APPENDICULAR MYOLOGY AND RELATIONSHIPS OF THE SHRIKES (AVES: PASSERIFORMES: LANIIDAE)

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ABSTRACT

The appendicular musculature was dissected in 18 species of passerine birds in the family Laniidae (shrikes and their allies). A cladistic analysis of variations in the limb muscles, supplemented by other information, was used to construct a hypothesis of evolutionary relationships in the family. Monophyly of the family as currently recognized was not refuted, but corroborating data are weak. The subfamily Malacontininae (bush-shrikes) is a coherent assemblage of primitive species. The true shrikes (subfamily Laniinae) have hind limb muscular specializations apparently unique among passerine birds. The helmet-shrikes (subfamily Prionopinae) have a distinct pattern of hind limb adaptations. The Bornean Bristlehead, Pityriasis gymnocephala (subfamily Pityriasiinae), an aberrant oscine of disputed affinities, is most likely the primitive sister taxon of the Prionopinae.

INTRODUCTION

Current opinions about the evolutionary relationships of the shrikes and their allies are based on the ideas of Sharpe (1877), who first defined the family Prionopidae, and Gadow (1883), who established the family Laniidae. Subsequent workers rearranged some genera, and

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removed many of them to other families. The taxonomic history of the group is reviewed by Sibley (1970:78–79) and Mayr and Amadon (1951). The modern concept of the shrike assemblage is expressed in the classification of the Laniidae by Rand (1960), which is summarized in Table 1.

Rand recognizes four subfamilies. The Prionopinae or helmet-shrikes include the genera *Eurocephalus* (two species) and *Prionops* (seven species) of Africa. Helmet-shrikes have specialized head feathering with stiffened feathers on the forehead, sometimes forming a crest. *Prionops*, furthermore, has distinctive eye wattles formed by fleshy outgrowths of the eyelid margins. The group has often been considered as a separate family Prionopidae, and as such is diagnosed by Van Tyne and Berger (1976:754) and Bannerman (1939:337). Sharpe (1877) defined the family by a detailed diagnosis, but most of his characters are either plesiomorphous or readily attributable to convergence. Mayr (1943) removed most of Sharpe’s genera to other families, and the remnant form the group as currently recognized.

The most diverse group in the Laniidae is the subfamily Malaconotinae or African bush-shrikes, which in Rand’s classification includes seven genera and 39 species. The bush-shrikes are variable in plumage, some being drab and others brightly colored. Some are birds of open country while others frequent woodlands. They are often arboreal gleaners, but some also forage on the ground. In general the subfamily appears to be a coherent group except for *Nilaus*, which differs from the other genera in the form of the tarsal envelope (podotheca). In

| Table 1.—Outline of Rand’s (1960) classification of the Laniidae. |
|-------------------|-----------------|-----------------|
| **Subfamilies**   | **Genera**      | **Number of species** | **Distribution** |
| Prionopinae       | *Eurocephalus*  | 2               | Africa           |
|                   | *Prionops*      | 7               | Africa           |
| Malaconotinae     | *Lanioturdus*   | 1               | Africa           |
|                   | *Nilaus*        | 1               | Africa           |
|                   | *Dryoscopus*    | 6               | Africa           |
|                   | *Tchagra*       | 6               | Africa           |
|                   | *Laniarius*     | 10              | Africa           |
|                   | *Telephorus*    | 10              | Africa           |
|                   | *Malaconotus*   | 5               | Africa           |
| Laniinae          | *Corvinella*    | 2               | Africa, Asia, Europe, North America, Philippines, Malaysia, New Guinea |
|                   | *Lanius*        | 23              | Africa, Asia, Europe, North America, Philippines, Malaysia, New Guinea |
| Pityriasinae       | *Pityriasis*    | 1               | Borneo           |
most bush-shrikes this has a row of large scutes on the anterior surface, with undivided (fused) laminae on either side of the planta tarsus. In *Nilaus*, however, the plantar surfaces have a row of separate scutes, resembling the condition in the Prionopinae. Perhaps on this basis, Sclater (1930) included *Nilaus* with the Prionopidae. Mayr (1943) transferred *Nilaus* to the Muscicapidae on the basis of plumage, considering that the shrike-like bill was a convergent feature. Chapin (1954) disagreed with both Sclater (1930) and Mayr (1943), and retained *Nilaus* among the shrikes.

The subfamily Laniinae contains the true or typical shrikes. The long-tailed genus *Corvinella* is restricted to Africa, but *Lanius* has spread throughout the Old World and into North America, and in the process has split into a great many species (Table 1). The true shrikes usually hunt by sitting on an exposed perch while scanning the ground. When it sights prey the bird flies down to capture it, and then returns to the same or another perch to feed. The Laniinae and Malaconotinae are sometimes grouped together as the family Laniidae when the Prionopidae are classified separately. This is based on the idea that they are closely related, though Mayr and Amadon (1951) questioned this. Diagnoses of the Laniidae in this form are given by Van Tyne and Berger (1976:753) and Bannerman (1939:348).

