# THE RELATIONSHIPS OF THE SHARPBILL (OXYRUNCUS CRISTATUS)

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ABSTRACT.—The Sharpbill (*Oxyruncus cristatus*) is a Neotropical suboscine passerine whose affinities have been unclear. The tyrant flycatchers, cotingas, and manakins of the superfamily Tyrannoidea have been suggested as the closest relatives of the Sharpbill. DNA-DNA hybridization comparisons between the radioiodine-labeled single-copy DNA of the Sharpbill and the DNAs of cotingas, manakins, tyrant flycatchers, and representatives of the other Neotropical superfamily, the Furnarioidea, indicate that *Oxyruncus* is a cotinga. We place it in the subfamily Cotinginae, family Tyrannidae.

The Sharpbill (Oxyruncus cristatus) is a medium-sized (ca. 16 cm) suboscine passerine with a straight, pointed bill and short rictal bristles. In the adult male the crested crown has a crimson center bordered by olive feathers tipped with black. The back is bright olivegreen, wings and tail blackish, underparts white with black spots, and the flanks pale greenishyellow. The plumage colors of the adult female are less intense than those of the male and the coronal stripe is inconspicuous.

The Sharpbill apparently has a discontinuous range in the humid montane forests of Costa Rica, Panama, southeastern Venezuela, southern Guyana and Surinam, northeastern and southeastern Brazil, southern Paraguay, and central Peru (Mees 1974, Traylor, 1979).

Extensive field observations of the Sharpbill have not been recorded but Sick (1971) reviewed the sparse literature and reported on his encounters with the species during his many years of field studies in Brazil. He found that Sharpbills tend to occur most often in dense tall forest, although they sometimes feed on fruits at the forest edge or in solitary trees. Fruits are the principal food but insects have been found in the stomachs of specimens and Sick observed Sharpbills hanging upside down from twigs to capture insect larvae. The vocalizations are relatively simple and similar to those of certain cotingas.

Sick found the birds most often in pairs and in mixed flocks of tanagers, furnariids, troupials, cotingas, woodpeckers, etc. feeding on fruiting trees. A captive Sharpbill ate fruits and cast hard pellets composed of the skins. Bangs and Barbour (1922) also observed Sharpbills feeding in fruiting trees with cotingas; Mees (1974) found them solitary, in pairs, and in mixed bird swarms in Surinam. Wetmore (1972:605) saw "four or five" together in Panama and recorded spiders, ants, and seeds from stomach contents.

Brooke et al. (1983) found the first recorded nest of the Sharpbill near the top of a 30-m tree in the montane forest of the Serra do Tingua, 50 km north of Rio de Janeiro, Brazil. The nest, which was built by the female, was "saddled onto a slender (ca. 3 cm) horizontal branch" and was a "simple ... shallow cup ... composed of roughly interlaced leguminous petioles . . . and a very few dry leaves." The outer surface "was a thin coat of mosses, liverworts, and spider's web... with a texture akin to thin cardboard, possibly resulting from the application and subsequent drying of saliva." The female fed the young by regurgitation, as do cotingas, rather than as in insectivorous tyrannids. Brooke et al. (1983) observed adult Sharpbills feeding in the ways described by Sick (1971).

# TAXONOMIC HISTORY

The genus Oxvruncus was described by Temminck (1820) who placed it in his Order VI, the "Anisodactyli." Bonaparte (1850) and Cabanis (1859) included it in the family "Anabatidae" (=Furnariidae) but Godman and Salvin (1888) placed it in a monotypic family. Most subsequent authors have also given the Sharpbill family status, including Sclater (1888), Sharpe (1901), Ridgway (1907), Hellmayr (1929), Wetmore (1930, 1960, 1972), Ames (1971), Storer (1971), Mees (1974), Traylor (1977, 1979), Wolters (1977), and Meyer de Schauensee and Phelps (1978). All of these authors have placed the Oxyruncidae near the Tyrannidae, the Cotingidae, the Pipridae, and the Phytotomidae, often with statements reflecting uncertainty about the relawedge-shaped bill and exaspidean tarsi." The exaspidean tarsal envelope in the tyrants, manakins, and Oxyruncus was used by Sclater (1888) as evidence that the Sharpbill should not be placed with the pycnaspidean cotingas. Ridgway (1907) noted considerable variation in the tarsal scutellation types and Pycraft (1906), Blaszyk (1935), Plotnick and Pergolani de Costa (1955), and Ames et al. (1968) have shown that this character has little or no value as evidence of family-level relationships.

