



The type of *Setophaga ruficoronata* (Kaup 1851) is a hybrid: implications for the taxonomy of *Myioborus* warblers (Passeriformes: Parulidae)

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Abstract

Hybridization, rapid diversification, and uncertainties surrounding type specimens add complexity to the already intricate taxonomy of high Andean *Myioborus* warblers of northern South America. In this study, we propose a reassessment of species boundaries within *M. ornatus* and *M. melanocephalus*, drawing on comparisons of name-bearing types. We also consider insights from a recent study of a hybrid zone in southern Colombia and northern Ecuador. We present three species delimitation alternatives that offer improved clarity compared to the current taxonomy, and discuss the rationale behind recognizing *chrysops* and *bairdi* as distinct species while redefining the species *ornatus* and *melanocephalus*, given the available evidence.

Resumen

La hibridación, la rápida diversificación y las ambigüedades de los especímenes tipo complican la ya confusa taxonomía de los *Myioborus* altoandinos del norte de Suramérica. Proponemos una reevaluación de los límites de especies en *M. ornatus* y *M. melanocephalus* con base en una revisión de todos los tipos nomenclaturales en el grupo, y teniendo en cuenta un estudio reciente de la zona híbrida del sur de Colombia y el norte de Ecuador. Presentamos tres alternativas de límites de especie que son preferibles al tratamiento taxonómico actual, y discutimos porqué la mejor opción dada la evidencia disponible es reconocer tanto a *chrysops* como a *bairdi* a nivel de especie, mientras que *ornatus* y *melanocephalus* son redefinidas.

Key words: birds, Colombia, Ecuador, holotype, hybridization, ornithology, type locality

Introduction

Parulid warblers represent a spectacular passerine radiation that has diversified widely (Lovette *et al.* 2010). That is the case of redstarts in the genus *Myioborus*, which stand out for their long, graduated white-and-black tail, flocking behavior, and montane distribution (Baird 1874; Curson *et al.* 1994). While variation in underparts color and wing pattern distinguish a few *Myioborus* species, for most, the combination of head pattern and coloration (of the face, crown, nape, and breast) has been used to diagnose taxonomic units (Bonaparte 1854; Salvin 1878; Sharpe 1885; Chapman 1927; Zimmer 1949). With the exception of *M. pictus*, and the widespread *M. miniatus* that occurs syntopically with other species at mid elevations, all taxa occur allopatrically in the highlands of northern South America and lower Central America. The distribution limits are less clear between two species of the northern tropical Andes (i.e., *M. melanocephalus* and *M. ornatus*), and their taxonomy is still an unsolved conundrum (Zimmer 1949; Pérez-Emán 2005).

The taxonomic complications in high Andean *Myioborus* (except in *M. albifrons* of the Venezuelan Andes) are rooted in rapid diversification of color patterns (Pérez-Emán 2005; Lovette *et al.* 2010), and hybridization (Céspedes-Arias *et al.* 2021), coupled with ambiguities of type specimens and localities (see below). Seven recognized forms are

currently grouped into one of two polytypic species: the northern *M. ornatus* with two subspecies, and the southern *M. melanocephalus* with five (Fig. 1). These two species maintain a hybrid zone where their ranges intersect in northern Ecuador and southern Colombia (Céspedes-Arias *et al.* 2021). Specifically, *M. ornatus* (subspecies *chrysops* Salvin 1878) of the western and central cordilleras of the Colombian Andes is replaced southerly by the northernmost taxon of *M. melanocephalus* (subspecies *ruficoronatus* Kaup, 1851). The subspecies *M. m. ruficoronatus* is thought to occur throughout the Ecuadorian Andes and southern Colombia (Chapman 1927; Meyer de Schauensee 1946; Zimmer 1949; Fjeldså & Krabbe 1990; Freile & Restall 2018). However, its type specimen presents problems that compromise the validity of the name *ruficoronatus*, and the integrity of the current taxonomy of this group. Here, we propose a reappraisal of the species limits of Andean *Myioborus* warblers based on a revision of name-bearing types of all described forms, and a better understanding of the evolution of the group.

***Myioborus melanocephalus ruficoronatus* is not a valid taxon**

The northern subspecies of *M. melanocephalus* was described as *Setophaga ruficoronata* Kaup, 1851 based on a single specimen collected by Adolphe De Lattre (Kaup 1851). The holotype is housed at the Vertebrate Zoology Collection, World Museum, National Museums Liverpool (formerly known as Museum of the Earl of Derby, Museum Derbyanum or Derby Museum), accession number NML-VZ D193. We examined photographs and an illustration of the type as it appeared in Salvin's (1878) monograph on *Myioborus* and other warblers grouped back then in the genus *Setophaga*. The color and pattern combination in the head and face of the type (see Kaup 1851; Bonaparte 1854; Baird 1874; Salvin 1878; Sharpe 1885) agrees with individuals of the center of the hybrid zone around Pasto, Department of Nariño, Colombia (Céspedes-Arias *et al.* 2021). Specifically, the type exhibits yellow lores and forehead (like the northern parental taxon: *M. o. chrysops*) a subtle black malar line, black auriculars, and a chestnut center of crown (like the southern parental taxon in central Ecuador). Assuming a complete lack of white auricular feathers, which cannot be confirmed from photographs, the hybrid score corresponding to this specimen is 0.59, lying near the middle in a scale ranging from 0 (phenotypically *M. o. chrysops*) to 1.0 (phenotypically Ecuadorian *M. melanocephalus*) (following methods and baseline data from Céspedes-Arias *et al.* 2021). Although the type of *S. ruficoronata* Kaup, 1851 agrees with specimens from central Nariño and the Sibundoy Valley (Department of Putumayo, Colombia), the presumed type locality is uncertain.

