 18.1), which was previously thought to be unique to the Eurylaimidae. This vinculum was found in all of the eurylaimids dissected, and also in *Philepitta*. However, careful dissection of both feet failed to show any trace of it in *Neodrepanis*. If the latter is most closely related to *Philepitta*, then it must have lost the vinculum after diverging from their most recent common ancestor. The Philepittidae, Eurylaimidae, and some Pittidae also share the lateral expansion of M. flexor hallucis brevis (character state 20.1). *Philepitta* and several eurylaimids also share a very distinctive derived state, the presence of M. gastrocnemius pars supramedialis (character state 12.1). Figure 35 suggests that this arose independently in *Philepitta* and a group of eurylaimids. Yet it is sufficiently unusual that it might have arisen only once, to be subsequently lost in *Neodrepanis* and several eurylaimids. Possibly Pars supramedialis and the attenuate form of

Pars medialis arose together as part of a single modification. In many passerines Pars medialis arises by two heads, superficial and deep (e.g., Raikow 1978, Fig. 6). Pars medialis might have originated by the superficial head separating completely from the deep head; this would explain why Pars medialis in these forms is reduced and lacks a division into two heads at its origin.

Monophyly of the Philepittidae has been implied by the previous recognition of the taxon, and is based on various similarities of external anatomy and of the syrinx. The most distinctive character is the eye wattles (character state 26.1). Eye wattles of a sort also occur in *Eurylaimus steeri,* but this condition is not homologous with the philepittid condition. In *E. steeri* the "wattles" are formed by fleshy expansions of the rims of the eyelids, a totally different situation from that in the Philepittidae (pers. obs.). The grouping is also supported by a unique form of M. iliotrochantericus medius (character 6.1). Although *Philepitta* and *Neodrepanis* are evidently closest relatives, they are rather distinct from each other morphologically in plumage and bill shape, and to this we may add myological differences. *Philepitta* has lost the intermediate head of M. flexor hallucis longus (character state 17.1) and has developed in the same region a femoral head of M. flexor digitorum longus (character state 19.1). *Neodrepanis,* as already noted, lacks both the plantar vinculum and M. gastrocnemius pars supramedialis, which are present in *Philepitta.* Thus, the two lineages of this small insular radiation have diverged considerably since their common origin.

Monophyly of the Eurylaimidae is supported by a rather modest attribute, the further lateral expansion of M. flexor hallucis brevis (character state 20.2), and by modification of M. flexor perforatus digiti IV (15.1), which is, however, absent, apparently by reversal, in *Calyptomena.* Thus, this family, which once seemed so well defined, is now only tenuously recognizable as being monophyletic. Many of the traditional eurylaimid characters were shown by Olson (1971) to be inconsistent, and the present study has eliminated the plantar vinculum as a unique eurylaimid character.

The foot has extensive fusion (syndactyly) between digits III and IV to the middle of the second phalanx of digit III in the majority of eurylaimids (character state 24.1), but not in *Pseudocalyptomena.*

Calyptomena is a well-defined genus, the two species dissected sharing two unique derived states (characters states 4.1 and 7.1). It also has a reduction of the postacetabular part of M. iliotibialis lateralis, a state that occurs to a more advanced degree in *Smithornis* (character state 2.1).

The remaining eurylaimid genera have the bill large, wide, and swollen (character state 25.1). This gives the Eurylaimidae their common name of "broadbills." As Olson (1971) pointed out, however, the bill does not achieve this condition in *Calyptomena* (although it is by no means small), and the same is true for *Pseudocalyptomena* (pers. obs.). The largest bill of all occurs in *Corydon,* which must, therefore, be part of this clade. Unfortunately no specimens of *Corydon* were available for dissection.

Eurylaimus, Cymbirhynchus, Serilophus, and *Psarisomus* form a terminal cluster that cannot be further resolved with the data of this study. They are virtually identical in their hind limb musculature. Perhaps future studies using different characters or methods of analysis will provide a better understanding of their relationships.

METHODOLOGICAL LIMITATIONS

An assessment of the results of this study might be aided by a brief consideration of the possible sources of error inherent in the methods utilized, and this analysis might be applicable more generally to other investigations of this type. Studies involving a cladistic analysis of morphological variation might encounter problems relating to (1) the specimens studied, (2) individual variation, and (3) the cladistic analysis. I have discussed some aspects of the first two sources of error in more detail elsewhere (Raikow 1985b).

PROBLEMS WITH SPECIMENS

Some problems arise from condition of museum specimens: (a) damage by shot or other injury, which might obscure or destroy critical details; (b) improper fixation, preservation, or storage, which might make dissection difficult because of decay or desiccation; (c) pathological conditions; and (d) the effects of dissection by previous investigators. These have posed little difficulty in the present study. More troublesome is the ambiguity inherent in some muscular structures that are not always easily classified within definitions of differing character states. For example, a muscle might be defined as arising by either one or two heads; yet in some cases an uncertain intermediate condition might occur in which a clear separation results more as an artifact of dissection than as an anatomical reality. The solution to this problem has simply been to proceed cautiously to reveal form without creating it.

INDIVIDUAL VARIATION

This is a potentially serious problem because, as in many studies, only one specimen was dissected of most species because of the unavailability of large series and the constraints of time. Little is known about individual variation in the avian muscular system, although we are now investigating this subject. The most frequent variations might be expected to be minor differences in the relative size and proportions of muscles, and I have not used these as characters in this study. Developmental anomalies pose a more serious problem, especially where atavistic anomalies might mimic primitive states; such conditions certainly occur in birds (Raikow 1975; Raikow et al. 1979; Hall 1984). In addition, we know little about widespread (polymorphic) variation in the avian muscular system, but there is evidence from current studies (McKitrick 1986) that such variations do occur in the avian limb musculature.

CLADISTIC ANALYSIS

If derived states never arose in separate lineages by convergence or parallelism, and if characters never reverted to secondarily primitive states, then there would be no character conflicts and all characters would combine to generate a single, unambiguous cladogram. Unfortunately, character conflicts are very common because of the frequent independent origin of similar derived conditions, especially at lower taxonomic levels where taxa share similar genomes. This problem is suspected of being especially prevalent with structurally simple modifications, like the loss and reappearance of small muscles.

Most workers seek the shortest cladogram consistent with the data: this is considered to be parsimonious because it requires the smallest number of ad hoc

hypotheses about independent origins. However, because the shortest tree is not necessarily the true historical phylogeny, this approach might well distort the true phylogeny by underestimating the frequency of independent origins. Such an effect might in part explain why cladograms often take a highly asymmetrical form, the "Hennigian comb" of Panchen (1982).

Another approach is to weight characters differentially according to some criteria that estimate the relative degrees to which they are subject to multiple origin. Hecht and Edwards (1977) provide such a scheme based on the idea that multiple origin is least likely in those characters that are the most structurally, developmentally, and (by inference) genetically complex. This approach might be criticized on the grounds that we know almost nothing about the genetic basis for the development of the structures under study, and I have not weighted characters differentially in this study.

These two approaches are responses to the fact that we frequently cannot distinguish between homologous and nonhomologous similarities. They do not solve the problem, but at least they provide methods for responding to it in a consistent way. I have adopted an approach of seeking the shortest tree consistent with the data, while at the same time discussing the relative levels of confidence in which the various clades are held: this depends on the number and complexity of the characters states defining each node (see also Swierczewski and Raikow 1981: 476–477).

Thus, with respect to the phylogenetic relationships of the Old World suboscines hypothesized herein, I consider that the overall pattern is strongly supported by the present morphological study. The proposed relationships among the genera of Eurylaimidae are less strongly supported, however, given the smaller number and more equivocal nature of the characters. It is possible that there is some underestimation of parallelism in muscular evolution here, so that the phylogeny hypothesized might be more asymmetrically branched than is the true phylogeny. Nevertheless, the overall directional picture of evolutionary change within the family, including the development of syndactyly, a heavy bill, and various trends in myological structure, is probably accurate in general if not in every detail.

COMPARISON WITH OTHER STUDIES

It is of interest to compare the results of this study with those of other investigations of passerine relationships. Sibley and Ahlquist (1985b and references therein) have pioneered the use of DNA-DNA hybridization in the analysis of avian phylogeny. In this technique the nucleotide sequences of the entire single-copy genomes of different species are compared and the degrees to which they share common sequences are measured. Based on the premise of a uniform average rate of nucleotide substitution over the genome as a whole, the genetic distances thus determined become direct measures of the relative divergence times between species. The phylogenies thus produced are based entirely on estimates of genetic distance, and no characters in the traditional sense are involved. Furthermore, there is no direct relationship between such distance measures and any particular class of morphological characters. Thus, if DNA and morphological studies generate similar phylogenies, the probable explanation is that they are not themselves coupled, but are correlated because they are independently tracing a third, common pattern, which is presumably the true historical genealogy. Thus, concordance

between the two methods might be taken as strong corroboration for the phylogenies on which they agree.

When DNA and morphological studies produce divergent results, however, the reason must lie in errors within one or both methods (McKitrick 1985). The morphological method entails several potential sources of error, as discussed above. Possible sources of error in the DNA hybridization method, however, have hardly been explored as yet, given the newness of the technique (but see Sibley and Ahlquist 1983:264–267).

A condensed version of the phylogeny proposed above (Fig. 35) is shown in Figure 37A, and is compared with a phylogeny of the same taxa (Fig. 37B) as hypothesized in the DNA hybridization studies of Sibley et al. (1982) and Sibley and Ahlquist (1985b). The similarity is striking, and indeed is even closer than it appears at first glance. The only significant difference is that I hypothesize the Acanthisittidae to be the sister group of the oscines, whereas Sibley et al. regard them as the sister group of the suboscines. Even this difference is minor because we agree that the New Zealand wrens are the descendants of an ancient lineage separate from the origin of the other suboscine groups. The remaining differences in the two diagrams do not represent disagreements but differences in coverage. I show the Furnarii, theTyranni, and the Old World suboscines as arising trichotomously from a single node, whereas Sibley et al. show the two former groups as sister taxa. This is not a disagreement, but rather the presence of an additional node in their phylogeny, because I failed to find any synapomorphies linking the two New World groups. Likewise, Sibley et al. do not indicate a precise position for the Philepittidae because they did not study this family, whereas I have been able to place them in the phylogeny as a result of my dissections. Based on the considerations discussed above, the close agreement between these two distinctly different approaches provides a strong feeling of confidence that the true history of the passerine birds is very close to that resulting from our studies.

This picture might be compared with the more traditional views that are reflected in the classifications of the last several decades. The classification of Wetmore (1960) might serve as an example because most of the others are similar. Figure 37C is a diagram of the hierarchical structure of Wetmore's classification. It is not exactly comparable to the other diagrams in Figure 37 because it is based on traditional methods in which relationships are hypothesized on a combination of genealogy and similarity, so that the pattern, although representing evolutionary relationships in some sense, is highly ambiguous (Raikow 1985a). Nevertheless, a rough comparison might be attempted. In Wetmore's classification the Menurae and Eurylaimidae are apparently separated off at a high categorical level on the basis of some combination of phylogenetic divergence and supposed morphological distinctiveness. The remaining suboscines are presumably grouped on the traditional basis of their "mesomyodian" syrinx, a morphological concept of dubious significance. The Tyranni (Wetmore's New World Tyrannoidea) are grouped with the Old World, non-eurylaimid suboscines in such classifications on the basis of a virtually undefinable "haploophone" syrinx (McKitrick 1985a).

CLASSIFICATION

A proposed classification embodying the phylogenetic conclusions of the present study is given in Table 3. It was constructed so that only monophyletic groups are recognized as taxa, with all taxa being ranked by a single method. Such a

TABLE 3

SUGGESTED CLASSIFICATION

Order Passeriformes	Suborder Passeres
Suborder Oligomyodi	Infraorder Acanthisittides
Infraorder Furnarii (*sedis mutabilis*)	Family Acanthisittidae
Infraorder Tyranni (*sedis mutabilis*)	Infraorder Polymyodi
Infraorder Pitti (*sedis mutabilis*)	
Family Pittidae	
Family Philepittidae	
Family Eurylaimidae	

classification assures that all taxa represent the same kind of biological phenomenon, and reflects in its hierarchical structure the phylogenetic relationships among its members. These characteristics are considered desirable in contrast to the vague and arbitrary nature of traditional "evolutionary" or "eclectic" methods.

In this classification the order Passeriformes is divided into the suborders Oligomyodi and Passeres, representing essentially the traditional suboscine and oscine groups. The Oligomyodi is divided into infraorders Furnarii, Tyranni, and Pitti. These are marked *sedis mutabilis* to indicate that their equal rank results from a trichotomy in the cladogram that is considered more likely to represent an unresolved pair of dichotomies than a simultaneous origin of three lineages. Within the Pitti, the families Pittidae, Philepittidae, and Eurylaimidae are sequenced in recognition of their pattern of origin.

The suborder Passeres includes an infraorder Acanthisittides for the Acanthisittidae, and Polymyodi for the traditional "oscine" or songbird radiation, now considered to include the former "Menurae." My views on avian classification are discussed fully elsewhere (Raikow 1985a).

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SUMMARY

The first detailed descriptions and illustrations are provided for the hindlimb musculature of the Old World suboscine families Acanthisittidae, Pittidae, Phile-

pittidae, and Eurylaimidae. Variations in the hindlimb musculature and several nonmyological characters are used in a numerical cladistic analysis to hypothesize the phylogenetic relationships among the genera of these families. The hindlimb musculature in general conforms to the expected morphology previously considered characteristic of the order Passeriformes, but considerable variation is described, including the discovery of a new muscle, M. gastrocnemius pars supramedialis. A plantar vinculum, connecting the tendons of Mm. flexor hallucis longus and flexor digitorum longus, is present in all eurylaimids dissected. Contrary to previous belief, however, this structure is not limited to the Eurylaimidae, but also occurs in *Philepitta castanea,* although not in *Neodrepanis coruscans,* of the family Philepittidae. The plantar vinculum is considered here to be a derived state within the Passeriformes, rather than a retained primitive state as previously believed.

