Taxonomy, nomenclature, and identification 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 has been muddled for two centuries. *Patagona* systematics were redefined in a study of migration, physiology, and genetics by Williamson et al. (2024), revealing two species with divergent genomes and seasonal range overlap: Southern Giant Hummingbird (*P. gigas*) and Northern Giant Hummingbird (*P. chaski*). However, the taxonomy and nomenclature of the genus need to be reconsidered in light of its newly-clarified biology and species limits. The species name *gigas* (Viellot 1824) and subspecies name *peruviana* (Boucard 1893) were both described based on multiple syntypes. Here, we designate a lectotype for each name and we critically consider the identity and usage of each. The lectotype of *P. gigas* appears to be a Southern Giant Hummingbird, albeit from unknown provenance, and the historic and ongoing usage of this name has been restricted to that entity. The *peruviana* lectotype appears to be a Northern Giant Hummingbird, but usage of the name throughout history has involved misdiagnosis and misapplication to entities that comprise variable mixtures of the two giant hummingbird species. Redefining *peruviana* to match Northern Giant Hummingbird would shift the entity to which this name has referred, sowing confusion due to its non-universal meaning. By contrast, the species name *chaski* was introduced concomitantly with the definitive discovery of the 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 Northern Giant Hummingbird. Lastly, we

report misidentified specimens in major museum collections, and we provide comprehensive information on species identification and seasonal ranges for these cryptic species.

Key words: Andes, *chaski*, cryptic species, elevation, giant hummingbirds, museum collections, *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 1824 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 first species description by Vieillot (Vieillot 1824) and that of the genus *Patagona* Gray 1840, and examine those of subsequently introduced taxon 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 relevant to our understanding of *Patagona* 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.

Taxonomic history of *Patagona gigas*

The species *Trochilus gigas* was described by Vieillot (1824) based on two syntypes from "Brésil" (Brazil) (Vieillot 1824). Vieillot wrote that one specimen "…appears to us to be only a young male; the old one is unknown to us; but we believe we recognize the female in an individual in the possession of Mr. Becœur, naturalist…" (Vieillot 1824). Lesson (1829) renamed the species *Ornismya tristis*, noting that its "homeland" was Chile (Lesson 1829). In 1840, Gray named the genus *Patagona*, listing *P. gigas* (ascribed to Vieillot, 1824) as the sole species (Gray

1840). In spite of other proposed names (e.g., *Hylocharis gigas*, *Ornismya gigantea*, *Trochilus tristis*, *Cynanthus tristis*, and *Hypermetra gigas*; see (Elliot 1879, Porter 1897, Hartert 1900), from this point forward, *Patagona gigas* entered into widespread use among ornithologists.

Vieillot's putative "young male" syntype, illustrated in Plate 180 and attributed to M. (or Mr.) Portier of the Ministry of the Navy (Vieillot 1824) has not been located and its current whereabouts are unknown to us. Vieillot's putative female syntype is NHMUK-1933.11.14.36, a taxidermied mount at the Natural History Museum at Tring (NHMUK (Warren 1966); Fig. 2). It is not known whether this individual was determined to be a female during dissection or whether sex was presumed based on plumage (the latter would be unreliable). This specimen was obtained by George Loddiges from Jean-Baptiste Bécouer, a pharmacist and collector known for his arsenical soap method of specimen preparation, who died in 1777 (Rookmaaker et al. 2006). This putative female syntype bears two sets of confusing labels (neither original), written at different times and in different hands (date and author unknown), that make its identity as a syntype questionable: One is a green tag that appears to state "*Trochilus gigas Vielliot female / gal. ois. 1.1e 29 p. 296 pl 180 / Loddiges Coll / May be type of female*" (note misspelling of "Vieillot"; Fig. 2). The other tag, a white British Museum label, reads on the front, "*Trochilus gigas female / Loddiges Colln. (Purchased)*"; and on the back states, "*1933-11-14-36. / ~~Not accepted as Viellot's type of female but~~ may be. See Type catalogue*" (again note misspelling of "Vieillot"). The line through the text "*Not accepted as Viellot's type of female but*" was done in blue ink at what appears to be a later date (NHMUK, *Pers. Comm.*; Fig. 2). Because specimens from the Loddiges collection, purchased by NHMUK in 1933, had no original labels, it is impossible to verify that Loddiges specimens are the types of the species they represent; thus, all are listed as probable holotypes or syntypes by the museum (Warren 1966).

Despite the unknown collection localities, provenance, and dates of Vieillot's two putative syntypes, much later, in 1932, Carl Hellmayr suggested that the (syn)type locality of Brazil described by Vieillot (1824) was an error, stating "…we suggest Valparaíso, Chile" (Hellmayr 1932). On pg. 231 of the *Birds of Chile*, Hellmayr provided his justification for the locality restriction, writing, "Oudart's plate of *T. gigas*, based on an evidently immature bird from "Brésil" in the collection of "M. Portier, attaché au ministère de la marine," while none too good, corresponds fairly well to certain bright-colored Chilean specimens, such as No. 61,676, Caldera, and accordingly I propose to restrict Vieillot's term to the small southern form suggesting Valparaiso [Region, Chile,] as type locality" (Hellmayr 1932). Hellmayr's statement that Oudart's plate illustrated an "immature" does not match Oudart's plate, which depicts a juvenile. Additionally, the specimen "No. 61,676" referenced by Hellmayr is FMNH-61676, an immature female from Caldera, Atacama Region, Chile, corresponding in plumage to the Southern Giant Hummingbird (the authors have confirmed by examining the specimen). Thus, Hellmayr's decision to restrict the specific (syn)type locality for *Patagona gigas* to Valparaíso Region, Chile was based on his comparison of an immature specimen, FMNH-61676, from the Atacama Region of Chile with Oudart's plate of a juvenile putative male (whose plumage differs from immature birds) from an unknown locality.

Further confusing the identity of putative (syn)types, in 1893, Adolph Boucard, a French ornithologist and specimen trader, wrote, "I have in my collection what I consider as the type of Vieillot 'Ex Coll Riocour'" (Boucard 1893). Boucard's text references obtaining Vieillot's type specimen from the Comte de Riocour collection, which he obtained most of in 1889 (Renshaw 1905). The specimen he mentions is MNHN-ZO-2023-396 (sex and locality undetermined; collection date prior to 1842) at the Muséum National d'Histoire Naturelle in Paris (MNHN),

which bears multiple tags, including Comte de Riocour tags with red outlines and Boucard Collection tags with purple outlines. The front side of the Boucard Collection tag reads, "*Patagona gigas / Ex. Col. Riocour Type Vieillot ?*" Boucard's tag includes a question mark ("?") after the words "type Vieillot", indicating doubt about the status of the specimen as a Vieillot (syn)type, which he indicated tentatively in his 1893 text by writing "…what I consider the type…" (Boucard 1893). However, we could find no evidence that the specimen MNHN-ZO-2023-396, which Boucard said was "Vieillot's type", is *the* type or even a syntype of *P. gigas*, nor any indication that this specimen was ever examined by Vieillot. MNHN-ZO-2023-396 was obtained by Boucard from the Comte de Riocour collection and resides at the MNHN. Vieillot described *P. gigas* based on two syntypes: one, the "young male" (current whereabouts unknown) came from M. (or Mr.) Portier of the Navy; the other, an adult female, is NHMUK-1933.11.14.36, which was collected by Jean-Baptiste Bécouer and was later obtained by George Loddiges before being purchased by NHMUK (Warren 1966). There is no evidence that Boucard (or Comte de Riocour before him) ever had access to George Loddiges' collection, which remained in the Loddiges family after George Loddiges' death in 1846 (NHMUK, *Pers. Comm.*). Consistent with this history, the specimen NHMUK-1933.11.14.36 does not bear original Boucard Collection tags, which would be expected had this specimen been "in my collection", as Boucard described.

Thus, the entity formerly known as the Giant Hummingbird (*Patagona gigas*) and currently known as the Southern Giant Hummingbird (*Patagona gigas*) was described based on a type series consisting of two syntypes with unknown collection dates, localities, and provenance, and whose history is uncertain.

A lectotype for *Patagona gigas* (now the Southern Giant Hummingbird)

In order to fix the identity of the unique species now known as the Southern Giant Hummingbird *Patagona gigas* (*sensu* Williamson et al. 2024), we designate as its lectotype Vieillot's (1824) putative female specimen NHMUK-1933.11.14.36, which is identifiable by plumage as a Southern Giant Hummingbird (Fig. 2). This specimen was obtained by NHMUK in 1933 after the purchase of George Loddiges' collection; Loddiges, in turn, acquired the specimen from Jean-Baptiste Bécouer. The timing of Bécouer's death in 1777 gives the lectotype NHMUK-1933.11.14.36 an estimated collection date prior to 1777. This lectotype 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. This designation fixes the identity of *Patagona gigas* to the adult specimen that is most likely to correspond to the individual described in Vieillot (1824). It also ensures nomenclatural stasis for the Southern Giant Hummingbird, consistent with the widely held view that stability should be paramount in biological nomenclature (ICZN 1999, Jiménez-Mejías et al. 2024).