From the original label of the *S. ruficoronata* type (Fig. 2) and its description (Kaup, 1851), Leadbeater presented the De Lattre specimen in December 1846, but no specific locality was given (Bonaparte 1854). However, a small label attached to the type reads "Caly." By the time Salvin (1878) revised the group, an additional label in the type stated "Cali, Colombia" as the collecting locality, but this was most likely an error induced by the interpretation of the small "Caly" label. First, Kaup (1851) did not indicate explicitly Cali or any locality whatsoever as the origin of the type (Bonaparte 1854). Ever since Salvin (1878), it has been assumed that De Lattre obtained the specimen at Cali (Chapman 1926; Zimmer 1949). Second, Cali lies at the bottom of the upper Cauca valley at 1000 m elevation, where no *Myioborus* warblers occur (Fig. 1). If De Lattre had collected *Myioborus* in the mountains surrounding Cali, as was formerly suspected (Chapman 1926; Hellmayr 1935), these would have corresponded to *M. miniatus* at low or *M. o. chrysops* at high elevations. Moreover, Salvin (1878) noticed that an additional specimen of *M. o. chrysops* taken by De Lattre at "Páramo of Popayán" (most likely in Puracé, Department of Cauca) in the Central Cordillera, ~110 km south of Cali, "agrees very closely with Mr. Salmon's examples" of *M. o. chrysops* from Department of Antioquia, also in the Central Cordillera. Although hybrid zones can move (Taylor *et al.* 2015; Aguillon & Rohwer 2022), that hybrids could have been observed as far north as Cali (3.5° N latitude) 180 years ago seem unlikely because the current approximate hybrid zone northern limit, as inferred from plumage variation, is located 200 km to the south (1.7° N latitude) in southern Cauca (Céspedes-Arias *et al.* 2021).

In addition to Cali, De Lattre collected birds in various other locations of southwestern Colombia (De Lattre & Bourcier 1846; Hellmayr 1911; Chapman 1917), including the Pacific lowlands (Buenaventura), the western (Juntas) and central cordilleras (Puracé, Popayán), and the southern Colombian Andes (Pasto). Hybrid individuals with an external appearance that closely resembles the *S. ruficoronata* type can be found near Pasto and surrounding areas (Céspedes-Arias *et al.* 2021). Because De Lattre took a fair number of specimens from Pasto (De Lattre & Bourcier 1846), it is possible that this corresponds to the real locality of collection of the *S. ruficoronata* type specimen.