The major phylogenetic conclusions are these: (1) The family Acanthisittidae is monophyletic, and is the sister taxon of the Oscines. Thus, the New Zealand wrens are not closely related to the other Old World suboscines. (2) The Pittidae, Philepittidae, and Eurylaimidae constitute a monophyletic group within a larger clade which also includes the New World suboscines. (3) The Pittidae is monophyletic and is the sister taxon of a clade which includes the Philepittidae and Eurylaimidae. (4) The Philepittidae is monophyletic and is the sister group of the Eurylaimidae. (5) The Eurylaimidae is monophyletic, although the evidence supporting this hypothesis is surprisingly modest considering the high rank previously accorded this group. (6) A radiation within the Eurylaimidae is suggested, with evolving characters that include the development of extreme syndactyly, the enlargement of the bill to the "broadbill" configuration, and numerous changes in the hindlimb muscles.

Limitations of the methodology employed are discussed. The most serious problem is that because of homoplasy, the occurrence of character conflicts makes it possible for one data set to support more than one cladogram. The choice of a preferred hypothesis might then be based on the parsimonious decision to select the cladogram with the smallest number of branch points. However, multiple solutions might still be possible given the opportunity to invoke different parsimony criteria and different character-weighting schemes. In the present work the approach was to depict the shortest cladograms using Wagner parsimony and equal character-weighting, and then to discuss the relative confidence in which the different clades are held.

The proposed phylogeny is compared to one suggested by C. G. Sibley and coworkers from their studies on DNA-DNA hybridization. Although not identical, the results of the two studies are so similar that the agreement cannot be attributed to chance. Given the unrelated nature of the data used in these different studies, the correspondence between their results must be due to their independent determination of an approximation of the true historical phylogeny. The relationships proposed in both investigations differ markedly from those in earlier, more traditional studies.

Based upon the phylogenetic conclusions of the present study, a classification is proposed in which all taxa are monophyletic, and in which the ranking of the taxa is done in a consistent way.

