A Preliminary Phylogenetic Hypothesis for the Cotingas (Cotingidae) Based on Mitochondrial DNA

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The cotingas (Cotingidae) are a diverse family of Neotropical suboscines that are thought to be closely related to manakins (Pipridae) and tyrant flycatchers (Tyrannidae) in the superfamily Tyrannoidea (Lanyon 1985; McKitrick 1985; Sibley and Ahlquist 1985, 1990; Prum 1990). The cotingas include species with a great variety of plumages, breeding systems, and ecologies, and they exhibit the largest range in body size of any passerine family (Snow 1982). Understanding the evolutionary history of variation in these traits requires a corroborated phylogenetic hypotheses for the group.

Toward this goal, we have conducted a preliminary molecular phylogenetic analysis to identify the major cotinga clades and reconstruct their interrelationships. Modern phylogenetic studies of the cotingas have included five analyses of morphological and molecular data. Some cotingas were included in phylogenetic studies based on allozyme electrophoresis (Lanyon 1985) and DNA-DNA hybridization (Sibley and Ahlquist 1985, 1990; Sibley et al. 1985). Furthermore, Prum (1990) performed a test of the monophyly of the cotingas based on morphology. Prum and Lanyon (1989) did a phylogenetic analysis of the *Schiffornis* group based on morphology, and Lanyon and Lanyon (1988) analyzed the relationships among the genera of the *Phytotoma* group using morphology and allozyme electrophoresis. Here, we analyze data from sequences of mitochondrial DNA from individuals of 32 cotinga species in 26 genera and 7 outgroup taxa.

Monophyly of cotingas.—First recognized in nearly its modern form by Sclater (1888), the Cotingidae has varied somewhat in taxonomic composition over the last century (Ridgway 1907; Hellmayr 1929; Snow 1979, 1982). Garrod (1876) first recognized the close relationship between manakins and cotingas based on the presence of an enlarged femoral artery. Prum (1990) established that the majority of cotingas and manakins possess the derived femoral artery condi-

tion, but that a few genera of putative cotingids lack the derived condition, viz. *Rupicola, Phoenicircus, Carpornis, Pipreola, Ampelioides, Lipaugus cryptolophus, L. subalaris,* and *Oxyruncus.*

Prum (1990) proposed a monophyletic Cotingidae on the basis of the shared possession of a derived insertion of an extrinsic syringeal muscle, M. tracheolateralis, on the lateral membrane between the A1 and B1 syringeal supporting elements. This clade included all of the cotingas sensu Snow (1979), with the addition of *Tityra* and *Phytotoma* and with the exclusion of *Laniisoma, Pipreola,* and *Ampelioides.* These family limits also left *Oxyruncus* and the six genera of the *Schiffornis* group (Prum and Lanyon 1989) unaligned within the tyrannoids. Subsequent morphological observations and a phylogenetic reanalysis of the data support the inclusion of all of these problematic genera within a single cotingid clade that includes the Cotingidae sensu Snow (1979), the *Schiffornis* group, *Tityra,* and *Phytotoma* (R. O. Prum unpubl. data).

Specifically, *Pipreola* and *Ampelioides* were incorrectly coded by Prum (1990); M. tracheolateralis in *Pipreola* and *Ampelioides* inserts on both the lateral A1/B1 membrane and the A1 element (R. O. Prum unpubl. data). Thus, these genera share the derived state of the cotingas and are members of the cotinga clade. Furthermore, the intrinsic syringeal muscles of the other problematic genera (*Oxyruncus* and the *Schiffornis* group) insert on the lateral A1/B1 membrane (Prum and Lanyon 1989, Prum 1990). The intrinsic syringeal muscles have evolved independently several times within the cotinga clade (e.g. *Lipaugus,* excluding *L. cryptolophus* and *L. subalaris,* and *Procnias*), and in each instance the intrinsic muscles insert on the lateral A1/B1 membrane, as does the primitive undifferentiated M. tracheolateralis within the cotinga clade. Ample additional evidence indicates that intrinsic syringeal muscles are evolutionarily derived from undifferentiated M. tracheolateralis (Ames 1971, Prum 1992). Thus, good support exists for the hypothesis that the intrinsic syringeal muscles of *Oxyruncus* and the *Schiffornis* group evolved subsequent to the derivation of the nearly unique insertion of M. tracheolateralis on the lateral membrane. *Oxyruncus* and the *Schiffornis* group also are members of the cotinga clade.

