# Taxonomy and nomenclature of the giant hummingbirds (*Patagona spp.*) (Aves: Trochilidae)

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**Abstract**

Giant hummingbirds (*Patagona* spp.) are extraordinarily large but nondescript hummingbirds whose taxonomy was muddled for two centuries. *Patagona* systematics were redefined in a study of migration and genetics by Williamson et al. (2024), revealing two species with divergent genomes and extensive seasonal range overlap. The latter study introduced a new name, *chaski*, for the Northern Giant Hummingbird; however, its brief nomenclatural justification omitted a key historical detail. Here, we revisit that justification by reviewing the taxonomy and nomenclature of the genus *Patagona* in light of its newly-clarified biology and species limits. First, we provide comprehensive information on identification of these cryptic species and report the extent of misidentification present in major collections. Second, we examine the validity of the name *peruviana* (Boucard 1893), long considered to be a poorly defined subspecies, and its potential application to the Northern Giant Hummingbird. Boucard's two putative syntypes are in fact known, and they appear to correspond to the northern genetic lineage; therefore, we designate a lectotype to clarify the entity originally associated with *peruviana*. We show that the entire subsequent history of *peruviana* has involved misapplication to entities that comprise variable mixtures of the two giant hummingbird species. Redefining *peruviana* to match the newly recognized Northern Giant Hummingbird would shift the limits of the entity to which this name refers, sowing confusion due to its non-universal meaning. By contrast, the name *chaski* was introduced concomitantly with the definitive discovery of two *Patagona* species and their taxonomic limits, morphology, physiology, migration, genetics, and year-round distributions. The Principle of Priority (Art. 23) of the International Code of Zoological Nomenclature provides a mechanism to suppress problematic senior synonyms. We invoke Art. 23.9.3 and urge

suppression of *peruviana* and adoption of *chaski*, the only name that applies specifically and uniquely to the Northern Giant Hummingbird.

**Key words:** Andes, *chaski*, elevation, giant hummingbirds, *Patagona*, taxonomy, migration, Trochilidae

## Introduction

Giant hummingbirds (*Patagona spp.*) comprise the most distinctive clade in the family Trochilidae because of their extraordinary size. Within the genus *Patagona*, however, morphological and plumage variation are subtle and it is difficult to disentangle geographic variation from age, wear, molt, sex and/or individual variation. Seasonal overlap among cryptic but distinct geographic breeding populations has exacerbated the challenge of characterizing the differences among genetic lineages and appropriately defining taxonomy.

A recent study made it possible to accurately adjudicate taxonomy and classification within *Patagona* for the first time by presenting new information about genetics, migration, and phenotypes (Williamson *et al.* 2024; Fig. 1). We now know that *Patagona* is a clade with two biological species that diverged ~2–3 Mya and that differ in breeding latitude and migratory behavior. The two lineages are largely allopatric during the breeding season. During the austral winter, the southern lineage, which breeds from central Chile through northwestern Argentina and likely throughout Bolivia, migrates to tropical latitudes of the central Peruvian Andes where it overlaps extensively with the northern, high-elevation resident lineage. The challenge of distinguishing the two cryptic species based on plumage and/or measurements has, until now, made it difficult to characterize their seasonal range overlap. However, the two lineages are reproductively isolated and experience no gene flow, making their status as biological species clear (Williamson *et al.* 2024). Each of the two species, the Northern Giant Hummingbird and Southern Giant Hummingbird, contains shallow geographic population structure. Additionally, the two species are vocally distinct (Williamson et al., *In. Prep*). The Northern Giant Hummingbird, which is a high-elevation resident, averages larger in bill length, wing chord, tail length, and tarsus length, although there is substantial overlap in morphological characteristics with the Southern Giant Hummingbird and only ~65–85% of individuals can be identified by

measurements alone when comparing sexes separately. Similarly, subtle plumage differences between northern and southern forms, which have been noted by previous scholars (e.g., Hellmayr 1932; Zimmer 1952) and clarified by Williamson et al. (2024), are useful for identification but not universally applicable across the range of individual variation (Fig. 1).

With unambiguous species status and newly defined taxon limits for the northern and southern forms, Williamson et al. (2024) evaluated what name should apply to the northern species. The name *peruviana* was introduced by Boucard (1893) in a brief description, and has since been applied, variably, as a subspecies comprising populations from northwestern Argentina and Bolivia northward. Williamson et al. (2024) argued that the name *peruviana* should not continue to be used for two main reasons: (1) Historic and persistent misalignment of the name *peruviana* with the northern genetic lineage; and (2) The type series (syntypes) appeared to have been comprised of a mix of the two giant hummingbird species. Williamson et al. (2024) therefore proposed the new species name, *chaski* (*Patagona chaski* sp. nov., Northern Giant Hummingbird, picaflor gigante del norte in Spanish) and designated a holotype.

The taxonomic description contained in Williamson, et al. (2024), omitted key information regarding the syntypes of *peruviana* that came to the attention of the authors after publication. We rectify this omission here. Williamson et al. (2024) did not know that the likely identities of the type series (syntypes) used by Boucard (1893) to designate *peruviana* were, in fact, known. Although Boucard did not provide identifiers for the specimens he referenced in his description, he stated that they were "…collected by Whitely in Peru" (Boucard 1893). At least 16 specimens were collected by Henry Whitely, Jr. in southern Peru from 1867–1873 or later (Table 1). At least one of these (AMNH-37502), which was assigned to the "northern" form, corresponds to the Southern Giant Hummingbird based on genetic evidence; a finding that is

expected because we now know that the southern lineage occurs in Peru during the austral winter. However, Williamson et al. (2024) were not aware of two specimens at the Muséum National d'Histoire Naturelle in Paris (MNHN; MNHN-ZO-MO-1989-340 and MNHN-ZO-MO-1989-341) that are considered to be Boucard's (1893) *peruviana* syntypes and are labeled accordingly (e.g., Jouanin 1950; Fig. 2a,b; Table 1). These syntypes appear to correspond to the northern lineage based on plumage features, although the female specimen is somewhat atypical. Their identifications should be considered tentative until confirmed using DNA sequencing.

A guiding purpose of the International Code of Zoological Nomenclature (the Code) is "to promote stability and universality in the scientific names of animals and to ensure that the name of each taxon is unique and distinct", thereby ensuring precision and consistency in the use of terms (ICZN 1999). Williamson et al. (2024) proposed the new species name, *chaski*, specifically because the name *peruviana* has been persistently misapplied, in variable ways, to an entity that is a mixture of both the northern and southern lineages of giant hummingbird. Based on new recognition that the likely syntypes of *peruviana* correspond to the northern lineage, the names *chaski* and *peruviana* should be considered synonyms, with *peruviana* senior and *chaski* junior. Art. 23.1 of the Code, the Principle of Priority, states the general principle that "the valid name of a taxon is the oldest name applied to it…" (ICZN 1999). However, the code allows for exceptions. For example, Art. 23.9, the Reversal of Precedence, provides a mechanism to favor a clear junior synonym over a confusingly applied older alternative. Art. 23.9.3 states, "If… an author considers that the use of the older synonym… would threaten stability or universality or cause confusion, and so wishes to maintain use of the younger synonym or homonym, he or she must refer the matter to the Commission for a ruling under the plenary power [Art. 81]. While

the case is under consideration use of the junior name is to be maintained [Art. 82]" (ICZN 1999).

Here, we present the taxonomic history and nomenclature of *Patagona* from 1840 to present, in light of the newly defined species and the new information about genetics and migration that clarifies seasonal range limits and methods for identification. We review the description of the genus *Patagona* Gray 1840, the original taxon (Vieillot 1824), and examine those of subsequently introduced names, *peruviana* and *boliviana* (Boucard 1893), within the genus, as well as the specimens key to historical identifications and naming. We further examine available information about the giant hummingbirds' distributions and migration that is relevant to our understanding of systematics. Next, we evaluate which name should be applied to the northern genetic lineage, the species-level entity now known under Northern Giant Hummingbird (*sensu* Williamson et al. 2024), with the aim of providing guidance to the International Commission on Zoological Nomenclature (ICZN). To this end, we ask whether instability, non-universality, or confusion would be caused by elevating the name *peruviana*, as is indicated by its persistent and continuous misapplication to a mixture of species.

**Taxonomy of the genus *Patagona***

The type specimen of the genus *Patagona* was described by Vieillot (1824) as *Trochilus gigas*, and was assigned to a type locality of "Brésil" (Brazil; Vieillot 1824). The type locality was later corrected to Chile by Lesson, who renamed the bird *Ornismiya gigas* (Lesson 1832). In 1840, Gray named the genus *Patagona*, listing *P. gigas* (ascribed to Vieillot, 1824) as the type species (Gray 1840). In spite of other proposed names (e.g., *Trochilus tristis*, *Cynanthus tristis*,

*Ornismya gigantea*, *Hypermetra gigas*; see Elliot 1879; Hartert 1900), from this point forward, *Patagona gigas* entered into widespread use among ornithologists and researchers.

**The Whitely series of *Patagona* specimens**

Henry H. Whitely, Jr., a British naturalist and explorer particularly interested in ornithology (Gladstone 1927; Sclater 1893), was a key figure in the history of *Patagona* taxonomy. For many years, Whitely collected specimens in southern Peru, with numerous trips throughout Arequipa and Cusco between the years of 1867 and 1873 (Chapman 1921; Sclater 1893; Sclater & Salvin 1867, 1869; Stephens & Traylor 1983). During this time, Whitely was credited with a number of new species discoveries, including the Bearded Mountaineer (*Oreonympha nobilis*; Sclater 1893). Many of Whitely's specimens were dispersed through the specimen trading business of his father, Henry Whitely, Sr. (Rasmussen & Prys-Jones 2003; Sharpe 1906). Although Whitely Sr., and to a lesser extent, Whitely Jr.'s, reputations have been questioned (Whitely, Sr. has been called 'reliably unreliable'; Rasmussen & Prys-Jones 2003), none of the specific problems that have been found have concerned the localities of Whitely's *Patagona* specimens.

Whitely collected at least 16 *Patagona* specimens in Peru from 1867 to 1873 (Table 1). In one letter about his 1867 Arequipa trip, Whitely noted, "… now commenced the worst part of the journey…the way, however, was enlivened by the sight of numerous birds, and especially, for some 2,000 feet, by the movements of the Giant Humming-bird (*Patagona gigas*)" (Sclater & Salvin 1867). Whitely's *Patagona* specimens, particularly those from Tinta, Cusco, Peru, have played a crucial role in history because they are thought to have formed the basis for a subsequent type description. Whitely collected in Tinta on several trips, including May–June 1868 and January 1869 (Sclater & Salvin 1869). The identities of at least three *Patagona*

specimens from his 1868 trip are known (MNHN-ZO-MO-1989-340, FMNH-45797, and FMNH-45798), and three others are suspected (AMNH-37500, AMNH-37501, and MNHN-ZO-MO-1989-34; Table 1). One specimen (AMNH-37501), housed at the American Museum of Natural History (AMNH) was designated as the "Type of Fig. 33, p. 67" in Giraud Elliot's 1879 synthesis, "*A classification and synopsis of the Trochilidae*" (Elliot 1879). This specimen, a male from Tinta, was noted in original ledgers as "figured in synopsis", as was AMNH-37502, a female collected from Cachupata, Cusco, Peru on August 21, 1873 (Table 1). These specimens, along with two other Whitely specimens, one each from Cachupata and Tinta (AMNH-37499 and AMNH-37500), were obtained by the AMNH in 1932 as part of the collection acquired from Walter Rothschild (Lanyon 1995;Table 1). Based on available data from gazetteers and related publications, AMNH-37500 and AMNH-37501 are suspected to have been collected during Whitely's June–August 1868 trip to Tinta. There are at least three other Whitely specimens (ANSP-50447, NHMUK 1887.3.22.700, and NHMUK 1913.3.20.291) collected during January 1869, and one additional specimen (ANSP-50448) is suspected to have been collected in either May–June 1868 or January 1869 (Table 1). At present, Whitely's *Patagona* specimens are known to reside at the AMNH, MNHN, Academy of Natural Sciences of Drexel University (ANSP), Field Museum of Natural History (FMNH) and Natural History Museum at Tring (NHMUK), and it is possible that there are additional Whitely *Patagona* specimens in other collections.