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APPENDIX I

LIST OF ABBREVIATIONS IN FIGURES

ABD4	abductor digiti IV
CF	caudofemoralis
EDL	extensor digitorum longus
EHL	extensor hallucis longus
FB	fibularis brevis
FCRLA	flexor cruris lateralis, pars accessoria
FCRLP	flexor cruris lateralis, pars pelvica
FCRM	flexor cruris medialis
FDL	flexor digitorum longus
FHB	flexor hallucis brevis
FHL	flexor hallucis longus
FIB	fibula
FL	fibularis longus
FPD2	flexor perforatus digiti II
FPD3	flexor perforatus digiti III
FPD4	flexor perforatus digiti IV
FPPD2	flexor perforans et perforatus digiti II
FPPD3	flexor perforans et perforatus digiti III
FT	flexor tendons
FTE	femorotibialis externus
FTED	femorotibialis externus, pars distalis
FTEP	femorotibialis externus, pars proximalis
FTI	femorotibialis internus
FTM	femorotibialis medius
G	gastrocnemius
GI	gastrocnemius, pars intermedia
GL	gastrocnemius, pars lateralis
GM	gastrocnemius, pars medialis
GS	gastrocnemius, pars supramedialis
ICR	iliotibialis cranialis
IF	iliofibularis
IFI	iliofemoralis internus
IL	iliotibialis lateralis
ILPO	iliotibialis lateralis, postacetabular belly
ILPR	iliotibialis lateralis, preacetabular belly
INT	intermediate portion
ISF	ischiofemoralis
ITCA	iliotrochantericus caudalis
ITCR	iliotrochantericus cranialis
ITM	iliotrochantericus medius
LAT	lateral portion
MED	medial portion
MTI	metatarsal I
OLD	obturatorius lateralis, pars dorsalis
OLV	obturatorius lateralis, pars ventralis
OM	obturatorius medialis
PIFCA	pubo-ischio-femoralis, pars caudalis
PIFCR	pubo-ischio-femoralis, pars cranialis
PL	plantaris
TCR	tibialis cranialis
TMT	tarsometatarsus
V	vinculum
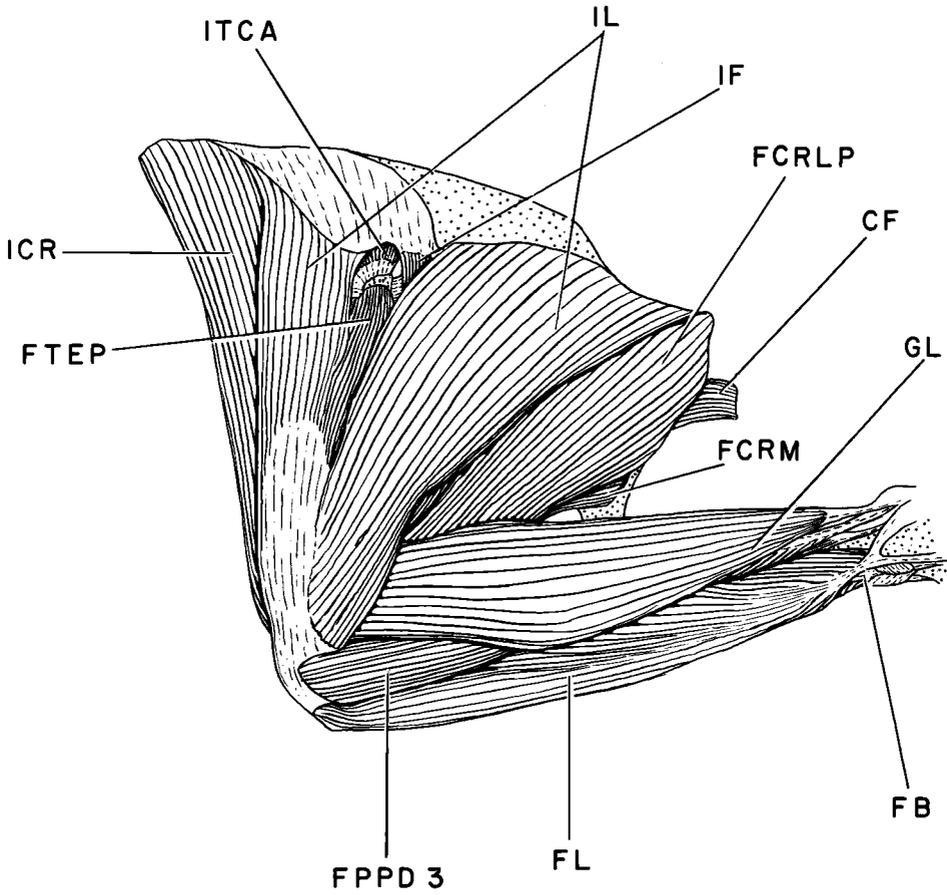
FIG. 1. Superficial musculature of the lateral surface of the thigh and crus in *Eurylaimus ochromalus*. Abbreviations in Appendix I.
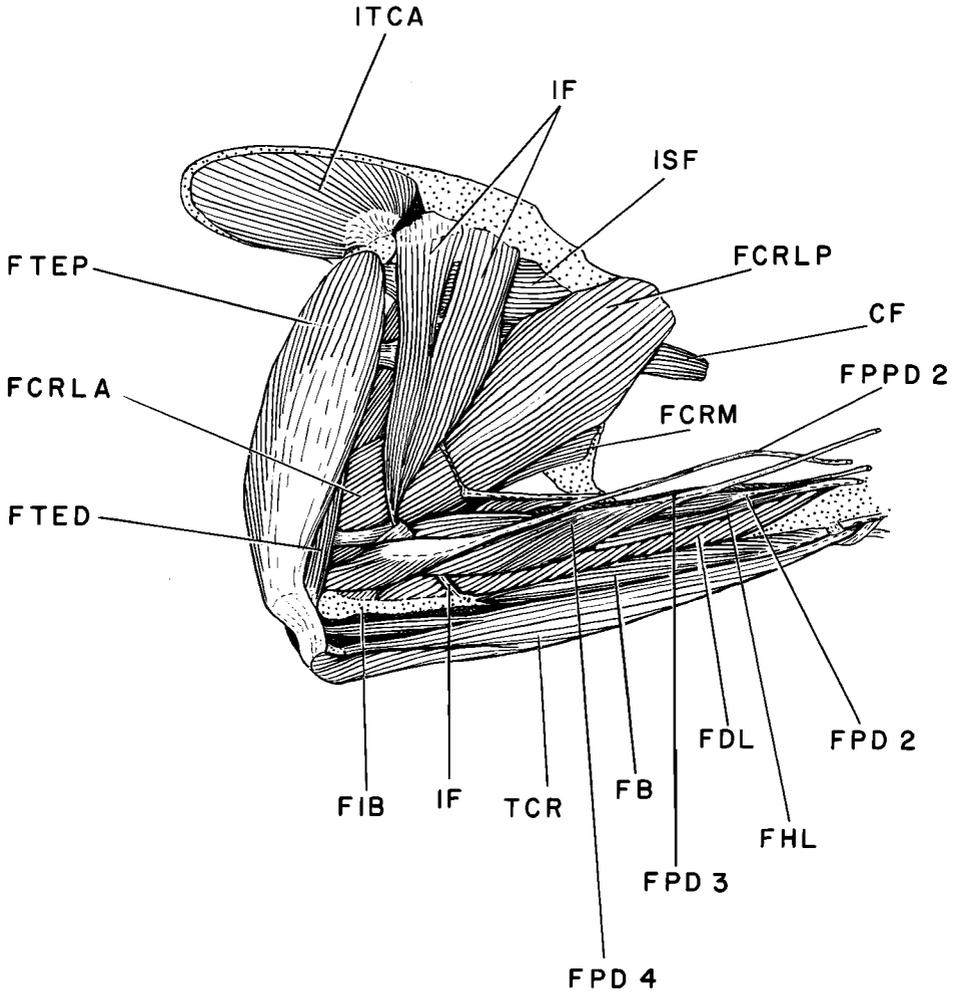
FIG. 2.   Second layer of muscles on the lateral surface of the thigh and crus in *Eurylaimus ochromalus*. Abbreviations in Appendix I.
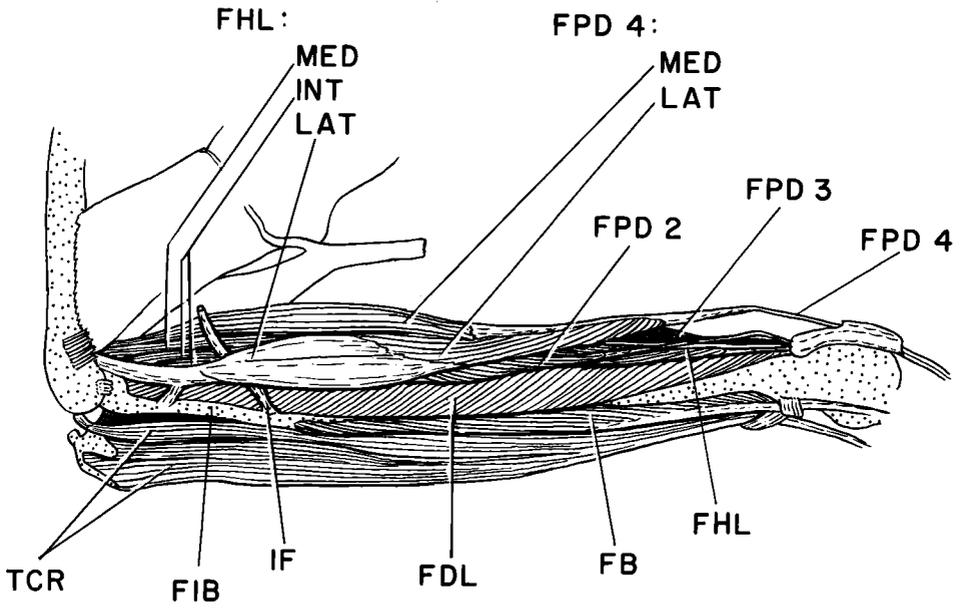
FIG. 3. Third layer of muscles on the lateral surface of the crus in *Eurylaimus ochromalus*. Abbreviations in Appendix I.