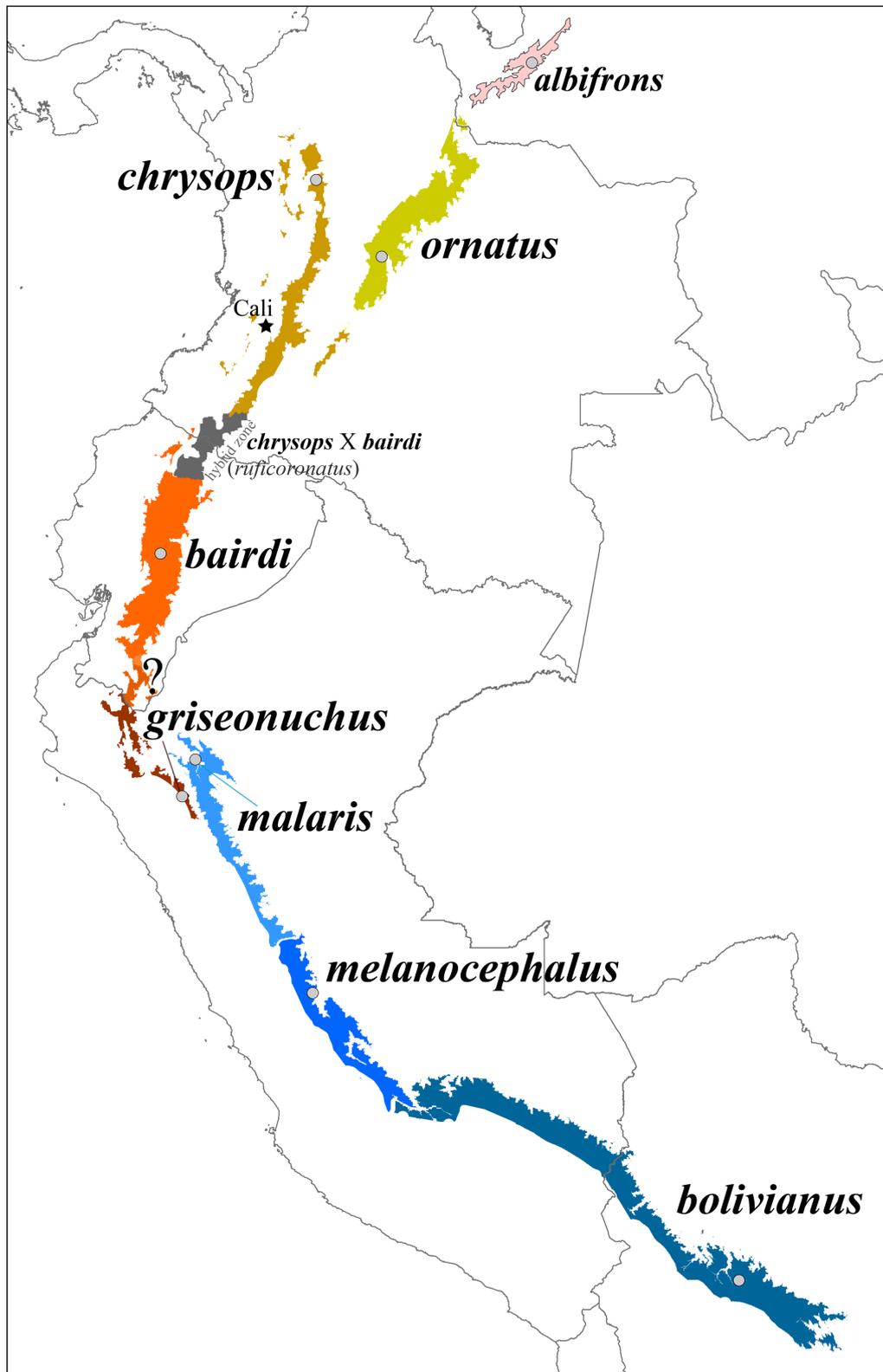


FIGURE 1. Map of northwestern South America showing the geographic distribution of high-elevation *Myioborus* warblers of the Northern Andes (*M. albifrons*, *M. ornatus* and *M. melanocephalus*). Each colored polygon represents the approximate geographic distribution of taxa recognized in this study, except for the one in dark gray, which shows the extent of the hybrid zone (Céspedes-Arias *et al.* 2021) between *chrysops* and *bairdi*. Gray dots indicate type localities of valid taxa, and the star the location of Cali, Colombia, the supposed type locality of *M. m. ruficoronatus*, which is most likely an error (see text). The question mark indicates the uncertainty in the geographic limits between *bairdi* and *griseonuchus* in southern Ecuador.



FIGURE 2. Photographs of the type specimen of *Setophaga ruficoronata* Kaup, 1851 (NML-VZ D1931) currently treated as *Myioborus melanocephalus ruficoronatus*. Side and dorsal views, with the detail of the front and face, and its label. The type exhibits intermediate facial color and pattern as observed in the center of the hybrid zone near Pasto, Department of Nariño, southern Colombia (Céspedes-Arias *et al.* 2021). Photographs by Tony Parker and John James Wilson (World Museum, National Museums Liverpool).

Because the name-bearing type is a hybrid individual, the name *ruficoronatus* Kaup, 1851 (currently applied to a subspecies of *M. melanocephalus*) is here rendered unavailable for the southern parental *Myioborus* population of the hybrid zone ranging in the Ecuadorian Andes. This type does not anchor any taxon at the species or subspecies level. In consequence, a name should be created or reinstated for the parental taxon south of the hybrid zone.

What is the name that should apply to the taxon hybridizing with *M. o. chrysops*?

Because the name *ruficoronatus* Kaup, 1851 is no longer available, nomenclatural action is necessary to define the southern parental taxon that hybridizes with *M. o. chrysops*. The hybrid form corresponding to the *ruficoronatus* type (e.g., yellow forehead and face, and chestnut crown) was thought to be a rare and poorly known bird that was distinct from the southern taxon *M. m. bairdi* Salvin, 1878 of central Ecuador (Baird 1874; Salvin 1878; Sharpe 1885; Hellmayr 1935), and from *M. m. griseonuchus* Chapman, 1927 from further south (Chapman 1927; Hellmayr 1935). These taxa have been ranked as subspecies of *M. melanocephalus* following Zimmer (1930), and adopted invariably ever since (Chapman 1927; Hellmayr 1935). However, inaccuracies of collecting localities and incomplete understanding of variation in head color patterns led ornithologists to treat specimens that were just like the *M. m. ruficoronatus* type (i.e., hybrids) to represent extremes of individual variation of *M. m. bairdi*, from central Ecuador (Meyer de Schauensee 1946; Zimmer 1949).

Based on this interpretation, and the principle of nomenclatural priority, *M. m. bairdi* was synonymized with *M. m. ruficoronatus* (Meyer de Schauensee 1946), but the latter name does not represent any taxon. This taxonomic scheme has been followed subsequently by taxonomic authorities and field guides to this date (Zimmer 1949; Meyer de Schauensee 1964; Fjeldså & Krabbe 1990; Curson *et al.* 1994; Clements 2007; Remsen *et al.* 2023).

The name *bairdi* Salvin, 1878 should be reinstated for the taxon occupying most of the Ecuadorian Andes

(type locality: Sicalpa Viejo, see below), and which is sandwiched between *M. o. chrysops* to the north (with which it forms a hybrid zone), and *M. m. griseonuchus* to the south (Fig. 1). Baird (1874) questioned the identification as *ruficoronata* in specimens from central Ecuador (e.g., Sclater 1855) as he noticed marked differences in facial pattern with Kaup's type, which description he found as "very unsatisfactory." Salvin (1878) confirmed Baird's observation of the marked differences between specimens that fully agreed with the *ruficoronatus* type (hybrids) and those from central Ecuador and described the latter as *Setophaga bairdi* Salvin, 1878.

In a subsequent taxonomic revision of the group, Sharpe (1885) further confirmed the validity of *bairdi*. Although several *bairdi* specimens were mentioned in its description (Salvin 1878), it was Sharpe (1885) who later designated a syntype (NHMUK 1885.3.8.801), which was collected by Clarence Buckley in "Sical", Ecuador (Fig. 3). This locality must refer to Sicalpa Viejo located in Colta, province of Chimborazo, which is nearby other Buckley's collecting sites such as Lago de Colta (see Paynter 1993). An illustration of *bairdi* by Johannes Gerardus Keulemans (in Salvin 1878; see Fig. 4) depicts its diagnostic differences with respect to *M. o. chrysops*, and from birds from the hybrid zone between the two (i.e., *M. m. ruficoronatus*).

