

THE PHYLOGENETIC RELATIONSHIPS OF THE *MARGARORNIS* ASSEMBLAGE (FURNARIIDAE)¹

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Abstract. We performed a phylogenetic analysis of the hindlimb musculature in the Passerine genera *Margarornis*, *Premnornis*, *Premnoplex*, and *Roraimia* (collectively known as the *Margarornis* assemblage or "treerunners") in order to determine their affinities with one another and with the Dendrocolaptinae, a related, monophyletic group with similar scansorial habits. We conclude that the treerunners are not part of the dendrocolaptine clade, for they lack the synapomorphies of that group. The treerunners themselves are shown to be monophyletic on the basis of five derived character states. *Lochmias nematura*, despite its outward similarity to *Margarornis squamiger*, is excluded from the treerunner assemblage by the absence of the derived character states diagnosing that clade.

Key words: *Margarornis assemblage*; *treerunners*; *phylogeny*; *myology*; *woodcreepers*; *Lochmias nematura*.

INTRODUCTION

REVIEW OF THE PROBLEM

The treerunners are a group of small, neotropical, scansorial birds of the family Furnariidae, subfamily Furnariinae (Sibley and Monroe 1990). They include the Fulvous-dotted Treerunner (*Margarornis stellatus*), the Pearled Treerunner (*Margarornis squamiger*), the Ruddy Treerunner (*Margarornis rubiginosus*), the Rusty-winged Barbtail (*Premnornis guttuligera*), the Spotted Barbtail (*Premnoplex brunnescens*), and the Roraimian Barbtail (*Roraimia adusta*). *Margarornis bellulus* and *Premnoplex tatei* were considered by Vaurie (1980) as conspecific with *Margarornis squamiger* and *Premnoplex brunnescens*, respectively, but Sibley and Monroe (1990) list them as species. In their scansorial habits, including some use of the tail as a prop, the treerunners resemble the woodcreepers or Dendrocolaptinae, a consideration that prompted Sclater (1890) to include them in his Dendrocolaptinae. In contrast, Feduccia (1973), favoring family status for the ovenbirds and for the woodcreepers, grouped the treerunners with the synallaxine furnariids, which he considered the most distantly related to the Dendrocolaptidae.

The ovenbirds and woodcreepers are widely regarded as together constituting a monophyletic group. This view is based both on morphology

(Ames 1971; Feduccia 1973; Raikow, unpubl. data) and on DNA-DNA hybridization (Sibley and Ahlquist 1985, 1990). They have been classified by various workers either as separate families (Furnariidae and Dendrocolaptidae; e.g., Vaurie 1980) or as subfamilies (Furnariinae and Dendrocolaptinae) within the family Furnariidae (e.g., Sibley and Ahlquist 1990). We consider the two groups as subfamilies, following Sibley and Monroe (1990).

The present paper is part of an ongoing study of the relationships of the ovenbirds and woodcreepers. In a previous paper (Rudge and Raikow 1992) we described the hindlimb myology of representatives of four treerunner genera in order to catalogue muscle variations and to assess the extent to which they are correlated with the scansorial habit. Recent work on the appendicular myology (Raikow, unpubl. data) has shown that the woodcreepers constitute a monophyletic group.

SPECIFIC AIMS

We will address the following four questions. (1) *Are the treerunners part of the Dendrocolaptinae?* Because the Dendrocolaptinae is monophyletic (Raikow, unpubl. data), we must show that the treerunners either do or do not exhibit the synapomorphies (shared derived character states) that diagnose the group. If the treerunners are members of this clade, possession of these character states would corroborate this. (2) *Are the treerunners a monophyletic group?* If the treerunners constitute a clade, they should exhibit shared derived characters lacking in other furnariids. (3)

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Is Lochmias nematura a member of the treerunner assemblage? Vaurie (1980:238) proposed this connection on the basis of plumage similarities with *Margarornis squamiger*. If *Lochmias* is a member of the treerunner assemblage, it should exhibit the synapomorphies of the group. (4) *What are the relationships of the treerunners to one another?* As with question (1) above, the answer will depend upon whether the treerunners are themselves monophyletic, plus the presence of derived character states within the assemblage that diagnose subordinate clades.