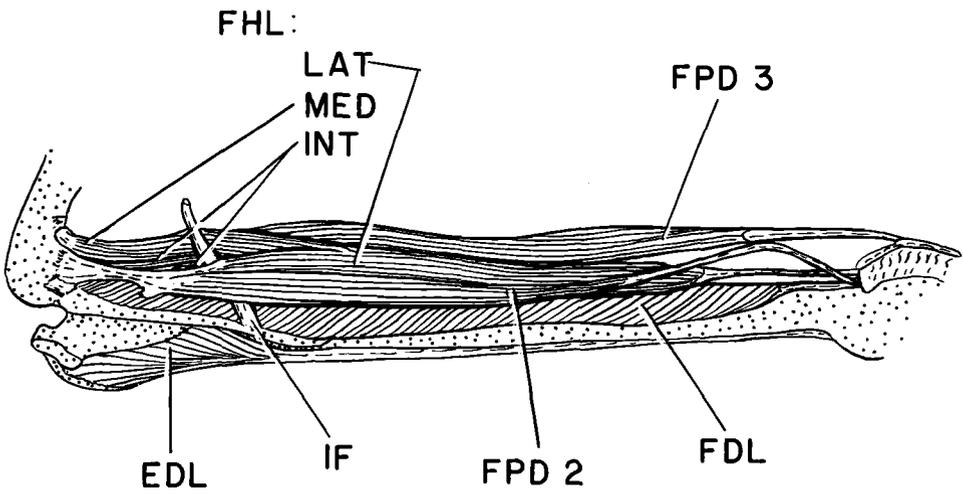
FIG. 4. Fourth layer of muscles on the lateral surface of the crus in *Eurylaimus ochromalus*. Abbreviations in Appendix I.
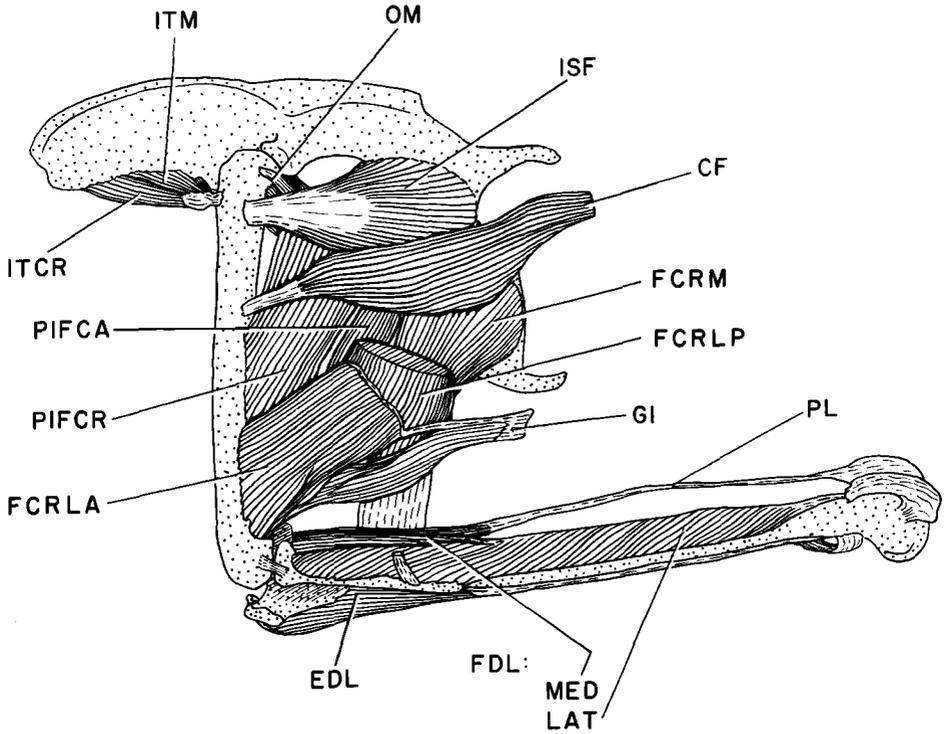
FIG. 5. Deep muscles on the lateral surface of the thigh and crus in *Eurylaimus ochromalus*. Abbreviations in Appendix I.
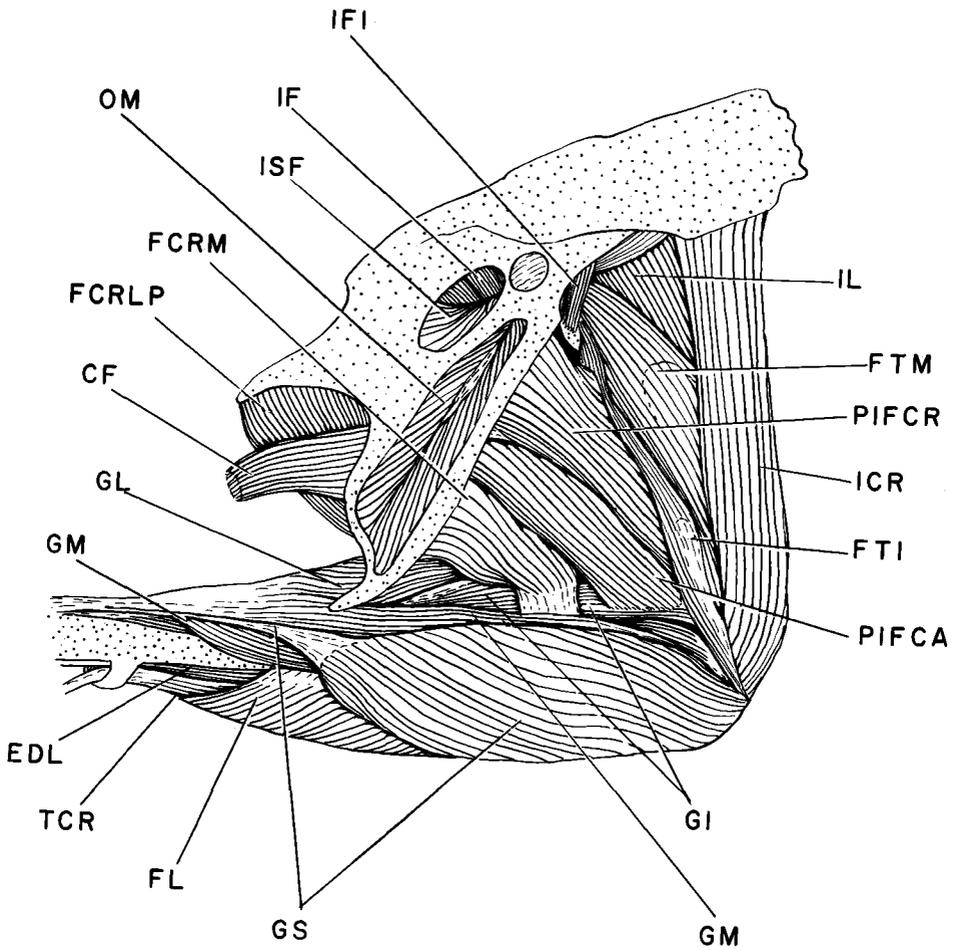
FIG. 6.   Superficial musculature on the medial surface of the thigh and crus in *Eurylaimus och-romalus*. M. gastrocnemius pars supramedialis (GS) has not previously been described, and overlies M. gastrocnemius pars medialis (GM), which in most birds is the most superficial muscle on the medial surface of the crus. Abbreviations in Appendix I.
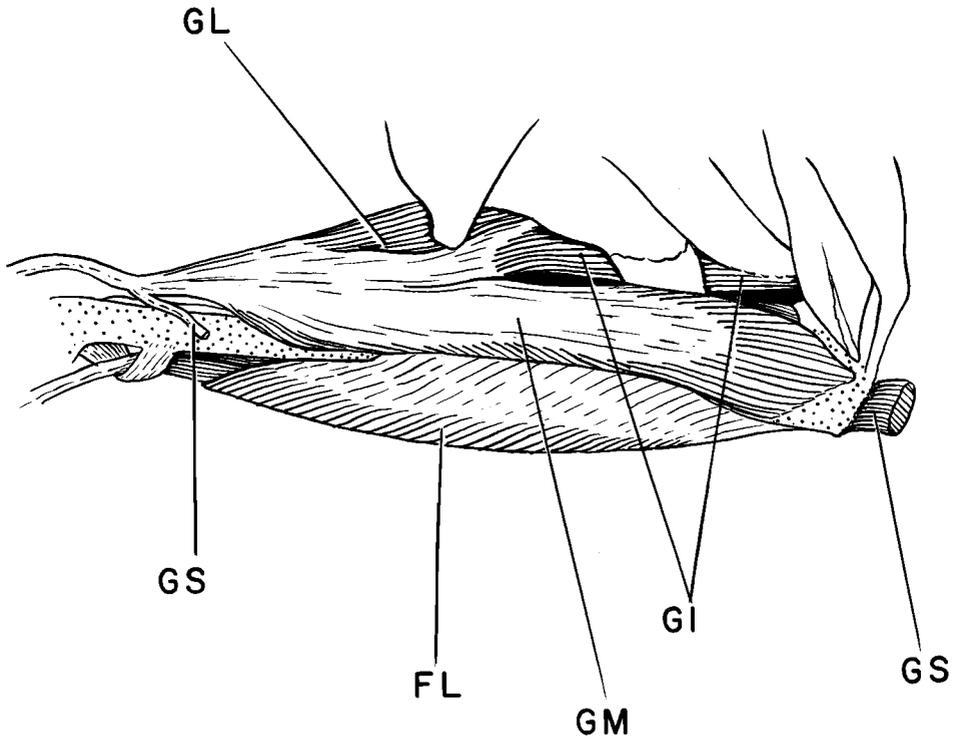
Fig. 7.   Muscles on the medial surface of the crus in *Eurylaimus ochromalus* following removal of M. gastrocnemius pars supramedialis (GS). Pars medialis (GM) shows the "attenuate" derived condition of reduced size, absence of separate superficial and deep heads, and concave cranial margin. Abbreviations in Appendix I.
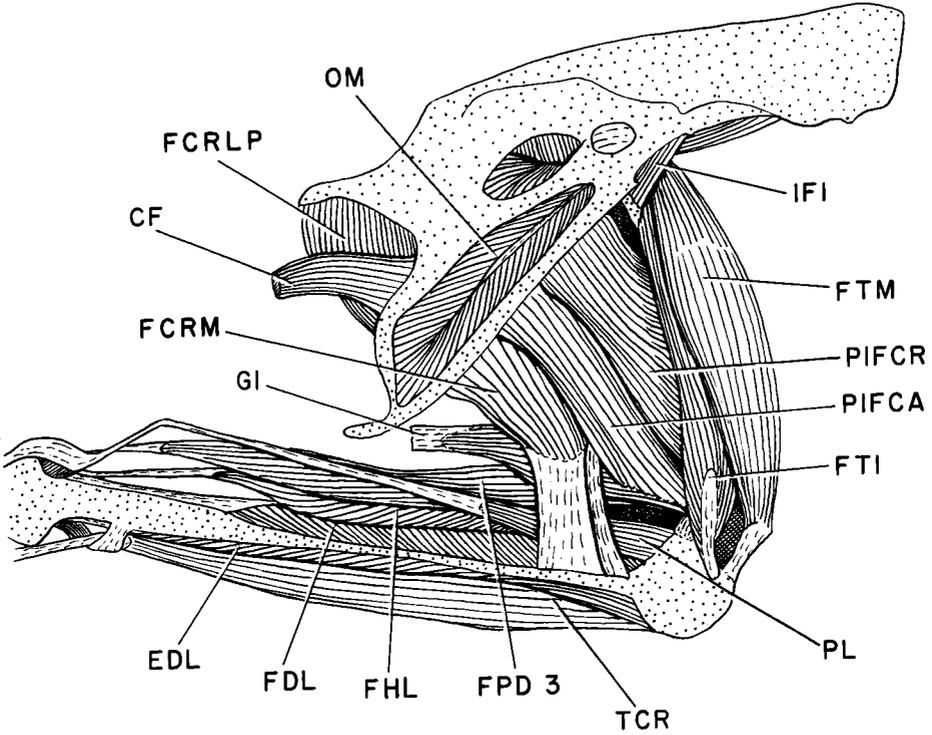
FIG. 8. Deeper layer of muscles on the medial surface of the thigh and crus in *Eurylaimus och-romalus*. Abbreviations in Appendix I.
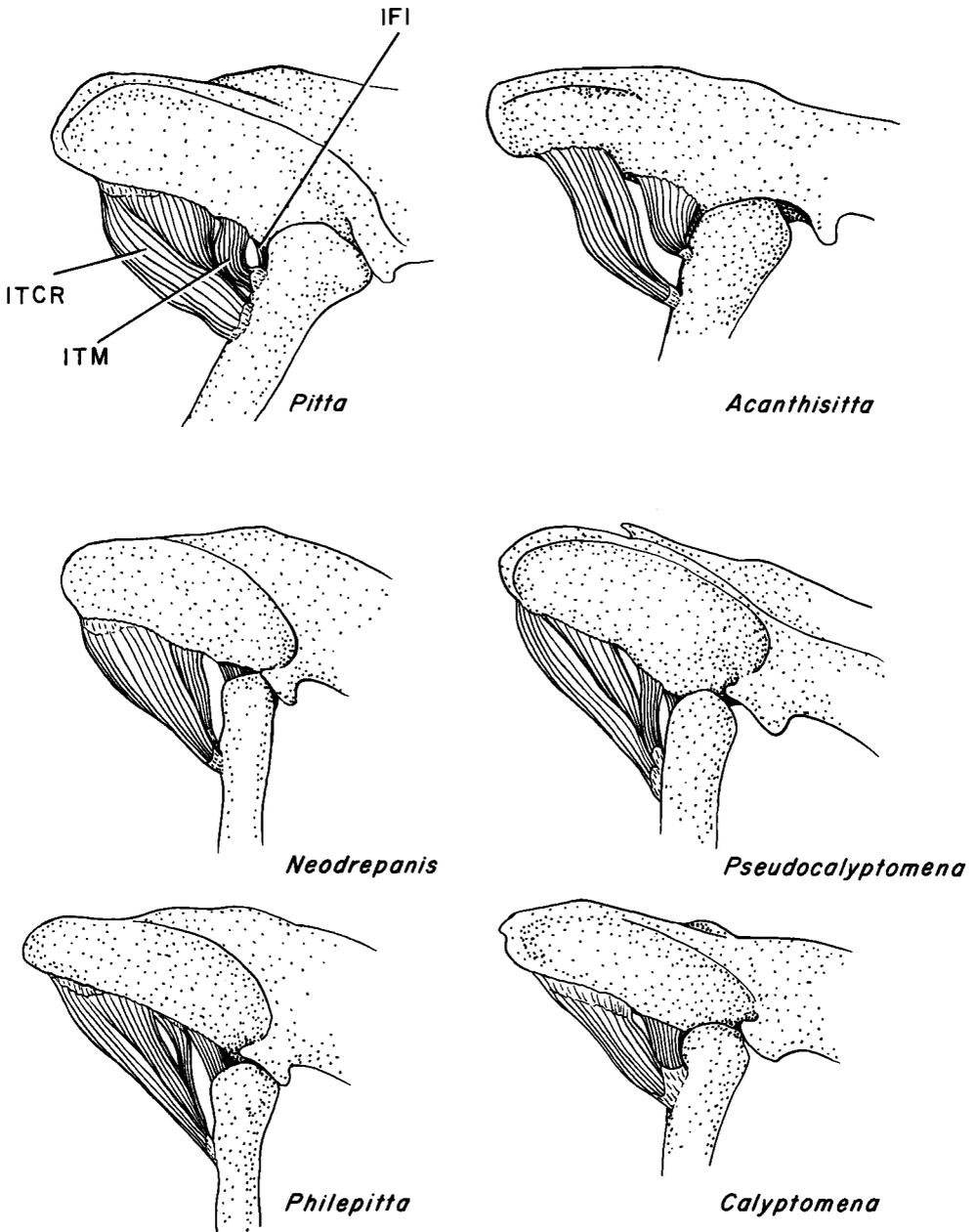
FIG. 9. Mm. iliotrochantericus cranialis (ITCR) and iliotrochantericus medius (ITM) in *Pitta versicolor, Neodrepanis coruscans, Philepitta castanea, Acanthisitta chloris, Pseudocalyptomena graueri,* and *Calyptomena viridis.* M. iliofemoralis internus (IFI) is also depicted. Abbreviations in Appendix I.
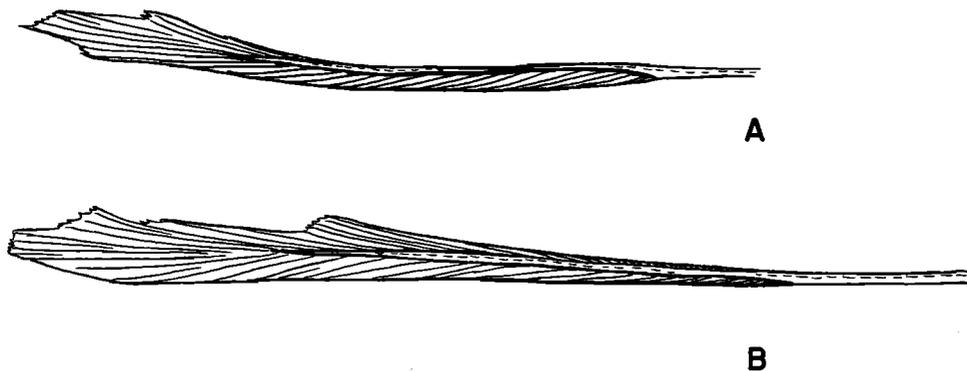
FIG. 10.   Variation in M. extensor digitorum longus. A. Primitive condition with highly asymmetrical belly as exemplified by *Eurylaimus ochromalus*; B. Derived symmetrical form illustrated by *Pitta brachyura.*
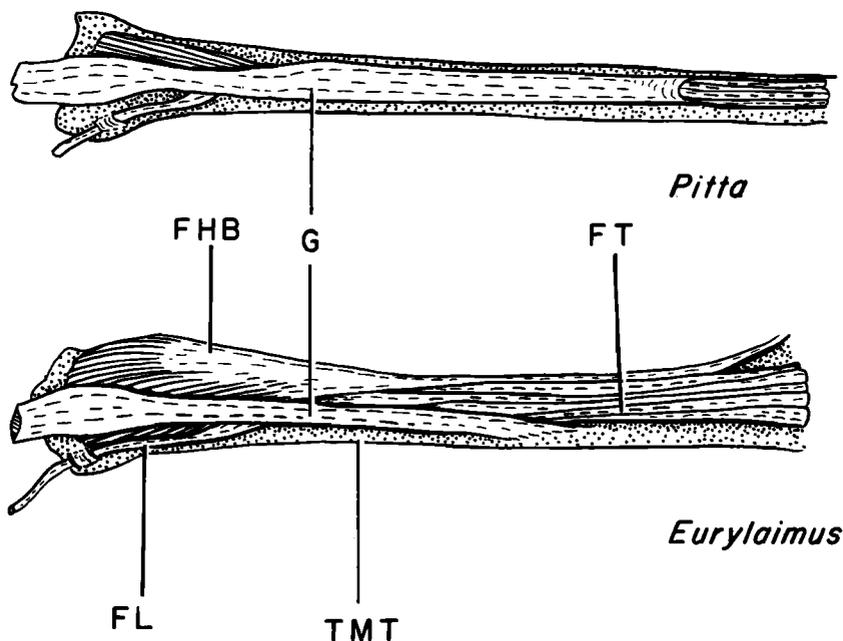
FIG. 11.   Plantar surface of tarsometatarsus showing variation in the insertion of M. gastrocnemius (G). *Pitta brachyura* illustrates the primitive condition in which the tendon of insertion ensheathes the flexor tendons (FT) and inserts on both sides of the tarsometatarsus (TMT). *Eurylaimus steeri* shows the derived condition of a restricted area of insertion. Abbreviations in Appendix I.