Discussion

Taken together, the revision of the nomenclatural history (Baird 1874; Salvin 1878; Chapman 1927; Meyer de Schauensee 1946; Zimmer 1949), the diagnosability of taxa represented by examined types, and insights derived from the evolutionary history and the study of the hybrid zone (Pérez-Emán 2005; Céspedes-Arias *et al.* 2021) underscore that a reevaluation of the existing *Myioborus* taxonomy is warranted. Currently, seven taxa are grouped within either of two polytypic species, namely *M. ornatus* and *M. melanocephalus*, while *M. albifrons* remains clearly defined and monotypic. Taxonomic checklists (e.g., Gill *et al.* 2023) that rely on classification committees employing typological species definitions have already split *M. chrysops* from *M. ornatus* (e.g., del Hoyo & Collar 2016). In contrast, others (e.g., Remsen *et al.* 2023) that prioritize criteria like reproductive isolation may tend to merge hybridizing taxa into one species.

Genetic differentiation in mitochondrial DNA across the high-elevation *Myioborus* taxa of the Northern Andes is relatively shallow, as shared variation is widespread likely due to recent divergence, and, potentially, introgression following secondary contact (Céspedes-Arias *et al.* 2021). Despite this shallow divergence four genetic clusters were largely correlated with geography, and partly with taxonomic units (Céspedes-Arias *et al.* 2021). One group included all *M. albifrons* samples, the sister clade to the *M. ornatus-melanocephalus* complex (Pérez-Emán 2005). A second group included *M. melanocephalus* samples from the east and south of the Marañón valley (i.e., *malaris*, *melanocephalus*, *bolivianus*). A third group was formed by *M. melanocephalus* samples from the west and north of the Marañón (i.e., *griseonuchus* and *bairdi*). The fourth group consisted of the Colombian taxa *M. o. ornatus* and *M. o. chrysops*. Hybrid samples clustered largely with the latter two groups (Céspedes-Arias *et al.* 2021). Nuclear genome data mostly agree with this pattern (LNCA unpublished data).

One of the three alternative schemes should preferably be adopted in lieu of the current taxonomic *status quo* (Table 1). In each of these schemes, the taxonomy of the Venezuelan Andes endemic *M. albifrons* remains unaltered. The first scheme (three-species alternative in Table 1) would retain a polytypic *M. ornatus*, with a revised delineation to encompass all taxa north and west of the Marañón river valley. Consequently, *M. ornatus* would comprise a variable group of subspecies, including the white-faced nominate form, the golden-faced *M. o. chrysops*, and the rufous-crowned forms *M. o. bairdi* and *M. o. griseonuchus*. Likewise, *M. melanocephalus* would be formed by the three black-crowned subspecies south of the Marañón valley (*M. m. melanocephalus*, *M. m. malaris*, *M. m. bolivianus*).

The second scheme (five-species alternative in Table 1) proposed the separation of both *M. ornatus* and *M. melanocephalus* into two distinct species each, as *chrysops* and *bairdi* are elevated to species rank. Hence, five species result from this approach: 1) the white-fronted *M. albifrons*, 2) white-faced *M. ornatus* sensu stricto, 3) the golden-faced *M. chrysops*, 4) the rufous-crowned *M. bairdi* (including two subspecies: *M. b. bairdi* and *M. b. griseonuchus*), and 5) the black-crowned *M. melanocephalus* (comprising three subspecies: *M. m. melanocephalus*, *M. m. malaris*, *M. m. bolivianus*). A third alternative would consider *griseonuchus* to be distinct from *M. bairdi*, based on its phenotypic diagnosability (six-species alternative in Table 1).



bairdi

griseonuchus

FIGURE 3. Top: the syntype of *Setophaga bairdi* Salvin, 1878 (NHMUK 1885.3.8.801). This specimen exhibits the facial color and pattern observed in individuals from most of the Ecuadorian Andes that are currently considered as the “pure” southern form hybridizing with *chrysops* (Céspedes-Arias *et al.* 2021). Photographs by Mark Adams (Natural History Museum, Tring). Bottom: the type of *Myioborus bairdi griseonuchus* Chapman, 1927 (AMNH 229332). This taxon is restricted to northern Peru (departments of Piura and Cajamarca). Photographs by Paul Sweet (American Museum of Natural History).