**Taxonomic history of the names *peruviana* and *boliviana***

In 1893, Adolph Boucard, a French ornithologist and specimen trader, proposed the names *Patagona peruviana* and *Patagona boliviana* for specimens in his collection, "…if the two should prove distinct species" (Boucard 1893). Boucard wrote, "I have in my collection what I

consider as the type of Vieillot 'Ex Coll Riocour.' My other specimens were collected in Chili by Reed. I have also three specimens collected by Whitely in Peru, and in Bolivia by Buckley" (Boucard 1893) (Fig. 2). Boucard appears to reference obtaining Vieillot's type specimen from the Comte de Riocour collection, of which he obtained most in 1889 (Renshaw 1905). Boucard's original text does not provide specific identifiers, collection dates, collecting localities, or sexes for the specimens in his collection from Chile, Peru, or Bolivia. However, two Whitely specimens at the Muséum National d'Histoire Naturelle in Paris (MNHN), MNHN-ZO-MO-1989-340 (a male from Tinta, collected 15 June 1868) and MNHN-ZO-MO-1989-341 (a female from Tinta, no date), were assigned equal status as syntypes for *peruviana*, while the specimen MNHN-ZO-MO-1989-342 (undetermined sex, no date; from Bolivia), collected by Clarence Buckley, was designated as the holotype *boliviana* (Jouanin 1950; Fig. 2; Table 1). The names *peruviana* and *boliviana*, in addition to the nominate *gigas*, were henceforth recognized and entered into use (e.g., Hartert 1900).

In 1921, Boucard's (1893) original description was contested by Eugène Simon, a naturalist and systematist from the MNHN. Simon wrote that *Patagona gigas* is a bird of the high mountains "…without presenting sufficient local variation to be considered as subspecies" (Simon 1921). Simon stated that Boucard (1893) had "…conditionally proposed the name *Patagona peruviana* for the specimens from Peru from Whitely's trip and *Patagona boliviana* for those brought back from Bolivia by Buckley" (Simon 1921). Then, Simon added, "…I have ascertained, by examining the types, that the coloration characters [Boucard] gives (in Gen. Humm. Birds. p. 61) are age-related or even completely illusory" (Simon 1921). In one footnote, Simon noted the white borders on the wing feathers and wing coverts and "the absence of a rufous part in front of the white uropygial band" on Boucard's types, which are characteristics of

*Patagona* juveniles and immatures (see Fig. 1). In a second footnote, Simon clarified his description of the phrase "completely illusory", noting that he was discussing, "…for example, the partly black throat of Peruvian birds" (Simon 1921). Simon did not provide specific identifiers of the supposed types, but it is presumed from his text that he examined the same specimens referenced in Boucard's (1893) original description.

In 1930, American ornithologist John Zimmer provided a brief account of *Patagona gigas peruviana* Boucard and *Patagona gigas boliviana* Boucard in *Birds of the Marshall field Peruvian expedition 1922-1923* (Zimmer 1930), recognizing Boucard's names as subspecific identifiers. Zimmer described examining four recently-collected *Patagona* specimens from Peru, compared with 23 previously-collected Peru specimens and 13 *gigas* specimens from central Chile and northwestern Argentina. Zimmer wrote, "The Peruvian birds, with one or two exceptions, are consistently larger than the Chilean skins, with longer wings and longer, heavier bills. They also, with one or two exceptions, are more rufescent on the under parts, sometimes markedly so. Since Dr. Hellmayr plans to discuss the characters of these two races in a forthcoming paper on the birds of Chile, I will leave further details to his able pen" (Zimmer 1930).

Two years later, Austrian ornithologist Carl Hellmayr published *The Birds of Chile* (Hellmayr 1932). In his account for the giant hummingbird, Hellmayr wrote, "Although the late Eugène Simon (Hist. Nat. Troch., p. 157) questioned the possibility of discriminating any geographic races of the Giant Humming bird, the study of between fifty and sixty properly labeled specimens from the whole range clearly indicates the existence of two forms" (Hellmayr 1932). Hellmayr said Simon's assessment that *P. peruviana* and *P. boliviana* were *nomina nuda* was a mistake, yet he agreed with Simon when he noted that "…several of the characters claimed

by Boucard prove to be individual" (Hellmayr 1932). Hellmayr went on to describe plumage differences of populations from Chile compared to those from Ecuador, Peru, and Bolivia, noting that the extent and intensity of rufous color to the underparts seemed to be "purely individual" and unrelated to sex or age (Hellmayr 1932). Hellmayr again agreed with Simon with respect to certain plumage features. Hellmayr concluded, "While the palest examples of the northern form can be closely matched by one or two unusually rufous-bellied birds from central Chile, the general run of the two series is easily told apart" (Hellmayr 1932). Hellmayr's resolute conclusion seemed to leave no doubt that there were two forms that were easily distinguished; this would later prove false (see below).

Based on his analyses of plumage, Hellmayr offered nomenclatural suggestions: "The larger northern race is entitled to the name *P. gigas peruviana*, tentatively proposed by Boucard for a specimen from Peru in his collection. The type, a male obtained by H. Whitely on June 15, 1868, at Tinta, Dept. Cuzco, agrees with the average of our Peruvian series, while *P. boliviana*, was based on an individual variant with wholly cinnamon-rufous under parts…" (Hellmayr 1932). Hellmayr thus cast doubt on the name *boliviana*, while bolstering the name *peruviana*. Hellmayr noted that "…An adult male from Tilcara, Jujuy (Nov. 24, 1905; L. Dinelli), and a couple from Lara, Tucuman (Feb. 12, 1903; G. A. Baer), all in the Tring Museum, are in every particular typical of the large northern form" (Hellmayr 1932). Years later, Hellmayr would add that specimen no. 868/48 collected by L. Dinelli on August 10, 1916, from Colalao del Valle, Tucumán, Argentina was "typical" of *peruviana* based on plumage and morphology (Revilliod *et al.* 1942).

Based on Hellmayr's account, largely regarded as definitive in the literature, subsequent authorities recognized *peruviana* as a valid subspecies and ceased recognizing *boliviana*, folding

*boliviana* into descriptions for *P. g. peruviana* (Peters 1945; Zimmer 1952). In *Check-list of the Birds of the World*, Peters wrote that "The breeding bird of northwestern Argentina (Jujuy, Catamarca, and Tucumán) is probably referable to [*P. g. peruviana*]" (Peters 1945).

In 1952, John Zimmer revisited *Patagona* taxonomy in *Studies of Peruvian Birds* (Zimmer 1952). Under his entry for *P. g. peruviana*, he stated, "This northern form of the species is fairly readily determinable in distinction from the southern *gigas gigas* when fully adult birds are compared, but young examples can be confusing" (Zimmer 1952). Zimmer went on to describe the difficulty of distinguishing juvenile birds by plumage. He noted, "All the adult examples from [the Urubamba Valley of Peru] are clearly *peruviana*. I have seen no Peruvian specimens that indicate the occurrence of *gigas gigas* in Perú, although there is evidence that the subspecies has some migratory tendencies, as noted by Hellmayr…" (Zimmer 1952). Zimmer presented a list of 83 specimens, from numerous localities and of both sexes, that he examined as part of his treatment. He wrote, "I would emend a statement made by Hellmayr (*loc. cit.*) with reference to certain Argentina specimens that he found to be 'in every particular typical of the large northern form.' Three females from Tilcara are fairly typical *peruviana* but the others are identifiable only by their measurements, since they are immature and in coloration resemble other young of both forms" (Zimmer 1952).

Historical descriptions of plumage and range by Hellmayr, Zimmer, and others, have since been regarded as definitive, without detailed examination of variation between the suspected races of *Patagona*. For example, in 1974, Fernando Ortiz-Crespo supported previous scholars, noting "[The race *peruviana*]…differs from the nominate race, occurring in central Chile, adjacent Argentina, and the southern Chilean provinces, in having a larger body size, a stouter, longer bill, and rufescent underparts" (Ortiz-Crespo 1974).

Thus, since ca. 1930, the giant hummingbird has been considered to contain two forms: The nominate *P. g. gigas*, a suspected migrant and apparently smaller-bodied bird with a shorter bill and shorter wings, stated to range from approximately central Chile to central Argentina; and *P. g. peruviana*, an apparently larger-bodied form with a longer bill and longer wings, thought to range (and breed) continuously from northern Chile through Peru and Ecuador, and through Bolivia and northwestern Argentina. Individuals of *peruviana* were believed to have more rufescent underparts and the two forms were described as being "easily distinguishable" based on plumage and morphology; we now know this is not the case (see below).

**Uncertainty about migration added to taxonomic confusion**

Inadequate information about migration contributed to longstanding uncertainty about *Patagona* taxonomy. Migration of the southern temperate populations was long suspected, and naturalists throughout history puzzled over where Chilean populations 'disappeared' to after breeding (Goodall *et al.* 1946). Even recently, the *Atlas of the Breeding Birds of Chile 2011-2016* called the winter whereabouts of Chilean-breeding giant hummingbirds an "unsolved mystery" (Medrano *et al.* 2018).

Darwin was among the earliest to note migration of southern giants: During his voyage on *The Beagle*, he remarked, "At Valparaíso, in the year 1834, I saw several of these birds in the middle of August, and I was informed they had only lately arrived from the parched deserts of the north" (Darwin 1839). German-Chilean botanist Federico Johow wrote that giant hummingbirds are "rather tropical" and were observed in central Chile only during the Chilean summer; he noted that their presence along the coast of Chile coincided with the flowering of *Lobelia* and columnar cacti, proposing that they wintered in the northern provinces of "…Peru,

Ecuador, etc." (Johow 1910, 1921). Hellmayr (1932) stated that *Patagona* is absent from central Chile during June–August, writing, "The birds probably migrate northwards, but a few, at least, cross the Andes on their migration, as is shown by specimens… which clearly pertain to the Chilean race" (Hellmayr 1932). Supporting this idea, *Birds of the High Andes* posited that Chilean breeders migrate across the Andes to adjacent western Argentina (Fjeldså & Krabbe 1990), while others have suggested that they migrate to northwestern Argentina (Sánchez Osés 2003). More recently, and without citing evidence, the guide "*Biodiversidad de Chile, patrimonio y desafíos*" stated that Chilean giant hummingbirds migrate to Ecuador for the austral fall (Ambiente 2008).