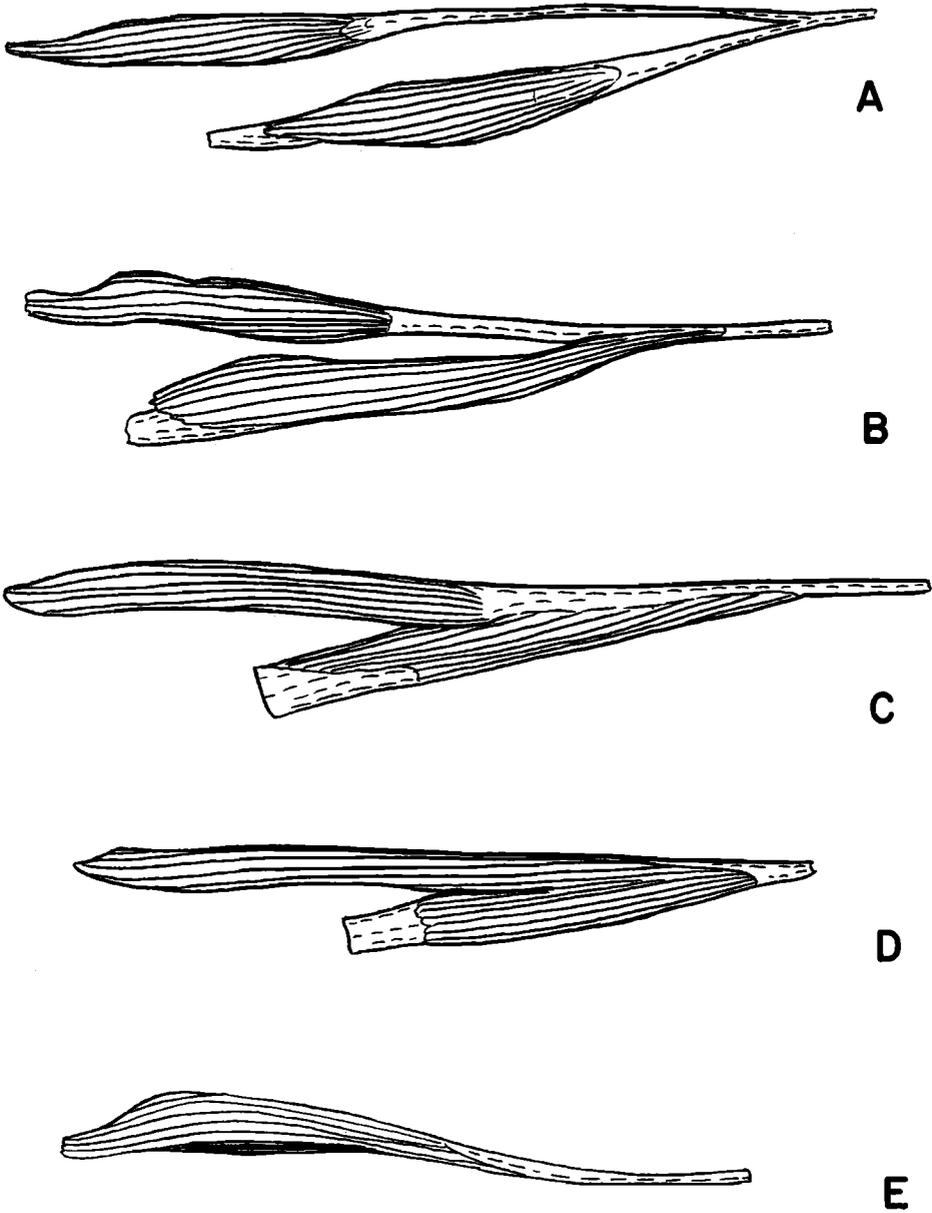
FIG. 12. Variation in M. flexor perforatus digiti IV (FPD4). A. Primitive Type 1 condition exemplified by *Philepitta castanea*. B. Derived Type 2a condition as shown by *Smithornis capensis*. C. Type 2b condition illustrated in *Eurylaimus ochromalus*. D. A different form of Type 2b exemplified by *Tyrannus tyrannus*. E. Type 3 condition illustrated in *Xenicus longipes*.
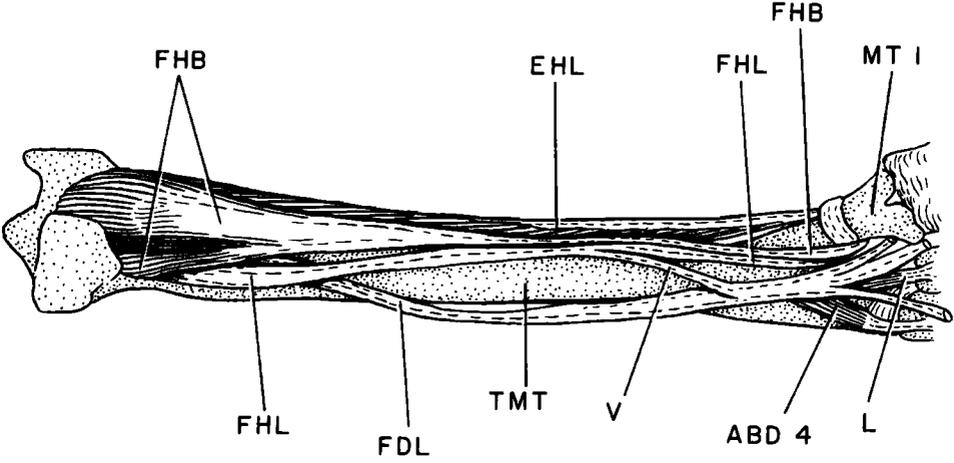
FIG. 13. Muscles and tendons on the plantar surface of the tarsometatarsus in *Eurylaimus och-romalus*. M. flexor hallucis brevis (FHB) shows the derived expanded and grooved condition. A plantar vinculum (V) connects the tendons of M. flexor hallucis longus (FHL) and M. flexor digitorum longus (FDL). Abbreviations in Appendix I.
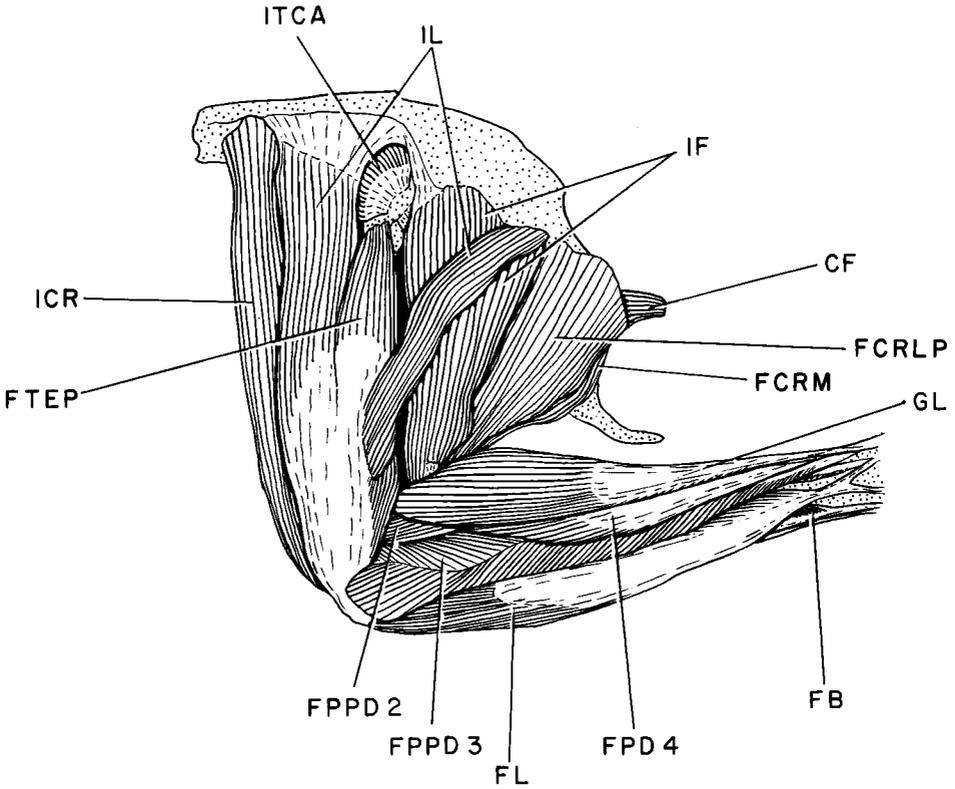
FIG. 14. Superficial lateral musculature of the thigh and crus in *Smithornis capensis*. The post-acetabular belly of M. iliotibialis lateralis (IL) is greatly reduced, whereas M. gastrocnemius pars lateralis (GL) is not enlarged. Compare with Figure 1. Abbreviations in Appendix I.
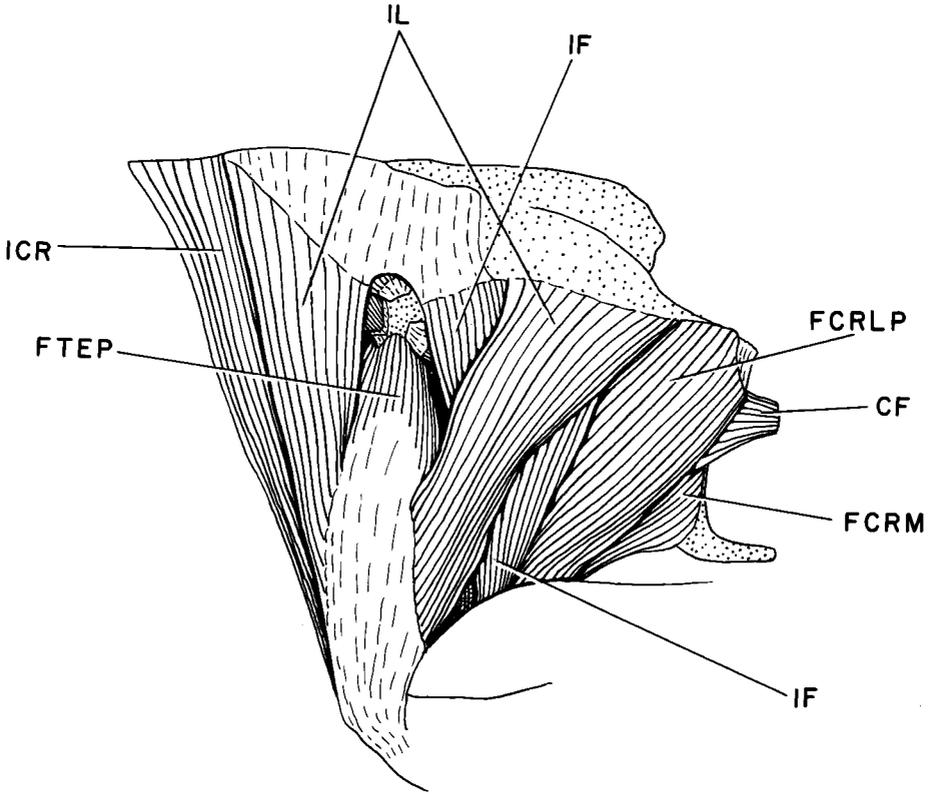
FIG. 15.   Superficial musculature on the lateral surface of the thigh in *Calyptomena viridis*. The postacetabular belly of M. iliotibialis lateralis (IL) is moderately reduced. Compare with Figures 1 and 14. Abbreviations in Appendix I.
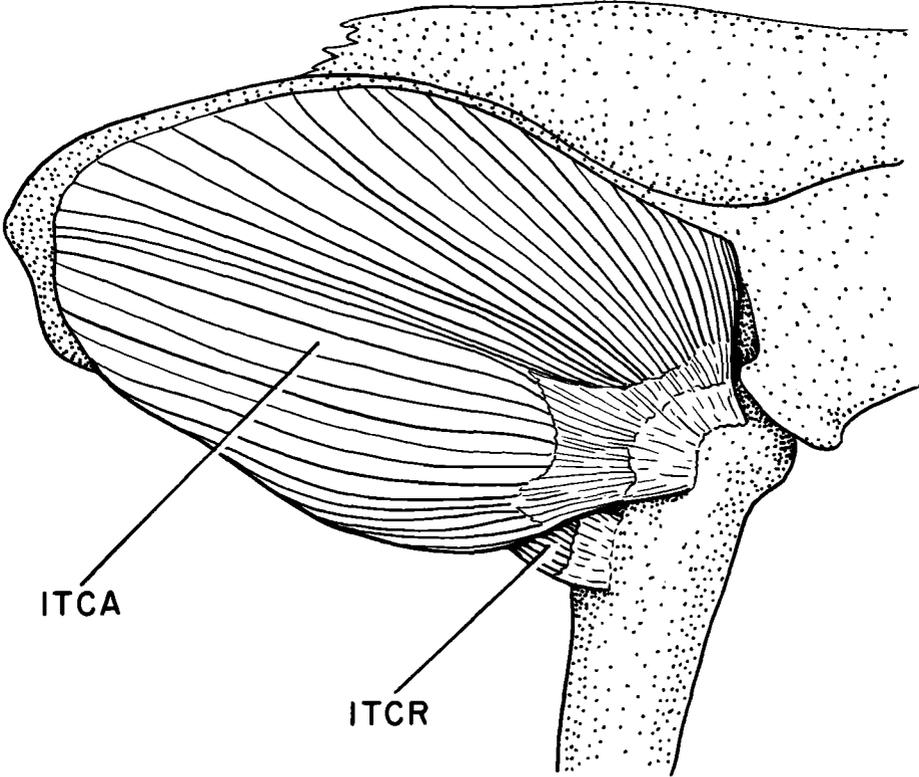
FIG. 16. M. iliotrochantericus caudalis (ITCA) in *Calyptomena whiteheadi* showing the derived condition with loss of superficial fascicles overlying the tendon of insertion. M. iliotrochantericus cranialis (ITCR) is also shown. Abbreviations in Appendix I.
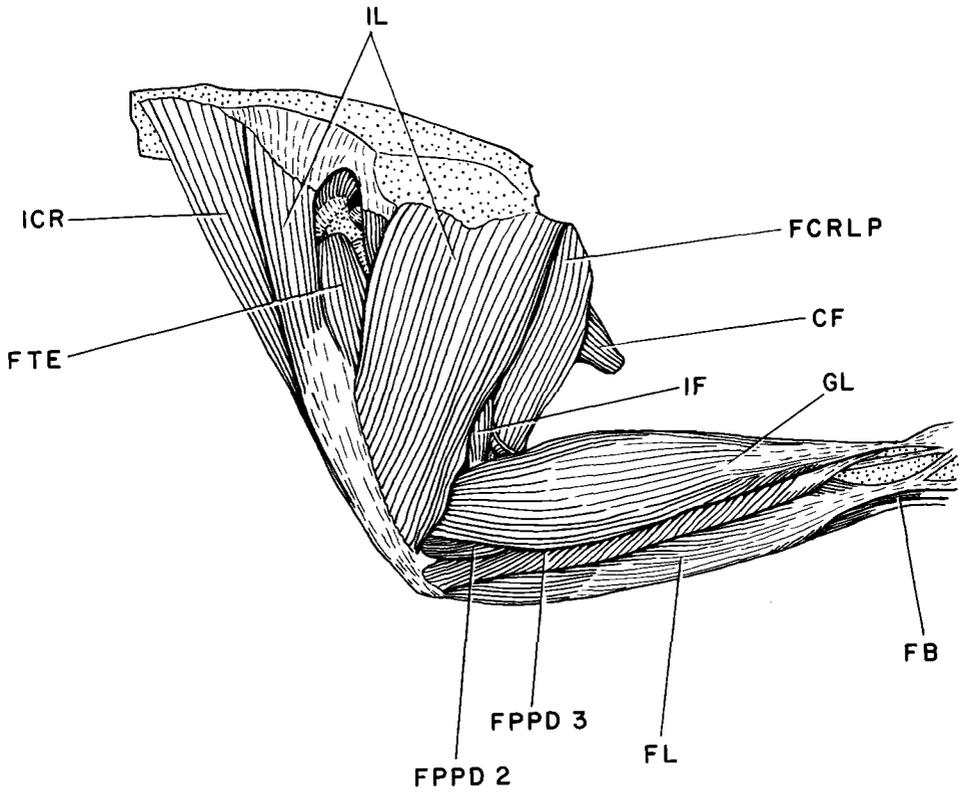
FIG. 17. Superficial musculature on the lateral surface of the thigh and crus in *Pseudocalyptomena graueri*. The preacetabular and postacetabular bellies of M. iliotibialis lateralis are separated by an acetabular gap. Abbreviations in Appendix I.
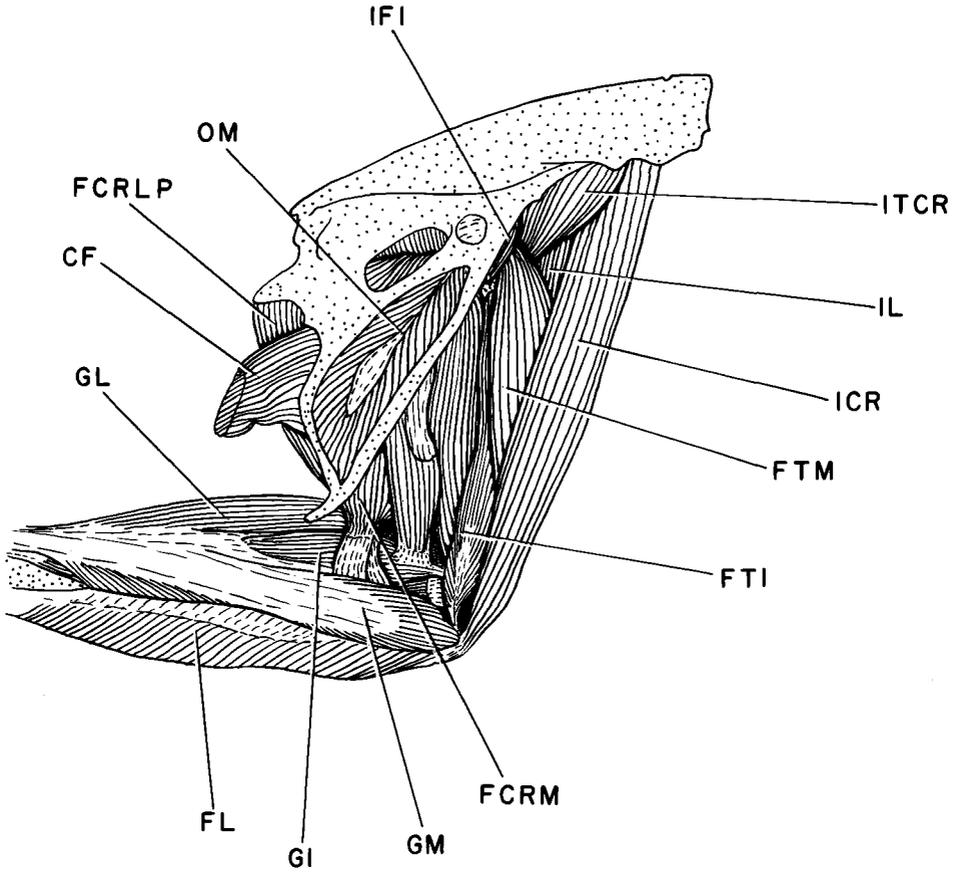