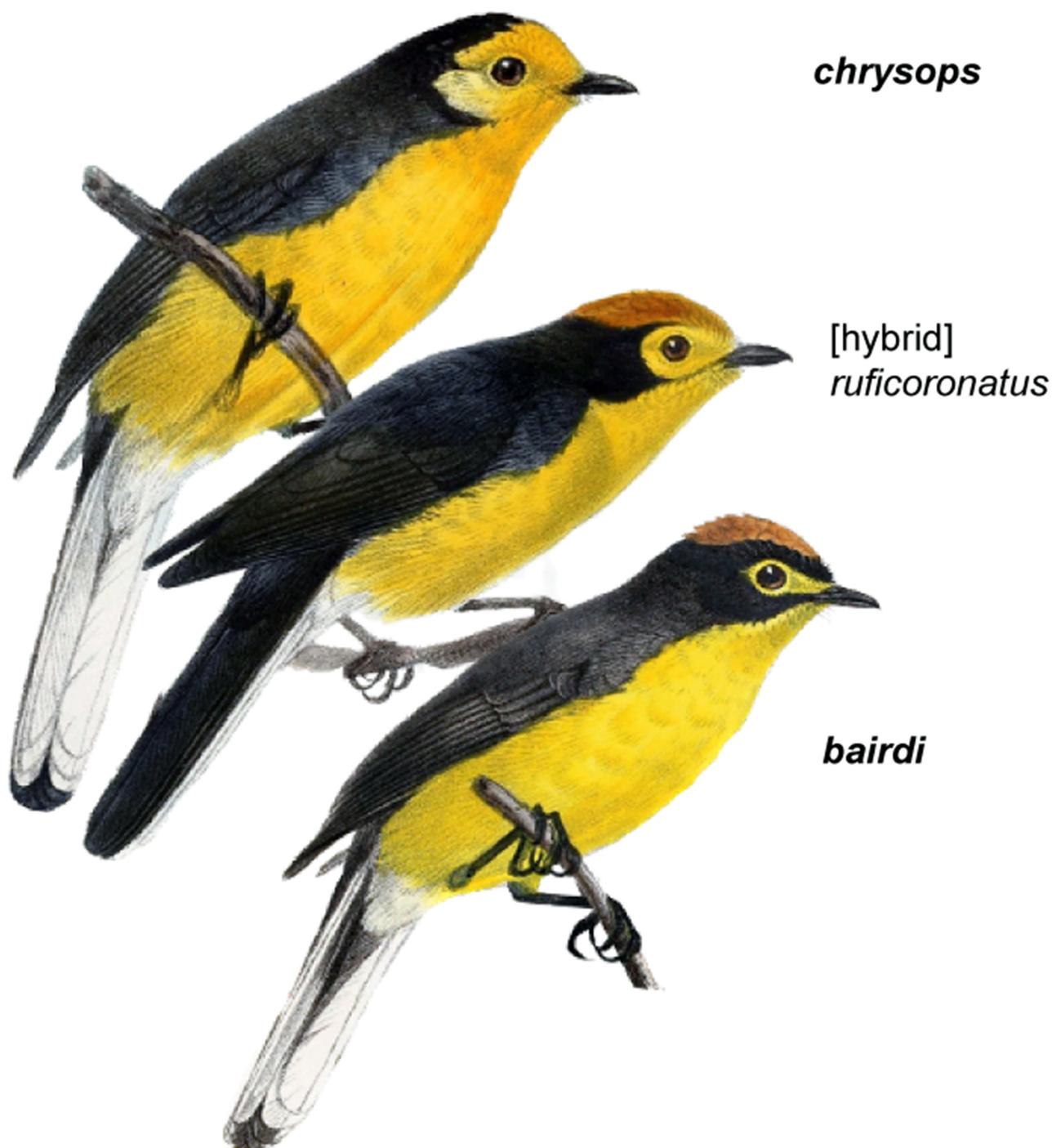


FIGURE 4. Illustrations of three Andean *Myioborus* as illustrated by Johannes Gerardus Keulemans in Salvin (1878). Top: *chrysops* of the Western and Central cordilleras of Colombia. Center: A hybrid individual painted based on the type of *Setophaga ruficoronata* (NML-VZ D1931, see Fig. 2). Bottom: *bairdi* based on a specimen assigned to *Setopopha bairdi* from Sical (sic) Ecuador (see Fig. 3). The taxon *bairdi* was until now considered a junior synonym of *ruficoronatus* (Meyer de Schauensee 1946). Illustrations from Salvin (1878) via the Biodiversity Heritage Library (<https://www.biodiversitylibrary.org/item/34861>)

In any scenario, within the framework of these alternatives, the redefined *M. melanocephalus* excludes the taxa *griseonuchus* and *bairdi*, which are either treated as a single species (*M. bairdi*, as proposed in the five-species alternative) or classified as subspecies of *M. ornatus* (as in the three-species alternative, Table 1). A least preferable approach, that all taxa be treated as conspecific under *M. ornatus*, was suggested at a time when the extent of hybridization and genetic variation was unknown (see Ridgely & Greenfield 2001).

TABLE 1. Four taxonomic schemes for the high-elevation *Myioborus* warblers of the Northern Andes. On the far left, the *status quo*, which is untenable considering the available data and discussion presented here. Next, a three-species approach that transfers from *M. melanocephalus* to *M. ornatus* the subspecies *griseonuchus* and *bairdi* (i.e., individuals formerly treated as *ruficoronatus*). A five-species approach recognizes consistent phenotypic divergence and is less in conflict with genetic variation than the previous two alternatives. Here, *Myioborus bairdi* is considered to contain two subspecies. On the far right, a six-species approach. The taxonomy of the Venezuelan Andes endemic *M. albifrons* remains unchanged.

Current treatment	Three-species alternative	Five-species alternative	Six-species alternative
<i>M. albifrons</i>	<i>M. albifrons</i>	<i>M. albifrons</i>	<i>M. albifrons</i>
<i>M. ornatus</i>	<i>M. ornatus</i>	<i>M. ornatus</i>	<i>M. ornatus</i>
<i>M. o. ornatus</i>	<i>M. o. ornatus</i>	<i>M. chrysops</i>	<i>M. chrysops</i>
<i>M. o. chrysops</i>	<i>M. o. chrysops</i>	<i>M. bairdi</i>	<i>M. bairdi</i>
<i>M. melanocephalus</i>	<i>M. o. bairdi</i>	<i>M. b. bairdi</i>	<i>M. griseonuchus</i>
<i>M. m. ruficoronatus</i> *	<i>M. o. griseonuchus</i>	<i>M. b. griseonuchus</i>	<i>M. melanocephalus</i>
<i>M. m. griseonuchus</i>	<i>M. melanocephalus</i>	<i>M. melanocephalus</i>	<i>M. m. melanocephalus</i>
<i>M. m. melanocephalus</i>	<i>M. m. melanocephalus</i>	<i>M. m. melanocephalus</i>	<i>M. m. malaris</i>
<i>M. m. malaris</i>	<i>M. m. malaris</i>	<i>M. m. malaris</i>	<i>M. m. bolivianus</i>
<i>M. m. bolivianus</i>	<i>M. m. bolivianus</i>	<i>M. m. bolivianus</i>	