MATERIALS AND METHODS

Twenty-five specimens of ten species of birds preserved in ethanol were dissected. Sample sizes and catalog numbers are given below in parentheses, with abbreviations for museums from which specimens were borrowed as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; FM, Field Museum of Natural History; LSU, Louisiana State University Museum of Natural Science; *Margarornis rubiginosus* (2: LSU/JPO 2289, LSU 64786); *Margarornis squamiger* (5: LSU 60811, LSU 75008, LSU 79559, LSU 79560, LSU 331197); *Premnoplex brunnescens* (7: FM 321530, FM 321531, LSU 70631, LSU 75010, LSU 85962, LSU 89447, LSU 95543); *Premnornis guttuligeria* (5: LSU 83865, LSU 89444, LSU 89445, LSU 107624, LSU 107625); *Roraimia adusta* (1: AMNH 7685); *Lochmias nematura* (1: LSU 79570); *Dendrocolaptes certhia* (1: CM 1380); *Deconychura longicauda* (1: LSU 107617); *Dendrocincla anabatina* (1: CM 3812); *Deconychura stictolaema* (1: LSU 114403). Dissection methods were described previously (Rudge and Raikow 1992).

Abbreviations for Figures 1–5 are as follows: FCRLA, *M. flexor cruris lateralis pars accessoria*; FCRLP, *M. flexor cruris lateralis pars pelvica*; FIB, head of the fibula; FL, *M. fibularis longus*; FPD4, *M. flexor perforatus digiti IV*; FPPD2, *M. flexor perforans et perforatus digiti II*; FPPD3, *M. flexor perforans et perforatus digiti III*; G, *M. gastrocnemius*; IF, *M. iliofibularis*.

RESULTS AND DISCUSSION

RELATIONSHIP TO THE DENDROCOLAPTINAE

(1) *Digit length.* In dendrocolaptines digit IV is elongated nearly to the length of digit III, a derived state in contrast to most passerine birds

(Raikow, unpubl. data). None of the treerunners were found to possess this character state.

(2) *Origin of *M. flexor digitorum longus* and *flexor hallucis longus*.* In the Dendrocolaptinae, *M. flexor digitorum longus* arises by the usual tibial and fibular heads, but also has a massive femoral head that occupies a position in the crus usually held by the medial head of *M. flexor hallucis longus* (Fig. 1A), which is correspondingly reduced. This condition is derived for the woodcreepers (Raikow, unpubl. data). In treerunners, however, *M. flexor digitorum longus* lacks a femoral head (Fig. 1B), and the medial head of *M. flexor hallucis longus* is not reduced. This is the primitive passerine arrangement, and fails to support the inclusion of the treerunners in the dendrocolaptine clade.

(3) *Tendon ossification.* The Dendrocolaptinae have evolved ossification of most of the crural tendons, in contrast to the usual passerine condition in which most of these tendons are not ossified. The treerunners lack ossified tendons except for the tarsal segment of the tendon of *M. flexor digitorum longus*, which alone is sometimes found in other passerines. The absence of this complex derived state argues against a grouping of the treerunners with the Dendrocolaptinae.

(4) *Insertion of *M. pubo-ischio-femoralis pars caudalis*.* In the Dendrocolaptinae, *M. pubo-ischio-femoralis pars caudalis* inserts onto the femur alone, a derived state, and not additionally upon *M. gastrocnemius pars intermedia* as in other passerine birds (Raikow, unpubl. data). The treerunners exhibit the typical passerine condition (Rudge and Raikow 1992, Figs. 7, 8) and do not exhibit the dendrocolaptine state for this character.

(5) *Insertion of *M. flexor cruris medialis*.* Raikow (unpubl. manuscript) pointed out that the Dendrocolaptinae exhibit changes in the size and insertion of the *M. flexor cruris medialis* tendon relative to the insertion of Tendon *M.* None of the treerunners exhibited such changes (Rudge and Raikow 1992, Fig. 8).

(6) *Curvature of the claws.* Raikow (unpubl. manuscript) reported that the claws of digits II–IV in woodcreepers have acquired a greater arc of curvature than those of ovenbirds. In the treerunners, however, the arcs of the claws remain within the range of nonscorsorial ovenbirds, and lack the derived specialization of the woodcreepers.