The subfamily Pityriasinae contains only the Bornean Bristlehead, *Pityriasis gymnocephala*. This is one of the strangest of all oscines, and its affinities are extremely obscure. Despite its name, it has no true bristles on its head (Stettenheim, 1974:226). It has a large, hooked bill, which is shrike-like in general form. Patches of contrastingly colored bristle-like contour feathers on the lower sides of the head, and a bare area of somewhat rough-textured skin around the eye suggest an affinity with the Prionopinae. The strangest feature is that the top of the head is covered with a dense carpet of finger-like outgrowths of the skin. These are not bristles, although they resemble them in a dry study skin. Examination of a spirit specimen shows that they are outgrowths of the skin itself. These peculiar structures are unique among birds, though probably representing some more generalized capability of the skin for such specializations as wattles, caruncles, and the like.

Mayr (1943) suggested tentatively that *Pityriasis* might be a starling (Sturnidae), mainly because the bare area around the eye resembles that in some mynahs. Mayr and Amadon (1951) pointed out the geographical difficulty of allying *Pityriasis* with the Prionopinae, but admitted that it has some possible affinities with that group, and could offer no better solution than to repeat the possible sturnid connection. Amadon (1943) reluctantly included it in the Sturnidae, while pointing out characters that argued against this position. Later (Amadon, 1956), he preferred to keep it in the Prionopidae. Delacour (1947) placed it
with the Sturnidae, but also with uncertainty. Thompson (1966) preferred to place Pityriasis in the Cracticidae, on the basis of a brief osteological study whose results he did not report. The overall impression that one receives from the literature is that nobody has been comfortable with any allocation of Pityriasis, and that the question of its affinities is still unresolved.

The present study is an attempt to clarify the problems of evolutionary relationships within the Laniidae, including the question of whether the family is monophyletic. This is done by a cladistic analysis of new information on the gross morphology of the limb muscles, combined with a reassessment of some of the characters analyzed by previous workers.

METHODS AND MATERIALS

All of the forelimb and hindlimb muscles were examined in the following species: Prionopinae—Prionops cristata, P. plumata, Eurocephalus rueppelli, E. anguitimens; Malaconotinae—Nilaus brubru, Dryoscopus sabini, D. cubla, Tchagra senegala, Laniarius ferrugineus, Telophorus sulfureopectus, T. zeylonus, T. dohertyi; Laniinae—Corvinella corvina, Lanius cristatus, L. collurio, L. vittatus; Pityriasinae—Pityriasis gymnocephala. In addition, certain muscles were also examined in Corvinella melanoleuca. This group includes at least one member of all genera admitted by Rand (1960) except for two of the Malaconotinae, namely Malaconotus and Lanioturdus, for which suitable specimens could not be obtained. For most species only one specimen was examined, but in several cases two or three were dissected. Specimens were studied under a stereomicroscope at magnifications of 6× to 25×, aided by an iodine muscle stain. Drawings were made directly from the specimens with the aid of a camera lucida microscope attachment.

For the analysis of evolutionary relationships, morphocline polarities were determined by the standard methods of cladistic analysis, especially by out-group comparisons with other groups of oscines. These methods are sufficiently common that they need not be explained in detail here. They are discussed by such workers as Gaffney (1979), Hecht and Edwards (1977), Kluge (1976), and Ross (1974), and in other papers cited therein.

MUSCLES OF THE FORELimb

All of the muscles described by Raikow (1977) for Loxops virens are also present in the species of Laniidae examined. The musculature of these species is generally uniform throughout the family and in most cases does not differ significantly from that of Loxops. In Pityriasis the bellies of M. deltoideus major cranialis and caudalis are fused for most of their length, while being easily separated in the other species. The bellies of M. pronator profundus and M. pronator superficialis are also more closely associated in Pityriasis than in the other species. The ventral head of origin of the humerotriceps in Pityriasis does not arise from nearly the entire inner surface of the pneumatic fossa as observed in the other species, but from the ventral wall of the fossa and ventral surface of the head of the humerus. In all species of Laniidae only one pneumatic fossa was observed.
Muscles of the Hind Limb

As in birds generally, the musculature of the hind limb in shrikes is much more diverse than that of the forelimb. All of the muscles reported for Loxops virens (Raikow, 1976) were present in the Laniidae, but most were not sufficiently different from those described therein to merit redescription here, nor do they require comment on any other basis. The following muscles did show variations requiring comment. These variations are summarized in Tables 2, 3, and 4.

*M. iliotibialis lateralis.*—In the Prionopinae (Fig. 1) the postacetabular part of the belly is reduced, its caudal margin lying farther cranially than in the other forms, and thereby failing to cover the underlying origin of *M. iliofibularis* (Table 2). The fully developed condition (“normal”) is considered to be the primitive state because it occurs most commonly in oscines, and because tendencies for the reduction of this muscle in one way or another occur in various passerine groups. The reduction is less extreme in Prionops than in Eurocephalus, and in one limb of one specimen of *P. plumata* the muscle was not reduced at all.