Chilean naturalist Rafael Barros offered what is perhaps the most detailed early treatment of *Patagona* migration. In 1952, Barros described Chilean-breeding giant hummingbirds as "…fleeing from the rainy season and the cold" (Barros 1952). Barros wrote, "It is not well elucidated if, when it leaves its places of residence…it actually moves to the provinces located to the north of Aconcagua (where my observations begin), or it crosses the high mountain range of the Andes and passes to the Republic of Argentina, or if it goes to winter in some regions of Bolivia or Peru. I know of no observations in this regard, and this is a problem to be solved, of great scientific interest" (Barros 1952). Barros posited the question: "Does it go up…to the heights of the Puna to cross the Andes?", later responding: "Based on what I have been able to observe for many years… I do not believe that it crosses the mountain range in the central part of the country, during its pilgrimages, either on its outward journey or on its return, because in the mountainous region it first reaches the lower parts, the pre-cordillera, the foothills of the Cordillera and fields beneath them, gaining altitude afterwards" (Barros 1952). In this same year, Zimmer cast doubt on the extent of northward travel of migratory temperate breeders, stating that

he had seen no Peruvian specimens indicating the occurrence of *P. gigas gigas* in Peru (Zimmer 1952).

In 1974, Ecuadorian ornithologist Fernando Ortiz-Crespo published a detailed treatment of the ecology of giant hummingbirds in Ecuador (Ortiz-Crespo 1974). Ortiz-Crespo briefly noted that the giant hummingbird population in central Chile "…builds up during the spring and summer", attributing their movement to northward migration (Ortiz-Crespo 1974). Ortiz-Crespo credited Johow (1910) and Darwin (1839) as his sources for migration information. In this same study, Ortiz-Crespo analyzed morphology between sexes and *Patagona* subspecies (which he assigned based on collection country), stating that his results "...do not seem to confirm the possibility that Ecuador is regularly visited on migration by birds which nest in central Chile, and whose winter quarters thus remain to be discovered" (Ortiz-Crespo 1974). Twelve years later, in a different manuscript about austral hummingbird migration, Ortiz-Crespo expressed similar uncertainty about *Patagona* migration, stating "…it is not known for sure where they winter" (Ortiz-Crespo 1986). He described examining 180 specimens, including 156 specimens from outside of Chile, only four of which (ANSP-145417 and FMNH-179394 from Bolivia, ANSP-167558 from Argentina, and FMNH-67518 from Peru) he said had measurements and coloration of the nominate form *gigas* (we examined these same specimens at ANSP and FMNH, and have confirmed that they are Southern Giant Hummingbirds). Ortiz-Crespo concluded, "This meager evidence suggests that southern populations disperse northward after nesting" (Ortiz-Crespo 1986), providing no additional specifics. He further suggested that examining specimens collected during the austral fall and winter from northwest Argentina and Bolivia would be important for understanding distribution and movement (Ortiz-Crespo 1986).

Since Darwin's mention of migration in 1839, many published accounts have mentioned *Patagona* migration or presence/absence of *Patagona* at certain times of the year in Chile with few additional details (e.g., (Aguirre 2001; Barros 1952; Estades *et al.* 2008; González-Gómez & Valdivia 2005; Gould 1861; Medel *et al.* 2022; Rueda-Uribe *et al.* 2023; Speziale & Lambertucci 2009; Velásquez-Noriega *et al.* 2021)). One publication stated that *Patagona* migrates 2,000 km (Rodríguez-Flores *et al.* 2019), but no information about the migratory route or sources for distance traveled were provided. The many, pre-2024 sources cited above corroborated the longstanding idea that Chilean *Patagona* populations migrate, but none provided detailed or definitive information about where these populations travel or how they get there.

Largely owing to a paucity of information about the migration of southern *Patagona* populations, the ranges and distributions of the putative giant hummingbird subspecies remained a source of confusion for their entire history. Gould (1861), though he did not mention forms, confirmed *Patagona* presence in Ecuador, Peru, Bolivia, and Chile, with no mention of Argentina (Gould 1861). Later, in his 1893 description, Boucard mentioned that the three forms (*gigas, peruviana, and boliviana*) were found in Ecuador, Peru, Bolivia, and Chile (Boucard 1893), providing no mention of Argentina. Hartert (1900), using Boucard's proposed names, noted that *P. peruviana* and *P. boliviana* were found in the "Andes from southern Ecuador to Chili and Argentina" (Hartert 1900). Hellmayr (1932) wrote that "*P. g. peruviana* … replaces the typical form in the Andes of Ecuador, Peru, Bolivia, and extreme northern Chile. It is probably also this race that nests in northwestern Argentina, although I have not been able to examine undoubted breeding specimens" (Hellmayr 1932). The idea that the race *peruviana* occurs in northwest Argentina was subsequently corroborated by many key historical accounts (Barros 1952; Fjeldså & Krabbe 1990; Koepcke 1983; Ruschí 1961; Zimmer 1952). In one, several

Southern Giant hummingbirds from Argentina and Bolivia were identified as *peruviana* (Zimmer 1952). This information continues to persist into recent years (e.g., Pearman & Areta 2020; Sánchez Osés 2003; Velásquez-Noriega *et al.* 2021). In *Birds of Chile: A Photo Guide*, Howell and Schmitt (2018) state that there is "no range overlap" between *peruviana* and *gigas* (Howell & Schmitt 2018). We now know northern Argentina contains only Southern Giant Hummingbirds, and that there is substantial range overlap of the two giant hummingbird species during the non-breeding season.

Uncertainty about migration, and confusion about the numbers of possible subspecies/forms and their respective distributions (e.g., Fjeldsa & Barbosa 1983), has additionally resulted in misleading generalizations about their elevations of residence. Woods (1998) suggested that the two forms, *peruviana* and *gigas*, might be elevational replacements and incompletely characterized the Southern Giant Hummingbird range, writing, "The northern subspecies of Giant Hummingbird *P. g. peruviana* regularly reaches paramo and puna habitats in Ecuador and Peru at 3,500-4,000 m, while the southern *P. g. gigas* occurs seasonally to below 2,000 m in central Chile and adjacent Argentina" (Woods *et al.* 1998). Woods does not mention latitudinal migration in southern temperate breeders. In a text about *P. g. peruviana*, Ruschi (1961) states that it is found in the Andes, varying in altitude from 2,500 to 5,000 meters (Ruschí 1961), but he does not mention *P. g. gigas* or its range. In many other texts, it is not possible to determine which form of giant hummingbird is being discussed.

The migration of Chilean giant hummingbirds has been suspected and discussed since at least 1834, but every aspect of the migratory journey had remained a mystery ever since, and no published works described population genetic connectivity until 2024. Two previous studies used open citizen science data to coarsely estimate the magnitude of elevational shift experienced

394 seasonally by Chilean-breeding populations (Rueda-Uribe *et al.* 2023; Williamson & Witt
395 2021b), and both studies underestimated the magnitude of elevational shift. Based on findings
396 from Williamson et al. (2024), we now know that the conspicuous giant hummingbirds are
397 comprised of two phenotypically cryptic species that overlap at the same sites and elevations
398 during the southern hemisphere winter, approximately May–September (Williamson *et al.* 2024).
399 The Southern Giant Hummingbird is a long-distance latitudinal migrant, traveling up to 8,300
400 km roundtrip in a circular loop across the Andes (Williamson *et al.* 2024). These data are even
401 more striking when put into a global context: The Southern Giant Hummingbird has one of the
402 two longest hummingbird migrations in the world, as its journey is similar to the typical distance
403 traveled by the Rufous Hummingbird (*Selasphorus rufus*), which flies up to ~8,200 km roundtrip
404 annually (Supp *et al.* 2015). At least some Southern Giant Hummingbird populations
405 shift >4,100 meters in elevation twice annually, making this species one of ~100 taxa that
406 undertake Elevational Niche-Shift Migration, or 'extreme' shifts in elevation between the
407 breeding and non-breeding seasons (Williamson *et al.* 2024; Williamson & Witt 2021b; a). These
408 discoveries, made possible with the use of miniaturized tracking devices and genomic
409 sequencing—technologies that were not available to Darwin, Johow, or any of the workers cited
410 above—have finally permitted the resolution of longstanding mysteries about migration and
411 distribution, clarifying taxonomy within this clade.
412
413 **Was a lectotype ever designated for *peruviana*?**
414 In their recent paper, Williamson et al. (2024) designated a holotype for the unique species
415 *Patagona chaski* (CORBIDI AV-012403, MSB:Bird:33080; PERU: dept. Cusco, Prov.
416 Urubamba, district Ollantaytambo, loc. Choquechaca, 13°11.620' S, 72°13.972' W, elev. 4,030

417 meters, 8 March 2009), based on diagnostic whole nuclear genomic and mitochondrial genomic
418 DNA-sequence data, confirmed locality, plumage, measurements, and physiological
419 characteristics. The name *chaski* is available and was registered on ZooBank (LSID:
420 urn:lsid:zoobank.org:pub:D2D498B7-1427-4A56-81F9-BFEA8C9CB6F5). Williamson et al.
421 (2024) introduced the name *chaski* on the grounds that the name *peruviana* was *nomen dubium*
422 and had never been applied consistently with the northern genetic lineage. An alternative path
423 would have been to designate a lectotype for *peruviana*. This raises the question of whether a
424 lectotype for *peruviana* has already been appropriately designated under the Code. Boucard's
425 (1893) mention of multiple specimens in the original description causes those specimens to
426 comprise syntypes, making it necessary to designate a single type, or lectotype. If Boucard had
427 instead designated a holotype for *peruviana*, the lectotype concept would have been unnecessary.
428 Confusion about the existence of a *peruviana* lectotype stems from pg. 231 in Hellmayr's
429 (1932) *Birds of Chile*, and possible ambiguity in the relevant section of the Code. In Boucard's
430 (1893) original description for *peruviana* and *boliviana*, he mentioned the existence of multiple
431 types ("…the specimens from Peru…") (Boucard 1893). However, Hellmayr noted that the name
432 *P. g. peruviana* was tentatively proposed by Boucard for "…a specimen from Peru in his
433 collection". Hellmayr called this individual, "the type", which he described as "…a male
434 obtained by H. Whitely on June 15, 1868, at Tinta, Dept. Cuzco…" (Hellmayr 1932). We cannot
435 be certain whether Hellmayr himself examined Boucard's putative syntypes, and no ledgers or
436 records exist at the MNHN to confirm that Hellmayr visited the collection (MNHN, *pers.*
437 *comm.*). Hellmayr wrote only "the type examined in the Paris Museum…" (Hellmayr 1932).
438 Under one interpretation of the Code, Hellmayr's assertion of the identity of "the type"
439 might constitute a lectotype designation. Art. 74.5 states that "…either the term "lectotype", or

440 an exact translation or equivalent expression (e.g. “the type”), must have been used or the author
441 must have unambiguously selected a particular syntype to act as the unique name-bearing type of
442 the taxon” (ICZN 1999). Furthermore, Art. 74.1.3 “…permanently deprives all other specimens
443 that were formerly syntypes of that nominal taxon of the status of syntype”. Under this
444 interpretation, MNHN-ZO-MO-1989-340 was designated as a lectotype by Hellmayr in 1932 and
445 the female from Boucard’s syntype series (MNHN-ZO-MO-1989-341) would therefore be a
446 paralectotype with no name-bearing function.
447 However, under an alternative interpretation of the Code, Hellmayr may not have
448 designated a lectotype. This is because Hellmayr’s assertion that there was a single “type”
449 contradicted Boucard’s original description of multiple “types” (Boucard 1893); if this was a
450 selection by Hellmayr, rather than an error, it was not made ‘unambiguously’. Art 74.6 of the
451 Code allows authors to restrict a type series to one holotype under certain conditions (“When it
452 has been accepted that a nominal species-group taxon was based on a single specimen and the
453 original description neither implies nor requires that there were syntypes, and if it is considered
454 subsequently that the original description was based on more than one specimen, the first author
455 to have published before 2000 the assumption that the species-group taxon was based upon a
456 single type specimen is deemed to have designated that specimen as the lectotype.”) Article 74.6
457 would therefore allow Hellmayr’s (1932) publication to constitute a lectotype designation if the
458 original description of the name *peruviana* (Boucard 1893) had never referred to a type series.
459 However, given that Boucard’s original description referenced “…the specimens from Peru…”
460 in the plural, he made it unequivocally clear that there was not only a single type specimen, a fact
461 confirmed by the MNHN (Jouanin 1950). Additionally, Art. 72.4.1 states that all specimens
462 mentioned in the original description are type specimens, unless explicitly excluded (“72.4.1.