Because of apparent homoplasy in the derived

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femoral artery condition within the cotingas (see above; Prum 1990), the monophyly of the cotingas cannot be strictly supported on current morphological data alone. However, the monophyly of this expanded cotinga clade can be supported assuming that the absence of the enlarged femoral artery is a secondary loss in *Rupicola, Phoenicircus, Carpornis, Pipreola, Ampelioides, Lipaugus cryptolophus, L. subalaris,* and *Oxyruncus.* This accelerated transition optimization of the femoral artery character is supported by the DNA-DNA hybridization dendrograms of Sibley and Ahlquist (1985, 1990) and by phylogenetic hypotheses based on allozymes (Lanyon 1985).

Three genera of former piprids (*Piprites, Neopelma,* and *Tyranneutes*) share the derived femoral artery character with manakins and cotingas but lack the known synapomorphies of either family (Prum 1990). Thus, the current resolution of the cotinga and manakin clades leaves the phylogenetic position of these three basal heteromerous genera unresolved. *Neopelma* and *Tyranneutes* are sister taxa (Prum 1990), but the relationships of the *Neopelma-Tyranneutes* clade and of *Piprites* to the cotinga or manakin clades have not been resolved.

Methods.—Freshly frozen or ethanol-preserved tissues (liver, heart, or muscle) were provided by the American Museum of Natural History (AMNH), the Academy of Natural Sciences of Philadelphia (ANSP), the Louisiana State University Museum of Natural Science (LSUMNS), and the University of Kansas Natural History Museum (KU) for 37 species of cotingas and related outgroups. The species examined, institutions, and tissue collection numbers are: *Ampelion rubrocristatus* (LSU 7664); *Doliornis sclateri* (LSU 3562); *Rupicola peruviana* (LSU 19004); *Rupicola rupicola* (LSU 7575); *Phoenicircus nigricollis* (LSU 2898); *Pipreola arcuata* (LSU 7654); *Pipreola chlorolepidota* (LSU 6989); *Ampeliodes tschudii* (LSU 5457); *Cotinga cayana* (LSU 2653); *Porphyrolaema porphyrolaema* (LSU 6989); *Conioptilon mcilhennyi* (LSU 1416); *Carpodectes hopkei* (ANSP 2381); *Xipholena punicea* (LSU 20833); *Gymnoderus foetidus* (LSU 9586); *Lipaugus unirufus* (ANSP 2399); *Lipaugus fuscocinereus* (ANSP 5039); *Lipaugus cryptolophus* (ANSP 4445); *Lipaugus subalaris* (ANSP 48784); *Procnias alba* (KU 1244); *Oxyruncus cristatus* (KU 220); *Cephalopterus ornatus* (LSU 12300); *Perissocephalus tricolor* (AMNH uncataloged); *Pyroderus scutatus* (LSU 8137); *Querula purpurata* (LSU 2785); *Haematoderus militaris* (KU 1348); *Iodopleura isabellae* (LSU 9553); *Pachyramphus marginatus* (LSU 2951); *Pachyramphus versicolor* (LSU 1702); *Schiffornis major* (KU 1426); *Laniisoma elegans* (ANSP 1558); *Tityra cayana* (LSU 9604); *Tityra inquisitor* (LSU 18568); *Piprites chloris* (KU 1415); *Pipra fasciicauda* (KU 1138); *Xenopipo atronitens* (KU 1228); *Machaeropterus pyrocephalus* (KU 1418); *Machaeropterus regulus striolatus* (KU 1043); *Machaeropterus regulus regulus* (KU uncataloged); and *Neopelma chrysocephalum* (KU 1376).

Genomic DNA was extracted from each sample using Qiamp tissue-extraction kits available from Qiagen. The 3′ end of the cytochrome-*b* gene (ca. 375 bp) was amplified using conventional thermal-cycling techniques, with a thermal profile of denaturing at 95°C for 30 s, annealing at 55°C for 30 s, and extension at 70°C for 90 s (Kocher et al. 1989). Extension time was lengthened by 4 s each cycle for 35 cycles. Cytochrome-*b* primers (L-15507 5′-CCAGACCTCC-TAGGAGACCCAGA-3′, H-15915 5′-AACTGCAGT-CATCTCCGGTTTACAAGAC-3′) were developed by Shannon Hackett (H and L refer to heavy and light strands, respectively, and numbers indicate relative position on reference chicken sequence; Desjardins and Morais 1990). Amplified product was purified on a low-melt (1%) NuSieve GTG agarose (FMC BioProducts) gel electrophoresed for 45 min at 85 to 95 volts; bands containing target products were excised from the gel, and DNA was recovered using Qiaquick spin columns (Qiagen).