The type locality for *Patagona gigas* was restricted by Hellmayr (1932) to "Valparaíso, Chile", based the associations that Hellmayr made between Oudart's plate of a juvenile putative male (illustrated in (Vieillot 1824)) and the immature female specimen FMNH-61676, collected September 23, 1924 from Caldera, Atacama Region, Chile, which is ~830 km north of Valparaíso, Chile. Neither the plate nor specimen FMNH-61676 have any known link to the lectotype NHMUK-1933.11.14.36 (and there is no evidence that Vieillot's "young male" and "adult female" syntypes were collected at the same time or from the same place). Because the lectotype NHMUK-1933.11.14.36 has an entirely unknown date of collection and provenance, because there is no evidence that Bécouer ever traveled to Chile (or South America) to acquire

his collection (Rookmaaker et al. 2006), and because there is reason to doubt the disconnected logic that Hellmayr used to restrict the type locality to Valparaíso, Chile, we hereby re-designate the locality of the *Patagona gigas* lectotype NHMUK-1933.11.14.36 to the entire range of the Southern Giant Hummingbird: Central Chile, western and northwestern Argentina, Andean regions of Bolivia, and southern and central Peru.

We additionally designate 16 *Patagona gigas* paralectotypes (9 females, 7 males), which serve no name-bearing function but which clarify the definition of the entity that is *Patagona gigas* by providing confirmed identification in conjunction with known collection dates and specific localities. Each of these specimens is a breeding adult, definitively identified by DNA sequence data (whole genomes or target capture of ultra-conserved elements) or unambiguous consilience of plumage and breeding season locality (Williamson et al. 2024). All paralectotypes were collected during December 2018 to January 2019 from Valparaíso Region, Chile. Specimens and tissues are housed at the Museum of Southwestern Biology (MSB) at the University of New Mexico, with additional tissue material at Pontificia Universidad Católica de Chile in Santiago, Chile. Together, the paralectotypes approximate the range of plumage variation typically observed in breeding adult Chilean *Patagona gigas*. Catalog numbers (MSB:BIRD numbers) of the paralectotypes are: 56142, 56153, 56208, 56207, 56321, 56253, 56256, 56264, 56284, 56328, 56262, 56271, 56289, 56254, 56129, 56229.

The Whitely series of *Patagona* specimens

Henry H. Whitely, Jr., a British naturalist and explorer particularly interested in ornithology (Sclater 1893, Gladstone 1927), was a key figure in the history of *Patagona* taxonomy. For many years, Whitely collected specimens in southern Peru, with numerous trips throughout Arequipa

258 and Cusco between the years of 1867 and 1873 (Sclater and Salvin 1867, 1869; Sclater 1893,
259 Chapman 1921, Stephens and Traylor 1983). During this time, Whitely was credited with a
260 number of new species discoveries, including the Bearded Mountaineer (*Oreonympha nobilis*;
261 (Sclater 1893). Many of Whitely's specimens were dispersed through the specimen trading
262 business of his father, Henry Whitely, Sr. (Sharpe 1906, Rasmussen and Prys-Jones 2003).
263 Although Whitely Sr., and to a lesser extent, Whitely Jr.'s, reputations have been questioned
264 (Whitely, Sr. has been called 'reliably unreliable'; (Rasmussen and Prys-Jones 2003), none of the
265 specific problems that have been found have concerned the localities of Whitely's *Patagona*
266 specimens.

267 Whitely collected at least 16 *Patagona* specimens in Peru from 1867 to 1873 (Table 1). In
268 one letter about his 1867 Arequipa trip, Whitely noted, "… now commenced the worst part of the
269 journey…the way, however, was enlivened by the sight of numerous birds, and especially, for
270 some 2,000 feet, by the movements of the Giant Humming-bird (*Patagona gigas*)" (Sclater and
271 Salvin 1867). Whitely's *Patagona* specimens, particularly those from Tinta, Cusco, Peru, have
272 played a crucial role in history because they are thought to have formed the basis for a
273 subsequent type description. Whitely collected in Tinta on several trips, including May–June
274 1868 and January 1869 (Sclater and Salvin 1869). The identities of at least three *Patagona*
275 specimens from his 1868 trip are known (MNHN-ZO-MO-1989-340, FMNH-45797, and
276 FMNH-45798), and three others are suspected (AMNH-37500, AMNH-37501, and MNHN-ZO-
277 MO-1989-34; Table 1). One specimen (AMNH-37501), housed at the American Museum of
278 Natural History (AMNH) was designated as the "Type of Fig. 33, p. 67" in Giraud Elliot's 1879
279 synthesis, "*A classification and synopsis of the Trochilidae*" (Elliot 1879). This specimen, a male
280 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 Tring Collection of birds, then in the possession of (and sold by) Lord Lionel Walter, Second Baron 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 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, Boucard 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 also three specimens collected by Whitely in Peru, and in Bolivia by Buckley" (Boucard 1893) (Fig. 3). 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 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-

304 MO-1989-342 (undetermined sex, no date; from Bolivia), collected by Clarence Buckley, was
305 designated as the holotype *boliviana* (Jouanin 1950); Fig. 3; Table 1). The names *peruviana* and
306 *boliviana*, in addition to the nominate *gigas*, were henceforth recognized and entered into use
307 (e.g., (Hartert 1900).

308 In 1921, Boucard's (1893) original description was contested by Eugène Simon, a
309 naturalist and systematist from the MNHN. Simon wrote that *Patagona gigas* is a bird of the
310 high mountains "…without presenting sufficient local variation to be considered as subspecies"
311 (Simon 1921). Simon stated that Boucard (1893) had "…conditionally proposed the name
312 *Patagona peruviana* for the specimens from Peru from Whitely's trip and *Patagona boliviana*
313 for those brought back from Bolivia by Buckley" (Simon 1921). Then, Simon added, "…I have
314 ascertained, by examining the types, that the coloration characters [Boucard] gives (in Gen.
315 Humm. Birds. p. 61) are age-related or even completely illusory" (Simon 1921). In one footnote,
316 Simon noted the white borders on the wing feathers and wing coverts and "the absence of a
317 rufous part in front of the white uropygial band" on Boucard's types, which are characteristics of
318 *Patagona* juveniles and immatures (see Fig. 1). In a second footnote, Simon clarified his
319 description of the phrase "completely illusory", noting that he was discussing, "…for example,
320 the partly black throat of Peruvian birds" (Simon 1921). Simon did not provide specific
321 identifiers of the supposed types, but it is presumed from his text that he examined the same
322 specimens referenced in Boucard's (1893) original description.

323 In 1930, American ornithologist John Zimmer provided a brief account of *Patagona*
324 *gigas peruviana* Boucard and *Patagona gigas boliviana* Boucard in *Birds of the Marshall field*
325 *Peruvian expedition 1922-1923* (Zimmer 1930), recognizing Boucard's names as subspecific
326 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; the specific distinction made by Hellmayr 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) from northwestern Argentina north through Bolivia, northern Chile, Peru and Ecuador (this range is substantially larger than the known range of the Northern Giant Hummingbird). 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 and 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,*

418 *patrimonio y desafíos*" stated that Chilean giant hummingbirds migrate to Ecuador for the austral
419 fall (Ambiente 2008).

420 Chilean naturalist Rafael Barros offered what is perhaps the most detailed early treatment
421 of *Patagona* migration. In 1952, Barros described Chilean-breeding giant hummingbirds as
422 "…fleeing from the rainy season and the cold" (Barros 1952). Barros wrote, "It is not well
423 elucidated if, when it leaves its places of residence…it actually moves to the provinces located to
424 the north of Aconcagua (where my observations begin), or it crosses the high mountain range of
425 the Andes and passes to the Republic of Argentina, or if it goes to winter in some regions of
426 Bolivia or Peru. I know of no observations in this regard, and this is a problem to be solved, of
427 great scientific interest" (Barros 1952). Barros posited the question: "Does it go up…to the
428 heights of the Puna to cross the Andes?", later responding: "Based on what I have been able to
429 observe for many years… I do not believe that it crosses the mountain range in the central part of
430 the country, during its pilgrimages, either on its outward journey or on its return, because in the
431 mountainous region it first reaches the lower parts, the pre-cordillera, the foothills of the
432 Cordillera and fields beneath them, gaining altitude afterwards" (Barros 1952). In this same year,
433 Zimmer cast doubt on the extent of northward travel of migratory temperate breeders, stating that
434 he had seen no Peruvian specimens indicating the occurrence of *P. gigas gigas* in Peru (Zimmer
435 1952).

436 In 1974, Ecuadorian ornithologist Fernando Ortiz-Crespo published a detailed treatment
437 of the ecology of giant hummingbirds in Ecuador (Ortiz-Crespo 1974). Ortiz-Crespo briefly
438 noted that the giant hummingbird population in central Chile "…builds up during the spring and
439 summer", attributing their movement to northward migration (Ortiz-Crespo 1974). Ortiz-Crespo
440 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., (Gould 1861, Barros 1952, Aguirre 2001, González-Gómez and Valdivia 2005, Estades et al. 2008, Speziale and Lambertucci 2009, Velásquez-Noriega et al. 2021, Medel et al. 2022, Rueda-Uribe et al. 2023)). 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, Zimmer 1952, Ruschí 1961, Koepcke 1983, Fjeldså and Krabbe 1990). 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., (Sánchez Osés 2003, Pearman and Areta 2020, 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 and 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.