*M. iliofemoralis externus.*—This small hip muscle arises from the ilium and inserts on the femur. It is usually absent in passerines, but
has been found in the Ptilonornynchidae and allies (Borecky, 1977). This muscle may also appear as a developmental anomaly in species that normally lack it. It has been suggested that the genetic information involved in the ontogenesis of this muscle was retained in passerines after the muscle itself was lost (Raikow, 1975), and that the occurrence of the muscle in the bowerbird group is due to its secondary reestablishment (Raikow et al., 1979). Another apparent example of this phenomenon was discovered in the present study. Distinct, well-developed iliofemoralis externus muscles were found bilaterally in one specimen each of Telophorus zeylonus and T. dohertyi, but the muscle was bilaterally absent in a specimen of T. sulphureopectus (Fig. 2), and in all other species studied. We cannot say whether these occurrences are typical of the first two species, or whether they are individual anomalies, because we examined only one specimen of each species. The occurrence of the muscle on both sides of the body in two species suggests, however, that it is a fairly common occurrence. Although

Table 2.—Variations in four hind limb muscles of Laniidae. Characters are discussed in the text.

| Species                  | M. illiotibialis lateralis | M. obturatorius lateralis pars dorsalis, insertion | M. gastrocnemius pars interna, Type | M. tibialis cranialis, Length of belly |
|--------------------------|----------------------------|---------------------------------------------------|------------------------------------|----------------------------------------|
| **Prionopinae**          |                            |                                                   |                                    |                                        |
| Prionops cristata        | reduced                    | proximal                                          | 3                                  | long                                  |
| Prionops plumata         | reduced                    | proximal                                          | 3                                  | long                                  |
| Eurocephalus rueppelli   | reduced                    | proximal                                          | 3                                  | long                                  |
| Eurocephalus anguitimens | reduced                    | proximal                                          | 3                                  | long                                  |
| **Malaconotinae**        |                            |                                                   |                                    |                                        |
| Nilaus brubru            | normal                     | distal                                            | 1                                  | short                                 |
| Dryoscopus sabini        | normal                     | distal                                            | 1                                  | short                                 |
| Dryoscopus cubla         | normal                     | distal                                            | 1                                  | short                                 |
| Tchagra senegala         | normal                     | distal                                            | 1                                  | short                                 |
| Laniarius ferrugineus    | normal                     | distal                                            | 1                                  | short                                 |
| Telophorus sulphureopectus | normal                   | distal                                            | 1                                  | short                                 |
| Telophorus zeylonus      | normal                     | distal                                            | 1                                  | short                                 |
| Telophorus dohertyi      | normal                     | distal                                            | 1                                  | short                                 |
| **Laniinae**             |                            |                                                   |                                    |                                        |
| Corvinella corvina       | normal                     | distal                                            | 1                                  | short                                 |
| Lanius cristatus         | normal                     | distal                                            | 1                                  | short                                 |
| Lanius collario          | normal                     | distal                                            | 1                                  | short                                 |
| Lanius vittatus          | normal                     | distal                                            | 1                                  | short                                 |
| **Pityriasinae**         |                            |                                                   |                                    |                                        |
| Pityriasis gymnocephala  | normal                     | distal                                            | 2                                  | long                                  |
Fig. 2.—Deep muscles of the hip in two species of Telophorus showing the presence and absence of M. iliofemoralis externus. Abbreviations: il. fem. ext., M. iliofemoralis externus; il. troch. caud., M. iliotrochantericus caudalis; il. troch. cran., M. iliotrochantericus cranialis.

This reappearance is a derived character state, its only taxonomic value in the present study is to suggest that the two species sharing it are more closely related to each other than to T. sulfureopectus.

M. obturatorius lateralis.—Pars dorsalis is not lost in any species studied herein, as it is in some passerines (Raikow, 1978; Bentz, 1979). In the Prionopinae pars dorsalis inserts more proximally relative to the insertion of M. obturatorius medialis, while in the other forms it inserts more distally, which is the more typical and probably primitive state (Table 2).

M. gastrocnemius.—Pars interna shows a range of variation similar to trends that occur in other passerine groups (Table 2). Three types are recognized (Raikow, 1978). In Type 1 pars interna has both a deep head and a superficial head at the origin, and the superficial head includes a patellar band, a strip of tissue arising from the patellar ligament. Type 2 possesses the superficial head but lacks the patellar band, and Type 3 lacks the superficial head as well. Type 1 is primitive in passerines, Type 2 derived, and Type 3 further derived. This determination is based on the widespread occurrence of Type 1 in passerines, and on the polarity of the morphocline in other groups, including the New World nine-primaried oscines (Raikow, 1978), the ploceid/estrildid complex (Bentz, 1979), and various other families (Borecky, 1977). In the Laniidae this morphocline is also correlated with various other polarities, which supports the conclusion that Type 1 is primitive. In Pityriasis the two heads are non-overlapping, an unusual con-
figuration for a Type 2 muscle. The Malaconotinae and Laniinae are Type 1, *Pityriasis* is Type 2, and the Prionopinae are Type 3. There was an exception to this, however; one specimen of *Eurocephalus rueppeli* was Type 1. This could be due to a reversional anomaly (see Raikow et al., 1979), or it might suggest that the group is still in the process of losing the patellar band and is variable. Dissection of a large series would be necessary to answer this question. In any event, the bulk of the data indicate that the reduction of the gastrocnemius pars interna is the characteristic state in the Prionopinae. This variation is illustrated elsewhere (Raikow, 1978: Fig. 6).