The purified PCR product was sequenced either manually on acrylamide gels with Promega cycle-sequencing chemistry, or amplified using only one primer (heavy or light) and sequenced with an ABI Prism Automated Sequencer (Model 310). The thermal profile used was denaturing at 96°C for 10 s, annealing at 50°C for 5 s, and extension at 60°C for 4 min, repeated for 25 cycles. Negative controls were used at each step of DNA preparation to test for reagent contamination. All taxa were sequenced entirely in both directions.

DNA sequences were inspected individually for quality and compared with the published *Gallus gallus* sequence (Desjardins and Morais 1990). For the sequences collected with the automated sequencer, variation between species was compared against the original electropherograms as a further check on sequence quality. The data were examined for possible site saturation by plotting pairwise comparisons for all ingroup and outgroup taxa of the number of transition and transversion substitutions against the Tamura-Nei genetic distance that was calculated using MEGA (Kumar et al. 1993).

The monophyly of the cotinga ingroup was assumed based on the shared-derived insertion of M. tracheolateralis or intrinsic syringeal musculature on the lateral membrane between the A1/B1 elements, and assuming the reversal of the enlarged femoral artery character within the ingroup (see above). Ingroup variation was rooted by outgroup comparison with *Neopelma chrysocephalum, Piprites chloris,* and the piprids (i.e. *Pipra filicauda, Xenopipo atronitens, Machaeropterus regulus,* and *Machaeropterus pyrocephalus*).

The equally weighted, unordered data set was analyzed using 100 replicates of PAUP 3.1.1 with random stepwise addition for starting trees and with the tree-bisection-and-reconnection branch swapping and MULPARS options in effect (Swofford

1993). The number of taxa was too large to employ the branch-and-bound algorithm. Additional analyses were performed in the same manner using 3:1 transversion-transition weighting, successive approximation (reweighting characters in subsequent parsimony analyses based on rescaled consistency indices of characters in the equally weighted analysis), removal of third-codon positions, and removal of third-codon transitions.

Decay indices (Bremer 1988) for clades in the equal-weighting hypothesis were calculated with PAUP 3.1.1 using a command file that performed 10 replicate heuristic searches, with random stepwise addition, while enforcing the reverse constraint for each of the resolved clades in the most parsimonious output tree. Bootstrap values for the equal-weighting hypothesis were calculated using 100 bootstrapped replicate character sets with 10 random-addition sequence heuristic searches each in PAUP 3.1.1.

Results.—Of the 375 bases sequenced, 339 unambiguous bases were available for all ingroup and outgroup taxa for analysis. All sequences have been deposited in GenBank (accession numbers AF123612 to AF123650). These 339 bases included 204 variable sites, 160 of which were phylogenetically informative. The percent sequence divergence varied among the ingroup taxa from 4.3% (*Cephalopterus ornatus* vs. *Perissocephalus tricolor*) to 25.7% (*Carpodectes hopkei* vs. *Laniisoma elegans*). Tamura-Nei distances were calculated for all pairs of ingroup and outgroup taxa. Graphs of pairwise comparisons for all taxa of Tamura-Nei distances and the number of transition and transversion substitutions were made for all codon positions, and for each of the three codon positions separately. These plots indicated that the relationship between transition and transversion substitutions and overall sequence divergence at all codon positions was linear, implying that saturation in these sequences was limited.

The result of the parsimony analysis of the equally weighted data was a single phylogenetic hypothesis of length 1,072, with a consistency index of 0.301 and a consistency index excluding autapomorphies of 0.269 (Fig. 1). The cotingas were identified as monophyletic if the network was rooted in any of the outgroup taxa (i.e. it was unnecessary to constrain the monophyly of the cotingas in the analysis). The tree included many resolved clades that are congruent with traditional taxonomies and with previous phylogenetic analyses of morphological and molecular characters.