The type series of a nominal species-group taxon consists of all the specimens included by the author in the new nominal taxon (whether directly or by bibliographic reference), except any that the author expressly excludes from the type series [Art. 72.4.6], or refers to as distinct variants (e.g. by name, letter or number), or doubtfully attributes to the taxon.”). Thus, under this interpretation, Hellmayr’s (1932) statements do not constitute designation of a lectotype, and the taxon *peruviana*, as validly described by Boucard (1893), continues to be based on a type series consisting of multiple syntypes.

**A lectotype for the taxon *peruviana***

In order to fix the identity on the taxonomic concept associated with the name *peruviana*, we re-designate or designate—depending on the interpretation of the Code—as its lectotype the male specimen (MNHN-ZO-MO-1989-340; Fig. 2a) collected in Tinta, Cusco, Peru, on June 15, 1868, by Henry Whitely, Jr. This is the same specimen that was subsequently singled out by Hellmayr (1932). The specimen is currently housed at the Muséum National d'Histoire Naturelle in Paris (MNHN). This designation satisfies Arts. 74.7.1, 74.7.2 and 74.7.3 (both original and amended versions; (ICZN 1999, 2003)), and is in accordance with Recommendations 74A and 74C. Importantly, this designation fixes the identity of *peruviana* to the individual described in Hellmayr (1932), thereby fulfilling a primary objective of the ICZN to promote stability of scientific names (ICZN 1999). Selection of MNHN-ZO-MO-1989-340 as the lectotype results in MNHN-ZO-MO-1989-341 (female, no date; Fig. 2b) becoming a paralectotype of *peruviana*. Selecting the female specimen as the lectotype would have needlessly contradicted Hellmayr’s (1932) text, which has been subsequently referenced by other authorities (e.g., (Peters 1945; Zimmer 1952).

By selecting the specimen MNHN-ZO-MO-1989-340, which appears to correspond to the northern giant hummingbird lineage, as the *peruviana* lectotype, it could be argued that *peruviana* has priority over *chaski* as the scientific name of the northern genetic lineage. However, we argue that *peruviana* has been applied with substantial taxonomic confusion and, as a result, it should be suppressed. To retain *peruviana* despite its tumultuous history and the inconsistency of its previous applications to mixtures of two distinct biological species would be promoting the continuation of instability and confusion rather than embracing the scientific advances that have finally clarified the taxonomy of giant hummingbirds. The single specimen that now underpins the name *peruviana* matches the northern genetic lineage due, in no small part, to chance. It was collected in an area and season where both lineages occur, and ornithological experts throughout history have never proven able to distinguish the two lineages consistently and without error. Because the name was misapplied for over a century, an adjustment in its meaning would comprise taxonomic instability and would cause the name to have multiple definitions throughout the literature (i.e., to be non-universal). All of this would lead to additional confusion. The Principle of Priority (Art. 23), a pillar of the Code, provides a remedy for this situation by allowing suppression of senior synonyms whose meaning has been similarly muddled.

**Unreliable historical identification of "*peruviana*" by morphology**

Hellmayr's (1932) account is often regarded as the definitive descriptive text for *Patagona* taxonomy and has been subsequently cited by numerous authorities, particularly in reference to distinguishing the nominate *gigas* from *peruviana*. Hellmayr examined "…between fifty and sixty properly labeled specimens from the whole range…", writing that there are "clearly" two

forms and that "…the general run of the two series is easily told apart" (Hellmayr 1932). In his text, Hellmayr presented a table of measurements from 45 specimens, from Ecuador (no localities given), Peru, Bolivia (one specimen; no locality), Argentina, and Chile. Hellmayr's data suggested that *P. g. gigas* was markedly smaller and did not overlap morphologically with *P. g. peruviana*, supporting his conclusion that there were two forms that were "clearly" and "easily" distinguished by morphology and plumage.

However, Hellmayr's conclusions about the ease with which *gigas* and *peruviana* could be distinguished are problematic when examined in detail. They directly contradict analyses conducted by Ortiz-Crespo (1974) and Williamson et al. (2024). Among 361 *Patagona* specimens from Ecuador, Peru, Bolivia, Argentina, and Chile, Williamson et al. (2024) found substantial overlap in morphological characteristics—including the same three measured traits studied by Hellmayr—between the two giant hummingbird species (Williamson *et al.* 2024). Williamson et al. (2024) found that Northern and Southern Giant Hummingbirds differed significantly, on average, in bill length, wing chord, and tail length, respectively; however, average trait differences were extremely subtle, on the scale of millimeters (e.g., ~1-5 mm)—size differences between the two species are not typically distinguishable by eye, and the ranges of trait values are similar for both species (Williamson *et al.* 2024). Similarly, within each giant hummingbird species, sexes differed significantly but not substantially in nearly all size measurements, although they are not sexually dimorphic in plumage. When analyzing morphological data separately for each sex, a Linear Discriminant Analyses using data from three traits (bill, wing, and tail) combined could distinguish Northern from Southern Giant Hummingbird adult females in only 65.4–82.8% of cases and adult males in 79.5–85.7% of cases, depending on the model set (Williamson *et al.* 2024). Additionally, Williamson et al.

532 (2024) found that the mass ranges of the two species are nearly identical. Thus, it would be
533 unwise to characterize the two giant hummingbird species on the basis of any single
534 morphological trait, and it would be imprudent to use any single measurement to attempt to
535 identify individuals to species. In light of this and the substantial degree of individual variation in
536 plumage (e.g., Fig. 1), the two giant hummingbird species are challenging to distinguish.

537 To understand how Hellmayr (1932) reached the conclusion that the two forms are easily
538 distinguished, we compared Hellmayr's original data (*n*=45 adults) with our own data, which
539 included published data from Williamson et al. (2024), measurements from wild-caught Northern
540 and Southern Giant Hummingbirds captured in Peru from July–August 2023, and data from
541 specimens at ANSP and FMNH (*n*=526 individuals total). After removing juveniles and filtering
542 only for individuals of known sex, locality, and age, our dataset included *n*=393 adults.

543 Hellmayr's data showed stark differences in bill, wing, and tail measurements for each
544 sex and species, with almost no overlap in trait distributions; these results sharply contrasted our
545 own, which showed substantial overlap in distributions for bill, wing, and tail measurements of
546 both sexes (Fig. 3). Hellmayr found significant differences between *gigas* and *peruviana* tail
547 measurements, for each males and females, where we found none between Southern and
548 Northern Giant Hummingbirds (Fig. 3c,f). Additionally, Hellmayr's *peruviana* measurements
549 were significantly greater than our Northern Giant Hummingbird measurements in comparisons
550 of male and female wing and tail, respectively (Fig. 3b–f). When we conducted a Principal
551 Components Analysis (PCA) using bill, wing, and tail measurements separately for each sex, we
552 found that Hellmayr's data clustered tightly and were shifted to the outer edges of the
553 distributions expected based on our much larger data set (Fig. 4). In this same analysis, the
554 MNHN male *peruviana* lectotype (MNHN-ZO-MO-1989-340), an apparent Northern Giant

555 Hummingbird, and the MNHN *boliviana* holotype (MNHN-ZO-MO-1989-342), a Southern
556 Giant Hummingbird, both fell within Hellmayr's range for *peruviana*, and within a
557 morphological zone of overlap between male Northern and Southern Giant Hummingbirds; when
558 analyzed with female data, MNHN-ZO-MO-1989-342 was an outlier for both species (Fig. 4).
559 The MNHN *peruviana* female paralectotype (MNHN-ZO-MO-1989-341), fell more closely in
560 line with measurements for Southern Giant Hummingbirds (Fig. 4). Taken together, these data
561 reinforce that individuals of each the Northern and Southern species may be difficult to
562 distinguish even with a suite of measurements used in concert.

563 The differences in trait means between forms in Hellmayr's dataset were noticeably
564 larger, and Hellmayr's CVs noticeably smaller, than those observed between species in our
565 dataset (Tables 2–4). For example, the difference between Hellmayr's *peruviana* and *gigas* mean
566 wing measurements was 2.64x greater for males and 4.21x greater for females than the
567 respective differences between Northern and Southern Giant Hummingbirds in our data (Fig. 3).
568 Hellmayr's tail measurements were particularly anomalous: Hellmayr's difference in tail lengths
569 between female *peruviana* and *gigas* was 19.57x greater than difference in tail lengths between
570 female Northern and Southern Giant Hummingbirds in our dataset (Fig. 3).

571 If Hellmayr's two groups, *peruviana* and *gigas*, corresponded to the northern and
572 southern species, respectively, the properties of his data should be consistent with trait
573 distributions from our much larger dataset of measurements from these two species. To test this,
574 we randomly subsampled our data, without replacement, to match Hellmayr's sample sizes, and
575 generated 10,000 random datasets. We did this separately for each sex and form (i.e., we
576 subsampled to $n$=8 for Southern males and $n$=4 for Southern females to match Hellmayr's *gigas*
577 sampling, and to $n$=25 for Northern males and $n$=8 for Northern females to match Hellmayr's

578 *peruviana* sampling). For each trait and sex, and for each of the 10,000 datasets generated, we
579 calculated trait means and CVs, resulting in expected distributions against which we could
580 compare Hellmayr's data. Using these 10,000 resampled data sets, we further calculated the
581 magnitudes of trait difference between the two giant hummingbird species, separately for each
582 sex and trait, yielding expected distributions for differences in trait means.

583 The CVs were smaller and magnitudes of trait difference were larger in Hellmayr's
584 (1932) data than in the expected distributions generated from our resampled datasets (Figs. 5–6,
585 Tables 2–5). For all sex-trait combinations, Hellmayr's data were statistically improbable (Figs.
586 5–6). For all traits and in both sexes, Hellmayr's differences in trait means fell on the outer right
587 tail of the expected distribution, based on 10,000 simulated datasets (Fig. 5). Across six trait-sex
588 combinations, the estimated probabilities of obtaining a difference of trait means as large or
589 larger than Hellmayr's ranged from 0.0001–0.014 probability (Fig. 5). Hellmayr's CVs were
590 realistic for some sex-trait combinations and unrealistically small for others, as they generally
591 fell on the outer left tails of the expected trait distributions (Fig. 6). The probabilities of obtaining
592 CVs as extreme or more extreme than Hellmayr's ranged from 0.001–0.301 for bill length,
593 0.000–0.178 for wing chord, and 0.0005–0.361 for tail length (Fig. 6).