**ruficoronatus* is heretofore unavailable, and the taxon it was supposedly representing should be recognized as *bairdi*

Taxonomy for high-elevation *Myioborus* warblers of the Northern Andes

Myioborus inhabiting the high elevation montane forests of the tropical Andes have been traditionally classified into three species: *M. albifrons*, *M. ornatus*, and *M. melanocephalus* (Table 1). However, that taxonomic structure is untenable for the latter two species given the rationale summarized above. No taxonomic treatment would fulfill all the criteria associated with alternative species concepts for *M. ornatus* and *M. melanocephalus*. Nevertheless, one undisputed result is that all populations of *M. melanocephalus* south of the Marañón valley form a cohesive entity, in terms of consistent phenotypic and genetic variation. Patterns are more complex north of the Marañón. Consequently, the various alternative schemes differ in whether to merge four of the northern taxa into one species (*ornatus*), separate them into three (*ornatus*, *chrysops*, *bairdi*) or four (*ornatus*, *chrysops*, *bairdi*, *griseonuchus*) distinct species.

One argument against separating *chrysops* and *bairdi*, and thus in favor of the three-species scheme (Table 1), is the evidence of hybridization. The *Myioborus* hybrid zone is extensive, encompassing a substantial population of hybrid individuals (Céspedes-Arias *et al.* 2021). However, cline theory (Barton & Hewitt 1985) suggest that some sort of selection against hybrids would be necessary to maintain the sharp phenotypic transition observed between *chrysops* and *bairdi*. The evidence of hybridization does not exclude the possibility of partial reproductive isolation (Rieseberg & Burke 2001; Cadena & Zapata 2021), implying that under certain interpretations of the biological species concept, *chrysops* and *bairdi* could indeed be recognized as distinct species. The presence of phenotypic differences between the parental species may reflect the cohesion of evolutionary lineages or species (Cadena & Zapata 2021).

Among the aforementioned taxonomic frameworks, we believe the five-species alternative aligns most congruently with the phenotypic diversity and is consistent with the known genetic structure in the group. In essence, recognizing five species even in the face of gene flow between some of these taxa appears as a robust hypothesis for delineating the evolutionary lineages in high Andean *Myioborus*. While we present three alternatives that will work best than the current taxonomy, we think the adoption of this five-species approach, denoting *M. albifrons*, *M. ornatus*, *M. chrysops*, *M. bairdi*, and *M. melanocephalus*, as the most appropriate course of action at this stage. Below, we provide details regarding the taxonomic entities, type specimens, English names, and geographic distributions as per this proposal.

***Myioborus albifrons* (Sclater & Salvin, 1871)**

English name: White-fronted Redstart (unchanged). Protonym: *Setophaga albifrons*. Type: NHMUK 1884.5.15.497. Type locality: Sierra Nevada of Mérida. Range of the species: Mérida Andes of Venezuela. Monotypic.

***Myioborus ornatus sensu stricto* (Boissonneau, 1840)**

Proposed English name: Clown Redstart. The name is a translation of the vernacular name used by locals: “payasito” (in Spanish), which refers to the white markings around bill and cheeks resembling a clown’s makeup. Protonym: *Setophaga ornata*. Type: MCZ 76106 (Fig. 5). Type locality: “Bogotá.” Range of the species: Eastern Andes of Colombia from Páramo de Sumapaz to the Tamá Massif in extreme western Venezuela. Monotypic. Unavailable names (synonyms):

flaveola (Lafresnaye, 1844). Protonym: *Setophaga flaveola*. The true type of *flaveola* (MCZ 76106, Fig. 6A) is a “Bogotá” skin in juvenile plumage corresponding to *M. ornatus*.

leucophomma (Kaup, 1851). Protonym: *Setophaga leucophomma*. The type (NML-VZ D2009, Fig. 6B) is a “Bogotá skin” corresponding to an immature *M. ornatus*.



FIGURE 5. Type of *Setophaga ornata* Boissonneau, 1840 (MCZ 76106), currently treated as *Myioborus ornatus sensu stricto*. Dorsal, ventral, and side views, with the detail of the face. This is a “Bogotá” skin. Photographs by Jeremiah Trimble (Museum Comparative Zoology, Harvard University).

***Myioborus chrysops* (Salvin, 1878), subspecies elevated to species rank**

Proposed English name: Colombian Redstart. Protonym: *Setophaga chrysops*. Type: NHMUK 1885.3.8.804 (Fig. 7). Type locality: Santa Elena, Antioquia, Colombia. Range of the species: Western and Central Andes, and the southern end of the Eastern Andes of Colombia (Páramo de Miraflores between Huila and Caquetá) south to the Colombian Massif in southern Cauca. Monotypic. *Myioborus chrysops* is the species hybridizing with *M. bairdi* in extreme southern Colombia and northern Ecuador.