Hellmayr (1929:1) placed the Oxyruncidae between the Tyrannidae and Pipridae, but commented in a footnote that "the affinities of this family are not satisfactorily determined, and it may become necessary to merge it with the Cotingidae."

Chapman (1939) declared that Oxyruncus "has no close relatives and its exact position in our system of classification has never been satisfactorily determined." After "consideration of the factual evidence" Chapman decided that "Oxyruncus is a relict species approaching extinction."

Wetmore (1960:17) noted that "if the sharpbills have other affinities it is doubtful that they are within the family Tyrannidae, where some have placed them." The latter reference was to Gadow (1893), Clark (1913), and Mayr and Amadon (1951) who had included *Oxyruncus* in the Tyrannidae.

Warter (1965) studied the cranial osteology of the Tyrannoidea and concluded that "the highly specialized skull [of *Oxyruncus*] argues against the inclusion of the genus in an otherwise so relatively homogeneous a family as the Tyrannidae."

Ames (1971:163) concluded that "the peculiar sharpbill ... has a basically tyrannid syrinx, ... but I cannot agree with Clark (1913) that its syrinx bears a "striking resemblance" to that of any particular genus of tyrannid, least of all to *Tyrannus* and *Sayornis*. The syringeal musculature of the sharpbill is strikingly like that of the becards (*Pachyramphus*) but there are substantial differences in the supporting cartilages. The type of musculature found in the sharpbill and the becards occurs elsewhere among the Tyrannidae, so the similarity should not be given too much weight."

The arguments of Warter and Ames convinced Traylor (1977:133–134) that Oxyruncus should be kept in a separate family.

Wetmore (1972:602) recorded his impres-

sion of the Sharpbill in life as resembling "some of the medium-sized species of Cotingidae" and Sick (1971:260) concluded that some of the facts he recorded seemed "to indicate more affinity to the cotingas than to the tyrant-flycatchers which are generally supposed to be the nearest relatives."

In this paper we address one principal question: namely, to which other group of the tyrannoid suboscine passerines is the Sharpbill most closely related, the tyrant flycatchers, the cotingas, or the manakins?

## METHODS

Sibley and Ahlquist have published moderately detailed descriptions (1981, 1983), and synoptic accounts (1982a-d), of the DNA-DNA hybridization procedures used to produce the data in Table 1. The delta  $T_{50}$ H values are measures of the average rate of nucleotide substitution, i.e., DNA evolution, and the same average rate occurs in all avian lineages. The delta T<sub>50</sub>H values are therefore measures of the relative times of divergence between the lineages represented by the two species whose DNAs were combined to produce a DNA-DNA hybrid. A preliminary calibration of delta  $T_{50}H$ values in absolute time indicates that each 1°C delta  $T_{50}H$  equals 4 to 5 million years since the time when the two lineages diverged, at least for delta values greater than ca. 6.0 (Sibley and Ahlquist 1981, 1982a; Sibley et al. 1982).

## **RESULTS AND DISCUSSION**

Table 1 presents the delta  $T_{50}$ H values for 23 DNA-DNA hybrids between the single-copy tracer DNA of the Sharpbill and the driver DNAs of 11 cotingas, two manakins, eight ty-rant flycatchers, and two species of the Furnarioidea as defined by Sibley and Ahlquist (in press a).