The most parsimonious tree (Fig. 1) places the *Schiffornis* group genera (Prum and Lanyon 1989), with the addition of *Tityra*, as the sister group to the rest of the cotingas. An *Ampelion* group that includes *Ampelion* and *Doliornis* is the sister group to the remaining cotingas (clade 2; Fig. 1). The next lineage includes a *Rupicola-Phoenicircus* clade as the sister group to a lineage composed of *Pipreola, Ampe-*

lioides, and *Oxyruncus* (clade 3; Fig. 1). Clade 3 is the sister group to a clade that includes a diverse assemblage of "core cotingas" (clade 4; Fig. 1): *Procnias; Cotinga;* the other canopy-dwelling lowland forest genera *Conioptilon, Porphyrolaema, Carpodectes, Xipholena,* and *Gymnoderus;* two separate clades of pihas (*Lipaugus* sensu stricto, and the *L. cryptolophus-L. subalaris* clade); and a well-resolved fruitcrow clade (clade 5; Fig. 1) that includes *Haematoderus, Querula, Pyroderus, Perissocephalus,* and *Cephalopterus.*

Decay (or Bremer) indices measure the number of additional evolutionary steps (ad hoc hypotheses of homoplasy) that are required before a clade is not supported by the data (Bremer 1988). Of the 30 resolved ingroup clades, 19 had decay indices of 1 and 11 had decay indices of more than 1 (Fig. 1). The *Schiffornis* group with *Tityra* and the core cotinga group each had decay indices of 2, whereas the *Rupicola* group has a decay index of 1. The best-supported clades include the *Ampelion* group with 3; the *Rupicola-Phoenicircus* clade with 4; *Lipaugus* (excluding *cryptolophus* and *subalaris*) with 6; the *Pipreola-Ampelioides-Oxyruncus* clade with 7; the *Cephalopterus, Perissocephalus-Pyroderus* clade with 5; and the *Carpodectes-Xipholena* clade with 8. Bootstrap values for all but a few clades were less than 50%.

These results are consistent with the hypothesis that *Neopelma* and *Tyranneutes* constitute the sister group to the manakin clade of Prum (1990). Accordingly, *Piprites,* or the piprids including *Neopelma* and *Tyranneutes,* could be the sister group to the cotingas.

We performed four other character analyses to evaluate the robustness of the equal-weighting analysis to alternative models of molecular evolution. First, transversion substitutions were weighted three times more than transition substitutions, and maximum-parsimony analysis yielded seven equally parsimonious trees of length 1,569. The majority of the phylogenetic relationships within the strict-consensus tree were congruent with the equal-weighting hypothesis. The main difference concerned relationships of the *Rupicola* and *Schiffornis* groups. In the strict consensus of the 3:1 weighted trees, the *Rupicola* group was split into the *Rupicola-Phoenicircus* and the *Pipreola-Ampelioides-Oxyruncus* clades, with unresolved relationships to each other and to the *Ampelion* and core cotinga groups. In all of the seven fundamental trees in the 3:1 weighting analysis, *Schiffornis* and *Laniisoma* formed a clade that was either the sister group to the rest of the *Schiffornis* group, or the sister group to the rest of the cotingas excluding the other *Schiffornis* group species. Most other details of the equal-weighting hypothesis were supported by the 3:1 weighting analyses. The relationships within the *Schiffornis* group genera differed between the two analyses, and the monophyly of the genus *Pipreola* was supported only by the differential-weighting hypothesis.