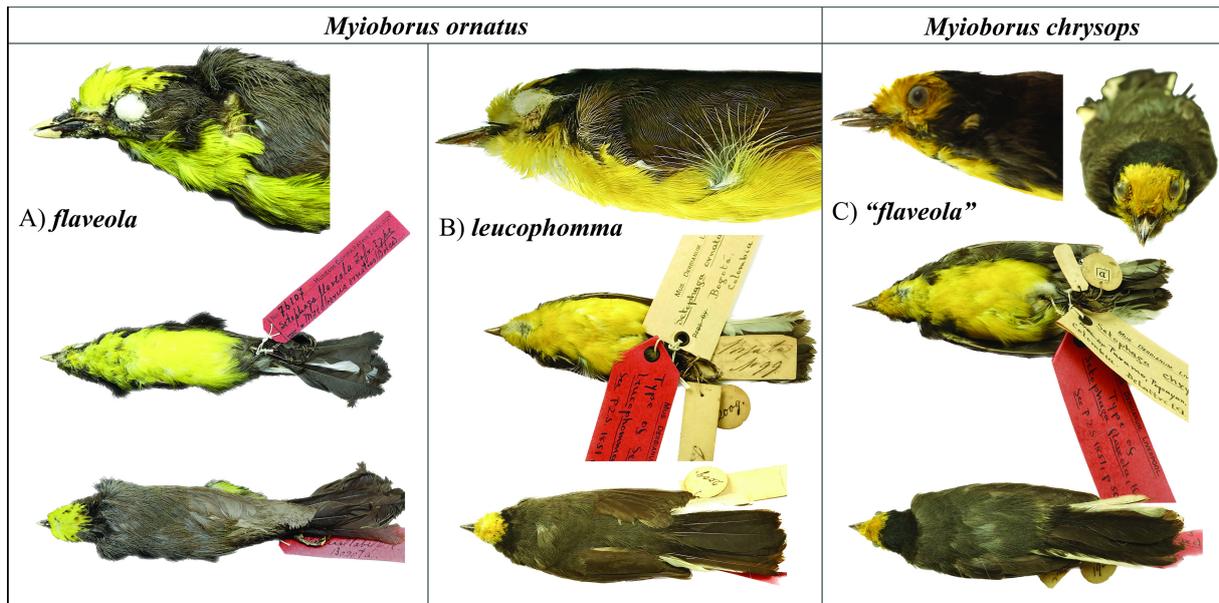


FIGURE 6. Type specimens of names synonymized with *Myioborus ornatus sensu stricto*, and *M. chrysops*. Types of *flaveola* (A, MCZ 76106) and *leucophomma* (B, NML-VZ D2009), which correspond to juvenile and immature individuals of *M. ornatus*, respectively. Kaup (1851) identified as *flaveola* a specimen that corresponds to *M. chrysops* (C, NML-VZ D1932), but this is not a true type specimen (see text). Photographs by Jeremiah Trimble (Museum Comparative Zoology, Harvard University), and by Tony Parker and John James Wilson (World Museum, National Museums Liverpool).



FIGURE 7. The type of *Setophaga chrysops* Salvin, 1878 (NHMUK 1885.3.8.804). Dorsal, ventral and side views, with the detail of the face. This taxon is currently treated as *M. ornatus chrysops*, and is the “pure” northern form hybridizing with *bairdi* in southern Colombia (see text). Photographs by Mark Adams (Natural History Museum, Tring).

A specimen (NML-VZ D1932, Fig. 6C) with a red label and marked as “type” for *flaveola* (not of Lafresnaye 1844, but one cited by Kaup, 1851) is not a proper name-bearing type. It corresponds to an adult *M. chrysops* that was identified by Kaup (1851) as *flaveola*, and collected by De Lattre at Puracé (Cauca, Colombia).

***Myioborus bairdi* (Salvin, 1878), name resurrected, and elevated to species rank**

Proposed English name: Ecuadorian Redstart. The name highlights that the distribution range of this species is mostly confined to the Andes of Ecuador. Protonym: *Setophaga bairdi*. Type: NHMUK 1885.3.8.801 (Fig. 3). Type locality: Sical = Sicalpa Viejo, Province of Chimborazo, Ecuador. Range of the species: western slope of the Andes in extreme southwestern Nariño, Colombia, south through both slopes of the Ecuadorian Andes to departments of Piura and Cajamarca, north of the Marañón river valley, Peru. Polytypic, with two subspecies:

Myioborus bairdi bairdi (Salvin, 1878). The nominate form occurs from southwestern Nariño, Colombia south to extreme southern Ecuador. (Chapman 1927; Zimmer 1949; Céspedes-Arias *et al.* 2021).

Myioborus bairdi griseonuchus Chapman, 1927. Type: AMNH 229332 (Fig. 3). Type locality: Taulis [Playa], Pacific slope NE Pascamayo, Department of Cajamarca, Peru. Range of subspecies: both slopes of the Andes west and north of the Marañón river valley in northern Peru to possibly extreme southern Ecuador. The range limits between *M. b. bairdi* and *M. b. griseonuchus* are not well known. This is complicated by variation observed in extreme southern Ecuador, where specimens have less black on hind crown (i.e., grayer nape) as in *griseonuchus*, but otherwise more closely resemble *bairdi* (Chapman 1927; Zimmer 1949; Céspedes-Arias *et al.* 2021). As in the case of *M. ornatus*, under the three-species alternative both subspecies included in *M. bairdi* would be subsumed under a polytypic *M. ornatus*. In the future, *griseonuchus* may prove to merit elevation to species rank, when nuclear genomic data are fully analyzed.