The cotingas in Table 1 range from 4.6 to 7.6 delta  $T_{50}H$  from Oxyruncus. These relatively low values, and the wide range of 3.0, indicate (1) that the Sharpbill is a member of the cotinga cluster, and (2) that, as expected, the other cotingas branched at various times from the lineage leading to the Sharpbill. We estimate that the divergences between the Sharpbill lineage and the other cotingas in Table 1 occurred between ca. 35 and 20 million years ago (MYA), from the early Oligocene to the mid-Miocene. However, the Sharpbill is probably even more closely related to some cotinga not represented in Table 1. Also, single delta T<sub>50</sub>H values may have an experimental error of as much as  $\pm 1.0$ . Thus Querula and Procnias are not necessarily more closely related to Oxyruncus than are some other cotingas. To determine the actual closest relative of

TABLE 1. DNA-DNA hybridization values between the radioiodine-labeled single-copy DNA of the Sharpbill (Oxy-
runcus cristatus) and the DNAs of other members of the Infraorder Tyrannides. Under "Group Index" the C = cotinga,
M = manakin, $Ti = tityrine$ , $T = tyrant flycatcher$ , $Mio = mionectid$ , $F = furnarioid$ , $Th = thamnophilid$ .

English name	Scientific name	Delta T <sub>50</sub> H	Group Index
Sharpbill	Oxyruncus cristatus	0.0	С
Purple-throated Fruitcrow	Querula purpurata	4.6	С
Bare-throated Bellbird	Procnias nudicollis	5.4	С
Bare-necked Fruitcrow	Gymnoderus foetidus	6.2	С
Ornate Umbrellabird	Cephalopterus ornatus	6.3	С
Barred Fruiteater	Pipreola arcuata	6.4	С
Andean Cock-of-the-Rock	Rupicola peruviana	6.5	С
Black-tailed Tityra	Tityra cayana	6.6	Ti
Masked Tityra	Tityra semifasciata	6.6	Ti
Red-crested Cotinga	Ampelion rubrocristatus	6.9	С
Pink-throated Becard	Platypsaris minor	7.4	Ti
Barred Becard	Pachyramphus versicolor	7.6	Ti
Golden-headed Manakin	Pipra erythrocephala	8.7	М
Green Manakin	Chloropipo holochroa	8.7	М
Whiskered Flycatcher	Myiobius barbatus	8.8	Т
White-crested Elaenia	Elaenia albiceps	8.8	Т
Brown-backed Chat-tyrant	Ochthoeca fumicolor	9.2	Т
Wied's Flycatcher	Myiarchus tyrannulus	9.4	Т
Streaked Attila	Attila spadiceus	9.6	Т
Grayish Mourner	Rhytipterna simplex	9.6	Т
Slaty-capped Flycatcher	Leptopogon superciliaris	10.0	Mio
Olive-striped Flycatcher	Mionectes olivaceus	10.5	Mio
Rufous Hornero	Furnarius rufus	14.0	F
Black-capped Antshrike	Thamnophilus schistaceus	14.4	Th

*Oxyruncus* would require several comparisons with each of the genera of cotingas, but we lack DNAs of all but those in Table 1. Thus, although the DNA data show that *Oxyruncus* is a cotinga, they do not reveal to which other cotingine genus it is most closely related.

The manakins *Pipra* and *Chloropipo*, at delta  $T_{50}H 8.7$  from *Oxyruncus*, indicate that the cotinga and manakin lineages diverged ca. 35– 40 MYA, in the late Eocene. This is supported by 21 DNA hybrids between cotingas and manakins, which have an average delta  $T_{50}H$ of 8.8  $\pm$  0.1 standard error (SE) and  $\pm$ 0.4 standard deviation (SD) (Sibley and Ahlquist, in press b).

The eight delta  $T_{50}H$  values between *Oxy*runcus and the tyrant flycatchers range from 8.8 to 10.5, a spread of 1.7. They average 9.5  $\pm$  0.2 SE,  $\pm$ 0.6 SD. A set of 62 DNA hybrids between cotingas plus manakins vs. tyrants has an average delta  $T_{50}H$  of 9.0  $\pm$  0.1,  $\pm$ 0.5. When the eight *Oxyruncus* × tyrant hybrids are added, making a total of 70, the average = 9.1  $\pm$  0.1,  $\pm$ 0.6. These data are included in Sibley and Ahlquist (in press b).