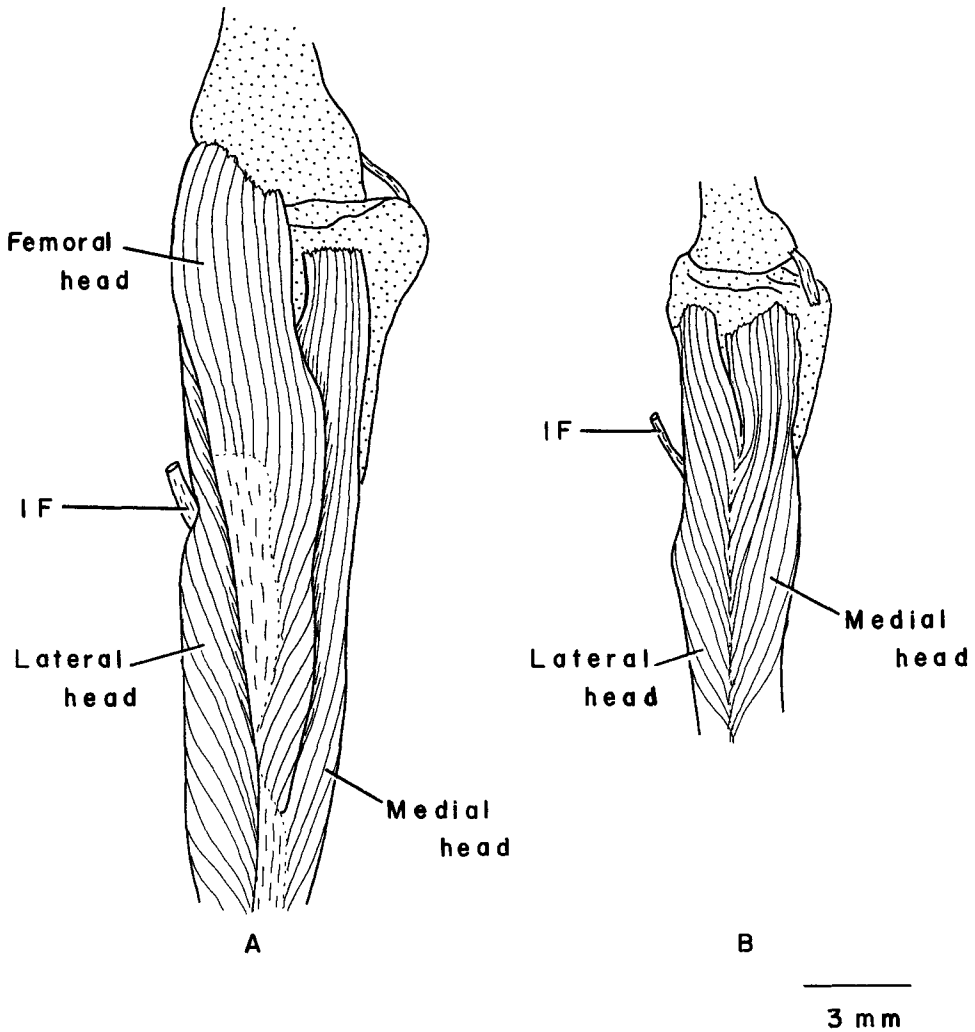


FIGURE 1. Comparison of the origin of *M. flexor digitorum longus* between: (A) *Dendrocolaptes certhia* CM 1380 (Dendrocolaptinae); and (B) *Premnoplex brunnescens* LSU 70631 (Furnariinae), illustrating the absence of a femoral head in the latter. Abbreviations for the figures are given under Materials and Methods.

(7) *Additional characters.* Other characters have been used to separate woodcreepers from other passerines. "Horns" on the syrinx (Ames 1971) argue for monophyly. In ovenbirds, "horns" were found only in *Geositta* (Ames 1971:154), however Ames (1971) apparently did not examine the syringes of the treerunners. Dendrocolaptines also characteristically possess a stiffened tail, but Vaurie (1980:230) indicated that the tail of treerunners is not notably stiffened.

In summary, none of the synapomorphic hindlimb character states that delimit the Dendrocolaptinae was found in any of the treerunner specimens, nor did the traditional characters

support inclusion of the treerunners in the dendrocolaptine clade.