*M. tibialis cranialis.*—In most forms the belly extends from \( \frac{1}{2} \) to \( \frac{2}{3} \) the length of the shank. In the Prionopinae it extends nearly the entire length of the shank, the muscular portion reaching as far distally as the transverse ligament. The same is true in *Pityriasis*, except that the fibers extend slightly beyond the transverse ligament (Table 2). The enlarged condition is considered derived by correlation with other characters.

*M. peroneus longus.*—As in most birds, this muscle gives rise to a tendon of insertion that bifurcates near the distal end of the shank. The short branch inserts on the tibial cartilage, while the long branch passes across the intertarsal joint to the plantar surface of the tarsus, where it fuses with the tendon of *M. flexor perforatus digiti* III. In most forms studied this muscle had the typical condition just described. In the Prionopinae, however, the long tendon is reduced in diameter to a fine strand, a derived state by out-group comparison. Also, in the Prionopinae and in *Pityriasis* the belly extends farther distally than in the other forms, extending beyond the point of bifurcation rather than ending before it (Fig. 3; Table 3).

*M. peroneus brevis.*—In a few passerines this muscle has a tibial head (Raikow, 1976, 1978), but in the Laniidae, as in most passerines so far examined, that structure is lacking.

*Mm. flexor perforatus digiti* III *and* flexor perforatus digiti IV.*— These muscles lie side by side in the shank, having a common origin also shared with the adjacent flexor hallucis longus. In most oscines the two muscles extend for about the same distance before giving rise to their tendons, but in the Laniidae their relative positions are shifted so that the flexor perforatus digiti IV arises somewhat more distally and thus extends farther distally than does the flexor perforatus digiti III (Fig. 4). This is listed in Table 3, where the length of the fleshy portion of the flexor perforatus digiti III is given as a decimal fraction of the length of the fleshy part of the flexor perforatus digiti IV, both measured from their common origin. Because this condition is atypical for passerines it is considered to be a derived state.
Fig. 3.—Variation in the distal end of M. peroneus longus. Lanius exemplifies the primitive condition, while Prionops illustrates two derived states, the extension of the fleshy belly beyond the bifurcation of the tendon, and the reduction in diameter of the long branch of the tendon.

*M. flexor hallucis longus (FHL).*—This large muscle is the main flexor of the hallux. In oscines it typically arises by three heads: the *lateral head* passes lateral to the iliofibularis tendon; the *intermediate head* passes medial to the iliofibularis tendon; and the *medial head* lies medial to the intermediate head. In some birds the latter two heads are partially fused together, but in most cases they are easily separable. Berger (1968; also in George and Berger, 1966) first pointed out this tripartite origin, and we have verified it extensively in other studies (Raikow, 1976, 1978; Bentz, 1979; Borecky, 1977). This condition also occurs among the Laniidae, but in addition some variations were found (Table 3) that by outgroup comparison are clearly derived states.
Fig. 4.—Variation in the relative position of two flexor muscles. The condition characteristic of most laniids is exemplified by *Lanius*, while *Hylocichla* illustrates the usual oscine arrangement. Abbreviations: flex. perf. dig. III, M. flexor perforatus digitii III; flex. perf. dig. IV, M. flexor perforatus digitii IV.

Table 3.—Variations in four hindlimb muscles of the Laniidae. Characters are discussed in the text.

| Species               | M. peroneus longus | Ratio of FPD3/FPD4 | M. flexor hallucis longus: |
|-----------------------|--------------------|--------------------|---------------------------|
|                       | Tendon  | Belly  | Lengths | Intermediate head | Lateral head |
| **Prionopinae**       |         |        |         |                 |              |
| *Prionops cristata*   | reduced | long   | 0.8     | normal          | normal       |
| *Prionops plumata*    | reduced | long   | 0.8     | normal          | normal       |
| *Eurocephalus rueppelli* | reduced  | long   | 0.7     | reduced         | normal       |
| *Eurocephalus anguitimens* | reduced | long   | 0.7     | reduced         | normal       |
| **Malaconotinae**     |         |        |         |                 |              |
| *Nilanus brubru*      | normal  | short  | 0.7     | normal          | normal       |
| *Dryoscopus sabini*   | normal  | short  | 0.8     | normal          | normal       |
| *Dryoscopus cubla*    | normal  | short  | 0.7     | normal          | normal       |
| *Tchagra senegala*    | normal  | short  | 0.9     | normal          | normal       |
| *Laniarius ferrugineus* | normal  | short  | 0.7     | normal          | normal       |
| *Telophorus sulfureopectus* | normal | short  | 0.8     | normal          | normal       |
| *Telophorus zeylonus* | normal  | short  | 0.8     | normal          | normal       |
| *Telophorus dohertyi* | normal  | short  | 0.8     | normal          | normal       |
| **Laniinae**          |         |        |         |                 |              |
| *Corvinella corvina*  | normal  | short  | 0.8     | reduced         | enlarged     |
| *Lanius cristatus*    | normal  | short  | 0.8     | absent          | enlarged     |
| *Lanius collurio*     | normal  | short  | 0.8     | absent          | enlarged     |
| *Lanius vittatus*     | normal  | short  | 0.8     | absent          | enlarged     |
| **Pityriasinae**      |         |        |         |                 |              |
| *Pityriasis gymnocephala* | normal  | long   | 0.9     | normal          | normal       |
The normal oscine condition is typified by *Laniarius* (Fig. 5). Here the lateral head is very small, arising by a long narrow tendon from the femur and a branch from the fibula, the common tendon of origin passing lateral to the iliofibularis tendon, and then giving rise to the small fleshy belly that fuses with the large intermediate head, which passes medial to the iliofibularis tendon. In *Corvinella* (both *C. corvina* and *C. melanoleuca*) the intermediate head is greatly reduced in size and fleshiness, its proximal portion being represented by a narrow tendon. The lateral head, however, is enlarged. Its fleshy portion is more massive, and arises more proximally, while its tendon of origin is shorter but wider, more so in *melanoleuca* than in *corvina*. This trend is continued further in *Lanius*, where the intermediate head has been lost completely, while the lateral head is still larger.