FIG. 18. Superficial musculature on the medial surface of the thigh and crus in *Pseudocalyptomena graueri*. Note the derived attenuate form of M. gastrocnemius pars medialis (GM) and the absence of Pars supramedialis. Abbreviations in Appendix I.
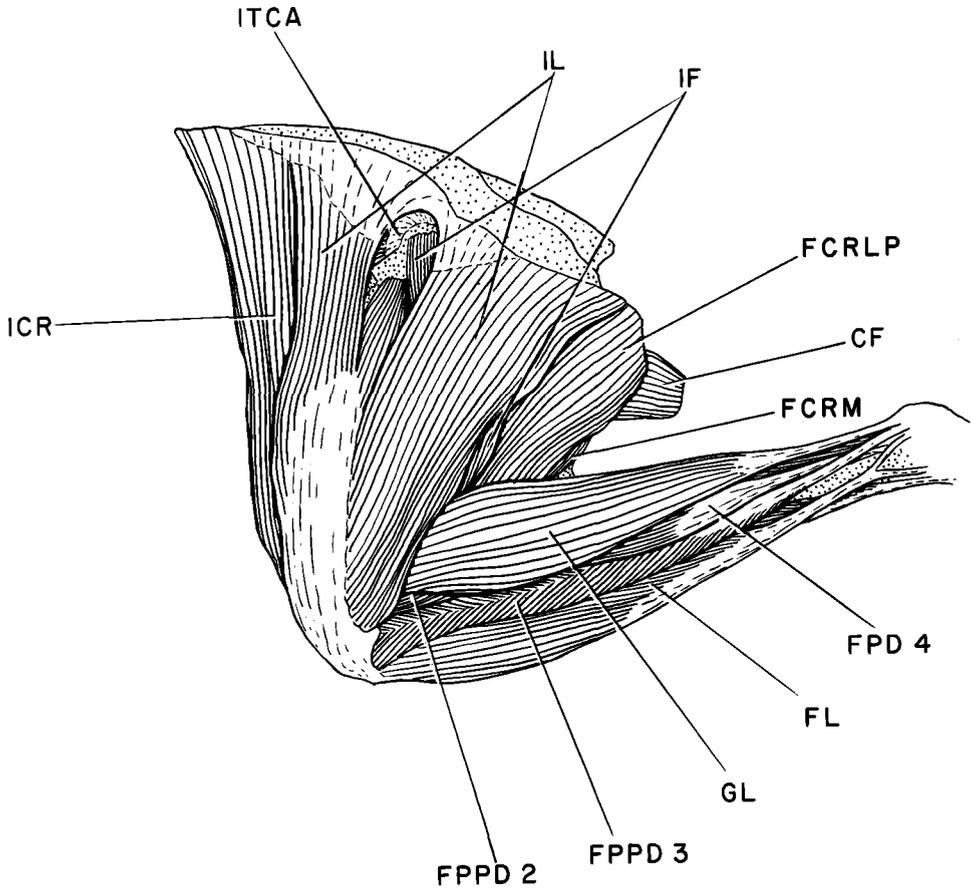
FIG. 19.   Superficial musculature on the lateral surface of the thigh and crus in *Philepitta castanea.*
Note the acetabular gap separating the two parts of M. iliotibialis lateralis (IL). Abbreviations in
Appendix I.
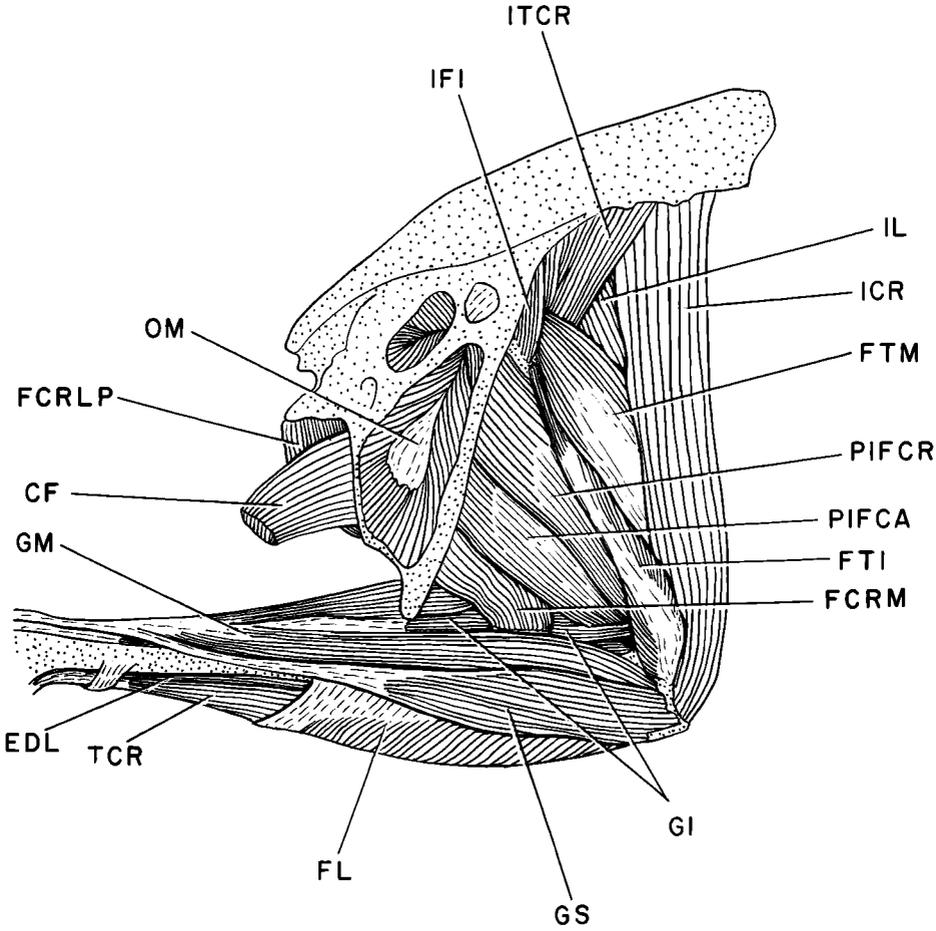
FIG. 20.   Superficial musculature on the medial surface of the thigh and crus in *Philepitta castanea*. A moderately developed M. gastrocnemius pars supramedialis (GS) is present. Abbreviations in Appendix I.
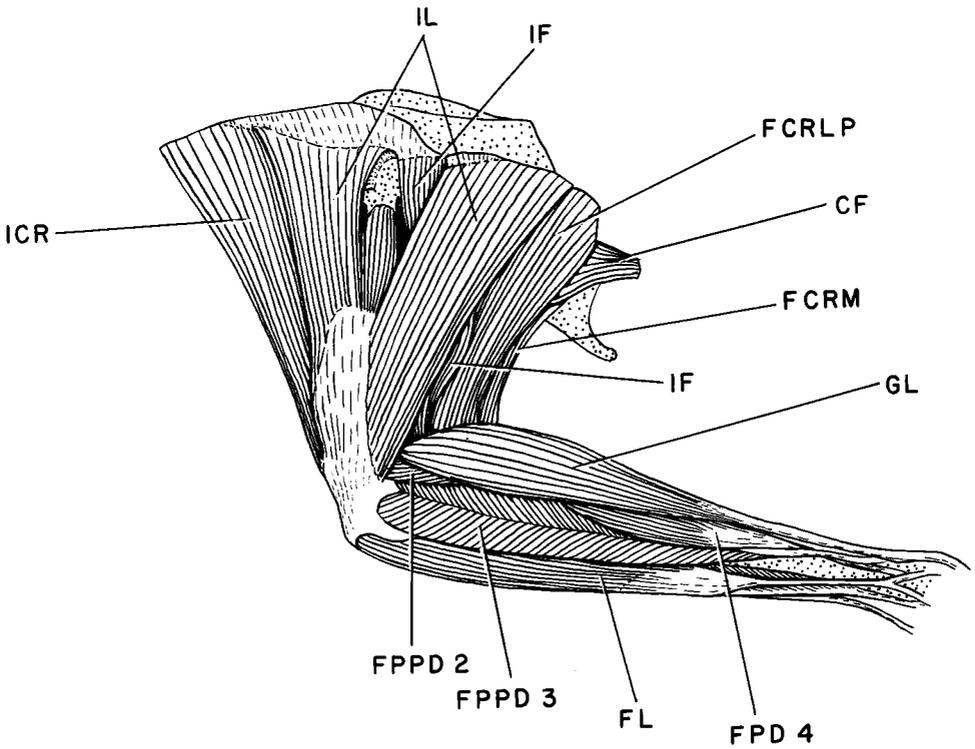
FIG. 21. Superficial musculature on the lateral surface of the thigh and crus in *Neodrepanis coruscans*, showing the acetabular gap in M. iliotibialis lateralis (IL) and the relatively slender development of the muscles in this diminutive species. Abbreviations in Appendix I.
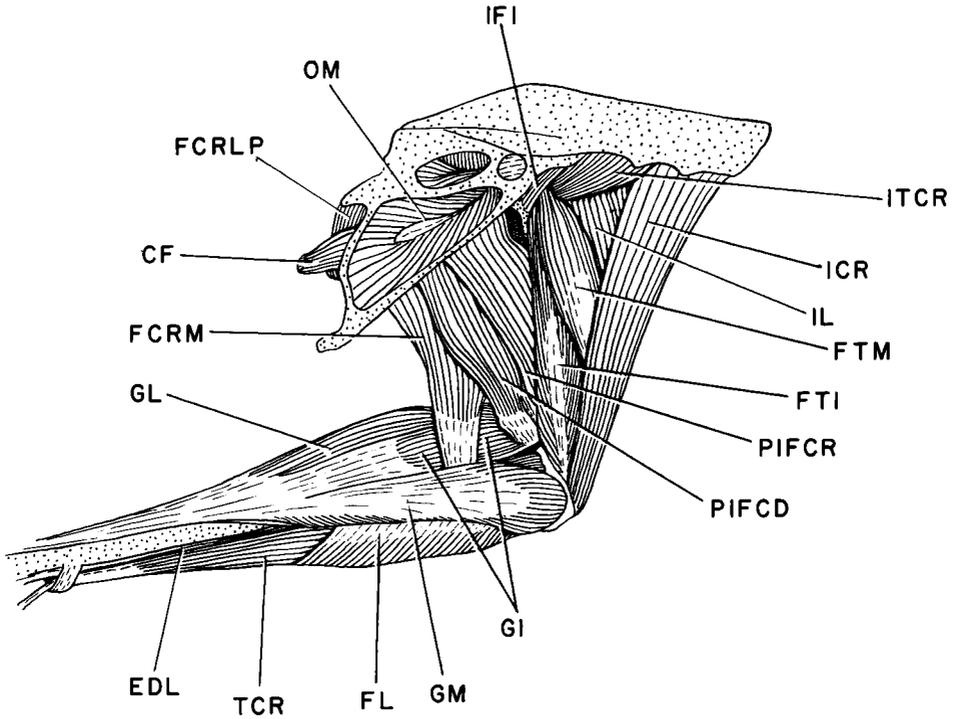
FIG. 22. Superficial musculature on the medial surface of the thigh and crus in *Neodrepanis coruscans*. Notable features are the derived attenuate form of M. gastrocnemius pars medialis (GM) and the absence of Pars supramedialis. Abbreviations in Appendix I.
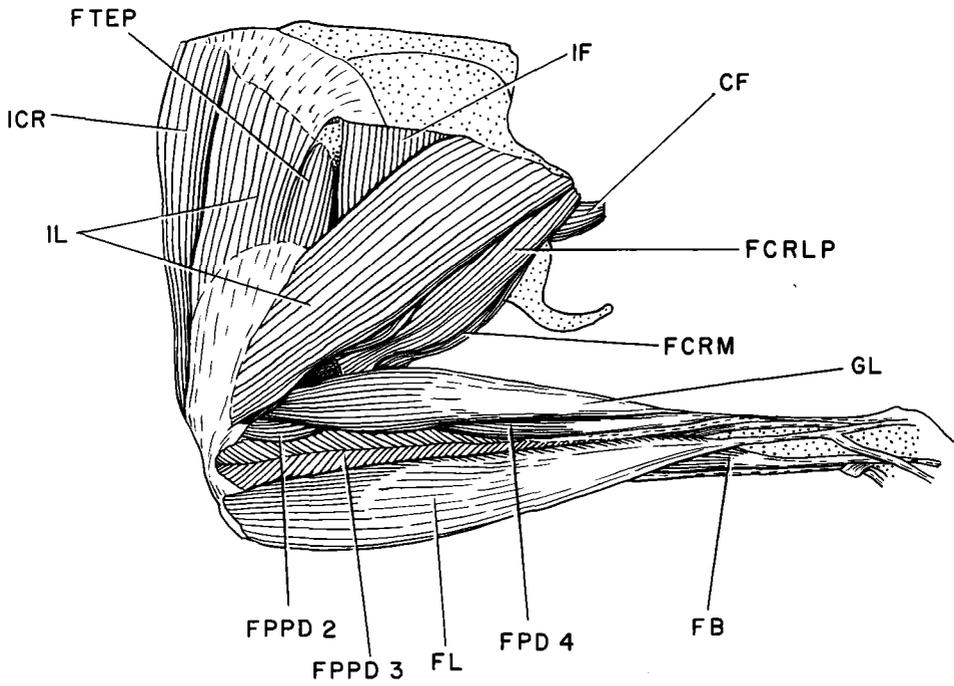
FIG. 23. Superficial musculature on the lateral surface of the thigh and crus in *Pitta versicolor*, showing the acetabular gap in M. iliotibialis lateralis (IL). Abbreviations in Appendix I.
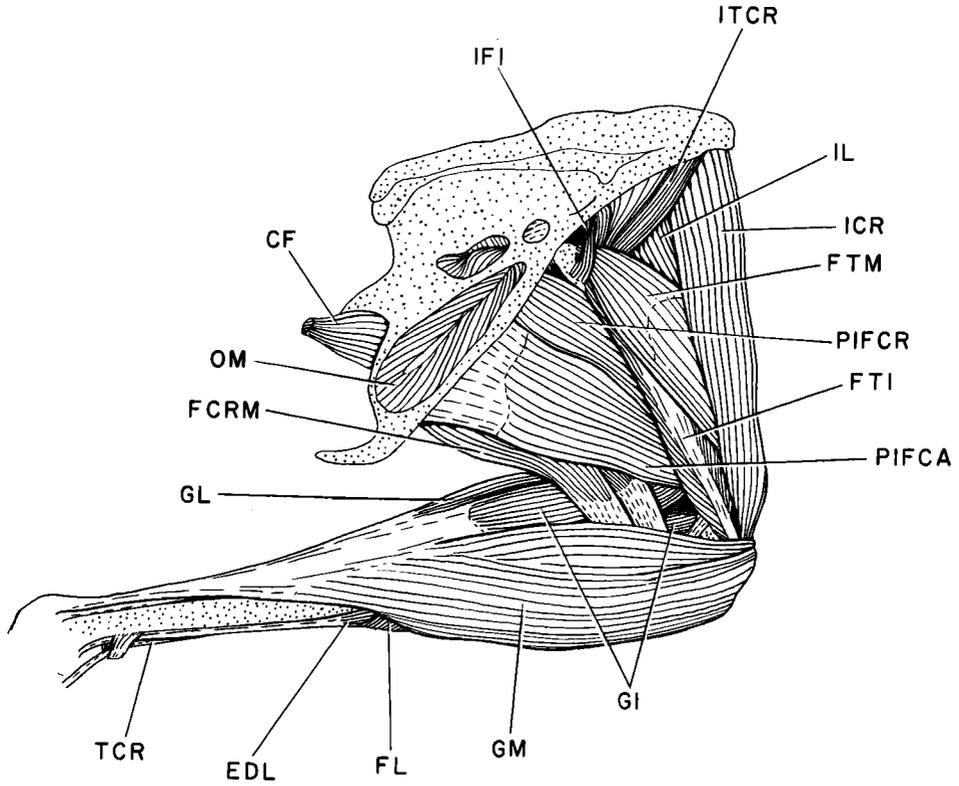
FIG. 24. Superficial musculature on the medial surface of the thigh and crus in *Pitta versicolor*. M. gastrocnemius pars medialis (GM) shows a primitive robust form with superficial and deep heads of origin, different from the derived attenuate condition in the Philepittidae and Eurylaimidae. There is no Pars supramedialis. M. pubo-ischio-femoralis pars caudalis (PIFCA) shows a caudad enlargement of its area of origin, a derived condition. Abbreviations in Appendix I.
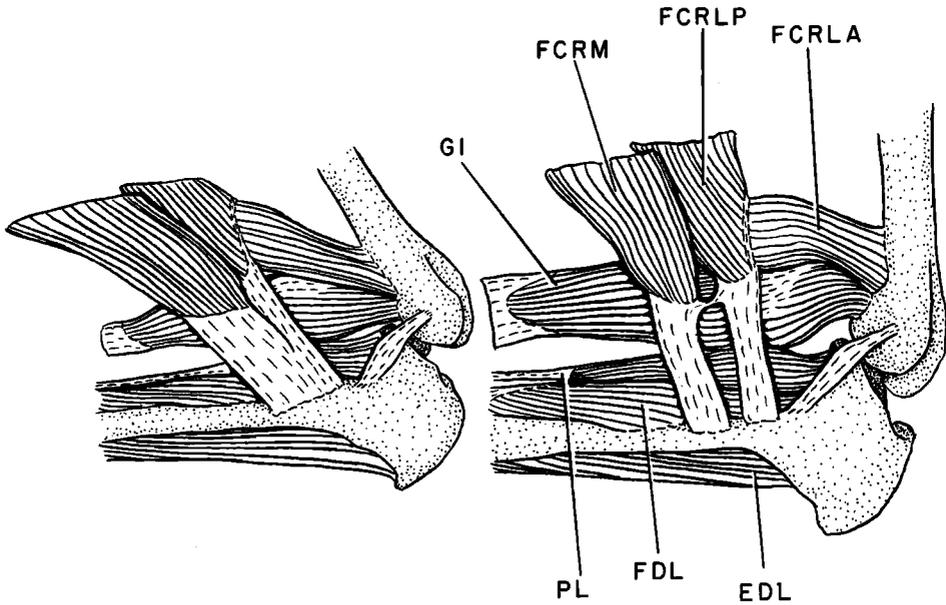