***Myioborus melanocephalus sensu stricto* (von Tschudi, 1844)**

Proposed English name: Black-crowned Redstart. The name reflects the etymology of the specific epithet, and highlights that its three subspecies are distinguish from all the above taxa in having a black center of crown. Protonym: *Setophaga melanocephalus*. Type: MHNN 92.9187 (Fig. 8). Type locality: Maraynioc, Junín, Peru (Zimmer 1949). Range of the species: Restricted the eastern slope of the Andes from south and east of the Marañón river valley in northern Peru to central Bolivia. The taxa *griseonuchus* and *bairdi* (and individuals formerly treated as *M. m. ruficoronatus*) are excluded from this redefined *M. melanocephalus*. Although the diagnosability and range limits between the three taxa included in *M. melanocephalus* are not clearly established (see photos of type, Figs. 8–10), we provisionally recommend maintaining those names at the subspecies level. Polytypic, with three subspecies:

Myioborus melanocephalus melanocephalus (Tschudi, 1844). The nominate subspecies occurs along the eastern slope of the Andes in central Peru. Its northern and southern range limits are not well known, but it might extend as far north as to the Huallaga valley in Huánuco, and as far south to the Apurímac valley, or even the Marcapata valley in Department of Cusco.

Myioborus melanocephalus malaris Zimmer, 1949. Type: AMNH 235067 (Fig. 9). Type locality: La Lejía, north of Chachapoyas, Department of Amazonas, Peru. Range of subspecies: south and east of the Marañón river valley in northern Peru in departments Amazonas and San Martín, Peru. Its southern range limit is unknown but may reach the Huallaga valley.

Myioborus melanocephalus bolivianus Chapman, 1919. Type: AMNH 137927 (Fig. 10). Type locality: Incachaca, Department of Cochabamba, Bolivia. Range of subspecies: the Yungas of the eastern Andean slope in southern Peru, probably from the Apurímac valley south through departments of Cusco and Puno to the Bolivian Department of Santa Cruz.



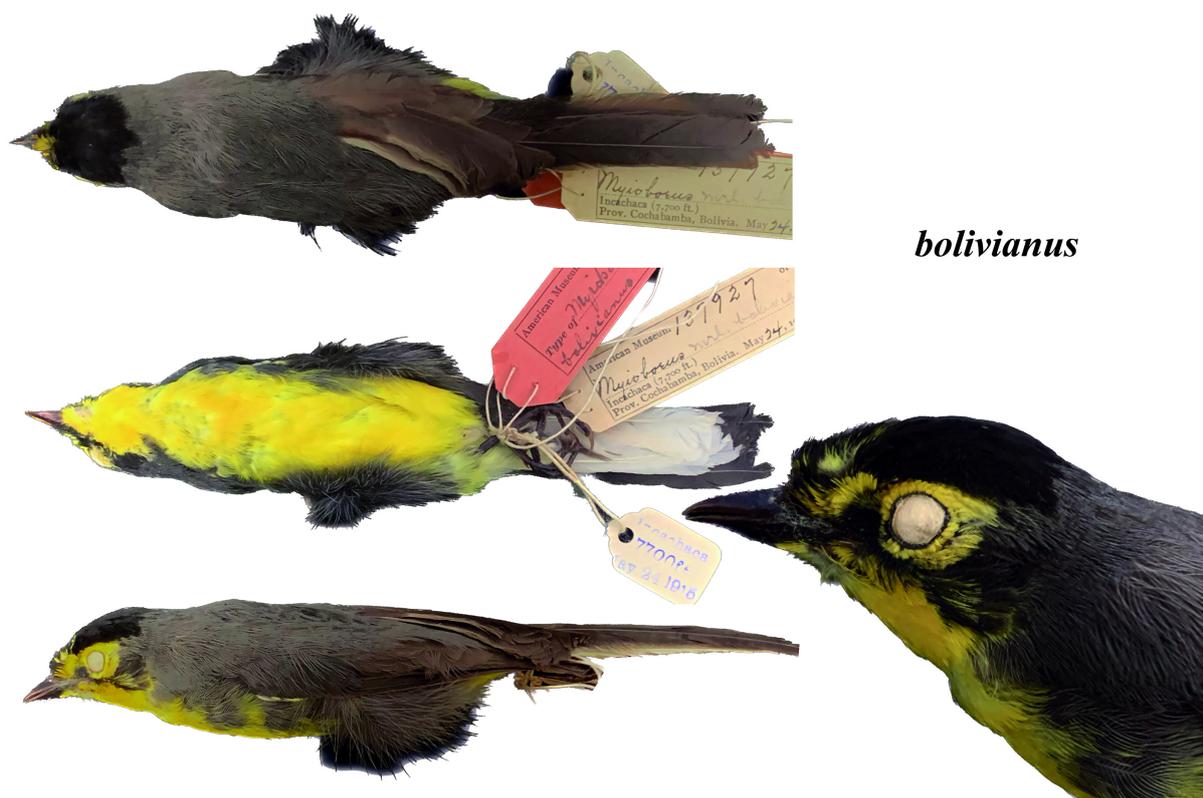
melanocephalus

FIGURE 8. The type of *Setophaga melanocephalus* Tschudi, 1844 (MHNN 92.9187). Dorsal, ventral and side views, with the detail of the face. Currently treated as the nominate subspecies of a polytypic species: *Myioborus melanocephalus*. Photographs by Maciej Czepiel and Celia Bueno (Musée d'Histoire Naturelle de Neuchâtel).



malaris

FIGURE 9. The type of *M. melanocephalus malaris* Zimmer, 1949 (AMNH 235067). Dorsal, ventral, and side views, with the detail of the face. Currently treated as a subspecies of a *Myioborus melanocephalus*. Photographs by Paul Sweet (American Museum of Natural History).



bolivianus

FIGURE 10. The type of *M. melanocephalus bolivianus* Chapman, 1919 (AMNH 37927). Dorsal, ventral and side views, with the detail of the face. Considered a subspecies of the polytypic species *Myioborus melanocephalus*. Note the lack of appreciable differences with respect to *M. m. malaris* (Fig. 10). Photographs by Paul Sweet (American Museum of Natural History).

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