The probable explanation for this trend is that in *Corvinella* and *Lanius* the flexor digitorum longus (FDL) has developed a new femoral head that lies between the intermediate and medial heads of the FHL. It may be that a crowding thereby results in this region, and that the reduction and loss of the intermediate head provides space for the new structure. The progressive enlargement of the lateral head of the FHL compensates for this loss so that this muscle does not suffer a reduction in strength. This is possible because the two heads are functionally equivalent, both contributing (along with the medial head) to the movement of their common tendon of insertion in bringing about flexion of the hallux.

A somewhat comparable situation has also evolved in the Prionopinae. *Prionops* lacks the femoral head of the FDL, and has a normal tripartite FHL. *Eurocephalus*, however, possesses a femoral head of FDL, and its FHL intermediate head is somewhat reduced. In one specimen of *E. rueppelli* the intermediate head was completely absent. There is little compensatory increase in the lateral head, however, such as occurs in the Laniinae.

*M. flexor digitorum longus*.—In most birds this muscle arises by two heads, one from the fibula and one from the tibiotarsus, but in some cases there is a third head arising across the back of the knee joint from the femur (Table 4). Such a femoral head (Fig. 5) occurs in *Lanius, Corvinella*, and *Eurocephalus* among the forms examined in the present study. The presence of a femoral head is considered a derived state, its absence primitive. This is based mainly on its pattern of distribution among birds. It is absent in most nonpasserine and passerine birds (George and Berger, 1966:450; Hudson, 1937:47; Raikow, 1978; Bentz, 1979; Borecky, 1977). Furthermore, in groups where it occurs it often appears only in an occasional form, for example, one thraupid and one sturnid out of many (Raikow, 1978; Borecky, 1977).

There is also variation in the insertion pattern of the three branches
Fig. 5.—Deep muscles of the lateral side of the shank, showing variations in M. flexor hallucis longus. The primitive state is exemplified by Laniarius, while Corvinella and Lanius show progressive stages in the reduction and loss of the intermediate head, and a correlated enlargement of the lateral head. Abbreviations: FDL. fem. hd., M. flexor digitorum longus femoral head; FDL. fib. hd., M. flexor digitorum longus fibular head; FHL. int. hd., M. flexor hallucis longus intermediate head; FHL. lat. hd., M. flexor hallucis longus lateral head; FHL. med. hd., M. flexor hallucis longus medial head; il. fib., tendon of insertion of M. iliofibularis.
Table 4.—Variations in three hindlimb muscles of the Laniidae. + = structure present, – = structure absent. Decimal values indicate length of fleshy belly relative to length of tarsus. Other characteristics are discussed in the text.

| Species                  | M. flexor digitorum longus | M. extensor hallucis longus | M. flexor hallucis brevis |
|--------------------------|----------------------------|----------------------------|---------------------------|
|                          | Femoral head | Insertion | Femoral head | Insertion | Femoral head | Insertion |
| **Prionopinae**           |              |           |              |           |              |           |
| Prionops cristata        | –            | AAB       | 0.8          | 0.5       |
| Prionops plumata         | –            | AAA       | 0.8          | 0.5       |
| Eurocephalus ruepelli    | +            | AAA       | 0.8          | 0.5       |
| Eurocephalus anguitimens | +            | AAA       | 0.9          | 0.5       |
| **Malaconotinae**        |              |           |              |           |              |           |
| Nilaus brubru            | –            | ABB       | 0.5          | 0.2       |
| Dryoscopus sabini        | –            | ABB       | 0.5          | 0.2       |
| Dryoscopus cubla         | –            | ABB       | 0.5          | 0.3       |
| Tchagra senegala         | –            | ABB       | 0.8          | 0.3       |
| Laniarius ferrugineus    | –            | ABB       | 0.7          | 0.3       |
| Telophorus sulphureopectus | –            | ABB       | 0.7          | 0.3       |
| Telophorus zeylonus      | –            | ABB       | 0.5          | 0.1       |
| Telophorus dohertyi      | –            |           | 0.5          | 0.2       |
| **Laniinae**             |              |           |              |           |              |           |
| Corvinella corvina      | +            | AAA       | 0.8          | 0.2       |
| Lanius cristatus        | +            | AAA       | 0.5          | 0.1       |
| Lanius collurio        | +            | AAB       | 0.5          |           |
| Lanius vittatus         | +            | AAA       | 0.5          | 0.1       |
| **Pityriasinae**         |              |           |              |           |              |           |
| Pityriasis gymnocephala | –            | AAB       | 1.0          | 0.7       |

of the tendon of this muscle, which insert on the plantar surfaces of digits II, III, and IV. The variation is in the number of accessory vincula, and is described by a code that is illustrated elsewhere (Raikow, 1978: Fig. 8). On the basis of outgroup comparison, it appears that condition ABB, which shows the largest number of vincula, is primitive. AAB is derived by the loss of one vinculum, and AAA is further derived by the loss of an additional vinculum (Table 4).