FIG. 25. Variation in the insertions of M. flexor cruris medialis (FCRM) and M. flexor cruris lateralis pars pelvica (FCRLP). Left: condition in *Pitta brachyura* showing the primitive condition of fusion of the two tendons. Right: derived condition exemplified by *P. versicolor* showing the derived separation of the two tendons of insertion. Abbreviations in Appendix I.
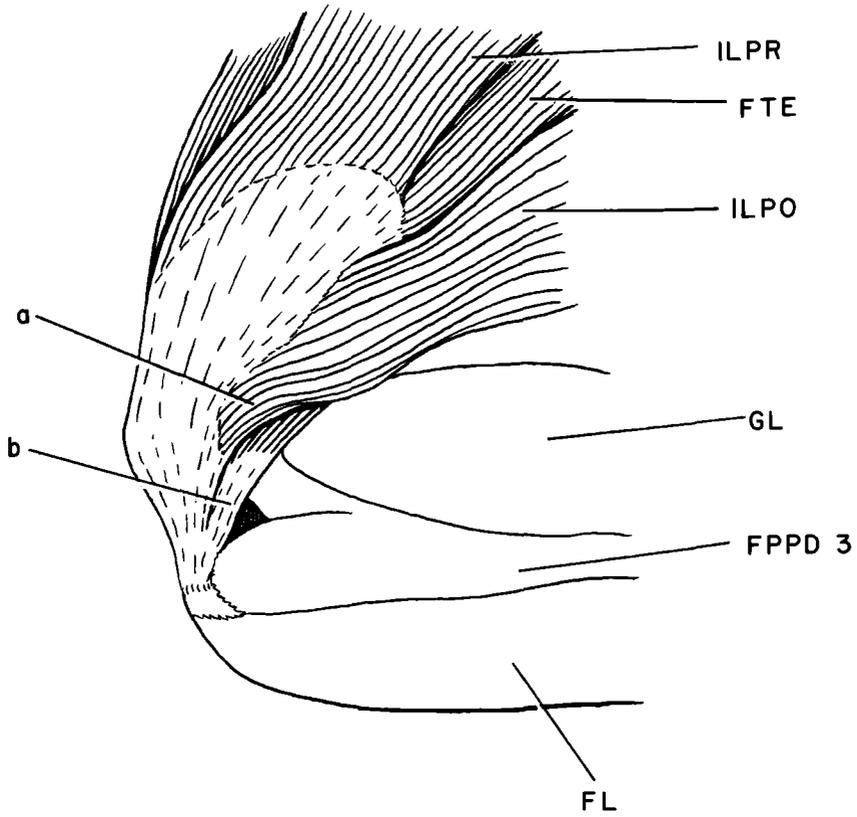
FIG. 26. Superficial muscles on the lateral surface of the knee in *Pitta brachyura*, illustrating a derived condition of pittas in which the distal part of the postacetabular belly of M. iliotibialis lateralis (ILPO) is divided into superficial (a) and deep (b) portions with separate insertions. Abbreviations in Appendix I.
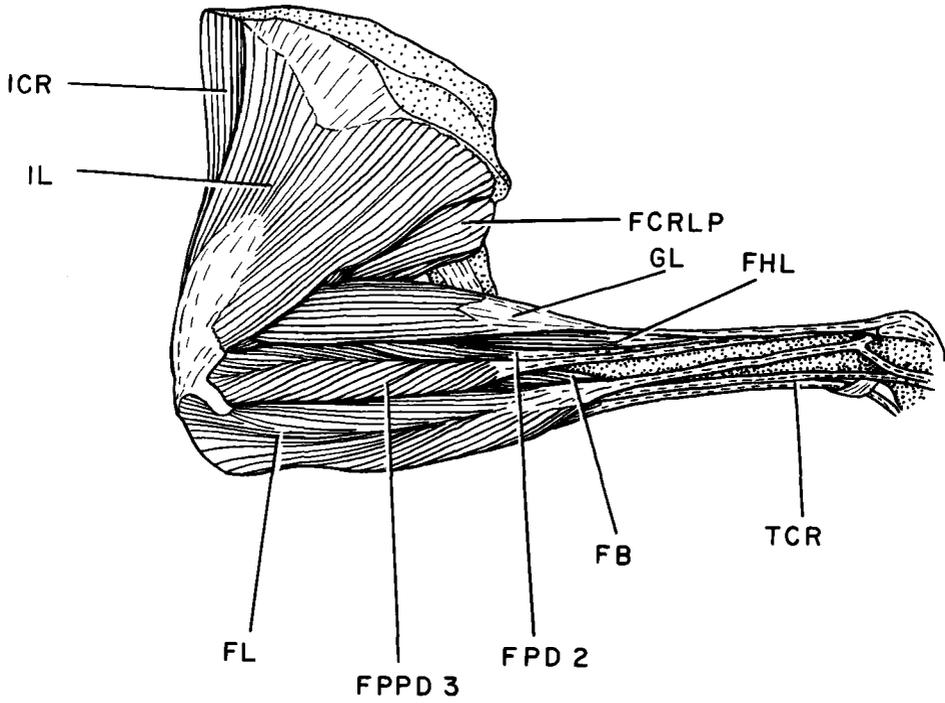
FIG. 27.   Superficial musculature on the lateral surface of the thigh and crus in *Acanthisitta chloris*. Note that in M. iliotibialis lateralis (IL) the pre- and postacetabular portions are not separated by an acetabular gap. Abbreviations in Appendix I.
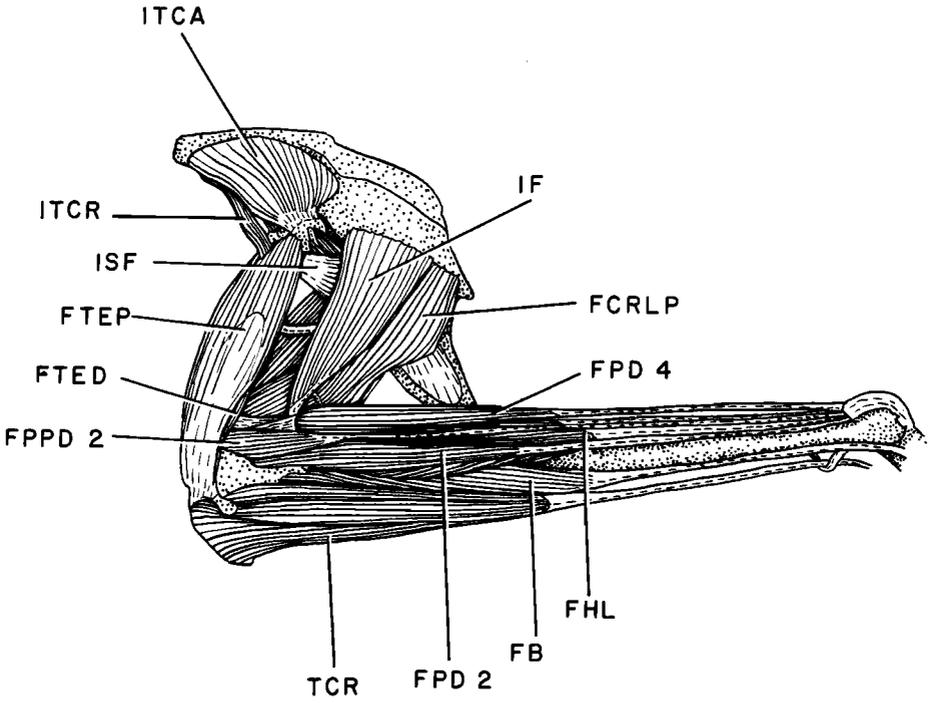
FIG. 28.   Second layer of muscles on the lateral surface of the thigh and crus in *Acanthisitta chloris*. Abbreviations in Appendix I.
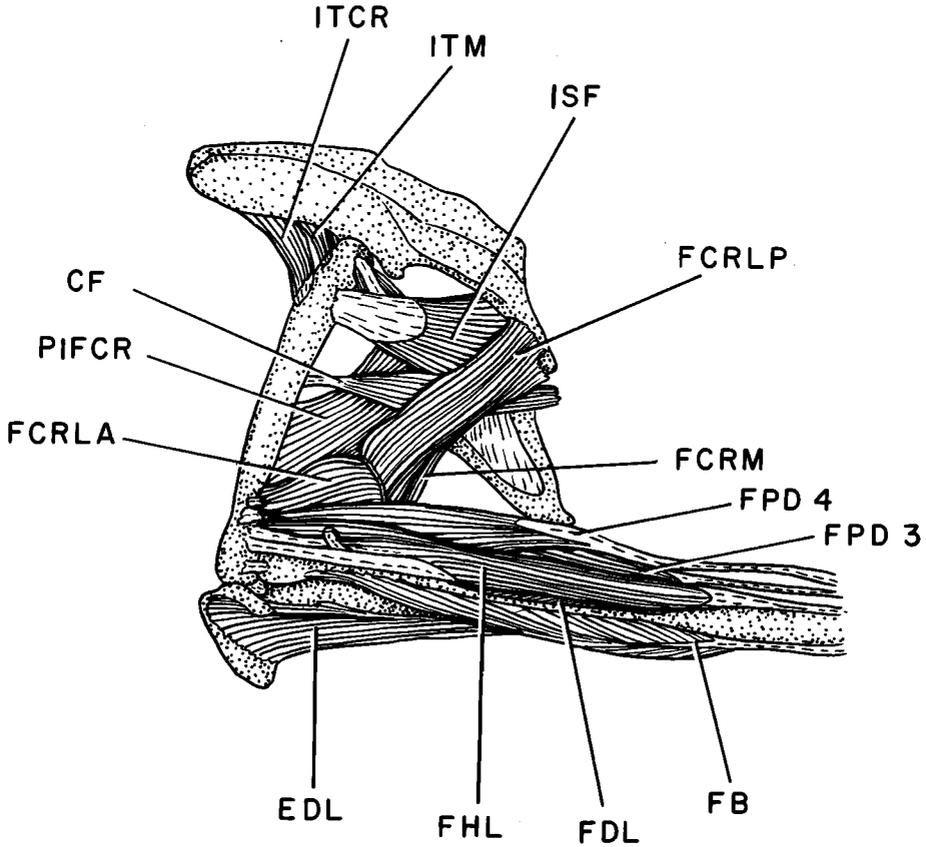
FIG. 29.   Third layer of muscles on the lateral surface of the thigh and crus in *Acanthisitta chloris*. Abbreviations in Appendix I.
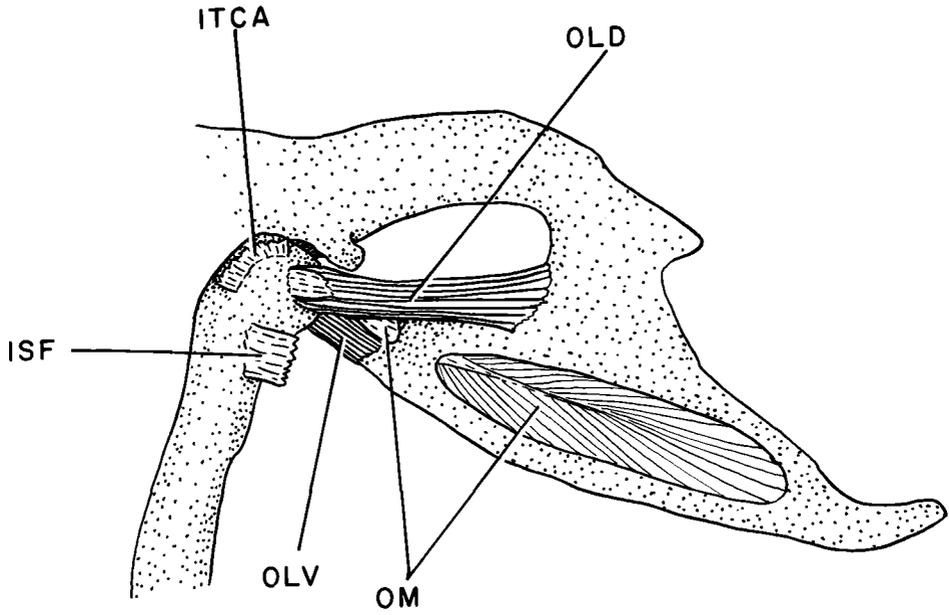
FIG. 30. Deep muscles of the hip in *Acanthisitta chloris*, showing the enlarged condition of M. obturatorius lateralis pars dorsalis (OLD). Abbreviations in Appendix I.
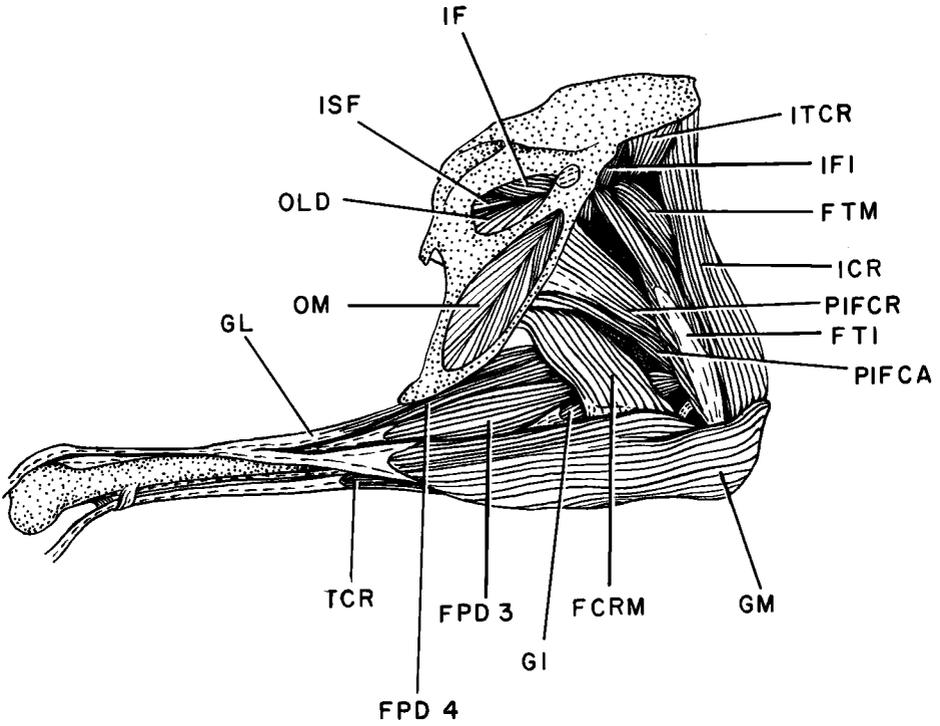
Fig. 31. Superficial muscles on the medial surface of the thigh and crus in *Acanthisitta chloris*. M. gastrocnemius pars medialis (GM) has a primitive form rather than the attenuate derived form of the Philepittidae and Eurylaimidae, and lacks Pars supramedialis. Abbreviations in Appendix I.
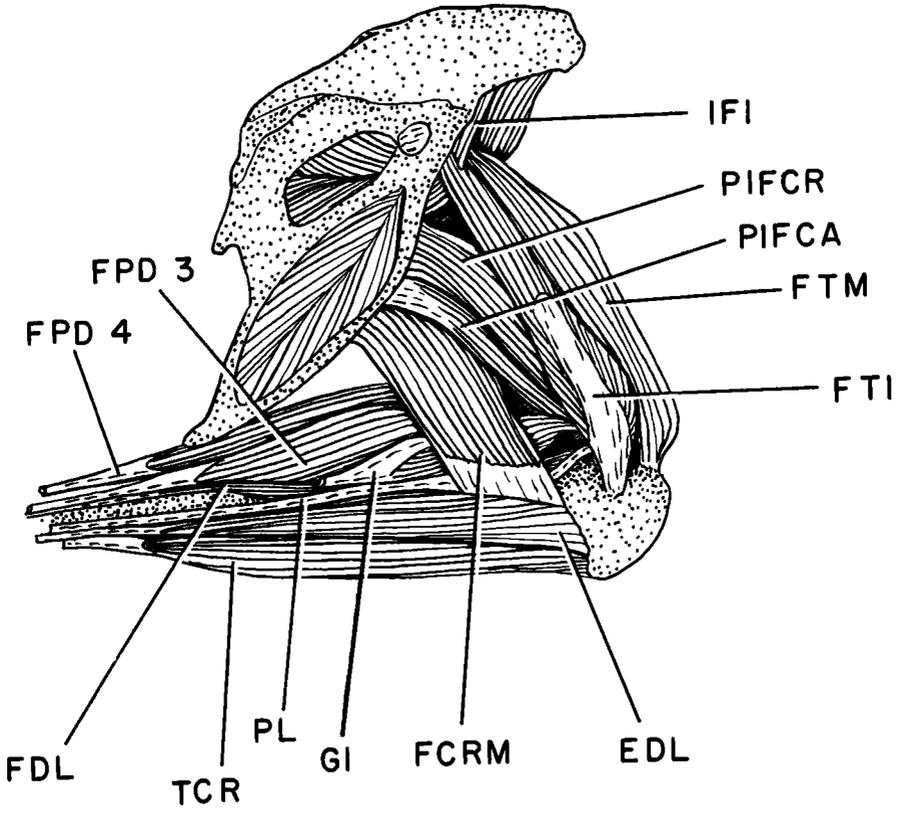
FIG. 32. Second layer of muscles on the medial surface of the thigh and crus in *Acanthisitta chloris*. Abbreviations in Appendix I.
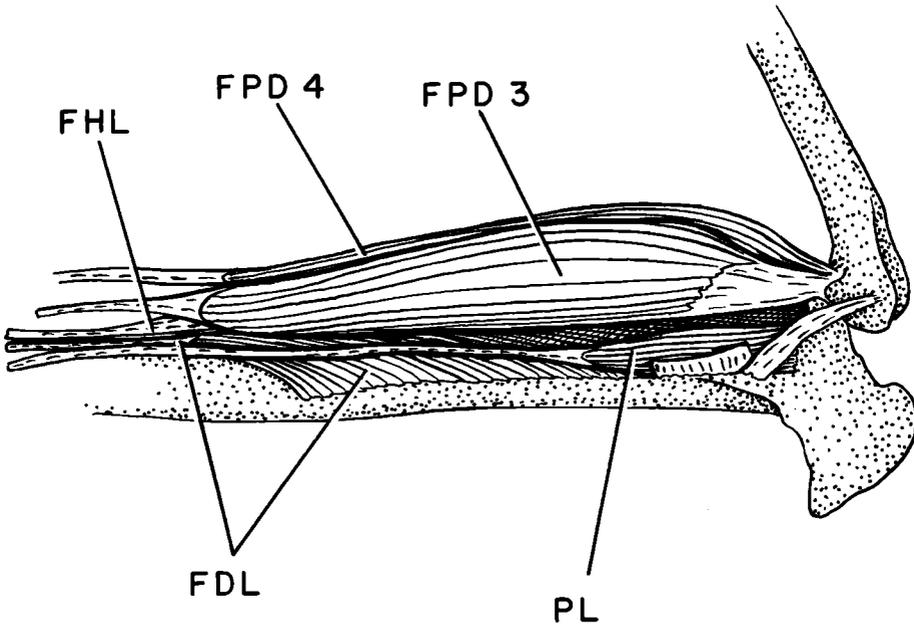