594 While Hellmayr's (1932) original data suggested strong morphological differences that
595 "clearly" indicated the existence of two forms, these data contradict robust comparisons by
596 Williamson et al. (2024), and our present comparison, which included data from an additional
597 165 individuals from across the *Patagona* range. Williamson et al. (2024) showed—and we
598 again demonstrate here—that there is substantial overlap in mensural traits between Northern
599 and Southern Giant hummingbirds, and between males and females of each species. Hellmayr's
600 data do not show the expected pattern of trait distribution overlap between giant hummingbird

601 forms, even when controlling for sex (Fig. 3). Hellmayr's *peruviana* measurements were
602 consistently greater than those in our larger dataset, sometimes significantly so, for all
603 comparisons except male bill length (Fig. 3). Importantly, Hellmayr's data are statistically
604 improbable: For example, based on 10,000 resampled datasets, there was only a 0.004
605 probability of finding as large of a taxon difference in male bill length as Hellmayr recovered
606 (Fig. 5). Similarly, there were only 0.002 and 0.007 probabilities of finding Hellmayr's
607 magnitudes of difference in male and female wing lengths, respectively, between his *gigas* and
608 *peruviana* categories. In sum, throughout Hellmayr's data, the differences between taxa are too
609 large and the variability within taxa is too low to have been produced by a random sampling of
610 the two genetic lineages (species) that we now know to exist.

611 Why were Hellmayr's (1932) data improbably decisive in distinguishing two *Patagona*
612 taxa in the paper in which he sought to resurrect the name *peruviana*? First, we must consider the
613 possibility that Hellmayr had included misidentified specimens in his dataset; we know this to be
614 true because at least several *P. gigas* were included in his "*peruviana*" series (see below).
615 Inclusion of misidentified individuals would have had the effect of diminishing between-taxon
616 differences and inflating the variability within taxa—the opposite of the pattern that we observed
617 in Hellmayr's data. The only remaining explanation is that Hellmayr did not report complete and
618 unaltered data. Rather than this being a case of scientific fraud, we speculate that Hellmayr may
619 have used a combination of plumage assessment, measurements, and locality to assign each
620 specimen to a taxonomic category; in other words, he may have started with the *a priori*
621 assumption that the two taxa were non-overlapping in size traits and range, and may then have
622 selectively included or omitted data that fit with his preconceived assumptions. Considering the
623 magnitude of the challenge inherent in identifying giant hummingbirds based on plumage, it may

have been Hellmayr's only option to make these educated guesses, seeking consilience of evidence as he tried to fit a taxonomy to this difficult group. However, his data cannot be considered valid scientific evidence because of the flawed selection process by which they appear to have been derived. Hellmayr's taxonomic conclusion that there were "clear" morphological differences between giant hummingbird forms held sway for nearly a century, but the distinction that he made was both scientifically invalid and taxonomically false.

**The subspecies name *peruviana* has been misapplied for 130 years**

Could the taxon name *peruviana* apply to the Northern Giant Hummingbird, a distinct and unique genetic lineage identified by Williamson et al. (2024), and to which its lectotype corresponds? Since Boucard's (1893) original description, there has been persistent uncertainty surrounding the diagnostic criteria and subspecies limits for *P. g. peruviana*, as well as the nominate *P. g. gigas*. While the work of scholars like Hellmayr and Zimmer was overall admirable and befitting of an era when neither genomic tools or miniature migration tracking devices existed, the characteristics presumed to be useful in diagnosing the two giant hummingbird forms have been found to be flawed (in the case of morphology); "illusory", as noted in 1921 by Simon (in the case of plumage), or misinformed (in the case of using misleading ideas about morphology and plumage in concert to assume latitudinal and elevational range limits). The name *peruviana* has been asserted to apply to "the large northern race" of giant hummingbird; yet, it has not been applied consistently to the taxon to which it is meant to denote. Instead, *peruviana* has been continuously and variably applied to a mixture of two distinct species on the basis of erroneous diagnoses of plumage characteristics, morphological measurements, and ranges. Widespread misclassification of the two *Patagona* taxa as subspecies

and misapplication of the name *peruviana* to both taxa has marked nearly a century of flawed taxonomy in this group. To continue using *peruviana* by altering its definition, concomitantly with its rank, would be confusing and would cause the name to have a non-universal definition pervading the literature, contrary to the spirit of the Principle of Priority (Art. 23).

Hellmayr's text is widely regarded as the definitive treatment for the entity *peruviana*. Although Hellmayr did not provide specimen identifiers, in a few cases he provides sufficient information to diagnose specimen identities. He describes three specimens that "…are in every particular typical of the large northern form…an adult male from Tilcara, Jujuy (Nov. 24, 1905; L. Dinelli), and a couple from Lara, Tucumán (Feb. 12, 1903; G. A. Baer), all in the Tring Museum" (Hellmayr 1932). These three specimens, formerly at Tring, were moved to the AMNH when Walter Rothschild sold his collection in 1932 (NHMUK, *pers. comm.*; AMHH, *pers. comm.*) The adult male from Tilcara described by Hellmayr is AMNH-479595, definitively identified as a Southern Giant Hummingbird, based on targeted sequence capture of ultra-conserved elements (UCEs), known breeding season collection locality, and definitive plumage characteristics (Williamson *et al.* 2024). The other two Lara, Tucumán individuals mentioned by Hellmayr, are AMNH-479593 and AMNH-479594—these two individuals are both juvenile Southern Giant Hummingbirds, for which Williamson et al. (2024) also provide UCE data. The fact that Hellmayr stated that these individuals were "in every particular typical" of the form *peruviana*, when in fact, they are Southern Giant Hummingbirds ranging in age from juveniles to adults, highlights that—despite claiming the two forms were "easily told apart"—he could not actually distinguish them consistently.

Importantly, the *Patagona* series collected by Henry Whitely from Tinta, Peru—of historical importance for its significance in the description of types—is a mixed series. The

Whitely specimens held at AMNH contain three Northern Giant Hummingbirds (AMNH-37400, AMNH-37500, AMNH-37501) and one Southern Giant Hummingbird (AMNH-37502), despite all being labeled "*peruviana*". That Boucard's apparent Whitely syntypes at the MNHN both appear to be Northern Giant Hummingbirds, based on plumage features (genetic identification is as yet unknown), has little bearing on whether the name *peruviana* has been correctly applied in the past, as the identities of these specimens are purely by chance: There is no evidence that any ornithologist or taxonomist of the 19$^{th}$ or 20$^{th}$ centuries was able to distinguish these two species or had any idea that they occurred together seasonally.

Misapplication of the name *peruviana* has persisted into the present. At least thirteen major museum collections whose specimens we have examined possess giant hummingbird specimens from each Peru, Bolivia, and Argentina that are labeled as *P. g. peruviana*, and which contain a mix of both the Northern and Southern Giant Hummingbird. Of the 557 specimens with locality data that we have examined, a total of 222 individuals (40%) are catalogued with subspecific identifiers. A total of 54 individuals (30.34% of specimens) that are labeled "*peruviana*" are actually Southern Giant Hummingbirds (e.g., AMNH-139179, LSUMNS-37404, CUMV-52570, MCZ-262196, FMNH-67518; Fig. 7). One individual (ANSP-145417) from Bolivia was labeled with both "*peruviana*" and "*gigas*" (and pencil marks are visible from where "*peruviana*" was erased and where "*gigas*" was instead written; this individual still bears "*peruviana*" on the back of its tag). Typically, individual *Patagona* collected in Ecuador, Peru, Bolivia, and northwestern Argentina that appeared large and had reddish underparts were assigned the name *peruviana* without greater scrutiny; by this measure, many reddish-toned *gigas* individuals appear to correspond to *peruviana* (e.g., Fig. 1). Thus, the name *peruviana* has been applied to specimens on the basis of erroneous information about morphology, plumage,

693 and assumptions about range. Perhaps as a consequence of this confusion, the extent to which
694 *peruviana* has been applied (or misapplied) in global collections appears to be limited, because
695 the vast majority of catalogued specimens (~60%) were not assigned subspecific identifiers.
696

697 **The world's largest hummingbird needs a robust name**

698 The migration-tracking, genomic, physiological, and morphological study conducted by
699 Williamson et al. (2024) demonstrated that high-elevation resident populations of the giant
700 hummingbird comprise a distinct species, a northern genetic lineage to which they assigned the
701 name *Patagona chaski* (Williamson *et al.* 2024). This was a novel taxonomic distinction and the
702 first time that analytical evidence had been presented supporting more than one species of giant
703 hummingbird. Although the authors were not aware at the time of evidence pertaining to the
704 identities of specific individual specimens that comprised the syntypes of *peruviana*, the fact that
705 those syntypes appear to correspond to the northern genetic lineage implies that *chaski* could
706 now be considered a junior synonym. However, based on the evidence presented above and Art.
707 23 of the Code, we conclude that use of *peruviana* should be suppressed because its application
708 has never aligned with the northern genetic lineage; as a result, its continued use would
709 perpetuate taxonomic and nomenclatural confusion and non-universality.

710 In accordance with the purpose of the Principle of Priority (Art. 23.2), "prevailing usage
711 must be maintained when the following conditions are both met (Art. 23.9.1): 1) the senior
712 synonym or homonym has not been used as a valid name after 1899 (Art. 23.9.1.1); and 2) the
713 junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in
714 at least 25 works, published by at least 10 authors in the immediately preceding 50 years and
715 encompassing a span of not less than 10 years" (Art. 23.9.1.2) (ICZN 1999). However, the Code

provides a mechanism to address situations of undue confusion and instability, such as this one: "If the conditions of 23.9.1 are not met but nevertheless an author considers that the use of the older synonym or homonym would threaten stability or universality or cause confusion, and so wishes to maintain use of the younger synonym or homonym, he or she must refer the matter to the Commission for a ruling under the plenary power [Art. 81]. While the case is under consideration use of the junior name is to be maintained [Art. 82]" (Art. 23.9.3).

In light of the evidence presented here, we recommend a reversal of precedence under Art. 23.9.3. We urge that the name *chaski* Williamson et al. 2024 take precedence and that the name *peruviana* Boucard 1893 be suppressed. In accordance with guidelines set forth by the Code (Art. 23.9.3), while under consideration of the plenary power of the Commission, the junior synonym, *chaski* in the present case, shall be maintained.