*M. extensor hallucis longus.*—This small intrinsic muscle of the foot extends the hallux in an action antagonistic to that of Mm. flexor hallucis longus and flexor hallucis brevis. Its size is generally correlated with that of M. flexor hallucis brevis, that is, in birds where the latter muscle is enlarged, this one generally is also. Variation in the size of this muscle occurs in the Laniidae (Table 4, Fig. 6). In the Malaconotinae and Laniinae the muscle is of a size typical for passerines; this will, therefore, be considered a primitive state, while the increased size seen in the Pityriasinae and Prionopinae is considered derived.
Fig. 6.—Variation in the development of two intrinsic muscles of the foot that move the hallux, Mm. extensor hallucis longus (ext. hal. long.) and flexor hallucis brevis (flex. hal. brev.). The relatively small size of these muscles as shown in Lanius is the primitive state, while Prionops and Pityriasis show progressive degrees of enlargement.

The reasoning behind this decision is similar to that given for M. flexor hallucis brevis.

M. flexor hallucis brevis.—This is one of the intrinsic muscles of the foot. It arises from the tarsometatarsus and in many birds, including passerines, ensheathes the tendon of M. flexor hallucis longus at the base of the first phalanx (George and Berger, 1966). This muscle flexes the hallux, augmenting the action of the much larger flexor hallucis longus. In most passerines this muscle is quite small (Raikow, 1978; Bentz, 1979; Borecky, 1977) and sometimes apparently absent. It appears likely that in many passerines, which are birds of relatively small size, both muscles are not needed for flexion of the hallux, and the small flexor tends toward reduction and loss. However, in some passerines this muscle becomes quite large. This is moderately true in the Vireonidae (Raikow, 1978) and more so in the Paradisaeidae and Ptilonorhynchidae as well as in Buphagus alone among the Sturnidae (Borecky, 1977). Change in size is probably an easily reversible evolutionary event, so caution should be used in postulating polarities with this character. However, it appears reasonable to suggest that extremely large size of this muscle is a derived state in passerine birds. One reason for this is that the muscle is small in the majority of pas-
serines. A second reason is that in many cases enlargement of this muscle is correlated (often with additional muscular specializations) with behavioral characteristics involving a strong grip. Among the Laniidae this muscle shows considerable enlargement in the Prionopinae, and even greater hypertrophy in *Pityriasis* (Fig. 6; Table 4).

**Discussion**

A cladogram representing a phylogenetic hypothesis is shown in Fig. 7. In the following discussion numbers in parentheses refer to the circled numbers in that figure; the dashed lines in the figure indicate uncertain relationships as discussed below. We must first ask whether the family Laniidae as defined by Rand (1960) is monophyletic. This hypothesis requires that the members of the family share at least one uniquely derived character state (synapomorphy) not found in other groups. This hypothesis is potentially capable of corroboration by the demonstration that such synapomorphies exist. It could be refuted by failing to discover such synapomorphies despite an earnest search for them, or by showing that at least one subgroup of the Laniidae is more closely related genealogically to some taxon outside the Laniidae than to the other taxa within the family. The problem is rendered difficult because it is unclear why Rand (1960) constructed the family as he did. As already noted, the family now consists basically of Sharpe’s (1877) Prionopidae and Gadow’s (1883) Laniidae, after the removal of various genera by subsequent workers. In essence, Rand’s Laniidae consists of those hook-billed oscines not included in other families.

A classification may be regarded as a hypothesis of relationships. To our knowledge, Rand did not publish an explanation of the basis for his classification. This makes it difficult to test the hypothesis because we do not know how it was developed. Nevertheless, we will attempt to reconstruct Rand’s hypothesis on the basis of what we perceive to be the concept of the Laniidae predominant among ornithologists today. This is that the Laniidae is a monophyletic group of oscines characterized by a hooked bill, a habit of feeding on relatively large animal prey, often using the feet to hold the prey, and resulting from an adaptive radiation centered in Africa, with one genus (*Lanius*) having spread throughout the Holarctic region, and another, perhaps relict Bornean form (*Pityriasis*), included with uncertainty.