487 Uncertainty about migration, and confusion about the numbers of possible
488 subspecies/forms and their respective distributions (e.g., (Fjeldsa and Barbosa 1983), has
489 additionally resulted in misleading generalizations about their elevations of residence. Woods
490 (1998) suggested that the two forms, *peruviana* and *gigas*, might be elevational replacements and
491 incompletely characterized the Southern Giant Hummingbird range, writing, "The northern
492 subspecies of Giant Hummingbird *P. g. peruviana* regularly reaches paramo and puna habitats in
493 Ecuador and Peru at 3,500-4,000 m, while the southern *P. g. gigas* occurs seasonally to below
494 2,000 m in central Chile and adjacent Argentina" (Woods et al. 1998). Woods does not mention
495 latitudinal migration in southern temperate breeders. In a text about *P. g. peruviana*, Ruschi
496 (1961) states that it is found in the Andes, varying in altitude from 2,500 to 5,000 meters (Ruschí
497 1961), but he does not mention *P. g. gigas* or its range. In many other texts, it is not possible to
498 determine which form of giant hummingbird is being discussed.
499 The migration of Chilean giant hummingbirds has been suspected and discussed since at
500 least 1834, but every aspect of the migratory journey had remained a mystery ever since, and no
501 published works described population genetic connectivity until 2024. Two previous studies used
502 open citizen science data to coarsely estimate the magnitude of elevational shift experienced
503 seasonally by Chilean-breeding populations (Williamson and Witt 2021a, Rueda-Uribe et al.
504 2023), and both studies underestimated the magnitude of elevational shift. Based on findings
505 from Williamson et al. (2024), we now know that the conspicuous giant hummingbirds are
506 comprised of two phenotypically cryptic species that overlap at the same sites and elevations
507 during the southern hemisphere winter, approximately May–September (Williamson et al. 2024).
508 The Southern Giant Hummingbird is a long-distance latitudinal migrant, traveling up to 8,300
509 km roundtrip in a circular loop across the Andes (Williamson et al. 2024). At least some

Southern Giant Hummingbird populations shift >4,100 meters in elevation twice annually, making this species one of ~100 taxa that undertake Elevational Niche-Shift Migration, or 'extreme' shifts in elevation between the breeding and non-breeding seasons (Williamson and Witt 2021a, b; Williamson et al. 2024). These discoveries, made possible with the use of miniaturized tracking devices and genomic sequencing—technologies that were not available to Darwin, Johow, or any of the workers cited above—have finally permitted the resolution of longstanding mysteries about migration and distribution, clarifying taxonomy within this clade.

Was a lectotype ever designated for *peruviana*?

In their recent paper, Williamson et al. (2024) designated a holotype for the unique species *Patagona chaski* (CORBIDI AV-012403, MSB:Bird:33080; PERU: dept. Cusco, Prov. Urubamba, district Ollantaytambo, loc. Choquechaca, 13°11.620' S, 72°13.972' W, elev. 4,030 meters, 8 March 2009), based on diagnostic whole nuclear genomic and mitochondrial genomic DNA-sequence data, confirmed locality, plumage, measurements, and physiological characteristics. The name *chaski* is available and was registered on ZooBank (LSID: urn:lsid:zoobank.org:pub:D2D498B7-1427-4A56-81F9-BFEA8C9CB6F5). Williamson et al. (2024) introduced the name *chaski* on the grounds that the name *peruviana* was *nomen dubium* and had never been applied consistently with the northern genetic lineage. An alternative path would have been to designate a lectotype for *peruviana*. This raises the question of whether a lectotype for *peruviana* has already been appropriately designated under the Code. Boucard's (1893) mention of multiple specimens in the original description causes those specimens to comprise syntypes, making it necessary to designate a single type, or lectotype. If Boucard had

532 instead designated a holotype for *peruviana*, the lectotype concept would; have been
533 unnecessary.
534 Confusion about the existence of a *peruviana* lectotype stems from pg. 231 in Hellmayr's
535 (1932) *Birds of Chile*, and possible ambiguity in the relevant section of the Code. In Boucard's
536 (1893) original description for *peruviana* and *boliviana*, he mentioned the existence of multiple
537 types ("…the specimens from Peru…") (Boucard 1893). However, Hellmayr noted that the name
538 *P. g. peruviana* was tentatively proposed by Boucard for "…a specimen from Peru in his
539 collection". Hellmayr called this individual, "the type", which he described as "…a male
540 obtained by H. Whitely on June 15, 1868, at Tinta, Dept. Cuzco…" (Hellmayr 1932). We cannot
541 be certain whether Hellmayr himself examined Boucard's putative syntypes, and no ledgers or
542 records exist at the MNHN to confirm that Hellmayr visited the collection (MNHN, *pers.*
543 *comm.*). Hellmayr wrote only "the type examined in the Paris Museum…" (Hellmayr 1932).
544 Under one interpretation of the Code, Hellmayr's assertion of the identity of "the type"
545 might constitute a lectotype designation. Art. 74.5 states that "…either the term "lectotype", or
546 an exact translation or equivalent expression (e.g. "the type"), must have been used or the author
547 must have unambiguously selected a particular syntype to act as the unique name-bearing type of
548 the taxon" (ICZN 1999). Furthermore, Art. 74.1.3 "…permanently deprives all other specimens
549 that were formerly syntypes of that nominal taxon of the status of syntype". Under this
550 interpretation, MNHN-ZO-MO-1989-340 was designated as a lectotype by Hellmayr in 1932 and
551 the female from Boucard's syntype series (MNHN-ZO-MO-1989-341) would therefore be a
552 paralectotype with no name-bearing function.
553 However, under an alternative interpretation of the Code, Hellmayr may not have
554 designated a lectotype. This is because Hellmayr's assertion that there was a single "type"

555 contradicted Boucard's original description of multiple "types" (Boucard 1893); if this was a
556 selection by Hellmayr, rather than an error, it was not made 'unambiguously'. Art 74.6 of the
557 Code allows authors to restrict a type series to one holotype under certain conditions ("When it
558 has been accepted that a nominal species-group taxon was based on a single specimen and the
559 original description neither implies nor requires that there were syntypes, and if it is considered
560 subsequently that the original description was based on more than one specimen, the first author
561 to have published before 2000 the assumption that the species-group taxon was based upon a
562 single type specimen is deemed to have designated that specimen as the lectotype.") Article 74.6
563 would therefore allow Hellmayr's (1932) publication to constitute a lectotype designation if the
564 original description of the name *peruviana* (Boucard 1893) had never referred to a type series.
565 However, given that Boucard's original description referenced "…the specimens from Peru…"
566 in the plural, he made it unequivocally clear that there was not only a single type specimen, a fact
567 confirmed by the MNHN (Jouanin 1950). Additionally, Art. 72.4.1 states that all specimens
568 mentioned in the original description are type specimens, unless explicitly excluded ("72.4.1.
569 The type series of a nominal species-group taxon consists of all the specimens included by the
570 author in the new nominal taxon (whether directly or by bibliographic reference), except any that
571 the author expressly excludes from the type series [Art. 72.4.6], or refers to as distinct variants
572 (e.g. by name, letter or number), or doubtfully attributes to the taxon."). Thus, under this
573 interpretation, Hellmayr's (1932) statements would not constitute designation of a lectotype, and
574 the taxon *peruviana*, as validly described by Boucard (1893), continues to be based on a type
575 series consisting of multiple syntypes.
576
577 **A lectotype for the taxon *peruviana***

578 In order to fix the identity on the taxonomic concept associated with the name *peruviana*, we re-
579 designate or designate—depending on the interpretation of the Code—as its lectotype the male
580 specimen (MNHN-ZO-MO-1989-340; Fig. 3a) collected in Tinta, Cusco, Peru, on June 15, 1868,
581 by Henry Whitely, Jr. This is the same specimen that was subsequently singled out by Hellmayr
582 (1932). The specimen is currently housed at the Muséum National d'Histoire Naturelle in Paris
583 (MNHN). This designation satisfies Arts. 74.7.1, 74.7.2 and 74.7.3 (both original and amended
584 versions; (ICZN 1999, 2003)), and is in accordance with Recommendations 74A and 74C.
585 Importantly, this designation fixes the identity of *peruviana* to the individual described in
586 Hellmayr (1932), thereby fulfilling a primary objective of the ICZN to promote stability of
587 scientific names (ICZN 1999). Selection of MNHN-ZO-MO-1989-340 as the lectotype results in
588 MNHN-ZO-MO-1989-341 (female, no date; Fig. 3b) becoming a paralectotype of *peruviana*.
589 Selecting the female specimen as the lectotype would have needlessly contradicted Hellmayr's
590 (1932) text, which has been subsequently referenced by other authorities (e.g., (Peters 1945,
591 Zimmer 1952).
592 By selecting the specimen MNHN-ZO-MO-1989-340, which appears to correspond to
593 the northern giant hummingbird lineage, as the *peruviana* lectotype, it could be argued that
594 *peruviana* has priority over *chaski* as the scientific name of the northern genetic lineage.
595 However, we argue that *peruviana* has been applied with substantial taxonomic confusion and, as
596 a result, it should be suppressed. To retain *peruviana* despite its tumultuous history and the
597 inconsistency of its previous applications to mixtures of two distinct biological species would be
598 promoting the continuation of instability and confusion rather than embracing the scientific
599 advances that have finally clarified the taxonomy of giant hummingbirds. The single specimen
600 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*"

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

To understand how Hellmayr (1932) reached the conclusion that the two forms are easily distinguished, we compared Hellmayr's original data (*n*=45 adults) with our own data, which included published data from Williamson et al. (2024), measurements from wild-caught Northern and Southern Giant Hummingbirds captured in Peru from July–August 2023, and data from

specimens at ANSP and FMNH (*n*=526 individuals total). After removing juveniles and filtering only for individuals of known sex, locality, and age, our dataset included *n*=393 adults.