**Conclusions**

Before the introduction of data on migration and genetics in 2024, the taxonomy of giant hummingbirds was impossible to disentangle, in part because of faulty assumptions about ranges and identification criteria. The taxon name *peruviana* has had a confusing history. To clarify its status, we (re)designated a lectotype for this taxon by selecting the same individual referenced by Hellmayr (1932) as "the type". By analyzing the descriptions and data presented by Hellmayr (1932), we uncovered that the morphological and plumage features thought to be key for distinguishing *peruviana* from the nominate *gigas* were erroneous; Hellmayr's data showing that the two giant hummingbird forms were "easily" discriminable were possibly derived from selective omission of data that did not fit with the overly optimistic assumption that the two taxa did not overlap in size. As a result, Hellmayr himself misidentified *gigas* specimens as

"*peruviana*", and in his attempt to resurrect the latter taxon, he erred in both its range and phenotypic diagnosis. The name *peruviana* has been misapplied throughout history, in variable, non-universal ways, to a mixture of two different giant hummingbird species. Applications of the name *peruviana* have always been misaligned with the unique species, the Northern Giant Hummingbird, that was identified and delimited by Williamson et al. (2024). There has been widespread and ongoing confusion as a result. Continued use of the name *peruviana* would foster a continuation of taxonomic confusion. The junior synonym, *chaski*, was introduced concomitantly with definitive discoveries of species limits, phenotypic characterizations, physiological and behavioral differences, and year-round distributions for the two *Patagona* species. It is the only name that has been applied specifically and uniquely to the genetically distinct entity that we now know as the Northern Giant Hummingbird. We therefore urge the continued use of *Patagona chaski* for the Northern Giant Hummingbird.

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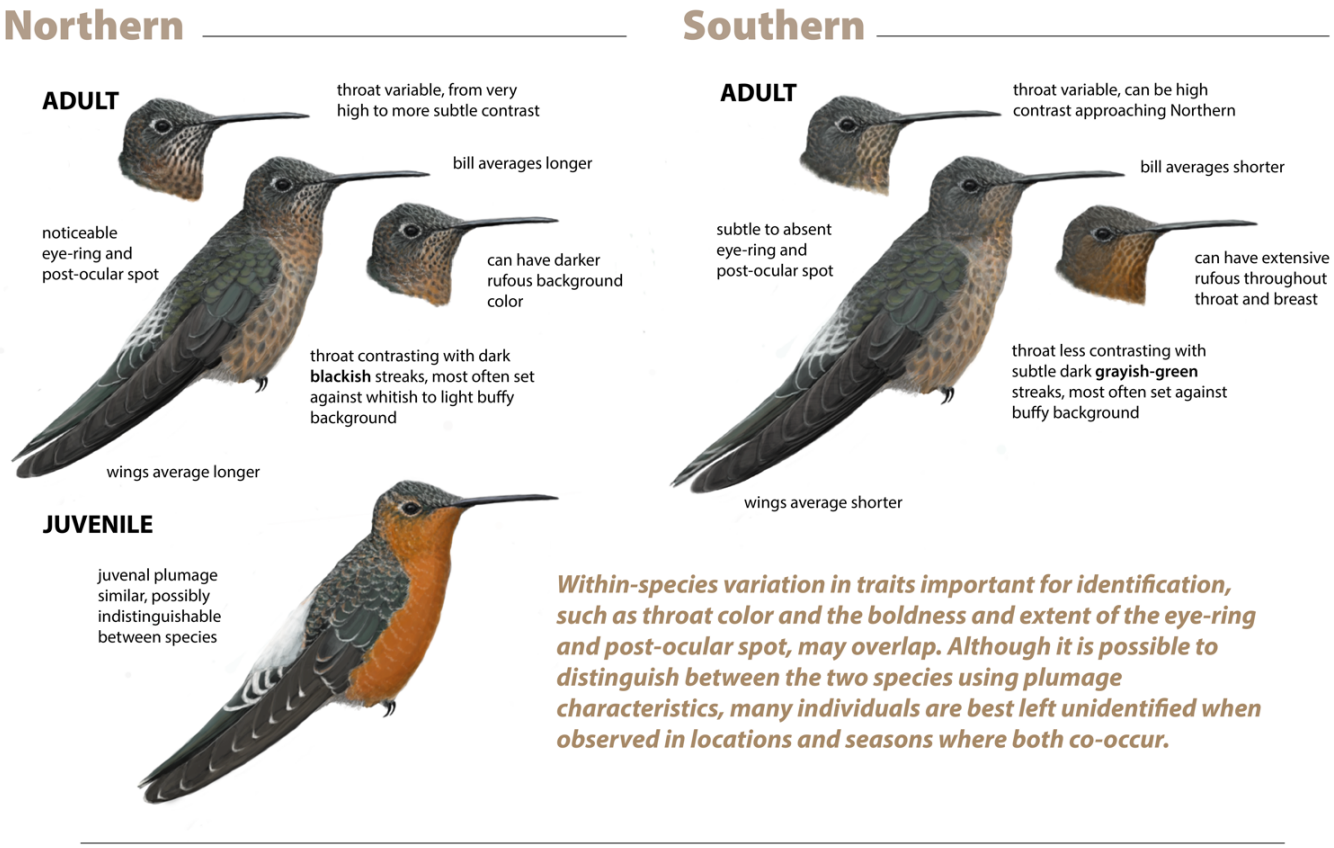


**Figure 1.** Key for distinguishing between Northern and Southern Giant Hummingbirds, highlighting important plumage characteristics described in (Williamson *et al.* 2024), including throat color and pattern and extent of eye-ring and post-ocular spot, as well as morphological characteristics, such as wing length and bill length. Juvenile is represented for comparison. Illustrations: Bryce W. Robinson.

**Figure 2. A–B,** Syntypes for the taxon *peruviana* from Boucard's (1893) collection described in Boucard (1893). **A** MNHN-ZO-MO-1989-340, a male, collected June 15, 1868. **B** MNHN-ZO-MO-1989-341, a female, no date. Both specimens were collected by Henry H. Whitely from Tinta, Peru. **C** Holotype for the taxon *boliviana* from Boucard's (1893) collection, MNHN-ZO-MO-1989-342, undetermined sex, collected in 1875 by Clarence Buckley from Bolivia. Photos: Muséum National d'Histoire Naturelle (MNHN), Paris.

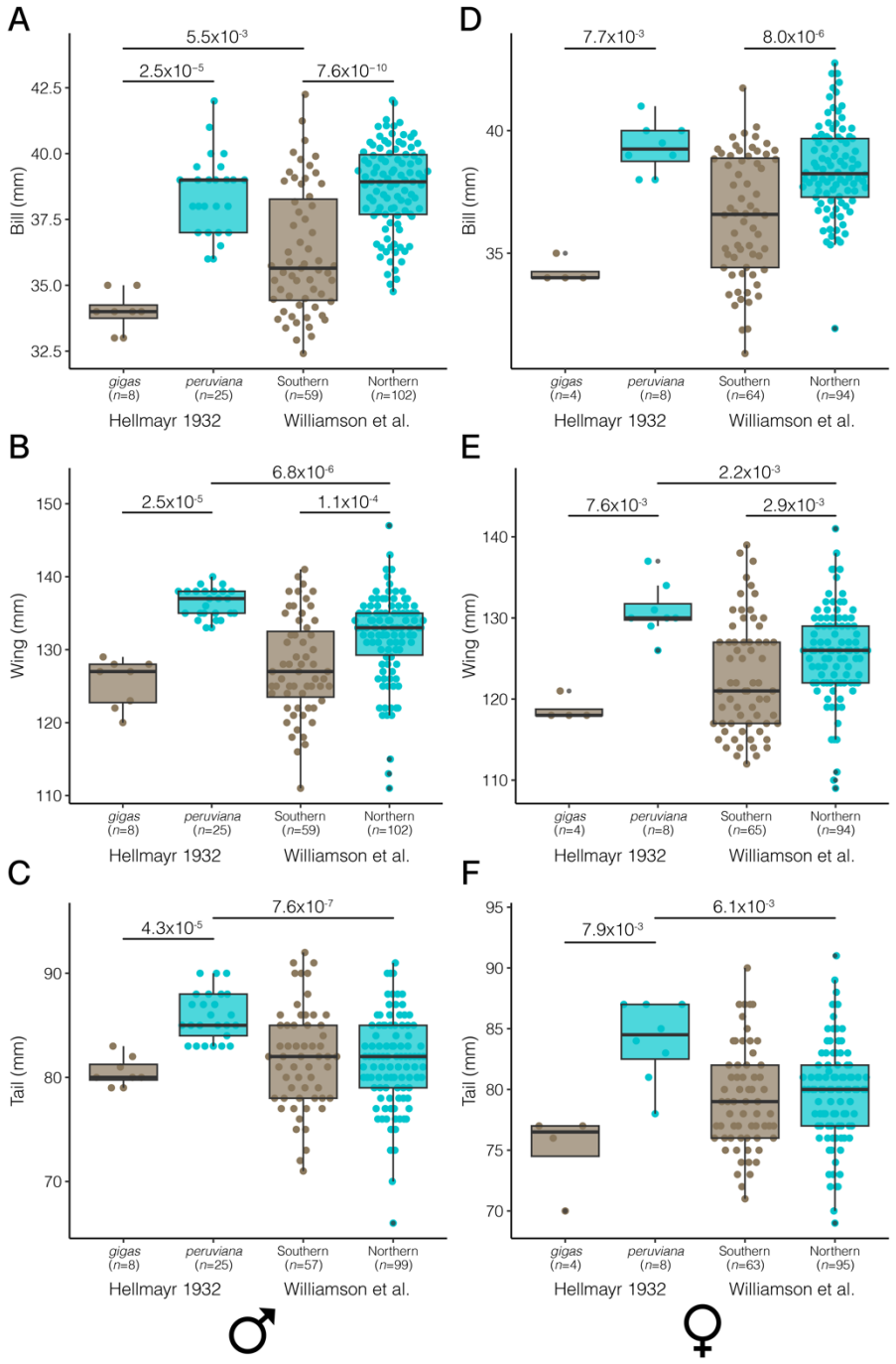


**Figure 3.** Comparison of morphological data (bill length, wing chord, and tail length; all in mm) between Hellmayr (1932) and Williamson et al. (present manuscript). **A–C** Males. **D–F** Females. Hellmayr compared adults of the two suspected forms, *gigas* and *peruviana*. Williamson et al. compared adults of the two species, the Southern and Northern Giant Hummingbird. Sample sizes for each comparison are reported on the x-axis and significant p-values are indicated above each comparison (from t-tests or non-parametric Wilcoxon Rank Sum tests). Box plot horizontal lines represent median values. Each point is a value from a single individual.