In Fig. 7, point (1) represents the traditional characteristics of the family as just defined. A hooked (and sometimes also toothed) bill is not uncommon in passerines. It occurs in various groups and, being structurally simple, could easily have originated independently several times. Convergence in such characters is widely recognized in birds, and bill shape is no longer considered convincing evidence of relationship. If the specific form of the bill were very similar in the different
Fig. 7.—A cladogram representing a hypothesis of phylogenetic relationships in the Laniidae. Dashed lines indicate portions of the phylogenetic hypothesis that are considered to be only weakly corroborated. Numbers refer to synapomorphies as follow: 1. Hooked bill and related predatory habits; 2. M. flexor perforatus digiti III reduced; 3. Back feathers fluffy; 4. Loss of a flexor digitorum longus vinculum giving AAB insertion pattern; 5. Flexor digitorum longus femoral head added; 6. Flexor hallucis longus intermediate head reduced; 7. Flexor hallucis longus lateral head enlarged; 8. Tail elongated; 9. Flexor hallucis longus intermediate head lost; 10. Flexor hallucis longus lateral head further enlarged; 11. Peroneus longus elongated; 12. Tibialis cranialis elongated; 13. Flexor hallucis brevis enlarged; 14. Extensor hallucis longus enlarged; 15. Gastrocnemius patellar band lost (Type 2); 16. Flexor hallucis brevis further enlarged; 17. Extensor hallucis longus further enlarged; 18. Head ornamentation; 19. Bellies of deltoideus major fused; 20. Gastrocnemius pars interna superficial head lost (Type 3); 21. Peroneus longus long tendon reduced; 22. Obturatorius lateralis pars dorsalis insertion proximal; 23. Loss of additional flexor digitorum longus vinculum giving AAA pattern; 24. Iliotibialis lateralis caudal margin reduced; 25. Flexor digitorum longus femoral head added; 26. Eye wattles.
shrike groups one might argue for monophyly, but the size and shape of the bill, and the presence of notches or "teeth" vary among members of the Laniidae. Because this characteristic is simple and easily subject to convergence, we cannot determine whether it arose once or more than once in the history of the Laniidae. For this reason bill shape will not refute a hypothesis of monophyly, but we do not consider that it offers convincing corroboration either. Thus, the main character on which the family is generally recognized must be considered equivocal at best.

In the present study only one myological trait was found to unite the Laniidae. The reduction of the flexor perforatus digiti III (2) is of general occurrence, but it is a simple structural character. We consider that at best it offers only weak and uncertain corroboration for the hypothesis that the family Laniidae is monophyletic.

The possibility that one subgroup of the Laniidae might be closely related to an outside group has been suggested. Mayr (1943) thought that Pityriasis might be an aberrant member of the Sturnidae. A comparison of the limb muscles of Pityriasis with those of the starlings (Borecky, 1977) does not support this view. Several authors have suggested a connection between the shrikes and the Corvidae; Sibley (1970) reviewed these ideas. Some characters, such as the pneumatic fossa of the humerus, and the sperm morphology, are probably plesiomorphous for passerines and hence of little value as indicators of relationship. In other cases only some of the four laniid subfamilies were considered. For example, Sibley (1970) found similarities between the electrophoretic patterns of the egg-white proteins of some Laniinae and Malaconotinae with those of the Corvidae. However, he had no data on the Prionopinae, so the comparison is meaningless with respect to the immediate question. A comparison of the limb muscles with those of the Corvidae (Borecky, 1977) shows some similarities, but the specializations characteristic of the Laniidae are lacking in the Corvidae. The Laniidae as a group may be close to the Corvidae, but there is no evidence that any one subfamily of the Laniidae is closer to the Corvidae than it is to the other laniid subfamilies. In general, we find no convincing evidence that any one laniid subfamily is more closely related to an outside group than to its confamilial taxa. Hence, the hypothesis of laniid monophyly is not refuted on this basis.

On the basis of the above discussion, we conclude that there is no compelling evidence to refute the hypothesis that the family Laniidae of Rand (1960) is monophyletic. On the other hand, the evidence corroborating this hypothesis is weak and circumstantial. In the absence of strong refutation we recommend retention of the family as defined by Rand, with the recognition that future studies may well permit a reassessment of this position.
The Malaconotinae are the most primitive group of shrikes in their limb musculature, lacking various specializations that are found in the other subfamilies, as discussed below. In this group the feathers of the back are soft and fluffy (3), an apparent derived state within this assemblage, though not otherwise unknown among oscines. This characteristic reaches its extreme in the “puff-backs” of the genus Dryoscopus.

The genus Nilaus differs from the others in its more fully scutellate tarsus; the other genera show more fusion of tarsal scutes. The reduction of scutellation through fusion is probably a derived trait, since the formation of separate horny scales is functionally associated with provision for mobility or bending of the skin, a factor of no consequence in the tarsus. Thus Nilaus appears to be a very primitive shrike. This is worth noting because Mayr (1943) was impressed by the similarity of its plumage with that of the muscicapid Batis. Mayr went so far as to consider Nilaus a “shrike-billed flycatcher,” and suggested that it be transferred to the Muscicapidae. It is possible that the Laniidae arose from the less specialized Muscicapidae, with Nilaus representing an intermediate form. The limb musculature unequivocally refutes the association of Nilaus with the Prionopidae as suggested by Sclater (1930).

The Malaconotinae have the primitive ABB pattern of insertion of the flexor digitorum longus. All other shrikes have lost at least one of the vincula of this muscle giving the AAB pattern (4) or an even more derived condition. Beyond this point the remaining groups separate as two lineages, one leading to the Laniinae and the other to the Pityriasinae and Prionopinae. Each group shows distinct trends in the evolution of the hind limb muscles. In some cases the functional or adaptive significance of the changes is not readily apparent, but in each lineage some of the changes are clearly associated with increasing the strength of the foot, especially the strength of the grip. This is undoubtedly related to the frequent use of the foot for holding prey.