MONOPHYLY OF THE TREERUNNERS

In order to demonstrate the monophyly of the treerunner assemblage, it is necessary to show that its members share synapomorphies lacking in other forms. We will consider whether any of the muscle variations found in our dissections is such a synapomorphy, using the method of outgroup comparison (Maddison et al. 1984, Raikow 1987:7-8). This method requires that the species in question belong to some more inclu-

sive clade (Raikow 1982:433). Raikow (unpubl. manuscript) has established that the ovenbird-woodcreeper assemblage is probably monophyletic. A rigorous application of outgroup comparison would demand a knowledge of the precise sister-group relationships of the treerunner assemblage. This is not available at the present time, but Raikow (unpubl. manuscript) dissected a representative sample of the Furnariinae, providing a basis for comparison. We used successive sister groups of the ovenbird-woodcreeper assemblage as outgroups (more distantly related Furnarii, including *Thamnophilus doliatus*, *Formicivora mentalis*, *Cercomacra tyrannina*, and *Acropternis orthonyx*; New World Tyranni; and Old World suboscines). We also made note of the condition of the character in question in the Dendrocolaptinae. These groupings represent the best current estimate of passerine phylogeny (Raikow 1987, Bledsoe and Raikow 1990, Sibley and Ahlquist 1990).

(1) *Origin of M. flexor cruris medialis*. In most passerines, the caudal extent of the origin of *M. flexor cruris medialis* arises from the edge of the dorsal rim of the ischiopubic fenestra; but in treerunners the origin extends from beyond the rim, forming a characteristic 'lip' (Rudge and Raikow 1992, Fig. 5). Despite some variation in size, this occurred in all specimens. Such an origin is unknown in other members of the furnariine-dendrocolaptine group (Raikow, unpubl. data). Its apparent absence in the other Furnarii mentioned above (Raikow, unpubl. manuscript), the New World Tyranni (McKittrick 1985:289; Raikow, unpubl. observ.), and the Old World suboscines (Raikow 1987:14) suggests that this is a derived condition in the Furnariidae and, thus, synapomorphic for the treerunner assemblage.

(2) *Origin of M. flexor perforans et perforatus digiti II*. In treerunners the origin of *M. flexor perforans et perforatus digiti II* extends from the laterodistal surface of the femur (as in other passerines) caudolaterally along the lateral collateral ligament, which joins the femur to the head of the fibula (Rudge and Raikow 1992, Fig. 8). The absence of such an extended origin among other members of the furnariine-dendrocolaptine assemblage (Fig. 2) and other suboscines (Raikow, unpubl. manuscript; McKittrick 1985:294; Raikow 1987:21), demonstrates that this is a derived state among furnariines. It has also been found unilaterally or bilaterally in a few dendrocolaptines (Raikow, unpubl. manuscript), where the

pattern of its occurrence suggests that it is due to individual variation. Therefore, we conclude that it has probably been independently derived in the treerunner assemblage and is a synapomorphy of the group.

(3) *Reduction of M. flexor perforatus digiti IV*. In suboscines, *M. flexor perforatus digiti IV* is composed of two separate bellies (Pars proximalis and Pars distalis), each of which gives rise to a tendon that joins with the other to form a common tendon of insertion. In treerunners, Pars proximalis is unusually small, and its insertion is reduced to a slender, hair-thin tendon (Fig. 3A). This condition is unknown in other members of the furnariine-dendrocolaptine assemblage (Fig. 3B) (Raikow, unpubl. data). The absence of this character state in other suboscines (Raikow, unpubl. manuscript; McKittrick 1985:296; Raikow 1987:22-23) suggests that it is a derived condition in the Furnariidae, and therefore synapomorphic for the treerunner assemblage.

(4) *M. flexor hallucis longus*. A swelling occurred in the insertion tendon of *M. flexor hallucis longus* (Rudge and Raikow 1992, Fig. 9) in all specimens. This condition is lacking in other members of the furnariine-dendrocolaptine assemblage (Raikow, unpubl. manuscript). It has not been reported in other suboscines (McKittrick 1985:304, Raikow 1987:23-25), suggesting that it is a derived condition in the Furnariidae and synapomorphic for the treerunner assemblage.

(5) *M. lumbricalis*. This is a small muscle that extends from the trifurcation of the *M. flexor digitorum longus* tendon to the joint pulleys of the forward toes. In treerunners, one or two additional bellies were found in all specimens (Rudge and Raikow 1992, Fig. 9). This is unknown in other members of the furnariine-dendrocolaptine assemblage or other Furnarii (Raikow, unpubl. manuscript), or the Old World suboscines (Raikow 1987:27). *M. lumbricalis* is absent among the New World Tyranni (McKittrick 1985:306). Although the presence of two bellies has been reported in some nonpasserine birds (i.e., *Gallicolumba luzonica* and *Opisthocomus hoazin*: George and Berger 1966:464), the absence in passerines of an association with the flexor hallucis longus tendon (found in those nonpasserines having a second belly) suggests that this condition has been independently derived and, as such, is a synapomorphy of the treerunner assemblage.