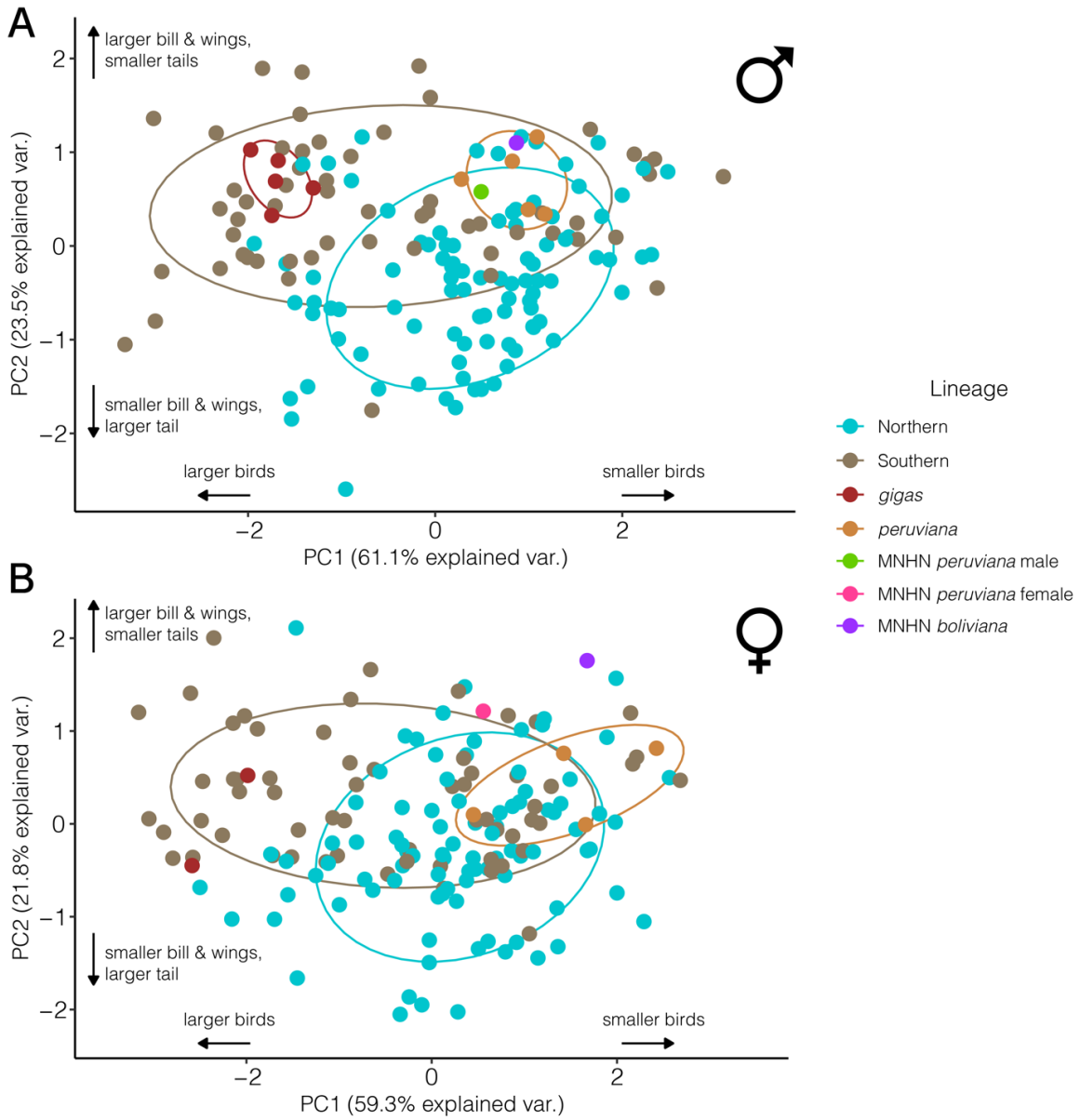


**Figure 4.** Principal Component Analysis (PCA) of bill, wing, and tail measurements for *gigas* and *peruviana* individuals from Hellmayr (1932) and Southern and Northern Giant Hummingbirds from Williamson et al. (present study) with MNHN *peruviana* syntypes and *boliviana* holotype. Because Hellmayr's data were organized numerically, rather than by individual, we have included only his records of single individuals per site to ensure accuracy. **A** Males (*n*=165 individuals); **B** Females (*n*=162 individuals). The male *peruviana* lectotype (MNHN-ZO-MO-1989-340), female *peruviana* paralectotype (MNHN-ZO-MO-1989-341), and *boliviana* holotype (MNHN-ZO-MO-1989-342) are plotted for reference; the *boliviana* holotype is of unknown sex and is therefore included in both PCAs. Although the female *peruviana* specimen is plotted, it should be noted that its maxilla is broken (MNHN, *pers. comm.*); however, *Patagona* maxilla and mandible lengths are typically equal. For reference, bill measurements: *peruviana* male: 35.7 mm; *peruviana* female 35.8 mm (mandible only); *boliviana*: 35.8 mm.

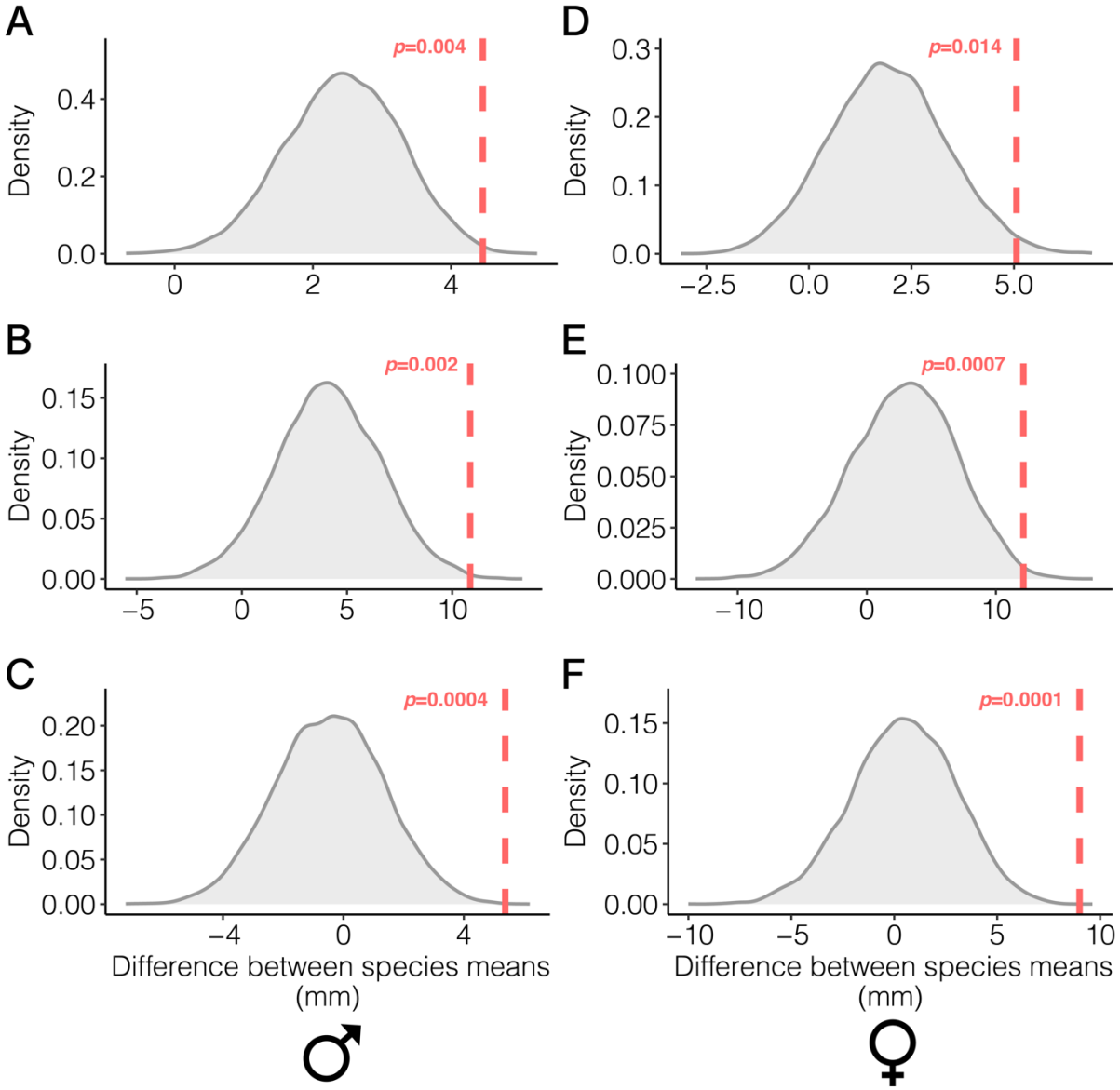


**Figure 5.** Expected distributions of trait mean differences between Northern and Southern Giant Hummingbirds, based on 10,000 resampled datasets generated from Williamson et al. (present study). **A–C** Expected male trait differences for each bill, wing, and tail; **D–F** Expected female trait differences for each bill, wing, and tail. Red dashed vertical lines indicate the differences between *gigas* and *peruviana* trait means from Hellmayr (1932) data, with the estimated probabilities of obtaining Hellmayr's values (red text). Estimated probabilities were calculated from 10,000 simulated datasets.

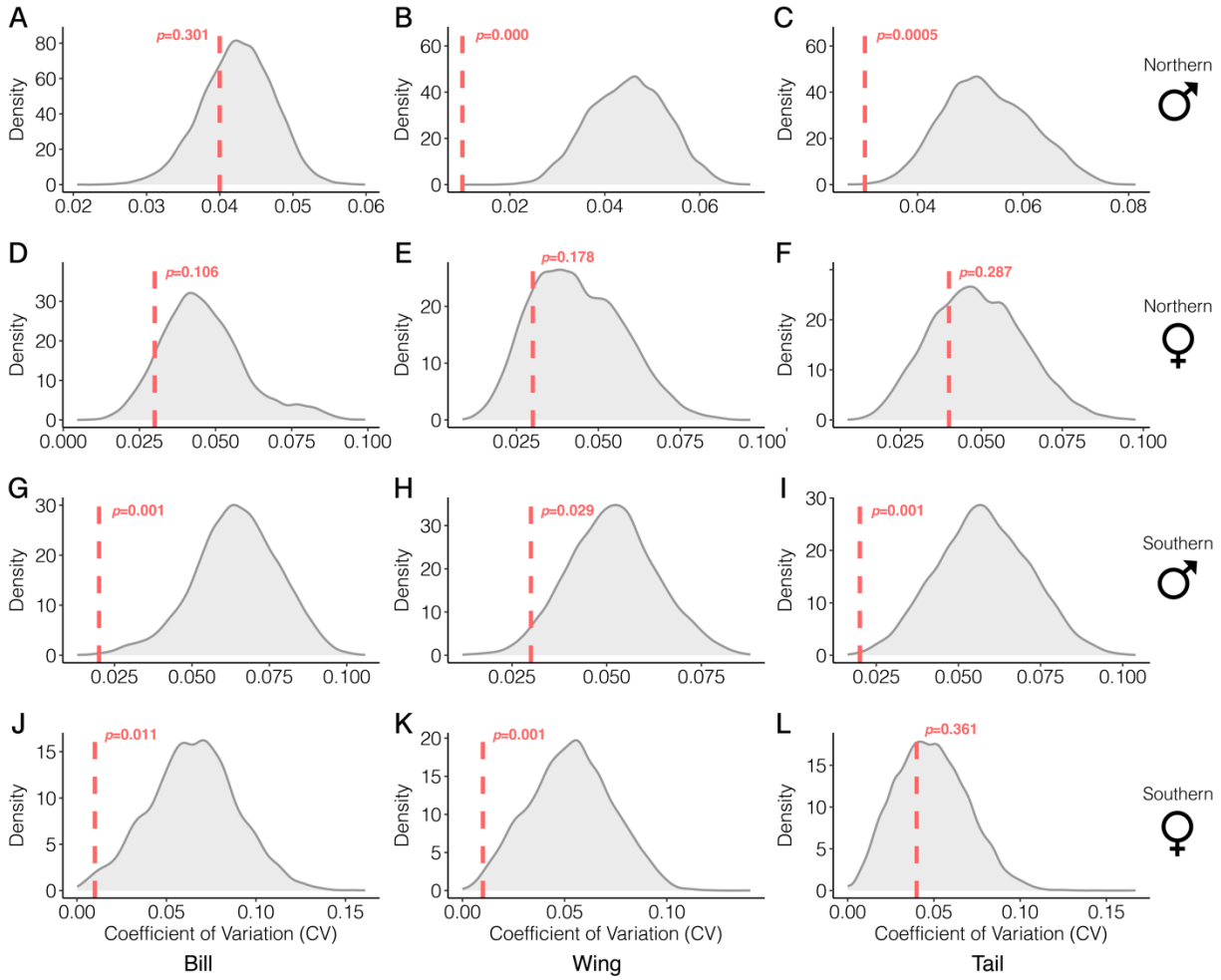


**Figure 6.** Expected distributions of coefficients of variation (CVs) for each Northern and Southern Giant Hummingbirds, based on 10,000 resampled datasets generated from Williamson et al. (present study). CVs were estimated separately for each species (Northern and Southern Giant Hummingbird), each sex (males and females), and each trait (bill, wing, and tail). **A–C** Northern males; **D–F** Northern females; **G–I** Southern males; **J–L** Southern females. Red dashed vertical lines indicate the CVs from Hellmayr's (1932) original data, with the estimated probabilities of obtaining Hellmayr's values (red text). Estimated probabilities were calculated from 10,000 simulated datasets.