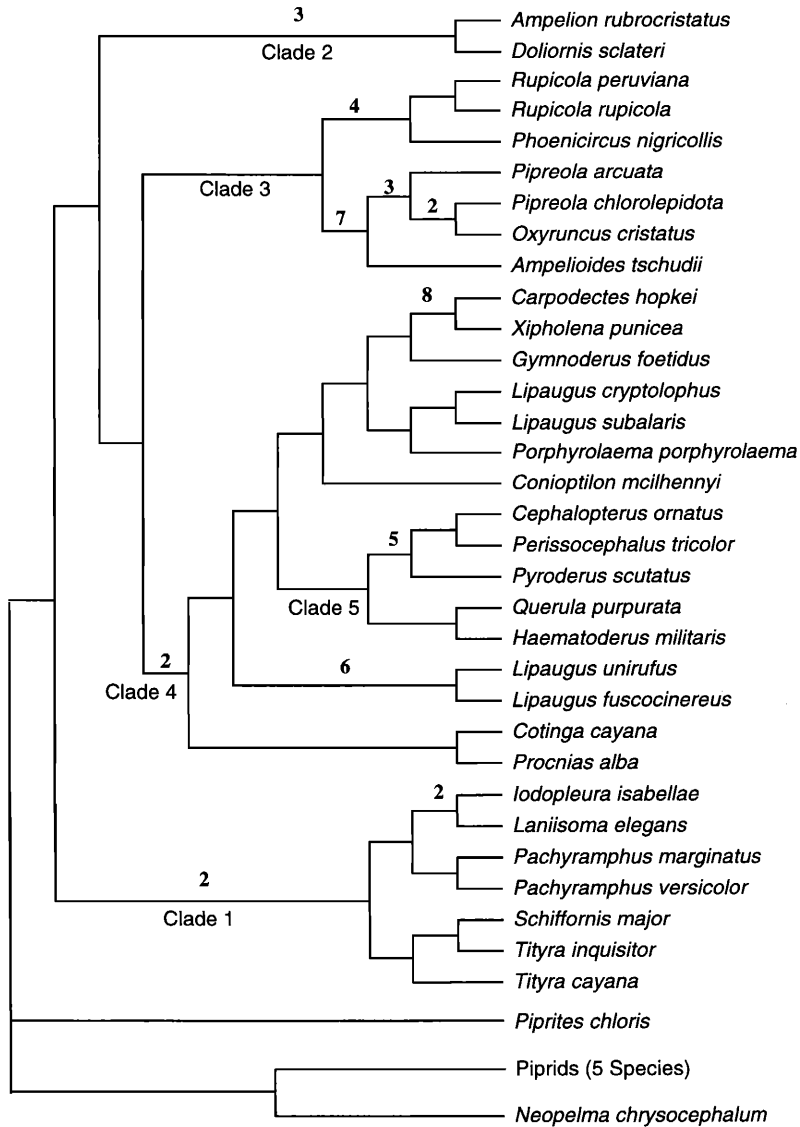Second, in a successive approximation analysis we

FIG. 1. The single most-parsimonious hypothesis for the phylogeny of the cotingas based on equally weighted cytochrome-*b* sequences. The numbers above some lineages are the decay indices that are greater than 1; other ingroup clades have a decay index of 1. The labeled clades (1 to 5) are referred to in the text. The piprid species include *Pipra filicauda*, *Xenopipo atronitens*, *Machaeropterus regulus*, and *M. pyrocephalus*.

recoded the characters (base weight = 1,000) based on their rescaled consistency indices from the most parsimonious equal-weighting tree. This resulted in a similar topology that identified many of the same relationships, except that the relationships among the *Schiffornis* group genera were different, and the monophyly of the *Rupicola* group was not supported. The *Pipreola-Ampelioides-Oxyruncus* clade was placed as the sister to the core cotingas (where the *Rupicola* group resides in the equal-weighting tree), but the

Rupicola-Phoenicircus clade was placed as the sister group to the large clade that included the *Ampelion* group, the *Pipreola-Ampelioides-Oxyruncus* clade, and the core cotingas. This topology was stable to additional reweighting after the first analysis.

Last, eliminating either all third-codon positions, or third-codon transition substitutions, resulted in poorly resolved ingroup relationships that contained only a few clades, most of which appeared in the equal-weighting hypothesis.

Discussion.—Prum and Lanyon (1989) identified the monophyletic *Schiffornis* group including six genera (*Schiffornis, Laniocera, Laniisoma, Iodopleura, Pachyramphus,* and *Xenopsaris*) based on morphological characters. The current molecular data set lacks two of these genera (*Laniocera* and *Xenopsaris*), but the other four genera are placed within a clade on the basis of these independent molecular data (clade 1; Fig. 1). However, the molecular data also include *Tityra* within this clade. *Tityra* was specifically excluded from the *Schiffornis* group on the basis of morphological characters (Prum and Lanyon 1989, Prum 1990). However, *Tityra* was hypothesized to be closely allied with *Pachyramphus* on the basis of other molecular data (Lanyon 1985; Sibley and Ahlquist 1985, 1990). Both hypotheses essentially could be correct if *Tityra* is the sister taxon to the *Schiffornis* group.