The average delta  $T_{50}$ H of 9.1 indicates that the cotinga-manakin lineage and the tyrant flycatcher lineage diverged in the late Eocene, ca. 40 MYA.

The 70 DNA hybrids used in the above calculations range from 8.6 to 10.5, a spread of 1.9. We believe this variation is due to experimental error, not to variable rates of nucleotide substitution. See Sibley and Ahlquist (1983) and Sibley et al. (1982) for additional information concerning the measurement and magnitude of experimental error.

For the branch between the Tyrannoidea and the Furnarioidea we have a total of 65 delta  $T_{50}$ H values which average 14.2  $\pm$  0.1,  $\pm$ 1.0. Sibley and Ahlquist (in press b) present the complete data.

The tyrannoid-furnarioid dichotomy occurred in the Paleocene, ca. 60–65 MYA. All divergence datings are subject to revision as the calibration between delta values and absolute time is improved and corrected.

We conclude that Oxyruncus cristatus is a cotinga and that it should be included in the Subfamily Cotinginae, Family Tyrannidae, Superfamily Tyrannoidea, Parvorder Tyranni, Infraorder Tyrannides. The Subfamily Piprinae is the sister group of the Cotinginae. This assignment of categories follows Sibley and Ahlquist (in press a) and is based upon the delta  $T_{50}$ H average values for divergence nodes because they are measures of the ages of origin, as proposed by Hennig (1966). The scale is as follows: up to delta  $T_{50}H 4 =$  members of the same genus, or closely related genera; delta 4-7 = members of the same Tribe; 7-9 =Subfamily; 9-11 = Family; 11-13 = Superfamily: 13-15 = Parvorder; 15-18 = Infraorder; 18-20 = Suborder; 20-22 = Order. It has been necessary to allow some flexibility in these boundaries to avoid excessive proliferation of categories and to accommodate the uncertainties in the time calibration.

The inclusion of the Sharpbill in the Cotinginae may be unacceptable to some avian systematists who prefer a classification in which specialized "grades" of morphologically distinctive taxa are recognized as separate categories above the generic level. We reject this procedure as subjective and leading to the recognition of arbitrary groupings that do not reflect degrees of genetic similarity. If the Sharpbill is placed in a separate subfamily or family, in spite of its close genetic relationship to the cotingas, then such morphologically distinctive genera as Cephalopterus, Procnias, and Rupicola should be treated likewise. However, Snow (1973, 1979, 1982), the most recent student of the cotingas, has included these genera in his concept of the Cotingidae and the DNA data support his arrangement. We have reduced the cotingas to a subfamily in the Tyrannidae to reflect the branching pattern of the phylogeny and to bring categorical levels into equivalence throughout the Passeriformes. The following classification of the Suborder Oligomyodi is that of Sibley and Ahlquist (in press a, b), which is based solely on the phylogeny derived from extensive DNA-DNA comparisons among all of the traditional families of suboscines except the Philepittidae.

- Order Passeriformes
- Suborder Oligomyodi
- Infraorder Acanthisittides
  - Family Acanthisittidae, New Zealand wrens

Infraorder Eurylaimides

Superfamily Pittoidea

Family Pittidae, pittas

- Family Eurylaimidae, broadbills
- (Family *inc. sedis* Philepittidae, asities)

Infraorder Tyrannides

Parvorder Tyranni

Superfamily Tyrannoidea

Family Tyrannidae

- Subfamily Tyranninae, tyrant flycatchers
- Subfamily Tityrinae
- Tribe Schiffornini, Schiffornis Tribe Tityrini, tityras, becards Subfamily Cotinginae, cotingas,
- plantcutters, Sharpbill Subfamily Piprinae, manakins
- Family Mionectidae, mionectid
- flycatchers
- Parvorder Furnarii
  - Superfamily Furnarioidea

Family Furnariidae Subfamily Furnariinae, ovenbirds Subfamily Dendrocolaptinae, woodcreepers Superfamily Formicarioidea Family Formicariidae, ground antbirds Family Rhinocryptidae, tapaculos Family Conopophagidae, gnateaters Parvorder Thamnophili Family Thamnophilidae, typical antbirds

Suborder Passeres

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