Hellmayr's data showed stark differences in bill, wing, and tail measurements for each sex and species, with almost no overlap in trait distributions; these results sharply contrasted our own, which showed substantial overlap in distributions for bill, wing, and tail measurements of both sexes (Fig. 4). Hellmayr found significant differences between *gigas* and *peruviana* tail measurements, for each males and females, where we found none between Southern and Northern Giant Hummingbirds (Fig. 4c,f). Additionally, Hellmayr's *peruviana* measurements were significantly greater than our Northern Giant Hummingbird measurements in comparisons of male and female wing and tail, respectively (Fig. 4b–f). When we conducted a Principal Components Analysis (PCA) using bill, wing, and tail measurements separately for each sex, we found that Hellmayr's data clustered tightly and were shifted to the outer edges of the distributions expected based on our much larger data set (Fig. 5). In this same analysis, the MNHN male *peruviana* lectotype (MNHN-ZO-MO-1989-340), an apparent Northern Giant Hummingbird, and the MNHN *boliviana* holotype (MNHN-ZO-MO-1989-342), a Southern Giant Hummingbird, both fell within Hellmayr's range for *peruviana*, and within a morphological zone of overlap between male Northern and Southern Giant Hummingbirds; when analyzed with female data, MNHN-ZO-MO-1989-342 was an outlier for both species (Fig. 5). The MNHN *peruviana* female paralectotype (MNHN-ZO-MO-1989-341), fell more closely in line with measurements for Southern Giant Hummingbirds (Fig. 5). Taken together, these data reinforce that individuals of each the Northern and Southern species may be difficult to distinguish even with a suite of measurements used in concert.

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

If Hellmayr's two groups, *peruviana* and *gigas*, corresponded to the northern and southern species, respectively, the properties of his data should be consistent with trait distributions from our much larger dataset of measurements from these two species. To test this, we randomly subsampled our data, without replacement, to match Hellmayr's sample sizes, and generated 10,000 random datasets. We did this separately for each sex and form (i.e., we subsampled to n=8 for Southern males and n=4 for Southern females to match Hellmayr's *gigas* sampling, and to n=25 for Northern males and n=8 for Northern females to match Hellmayr's *peruviana* sampling). For each trait and sex, and for each of the 10,000 datasets generated, we calculated trait means and CVs, resulting in expected distributions against which we could compare Hellmayr's data. Using these 10,000 resampled data sets, we further calculated the magnitudes of trait difference between the two giant hummingbird species, separately for each sex and trait, yielding expected distributions for differences in trait means.

The CVs were smaller and magnitudes of trait difference were larger in Hellmayr's (1932) data than in the expected distributions generated from our resampled datasets (Figs. 5–6, Tables 2–5). For all sex-trait combinations, Hellmayr's data were statistically improbable (Figs.

692 5–6). For all traits and in both sexes, Hellmayr's differences in trait means fell on the outer right
693 tail of the expected distribution, based on 10,000 simulated datasets (Fig. 6). Across six trait-sex
694 combinations, the estimated probabilities of obtaining a difference of trait means as large or
695 larger than Hellmayr's ranged from 0.0001–0.014 probability (Fig. 5). Hellmayr's CVs were
696 realistic for some sex-trait combinations and unrealistically small for others, as they generally
697 fell on the outer left tails of the expected trait distributions (Fig. 7). The probabilities of obtaining
698 CVs as extreme or more extreme than Hellmayr's ranged from 0.001–0.301 for bill length,
699 0.000–0.178 for wing chord, and 0.0005–0.361 for tail length (Fig. 7).

700 While Hellmayr's (1932) original data suggested strong morphological differences that
701 "clearly" indicated the existence of two forms, these data contradict robust comparisons by
702 Williamson et al. (2024), and our present comparison, which included data from an additional
703 165 individuals from across the *Patagona* range. Williamson et al. (2024) showed—and we
704 again demonstrate here—that there is substantial overlap in mensural traits between Northern
705 and Southern Giant hummingbirds, and between males and females of each species. Hellmayr's
706 data do not show the expected pattern of trait distribution overlap between giant hummingbird
707 forms, even when controlling for sex (Fig. 4). Hellmayr's *peruviana* measurements were
708 consistently greater than those in our larger dataset, sometimes significantly so, for all
709 comparisons except male bill length (Fig. 4). Importantly, Hellmayr's data are statistically
710 improbable: For example, based on 10,000 resampled datasets, there was only a 0.004
711 probability of finding as large of a taxon difference in male bill length as Hellmayr recovered
712 (Fig. 5). Similarly, there were only 0.002 and 0.007 probabilities of finding Hellmayr's
713 magnitudes of difference in male and female wing lengths, respectively, between his *gigas* and
714 *peruviana* categories. In sum, throughout Hellmayr's data, the differences between taxa are too

large and the variability within taxa is too low to have been produced by a random sampling of the two genetic lineages (species) that we now know to exist.

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

761 particular typical of the large northern form…an adult male from Tilcara, Jujuy (Nov. 24, 1905;
762 L. Dinelli), and a couple from Lara, Tucumán (Feb. 12, 1903; G. A. Baer), all in the Tring
763 Museum" (Hellmayr 1932). These three specimens were formerly at Tring but were moved to the
764 AMNH in 1932 after Lord Rothschild sold his collection (Lanyon 1995, Roselaar 2003);
765 NHMUK *Pers. Comm.*, AMNH *Pers. Comm.*) The adult male from Tilcara described by
766 Hellmayr is AMNH-479595, definitively identified as a Southern Giant Hummingbird, based on
767 targeted sequence capture of ultra-conserved elements (UCEs), known breeding season
768 collection locality, and definitive plumage characteristics (Williamson et al. 2024). The other two
769 Lara, Tucumán individuals mentioned by Hellmayr, are AMNH-479593 and AMNH-479594—
770 these two individuals are both juvenile Southern Giant Hummingbirds, for which Williamson et
771 al. (2024) also provide UCE data. The fact that Hellmayr stated that these individuals were "in
772 every particular typical" of the form *peruviana*, when in fact, they are Southern Giant
773 Hummingbirds ranging in age from juveniles to adults, highlights that—despite claiming the two
774 forms were "easily told apart"—he could not actually distinguish them consistently.
775 Importantly, the *Patagona* series collected by Henry Whitely from Tinta, Peru—of
776 historical importance for its significance in the description of types—is a mixed series. The
777 Whitely specimens held at AMNH contain three Northern Giant Hummingbirds (AMNH-37400,
778 AMNH-37500, AMNH-37501) and one Southern Giant Hummingbird (AMNH-37502), despite
779 all being labeled "*peruviana*". That Boucard's apparent Whitely syntypes at the MNHN both
780 appear to be Northern Giant Hummingbirds, based on plumage features (genetic identification is
781 as yet unknown), has little bearing on whether the name *peruviana* has been correctly applied in
782 the past, as the identities of these specimens are purely by chance: There is no evidence that any

783 ornithologist or taxonomist of the 19th or 20th centuries was able to distinguish these two species
784 or had any idea that they occurred together seasonally.