The Laniinae have a femoral head (5) to the flexor digitorum longus (FDL), in addition to the usual fibular and tibiotarsal heads, as described earlier. As this is a multijoint muscle, operating across the knee, the intertarsal (“heel”) joint, and the several joints of digits II, III, and IV, a precise inference as to the functional modifications resulting from the addition of the femoral head is impossible. However, it seems probable that the muscle’s primary focus of action is in its unique capability to flex the three forward toes simultaneously. The addition of the femoral head adds a new mass of fibers to the muscle, which complements the preexisting portion in exerting tension on its tendon of insertion. In other words, it appears that the major effect of
the addition of the femoral head is to increase the strength of flexion of the three forward toes.

As previously described, the flexor hallucis longus (FHL) arises by three heads in most oscines. The intermediate head is reduced in Corvinella (6), however, and lost completely in Lanius (9). As noted above, this makes space available for the newly added femoral head of FDL. The lateral head of FHL is enlarged in Corvinella (7), and further enlarged in Lanius (10) to compensate for the reduction and loss of the intermediate head. These evolutionary changes in the flexor of the forward three toes (FDL) and its antagonist the hallux (FHL) constitute an adaptation for increasing the strength of the grip in the Laniinae. Corvinella is less advanced in these trends than is Lanius. Because both species of Corvinella show these traits, the inclusion of melanoleuca in this genus instead of its previous separation in the genus Urolestes is supported. The elongated tail of Corvinella (8) is an autapomorphic feature of this genus.

The lineage including the Pityriasinae and Prionopinae also shows myological adaptations for increased foot strength, but mainly of a different sort than in the Laniinae. The peroneus longus (11) and tibialis cranialis (12) are enlarged compared to the Malaconotinae and Laniinae. These muscles are principal extensors and flexors, respectively of the foot as a whole, operating on the tarsometatarsus. Enlargement also occurs in the flexor hallucis brevis (13) and extensor hallucis longus (14), which flex and extend the hallux. In this group also, the patellar band of the gastrocnemius is lost (15). Enlargement of the hallucal muscles reaches an extreme in Pityriasis (16, 17).

Pityriasis has peculiar head ornamentation (18), as described above. Comparable specializations are also found in the Prionopinae, in the form of eye wattles (26) and sometimes crests. Mayr and Amadon (1951) suggested hesitantly that such head ornamentation might link Pityriasis with the Prionopinae, but it is difficult to suggest any sort of homology between vague “tendencies” when the actual structures are quite different. For this reason we have considered the specializations in the two groups to be autapomorphic (18, 26) rather than suggesting that a tendency for head ornamentation is a synapomorphy linking Pityriasis with the helmet shrikes. Pityriasis has some fusion of the two parts of the deltoideus major (19).

Eurocephalus and Prionops are undoubtedly each other’s closest relatives. They are linked by a number of derived states in the limb musculature (20–24). Eurocephalus has one important autapomorphy in the presence of a femoral head to the flexor digitorum longus (25), which also occurs in the Laniinae (5). This is the only important character conflict in the present study. This structure must have arisen
independently in the two groups because of the many other characters (Fig. 7) supporting the proposed phylogeny. The development of eye wattles is autapomorphic for *Prionops* (26).

**Conclusions**

1. The family Laniidae (Rand, 1960) is a poorly-defined assemblage of hook-billed oscines mainly centered in Africa, but with one genus (*Lanius*) distributed through Eurasia and North America, and another (*Pityrias*is) in Borneo. The present study of limb myology and a review of other characters was undertaken to clarify phylogenetic relationships within the group, including the question of whether it is monophyletic as implied by Rand’s classification.

2. No evidence was found to refute the hypothesis of monophyly, but only weak and uncertain corroborating evidence was obtained. For the present it is, therefore, concluded that the practical course is to retain the family as a taxonomic unit, with the recognition that it is still not rigorously demonstrated to be a clade.

3. The subfamily Malaconotinae (bush-shrikes) is relatively uniform in its limb muscles, which are generally primitive and of typical oscine form.

4. The members of the subfamily Laniinae (true shrikes) have an unusual configuration of certain hind limb muscles, including the presence of a femoral head of the flexor digitorum longus. The intermediate head of the flexor hallucis longus is reduced in *Corvinella* and lost in *Lanius*, while the lateral head is enlarged in the former genus and further enlarged in the latter. These modifications are believed to increase the strength of the grip of the foot, with *Lanius* being more advanced than *Corvinella*.

5. The members of the subfamily Prionopinae (helmet-strikes), *Prionops* and *Eurocephalus*, are confirmed as being each other’s closest relatives by the shared possession of several derived states in the pelvic musculature.

6. The enigmatic Bornean Bristlehead (*Pityrias*is gymnocephala), sole member of the subfamily Pityriasinae, has been placed by previous workers in several different families. The limb musculature strongly supports its inclusion in the Laniidae, and indicates that it is the primitive sister taxon of the Prionopinae.

7. A cladogram representing the preferred hypothesis of phylogenetic relationships is presented (Fig. 7).

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