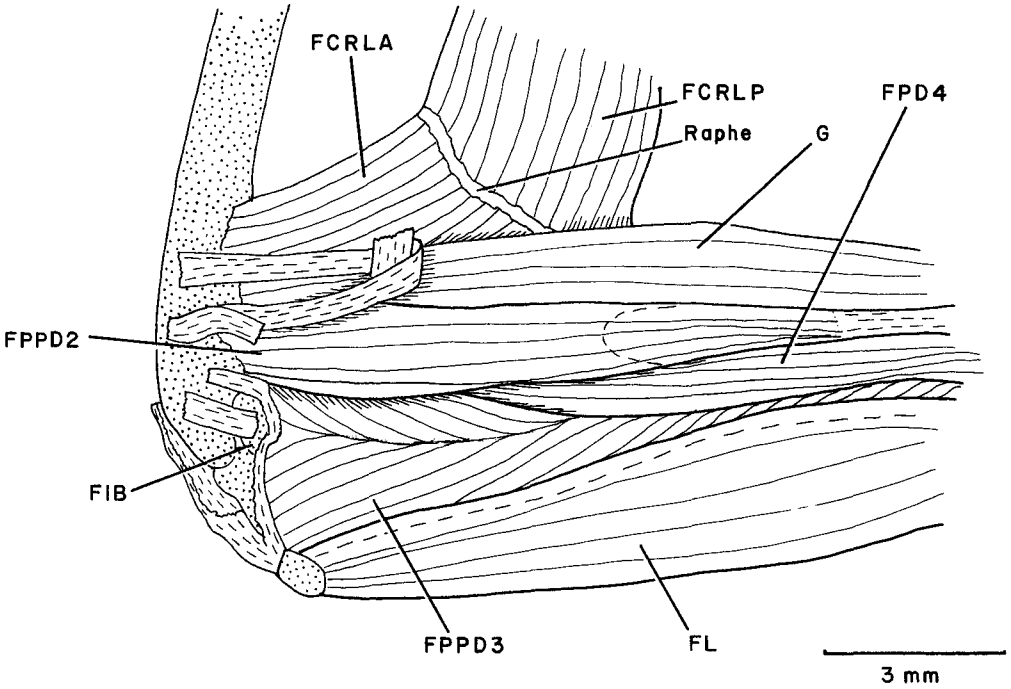


FIGURE 2. Origin of *M. flexor perforans et perforatus digiti II* (FPPD2) in the dendrocolaptine *Deconychura stictolaema* LSU 114403, showing the absence of an origin from the head of the fibula (FIB).

Thus, our dissections suggest five synapomorphic characters that appear to demarcate a tree-runner clade from other members of the ovenbird-woodcreeper assemblage.

RELATIONSHIP OF *LOCHMIAS* TO THE TREERUNNER ASSEMBLAGE

Lochmias nematura has been suspected of affinities with *Margarornis squamiger* on the basis of

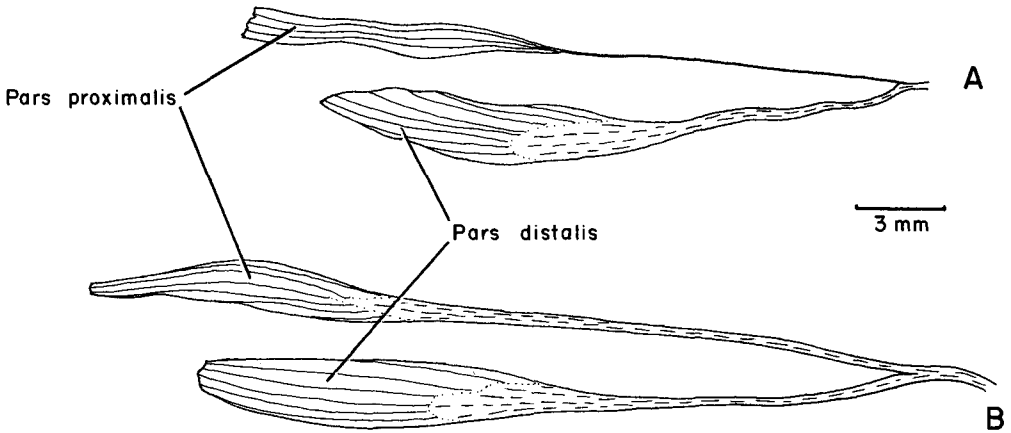


FIGURE 3. Comparison of *M. flexor perforatus digiti IV* in (A) *Margarornis squamiger* LSU 75008; and (B) *Dendrocolaptes certhia* CM 1380. Note the reduction of Pars proximalis and its fine, hairlike tendon in the treerunners compared to its condition in the Dendrocolaptinae.