785 Misapplication of the name *peruviana* has persisted into the present. At least thirteen
786 major museum collections whose specimens we have examined possess giant hummingbird
787 specimens from each Peru, Bolivia, Argentina, and Chile that are labeled as *P. g. peruviana*, and
788 which contain a mix of both the Northern and Southern Giant Hummingbird. Of the 557
789 specimens with locality data that we have examined, a total of 222 individuals (40%) are
790 catalogued with subspecific identifiers. A total of 54 individuals (30.34% of specimens) that are
791 labeled "*peruviana*" are actually Southern Giant Hummingbirds (e.g., AMNH-139179,
792 LSUMNS-37404, CUMV-52570, MCZ-262196, FMNH-67518; Fig. 8). One individual (ANSP-
793 145417) from Bolivia was labeled with both "*peruviana*" and "*gigas*" (and pencil marks are
794 visible from where "*peruviana*" was erased and where "*gigas*" was instead written; this
795 individual still bears "*peruviana*" on the back of its tag). Typically, individual *Patagona*
796 collected in Ecuador, Peru, Bolivia, and northwestern Argentina that appeared large and had
797 reddish underparts were assigned the name *peruviana* without greater scrutiny; by this measure,
798 many reddish-toned *gigas* individuals would appear to correspond to *peruviana* (e.g., Fig. 1).
799 Thus, the name *peruviana* has been incorrectly applied to specimens on the basis of erroneous
800 information about morphology, plumage, and assumptions about range. Perhaps as a
801 consequence of this confusion, the extent to which *peruviana* has been applied (or misapplied) in
802 global collections appears to be limited, because the vast majority of catalogued specimens
803 (~60%) were not assigned subspecific identifiers.
804

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

806 The migration-tracking, genomic, physiological, and morphological study conducted by
807 Williamson et al. (2024) demonstrated that high-elevation resident populations of the giant
808 hummingbird comprise a distinct species, a northern genetic lineage to which they assigned the
809 name *Patagona chaski* (Williamson et al. 2024). This was a novel taxonomic distinction and the
810 first time that analytical evidence had been presented supporting more than one species of giant
811 hummingbird. Although the authors were not aware at the time of evidence pertaining to the
812 identities of specific individual specimens that comprised the syntypes of *peruviana*, the fact that
813 those syntypes appear to correspond to the northern genetic lineage implies that *chaski* could
814 now be considered a junior synonym. However, based on the evidence presented above and Art.
815 23 of the Code, we conclude that use of *peruviana* should be suppressed because its application
816 has never aligned with the northern genetic lineage; as a result, its continued use would
817 perpetuate taxonomic and nomenclatural confusion and non-universality.
818 In accordance with the purpose of the Principle of Priority (Art. 23.2), "prevailing usage
819 must be maintained when the following conditions are both met (Art. 23.9.1): 1) the senior
820 synonym or homonym has not been used as a valid name after 1899 (Art. 23.9.1.1); and 2) the
821 junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in
822 at least 25 works, published by at least 10 authors in the immediately preceding 50 years and
823 encompassing a span of not less than 10 years" (Art. 23.9.1.2) (ICZN 1999). However, the Code
824 provides a mechanism to address situations of undue confusion and instability, such as this one:
825 "If the conditions of 23.9.1 are not met but nevertheless an author considers that the use of the
826 older synonym or homonym would threaten stability or universality or cause confusion, and so
827 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.

Nomenclatural 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 first described species in the genus *Patagona*, *Patagona gigas,* and the subspecies *peruviana* have had confusing histories. To clarify the status of the entity currently known as the Southern Giant Hummingbird (*Patagona gigas*; *sensu* Williamson et al. 2024) and the taxon name *peruviana*, we designated a lectotype for *P. gigas* by selecting the same putative adult female likely examined by Vieillot (1824) and we (re)designated a lectotype for *peruviana* by selecting the same individual referenced by Hellmayr (1932) as "the type". Throughout history, the name *Patagona gigas* has always been applied correctly to the Southern Giant Hummingbird, and thus, we argue for continued use of this name. However, 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 his

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.

Distribution and identification of the two cryptic giant hummingbird species

The two giant hummingbird species are phenotypically cryptic and challenging to distinguish. Here, we provide details about their identification, seasonal distributions, elevational ranges relevant to ornithologists and birders. Although it is possible to distinguish between the two species using plumage characteristics, within-species variation in traits important for identification may overlap; as such, many individuals are best left unidentified when observed during locations and seasons of co-occurrence. Vocal differences may be important for distinguishing the two species in the field, particularly when they co-occur (Williamson et al., *In*

Prep.) Gaining a clearer understanding of the annual elevational and latitudinal ranges of both species will be essential to further understanding migration, seasonal zones of overlap, and regions where the two species hybridize.

Northern Giant Hummingbird (Patagona chaski)

Plumage: Adult Northern Giant Hummingbirds typically have whitish or buffy-colored throats with dark blackish streaks (but note that throat color is variable, from very high to more subtle contrast), a subtle cinnamon patch at the base of the throat (giving the throat base a more rufous color), and a whitish eye-ring with post-ocular spot (Fig. 1). Wings and bill average longer, but identification by plumage and/or measurements alone is unreliable.

Distribution and range: The Northern Giant Hummingbird is found year-round in extreme southern Colombia, Ecuador, Peru and northern Chile (Arica y Parinacota Region); more information is needed to confirm whether this species occurs in Bolivia. *P. chaski* spans an elevational range of ~1,800-3,600 m in Ecuador, ~1,900-4,300 in Peru, and ~1,900-3,800 m in Chile. In Peru, observers should carefully scrutinize giant hummingbirds during periods of seasonal overlap (~May–Sept), as the two *Patagona* species co-occur in many of the same sites and elevations. Individuals observed throughout Peru from November–April are Northern Giant Hummingbirds; individuals observed in central to southern Peru from May–September could plausibly be either Northern or Southern Giant Hummingbirds. The Northern Giant Hummingbird may appear very similar in plumage to the Southern Giant Hummingbird (Fig. 1), particularly in poor lighting conditions in the field or when seen in flight. *P. chaski* is found in arid and semi-arid habitats on the west slope of the Andes and in intermontane valleys, including montane scrub, hedgerows, agricultural areas, open woods (including *Polylepis*), and gardens,

often with *Agave*, *Puya*, and Cactaceae spp. Across its range, it tends to associate with fast-flowing streams.

Southern Giant Hummingbird (Patagona gigas)

Plumage: The Southern Giant Hummingbird tends to have a warm brown to cinnamon throat with subtly contrasting grayish-green streaks (but note that throat contrast is variable and may approach Northern in coloration), occasionally with a subtle cinnamon patch at the base; some individuals may have extensive rufous throughout the throat and breast. The eye-ring and post-ocular spot are subtle (buffy-colored, if present) to absent, giving Southern individuals a 'blank-faced' appearance (Fig. 1). Wings and bill average shorter, but identification by morphology alone is unreliable.

Distribution and range: The Southern Giant Hummingbird is found in central Chile, central through northwestern Argentina, Bolivia, and Peru (through central Ancash Department). This species breeds from sea level to ~2,000 m in Chile, above ~2,500 m in Argentina, and ~2,100–4,150 m in Bolivia. After breeding, *P. gigas* in central Chile migrate (starting ~mid-February to March) to Peru, passing through the breeding grounds of populations from northwest Argentina. At least some populations breeding in northwest Argentina also migrate to central Peru, but details about migration are as yet unknown. In Peru, *P. gigas* is found on the nonbreeding grounds in Peru, up to 4,300 m, at the same sites and elevations as the Northern Giant Hummingbird. Southern Giant hummingbirds are estimated to comprise ~20–40% of the nonbreeding population in Peru during May–September (Williamson et al. 2024); however, further work is needed to refine our understanding of this species migratory stopover sites and nonbreeding range. Individuals observed in Bolivia should be carefully evaluated, particularly in

the north, to rule out presence of the Northern Giant Hummingbird. Individuals in Chile and Argentina may overwinter. Observers should carefully scrutinize individuals in northern Chile (Arica y Parinacota Region), particularly during August–October when Southern Giant hummingbirds migrate through the region (and may pass through the range of Northern Giant hummingbirds).

Juvenile giant hummingbirds

The juvenal plumage of both juvenile giant hummingbirds is nearly identical, and possibly indistinguishable; several previous researchers have noted the difficulty of distinguishing the forms (e.g., (Zimmer 1952, Ortiz-Crespo 1974)). The juveniles of both species have deep cinnamon throats, breasts, and bellies that fade to duller brown as birds molt into immature plumage; emerald-toned heads, backs, and wings with buffy-tips to contour feathers; a pronounced white rump patch that may extent mid-way up the back; and fresh white tips to primaries and rectrices ((Mulsant and Verreaux 1876); Fig. 1). Dark black streaking seems to appear occur sooner on the throats of northern juveniles; presence of this character may prove useful for identification. Season and locality should be carefully evaluated when observing juveniles.

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Data deposits: Raw data will be uploaded to Dryad upon manuscript acceptance.