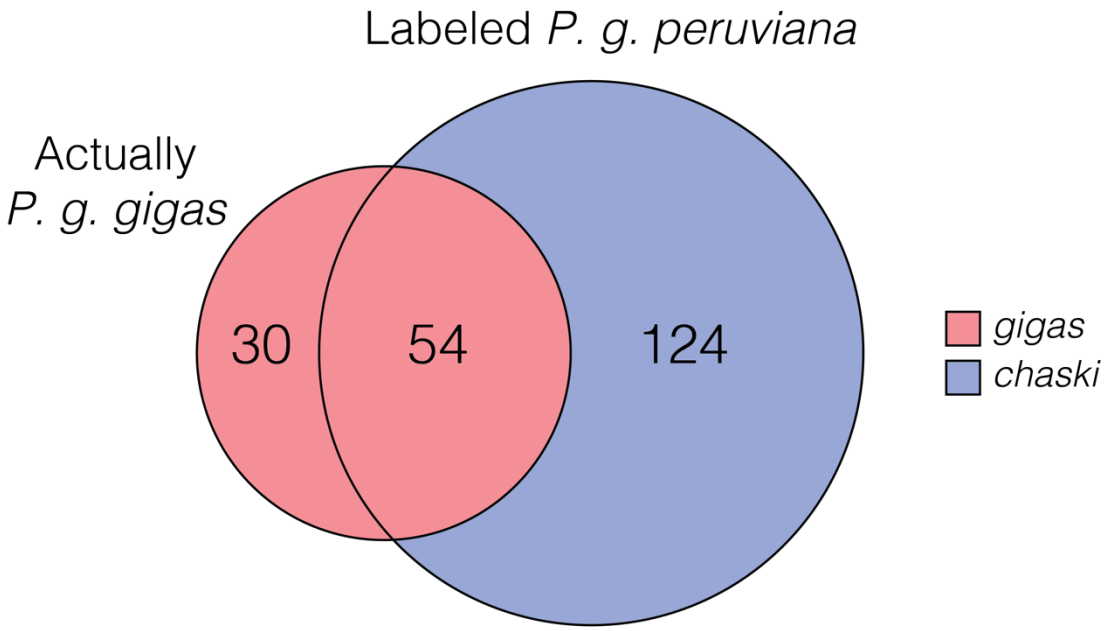


**Figure 7.** Visual representation of the *Patagona* specimen record as it pertains to previous versus current identifications. A total of 557 specimens were examined from 13 museum collections. Of these, 30 specimens are labeled as *P. g. gigas* and pertain to the Southern Giant Hummingbird (*Patagona gigas*). A total of 178 specimens are labeled as *P. g. peruviana*; of these, 124 specimens pertain to the Northern Giant Hummingbird (*Patagona chaski*) and 54 specimens pertain to the Southern Giant Hummingbird (*Patagona gigas*).

**Table 1.** Summary of *Patagona* specimens collected from southern Peru by Henry H. Whitely, Jr. One additional individual (collected ca. July 20, 1867 in Arequipa; known from Whitely's letter to Philip Lutley Sclater and Osbert Salvin, 1867; (Sclater & Salvin 1867)) is suspected but remains unidentified. Additionally, ANSP-50448 appears to be a Whitely specimen, but its origins and provenance are unknown (ANSP, *pers. comm.*) Museums: AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences of Drexel University; FMNH = Field Museum of Natural History; MNHN = Muséum National d'Histoire Naturelle; NHMUK = The Natural History Museum at Tring. *Indicates status as "type of fig" in Elliot 1879. **Equal status in AMNH ledgers with AMNH-37501. ‡Indicates status as a *peruviana* syntype (Jouanin 1950). ^MNHN-ZO-MO-1989-341 is listed in the MNHN database as having a collection date of "ca. 1868", which was estimated based on Whitely's Peru collection dates. However, the specimen has no date information, but was likely collected during 1868–1878 (MNHN, *pers. comm.*), and definitively before Whitely's death in 1892.

| Specimen identifier | Museum | Country | Department | Specific Locality | Collection Date | Putative Identification | Evidence |
|---|---|---|---|---|---|---|---|
| AMNH-37500 | AMNH | Peru | Cusco | Tinta | no date | Northern | Genomic data; plumage not diagnostic |
| AMNH-37501* | AMNH | Peru | Cusco | Tinta | no date | Northern | Genomic data; plumage not diagnostic |
| AMNH-37499 | AMNH | Peru | Cusco | Cachupata | 21 Aug 1873 | Northern | Genomic data; plumage not diagnostic |
| AMNH-37502** | AMNH | Peru | Cusco | Cachupata | 21 Aug 1873 | Southern | Genomic data; plumage not diagnostic |
| MNHN-ZO-MO-1989-340‡ | MNHN | Peru | Cusco | Tinta | 15 June 1868 | Northern | Plumage (diagnostic) |
| MNHN-ZO-MO-1989-341‡^ | MNHN | Peru | Cusco | Tinta | no date | Northern | Plumage (suggestive) |
| FMNH-45797 | FMNH | Peru | Cusco | Tinta | 25 May 1868 | Northern | Plumage (diagnostic) |
| FMNH-45798 | FMNH | Peru | Cusco | Tinta | 20 June 1868 | Northern | Plumage (diagnostic) |
| ANSP-50447 | ANSP | Peru | Cusco | Tinta | 4 Jan 1869 | Northern | Plumage (diagnostic) |
| NHMUK 1887.3.22.700 | NHMUK | Peru | Cusco | Tinta | 4 Jan 1869 | Northern | Plumage (diagnostic) |
| NHMUK 1913.3.20.291 | NHMUK | Peru | Cusco | Tinta | 4 Jan 1869 | Northern | Plumage (diagnostic) |
| NHMUK 1913.3.20.293 | NHMUK | Peru | unknown | W. Peru | no date | Northern | Plumage (diagnostic) |
| NHMUK 1887.3.22.701 | NHMUK | Peru | Arequipa | Chiguata | 10 June 1867 | Unknown (juvenile) | – |
| NHMUK unregistered | NHMUK | Peru | Arequipa | Chiguata | 10 June 1867 | Unknown (juvenile) | – |
| NHMUK 1913.3.20.294 | NHMUK | Peru | unknown | W. Peru | no date | Unknown (juvenile) | – |

**Table 2.** Morphological summary statistics for *gigas* (Hellmayr 1932) and Southern Giant Hummingbird (Williamson et al., present study) males and females. For each measured parameter, we provide sample size (*n*), mean, standard deviation, range (minimum and maximum values), and coefficient of variation.

| Dataset | Sex | Parameter (units) | *n* | Mean | Standard Deviation | Minimum | Maximum | Coefficient of Variation |
|---|---|---|---|---|---|---|---|---|
| Hellmayr 1932 | Male | Bill | 8 | 34 | 0.76 | 33 | 35 | 0.02 |
| | | Wing | 8 | 125.5 | 3.34 | 120 | 129 | 0.03 |
| | | Tail | 8 | 80.5 | 1.41 | 79 | 83 | 0.02 |
| Williamson et al. (present study) | | Bill | 59 | 36.27 | 2.4 | 32.41 | 42.25 | 0.07 |
| | | Wing | 59 | 127.64 | 6.74 | 111 | 141 | 0.05 |
| | | Tail | 57 | 81.88 | 4.86 | 71 | 92 | 0.06 |
| Hellmayr 1932 | Female | Bill | 4 | 34.25 | 0.5 | 34 | 35 | 0.01 |
| | | Wing | 4 | 118.75 | 1.5 | 118 | 121 | 0.01 |
| | | Tail | 4 | 75 | 3.37 | 70 | 77 | 0.04 |
| Williamson et al. (present study) | | Bill | 64 | 36.5 | 2.51 | 30.91 | 41.74 | 0.07 |
| | | Wing | 65 | 122.77 | 7.01 | 112 | 139 | 0.06 |
| | | Tail | 63 | 79.17 | 4.19 | 71 | 90 | 0.05 |

**Table 3.** Morphological summary statistics for *peruviana* (Hellmayr 1932) and Northern Giant Hummingbird (Williamson et al., present study) males and females For each measured parameter, we provide sample size (*n*), mean, standard deviation, range (minimum and maximum values), and coefficient of variation.

| Dataset | Sex | Parameter (units) | *n* | Mean | Standard Deviation | Minimum | Maximum | Coefficient of Variation |
|---|---|---|---|---|---|---|---|---|
| Hellmayr 1932 | Male | Bill | 25 | 38.46 | 1.49 | 36 | 42 | 0.04 |
| | | Wing | 25 | 136.36 | 2.02 | 133 | 140 | 0.01 |
| | | Tail | 25 | 85.88 | 2.33 | 83 | 90 | 0.03 |
| Williamson et al. (present study) | | Bill | 102 | 38.71 | 1.65 | 34.76 | 42.03 | 0.04 |
| | | Wing | 102 | 131.76 | 6 | 111 | 147 | 0.05 |
| | | Tail | 99 | 81.42 | 4.38 | 66 | 91 | 0.05 |
| Hellmayr 1932 | Female | Bill | 8 | 39.31 | 1.03 | 38 | 41 | 0.03 |
| | | Wing | 8 | 130.88 | 3.31 | 126 | 137 | 0.03 |
| | | Tail | 8 | 84 | 3.25 | 78 | 87 | 0.04 |
| Williamson et al. (present study) | | Bill | 94 | 38.41 | 1.85 | 31.93 | 42.76 | 0.05 |
| | | Wing | 94 | 125.65 | 5.74 | 109 | 141 | 0.05 |
| | | Tail | 95 | 79.64 | 4.04 | 69 | 91 | 0.05 |

**Table 4.** Difference between taxon-mean trait values from Hellmayr (1932) (i.e., between '*peruviana'* and *gigas*) and Williamson et al. (i.e., between the Northern Giant Hummingbird and Southern Giant Hummingbird).

| | | Difference between species means (mm) | | |
|---|---|---|---|---|
| **Sex** | **Source** | **Bill length** | **Wing chord** | **Tail length** |
| Male | Hellmayr 1932 | 4.46 | 10.86 | 5.38 |
| | Williamson et al. (present study) | 2.44 | 4.12 | -0.45 |
| Female | Hellmayr 1932 | 5.06 | 12.12 | 9.0 |
| | Williamson et al. (present study) | 1.91 | 2.88 | 0.46 |