a similar pearly plumage pattern and similarities in the tail (Vaurie 1980:238). If *Lochmias* is a member of the treerunner assemblage, it should exhibit the synapomorphies of that group. In *Lochmias* *M. flexor cruris medialis* does not have a caudally extended origin as in the treerunner assemblage; its origin extends only to the rim of the ischiopubic fenestra. *M. lumbricalis* consists of only one belly in *Lochmias*. *M. flexor perforans et perforatus digiti II* in *Lochmias* lacks an extended origin onto the head of the fibula, but retains the typical origin found in other subspecies. *M. flexor perforatus digiti IV* in *Lochmias* has neither the reduced belly nor the fine, hairlike tendon characteristic of the treerunner assemblage. *Lochmias* does have a slight stiffening in the region of the swelling of *M. flexor hallucis longus* noted in the description of this muscle above, but no swelling is present. We interpret this as not being sufficiently similar to constitute a character state shared with the treerunner assemblage. In conclusion, *Lochmias* has none of the synapomorphies of the treerunners, and we therefore conclude that it is not a member of that group.

INTERRELATIONSHIPS OF THE TREERUNNERS

The caudal extent of the postacetabular belly of *M. iliotibialis lateralis* was reduced in all *Margarornis* specimens, in contrast to the other species of this study (Rudge and Raikow 1992, Figs. 1, 2). Such reductional trends have been observed in a number of passerine groups (e.g., McKittrick 1985:308, Raikow 1987:28) including a few furnariines and dendrocolaptines (Raikow, unpubl. manuscript). This outgroup comparison is therefore somewhat equivocal. However, as most outgroups either lack this character, or have it in some but not all species, it probably represents a derived state in the treerunners as well, and constitutes a synapomorphy for the two *Margarornis* species.

In *Premnoplex brunnescens* and *Premnornis guttuligera*, Tendon M originates entirely from the tibial lobe of *M. flexor cruris lateralis* pars pelvica (Rudge and Raikow 1992, Figs. 7, 8). A similar modification has also been found among dendrocolaptines (Raikow, unpubl. manuscript). This condition is lacking in other Furnarii and in the more distant New World Tyranni, and, given the monophyly of the treerunners, is de-

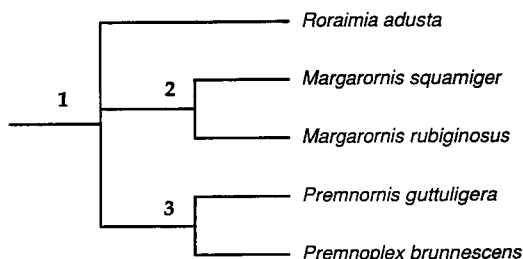


FIGURE 4. Phylogenetic tree illustrating relationships of the *Margarornis* assemblage based upon hindlimb muscle synapomorphies: (1) *M. flexor cruris medialis* origin extended; *M. flexor perforans et perforatus digiti II* origin extended; *M. flexor perforatus digiti IV* pars proximalis belly and tendon reduced; swelling in tendon of *M. flexor hallucis longus*; *M. lumbricalis* possession of two bellies; (2) *M. iliotibialis lateralis* pars postacetabularis belly reduced; (3) Tendon M originates from the tibial lobe of *M. flexor cruris lateralis* pars pelvica; *M. lumbricalis* possession of third intermediate belly.

rived for the clade consisting of *Premnoplex brunnescens* and *Premnornis guttuligera*.

One of the more striking differences among the species of the present study is the presence of a third belly of *M. lumbricalis* (Rudge and Raikow 1992, Fig. 9) in *Premnornis guttuligera* and *Premnoplex brunnescens*. Some individual exceptions were found in both these species, but this may be due to dissection artifact, given the tiny size of the structure. No other birds in this study had a third belly, which is also unknown in other birds (George and Berger 1966:483-484). We conclude that this condition represents a synapomorphy for these two species.

Our conclusions are presented in the form of a tree (Fig. 4). Information from the hindlimb musculature is insufficient to completely resolve the phylogeny of the treerunners, but it does provide a documented hypothesis for future comparison with other studies.

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