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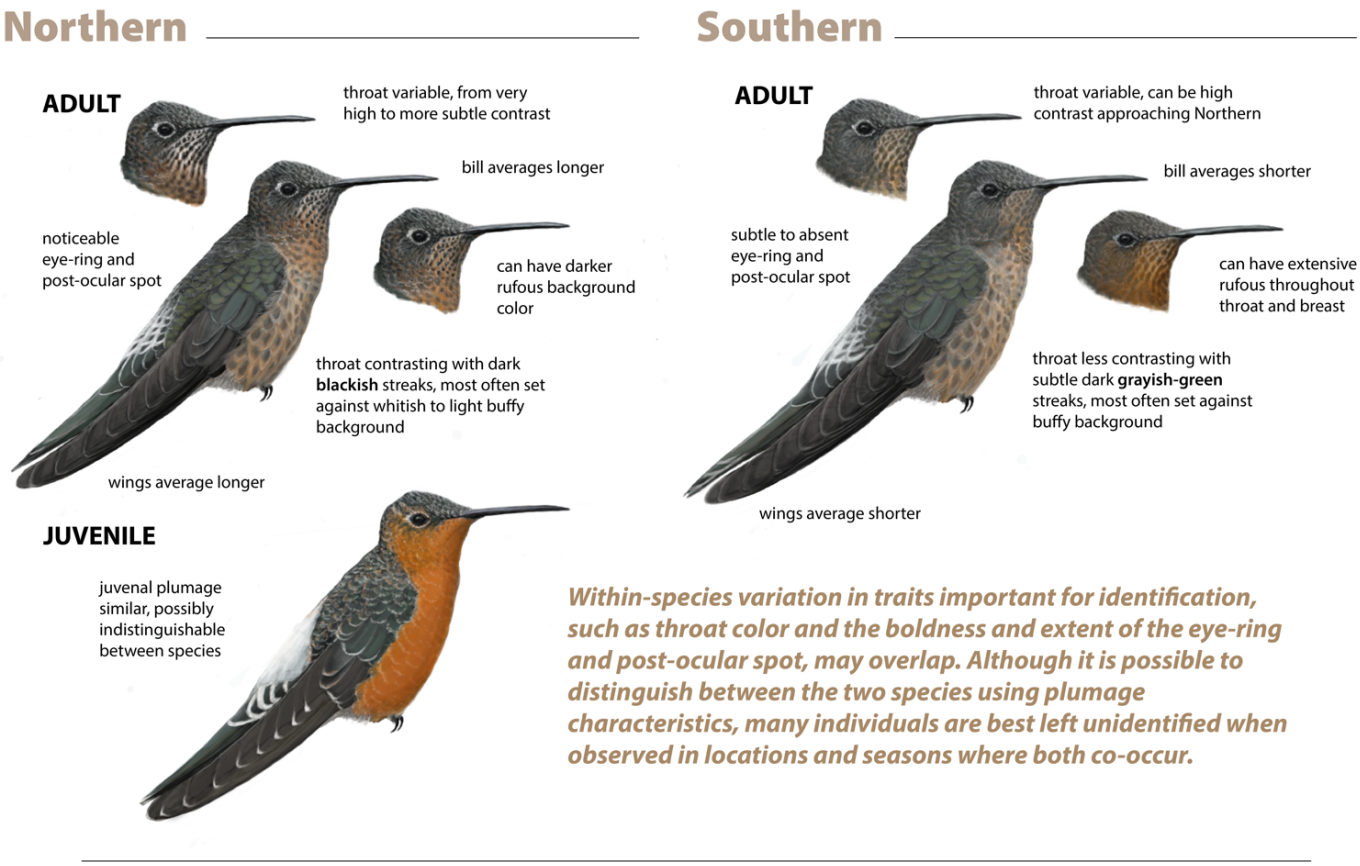

Figure 1. Key for distinguishing between Northern and Southern Giant Hummingbirds, highlighting important plumage characteristics described in, including throat color and pattern and extent of eye-ring and post-ocular spot, as well as morphological characteristics, such as wing length and bill length.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

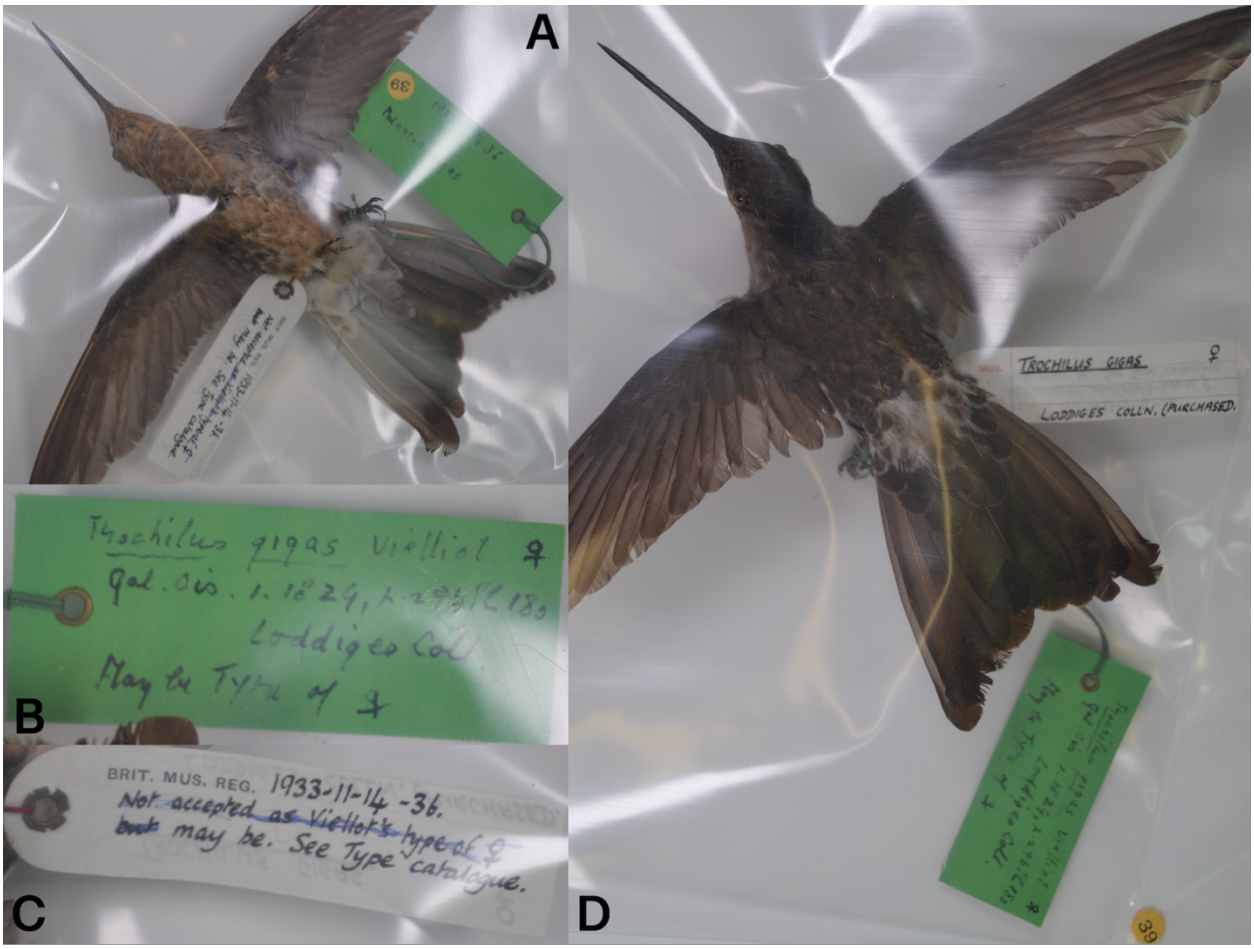

Figure 2. The lectotype, designated here, for the species *Patagona gigas*, formerly known as the Giant Hummingbird and currently known as the Southern Giant Hummingbird (*sensu* Williamson et al. 2024). The specimen shown is NHMUK-1933.11.14.36, a female with no collection date and no specific locality (provenance unknown), first acquired by Jean-Baptiste Bécouer. This specimen, a taxidermied mount, is thought to be one of two syntypes used to describe *Patagona gigas* by Vieillot (1824), but see specimen tag notes. **A** Ventral view showing the bird's throat, which is a clear match for the Southern Giant Hummingbird; **B–C** Non-original specimen labels (the specimen does not possess original labels) indicating uncertainty about whether NHMUK-1933.11.14.36 was one of Vieillot's (1824) syntypes; **D** Dorsal view of the specimen. Photos: Natural History Museum at Tring (NHMUK).

Figure 3. 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.