These molecular sequence data also corroborate the existence of the *Ampelion* group, which was recognized by Lanyon and Lanyon (1988) on the basis of syringeal morphology and allozyme data. Lanyon and Lanyon (1988) presented compelling molecular and morphological evidence that *Phytotoma* and *Zaratornis* are closely related to *Ampelion* and *Doliornis,* so we conclude that the these genera are also within the *Ampelion* clade identified here. Furthermore, our results support the monophyly of a *Rupicola-Phoenicircus* clade that was first suggested by Lanyon (1985) and is congruent with morphological data (R. O. Prum unpubl. data).

This phylogenetic hypothesis suggests close phylogenetic relationships among several groups of taxa that have been closely associated in pre-phylogenetic classifications of the family (e.g. Snow 1979). The fruitcrow clade (clade 5; Fig. 1) differs little in composition from the classification of Snow (1979, 1982), including four large-bodied genera (*Haematoderus, Perissocephalus, Pyroderus,* and *Cephalopterus*) and the smaller-bodied *Querula,* but excluding the large-bodied *Gymnoderus* that traditionally is a member of this group. Furthermore, the core-cotinga clade (clade 4; Fig. 1) includes a diversity of genera that have been considered as closely related within the family. Within the core cotingas, the close relationship between *Carpodectes* and *Xipholena* that was implied by traditional classifications (Snow 1979, 1982) was strongly supported. However, the close relationship traditionally suggested between *Cotinga* and *Porphyrolaema* is not supported by these data. The other relationships among the core cotinga genera are not strongly supported and need to be confirmed by additional data.

The molecular phylogenetic analysis identifies a clade including *Rupicola, Phoenicircus, Pipreola, Ampelioides,* and *Oxyruncus* (clade 3). This clade is corroborated by independent morphological data (Prum 1990). All five genera lack the derived enlarged femoral artery condition in an apparent reversal of the synapomorphy of the cotinga-manakin clade. The in-

dependent identification of these genera within a clade supports the hypothesis that the enlarged femoral artery was lost a single time in the common ancestor of the *Rupicola* group and a second time in *Lipaugus cryptolophus -L. subalaris* clade within the core cotinga assemblage. This result further supports the conclusion that the absence of the derived hindlimb artery character in these genera is a secondary loss, and that the heteromerous cotingas and manakins constitute a clade.

The monophyly of a number of genera was explicitly supported in this analysis, including *Rupicola* and *Pachyramphus.* These molecular data also confirm Prum's (1990) hypothesis, based on morphology, that the genus *Lipaugus* as currently constituted (Snow 1979, 1982) is a polyphyletic assemblage of two clades. In all analyses, *Lipaugus cryptolophus* and *L. subalaris* form a well-supported clade that is not closely related to rest of the genus *Lipaugus,* represented here by *L. unirufus* and *L. fuscocinereus.* Two cotinga genera were hypothesized to be paraphyletic: *Pipreola* (including *Oxyruncus cristatus*) and *Tityra* (including *Schiffornis*). However, the monophyly of *Pipreola* and *Tityra* are each strongly supported by additional morphological and plumage synapomorphies that were not analyzed here. The molecular evidence for their paraphyly presented here is not strongly supported.

Our results are not sufficiently complete to propose an entire phylogenetic classification for the cotingas. However, the four main corroborated clades could be recognized as subfamilies of the Cotingidae:

Tityrinae (type genus *Tityra* Vieillot 1816), including *Tityra, Schiffornis, Laniocera, Laniisoma, Iodopleura, Pachyramphus,* and *Xenopsaris;*

Phytotominae (type genus *Phytotoma* Molina 1782), including *Ampelion, Doliornis, Zaratornis,* and *Phytotoma;*

Rupicolinae (type genus *Rupicola* Brisson 1760), including *Rupicola, Phoenicircus, Pipreola, Ampelioides,* and *Oxyruncus;* and

Cotinginae (type genus *Cotinga* Brisson 1760), including *Cotinga, Conioptilon, Porphyrolaema, Carpodectes, Xipholena, Lipaugus* (sensu stricto), *Lipaugus cryptolophus, L. subalaris, Gymnoderus, Procnias, Haematoderus, Querula, Perissocephalus, Pyroderus,* and *Cephalopterus.*

Each of these taxa has appeared in previous classifications (Bock 1994). Future phylogenetic efforts should focus on testing the monophyly of these clades and further corroborating the interrelationships of the species within them.

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