FIG. 33.   Deep caudomedial muscles of the crus in *Acanthisitta chloris*. Abbreviations in Appendix I.
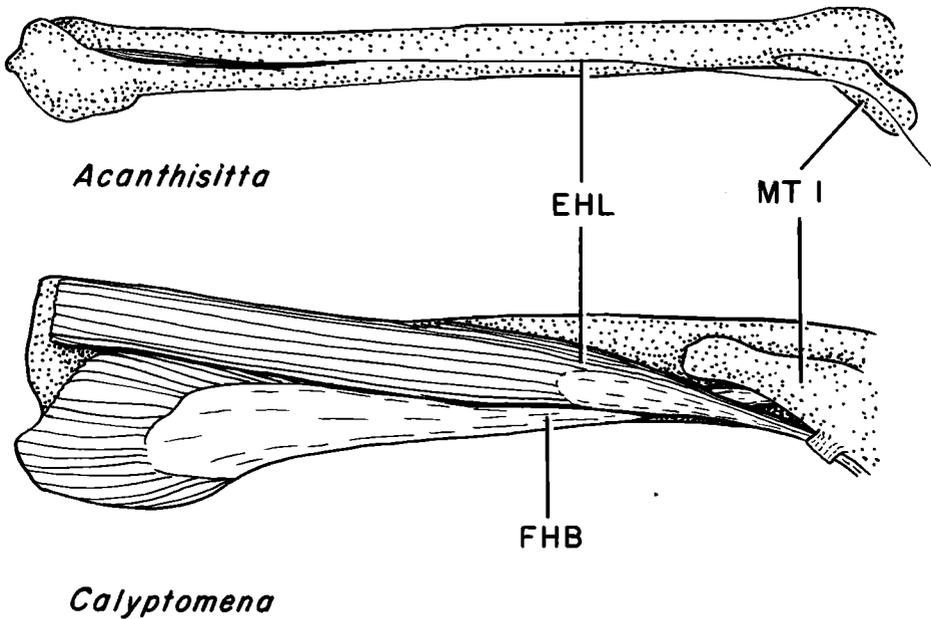
FIG. 34.   Extremes of variation in the development of two intrinsic muscles of the pes, Mm. extensor hallucis longus (EHL) and flexor hallucis brevis (FHB) as illustrated by *Acanthisitta chloris* and *Calyptomena viridis*. MTI is metatarsal I. Abbreviations in Appendix I.
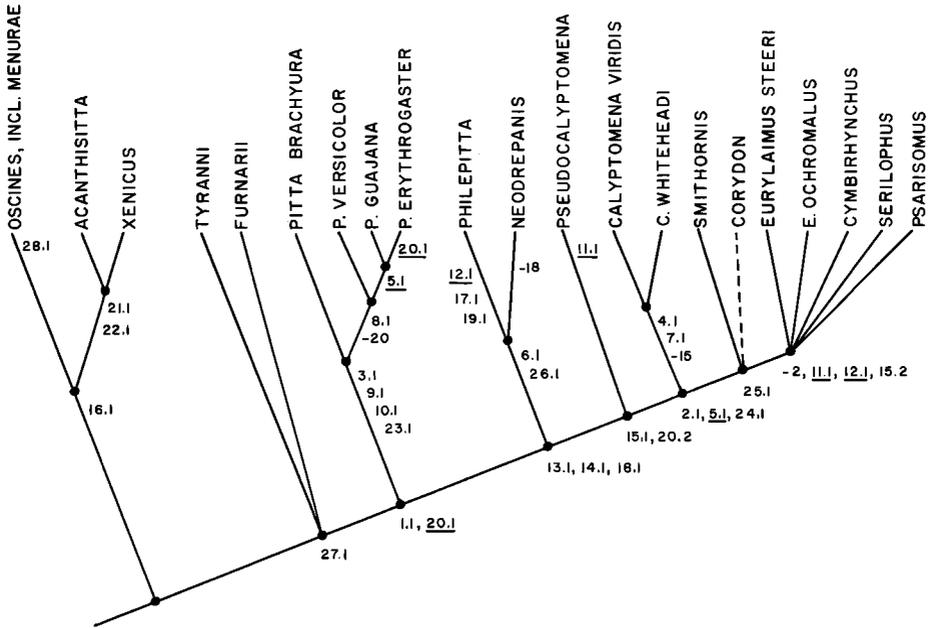
FIG. 35. One of four similar and equally parsimonious cladograms showing the relationships of the Old World suboscines to each other and to the other passerine birds. They were generated by PAUP and have a consistency index of 0.771, excluding autapomorphic character states. The numbers designate the character states as in Tables 1 and 2. A minus sign indicates an evolutionary reversal. Derived states postulated to have arisen independently in two different lineages are underlined. *Corydon* was not dissected, and is included tentatively on the basis of bill shape alone; it was not included in the computer analysis.
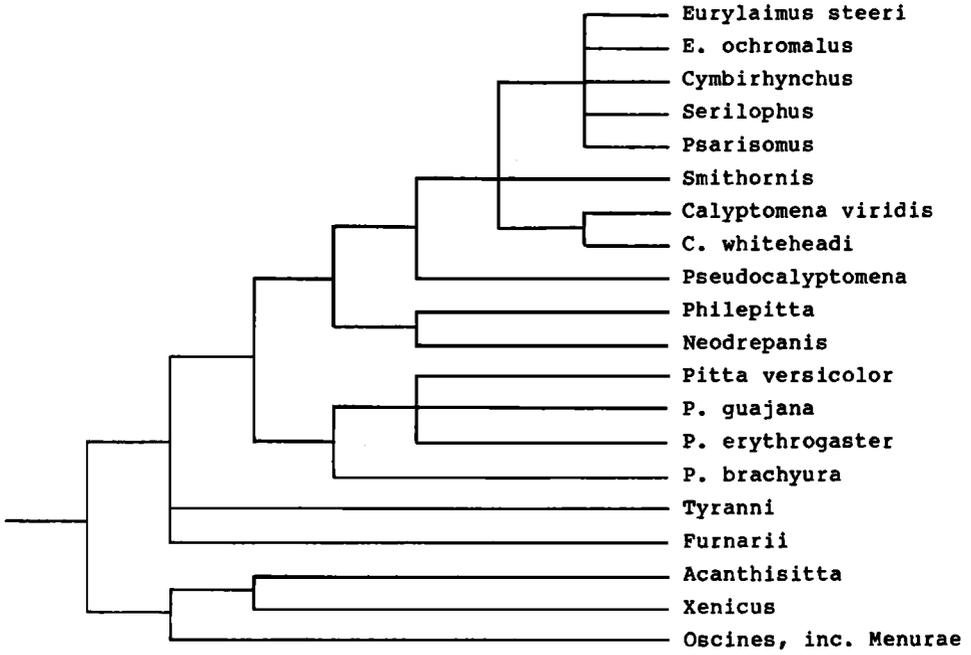
FIG. 36.   Strict consensus tree for four similar cladograms, one of which is shown in Figure 35. This is the basic phylogenetic hypothesis of the present investigation.
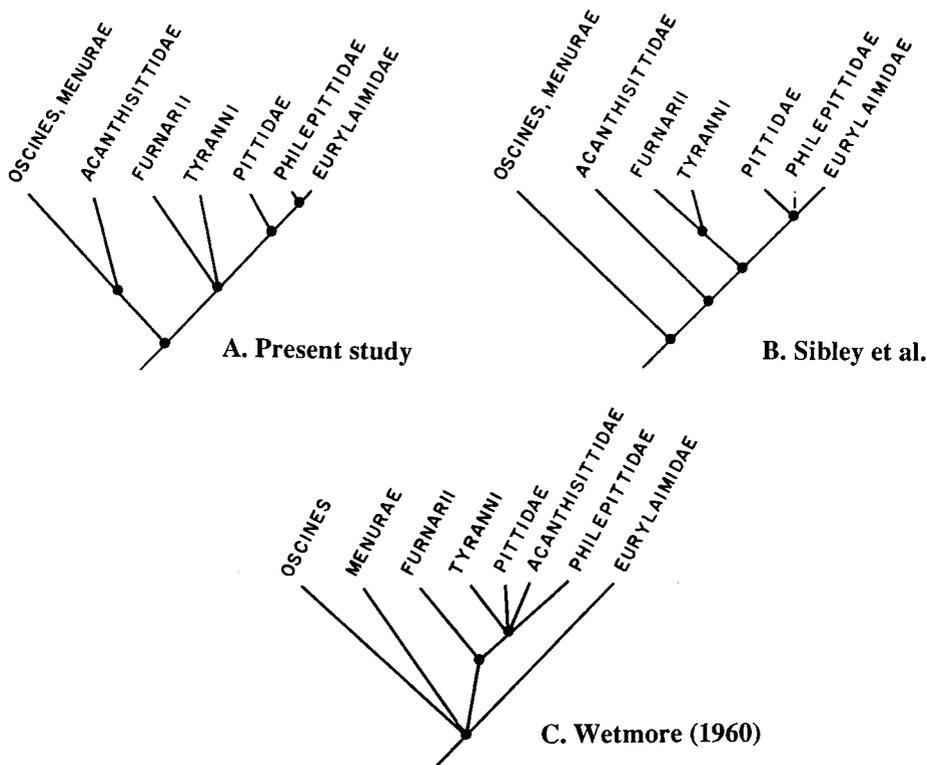
FIG. 37. A comparison of the results of three different studies of passeriform relationships. A. Simplified cladogram showing results of the present morphological study. B. Simplified cladogram of the results of the DNA hybridization study of Sibley et al. (1982) and Sibley and Ahlquist (1985b). C. The hierarchical structure of the classification of Wetmore (1960). A single nomenclature is used for ease of comparison. The taxon Furnarii corresponds to the Furnarioidea of Sibley et al. (1982) and of Wetmore (1960), and to a corresponding but unnamed taxon of Sibley and Ahlquist (1985b). The taxon Tyranni corresponds to the Tyrannoidea of Sibley et al. (1982), the Tyranni of Sibley and Ahlquist (1985b), and to the New World families of Wetmore's (1960) taxon Tyrannoidea.

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