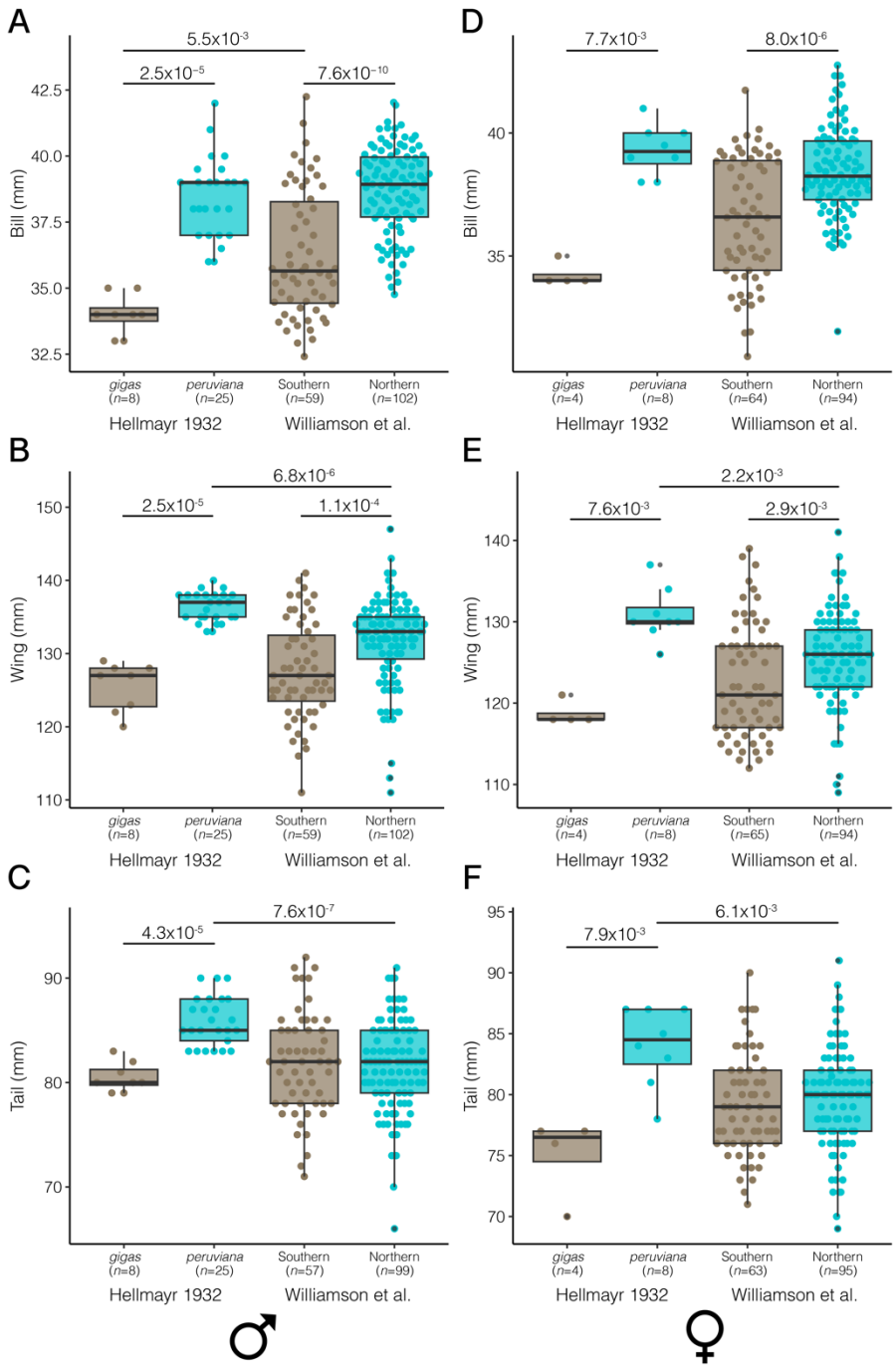

Figure 4. Comparison of morphological data (bill length, wing chord, and tail length; all in mm) between Hellmayr (1932) and Williamson et al. (present manuscript). **A–C** Males. **D–F** Females. Hellmayr compared adults of the two suspected forms, *gigas* and *peruviana*. Williamson et al. compared adults of the two species, the Southern and Northern Giant Hummingbird. Sample

1191 sizes for each comparison are reported on the x-axis and significant p-values are indicated above

1192 each comparison (from t-tests or non-parametric Wilcoxon Rank Sum tests). Box plot horizontal

1193 lines represent median values. Each point is a value from a single individual.

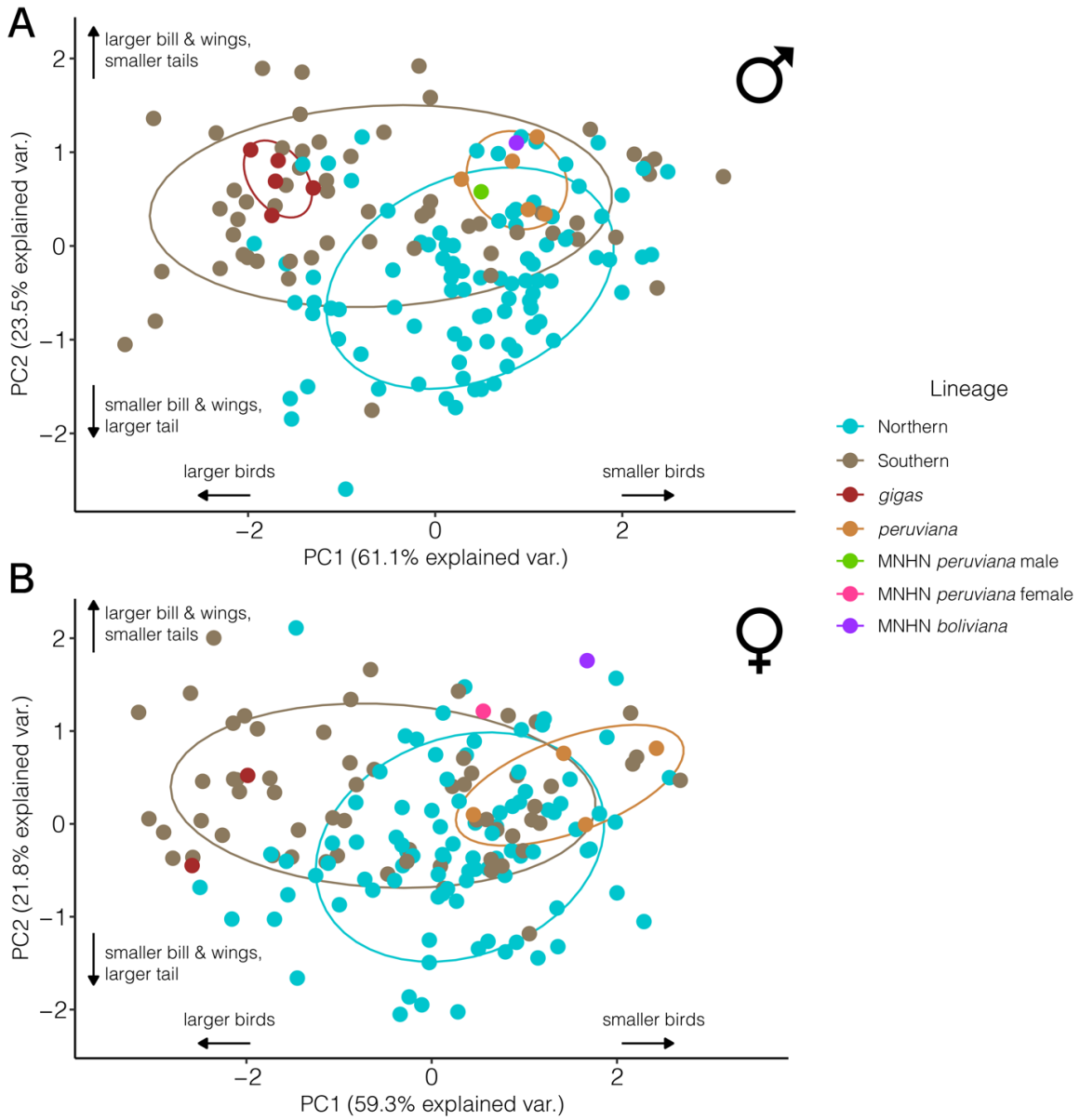

Figure 5. Principal Component Analysis (PCA) of bill, wing, and tail measurements for *gigas* and *peruviana* individuals from Hellmayr (1932) and Southern and Northern Giant Hummingbirds from Williamson et al. (present study) with MNHN *peruviana* syntypes and *boliviana* holotype. Because Hellmayr's 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.

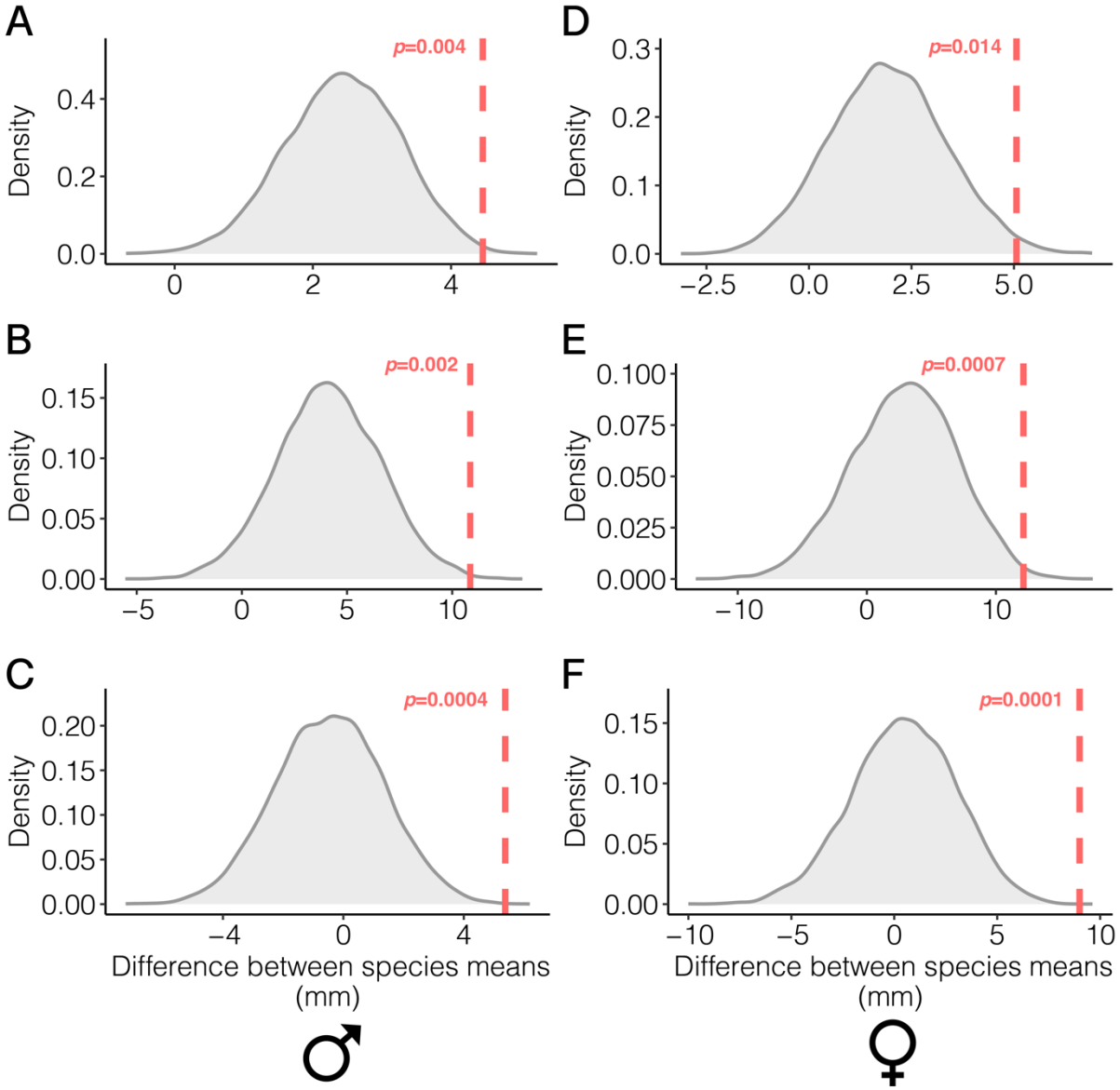

Figure 6. Expected distributions of trait mean differences between Northern and Southern Giant Hummingbirds, based on 10,000 resampled datasets generated from Williamson et al. (present study). **A–C** Expected male trait differences for each bill, wing, and tail; **D–F** Expected female trait differences 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.

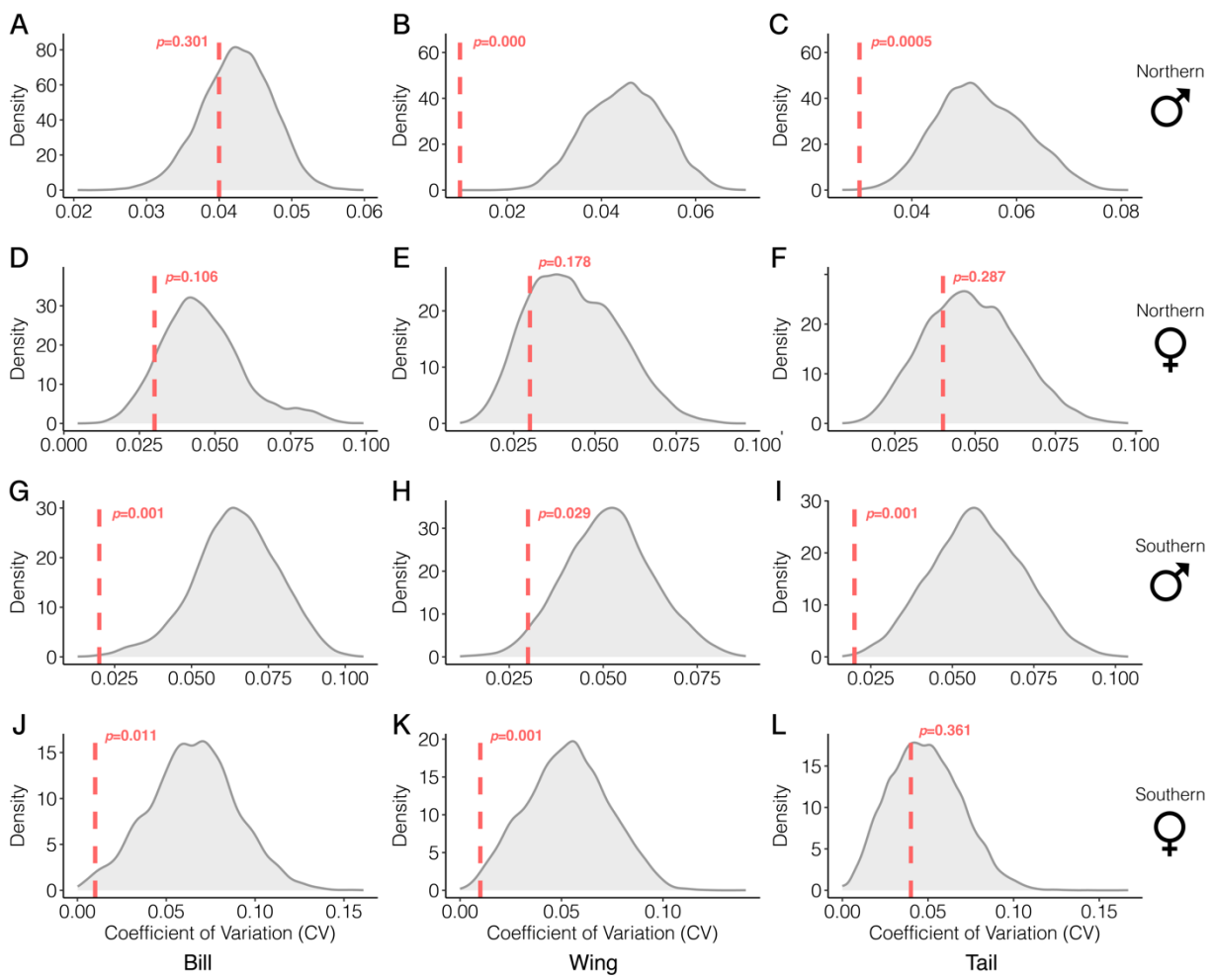

Figure 7. Expected distributions of coefficients of variation (CVs) for each Northern and Southern Giant Hummingbirds, based on 10,000 resampled datasets generated from Williamson et al. (present study). CVs were estimated separately for each species (Northern and Southern Giant Hummingbird), each sex (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.

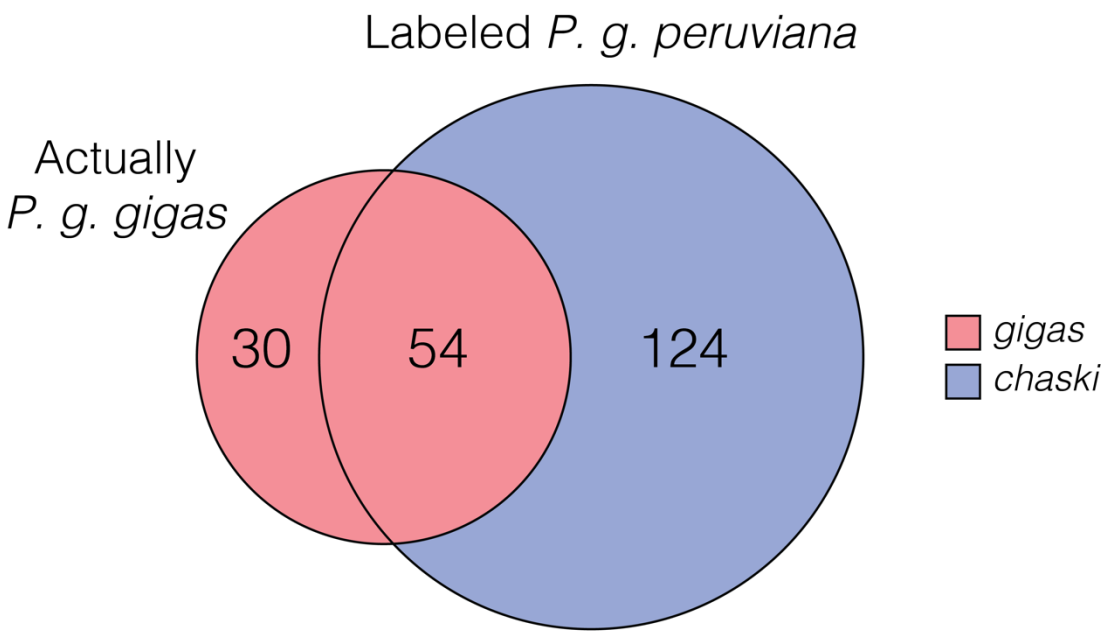

Figure 8. Visual representation of the *Patagona* specimen record as it pertains to previous versus current identifications. A total of 557 specimens were examined from 13 museum collections. Of these, 30 specimens are labeled as *P. g. gigas* and pertain to the Southern Giant Hummingbird (*Patagona 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 and 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)	–

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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

1262 **Table 3.** Morphological summary statistics for *peruviana* (Hellmayr 1932) and Northern Giant Hummingbird (Williamson et al.,
1263 present study) males and females For each measured parameter, we provide sample size (*n*), mean, standard deviation, range
1264 (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

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1266 **Table 4.** Difference between taxon-mean trait values from Hellmayr (1932) (i.e., between

1267 '*peruviana'* and *gigas*) and Williamson et al. (i.e., between the Northern Giant Hummingbird and

1268 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

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