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Taxonomic status of the Western Hemispingus *Sphenopsis ochracea* (Thraupidae) and a review of species limits in the genus *Sphenopsis* P. L. Sclater, 1861

by Matthew R. Halley

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SUMMARY.—The genus *Sphenopsis* P. L. Sclater, 1861, has recently been restored to recognise the genetic monophyly of four Neotropical tanager species, formerly placed in the genus *Hemispingus* Cabanis, 1851, which are little known and poorly represented in museum collections: Oleaginous Hemispingus *Sphenopsis frontalis* (von Tschudi, 1844), Black-eared Hemispingus *S. melanotis* (P. L. Sclater, 1855), Western Hemispingus *S. ochracea* (von Berlepsch & Taczanowski, 1884) and Piura Hemispingus *S. piurae* (Chapman, 1923). Only ten study skins of *S. ochracea* are known in collections; prior to this study, just seven were known and no collection had adults of both sexes. The paucity of specimens has caused a considerable amount of confusion about the morphology of *S. ochracea*, both in published literature and private discussions among ornithologists. To review species limits, I assembled and photographed a comprehensive sample of study skins of *Sphenopsis* species, including *S. ochracea* study skins of both sexes, under a single light source, and compared plumage characters to published colour standards. I also quantified and analysed morphometric variation. These data expose multiple errors in published literature and scientific illustrations, and support recognition of *S. ochracea* and *S. piurae* at species rank.

In June 2021, the chance discovery of three study skins of Western Hemispingus *Sphenopsis ochracea* (von Berlepsch & Taczanowski, 1884), a poorly known species of montane tanager (Thraupidae), in the Delaware Museum of Natural History (DMNH, now Delaware Museum of Nature & Science), prompted me to undertake a critical review of the genus *Sphenopsis* P. L. Sclater, 1861. At present, there is disagreement among the four major world checklists with respect to the number of species recognised in the genus (Table 1). In particular, the taxonomic status of *S. ochracea*, of which specimens are rare in collections, and *S. piurae* (Chapman, 1923) remain contentious. Here, I identify and rectify several sources of confusion, via specimen comparisons and a critical analysis of the literature.

On 22 April 2017, the South American Checklist Committee (SACC) of the American Ornithological Society (AOS) passed a measure to ‘Resurrect *Sphenopsis* for *Hemispingus melanotis* and *H. frontalis*’ (Proposal 730.10). The four major world checklists have also recognised the name *Sphenopsis* for these taxa, although some nomenclatural confusion remains. Burns *et al.* (2014) first proposed restoring the genus ‘*Sphenops* Sclater, 1862’ for this clade, then suggested ‘*Sphenopsis* Sclater, 1862’ (Burns *et al.* 2016). The first 192 pages of P. L. Sclater’s *Catalogue of a collection of American birds* (‘1862’), in which the name *Sphenops* first appeared, were published in late 1861 (see Coues 1879: 278). After the remaining pages (193–368) were published in 1862, an ‘Errata et Emendanda’ page was added to this work, which stated ‘for *Sphenops* read *Sphenopsis* in several places’. This retroactive amendment was intended to bring the earlier work in line with the ‘1861’ volume of *Proceedings of the Zoological Society of London*, published in April 1862, where the name *Sphenopsis* first

TABLE 1

Five alternative taxonomies of the genus *Sphenopsis* as presented in (from left to right) the present study; eBird/Clements checklist v.2021 (Clements *et al.* 2021); IOC world bird list v.12.1 (Gill *et al.* 2021); Howard & Moore v.4 (Dickinson & Christidis 2014); HBW/Birdlife International digital checklist v.6 (HBW & BirdLife International 2021). The South American Checklist Committee (SACC) of the American Ornithological Society (AOS) currently recognises two species (*S. melanotis*, *S. frontalis*) in line with eBird/Clements and Howard & Moore. The ‘linearised’ taxonomic sequence used in this study (see Appendix) was based on Price-Waldman (2019), wherein *S. melanotis* (*sensu lato*, as treated by eBird/Clements and Howard & Moore) was reconstructed as paraphyletic. Taxa recognised at species rank within each taxonomy are shown in boldface. Taxa for which study skins were not personally examined in the present study are denoted thus (—).

Present study	eBird/Clements	IOC	Howard & Moore	HBW/Birdlife
<i>S. melanotis melanotis</i>	<i>S. m. melanotis</i>	<i>S. m. melanotis</i>	<i>S. m. melanotis</i>	<i>S. m. melanotis</i>
<i>S. m. castaneicollis</i>	<i>S. m. castaneicollis</i>	<i>S. m. castaneicollis</i>	<i>S. m. castaneicollis</i>	<i>S. m. castaneicollis</i>
<i>S. frontalis frontalis</i>	<i>S. f. frontalis</i>	<i>S. f. frontalis</i>	<i>S. f. frontalis</i>	<i>S. f. frontalis</i>
<i>S. f. hanieli</i>	<i>S. f. hanieli</i>	<i>S. f. hanieli</i>	<i>S. f. hanieli</i>	<i>S. f. hanieli</i>
—	<i>S. f. ignobilis</i>	<i>S. f. ignobilis</i>	<i>S. f. ignobilis</i>	<i>S. f. ignobilis</i>
—	<i>S. f. flavidorsalis</i>	<i>S. f. flavidorsalis</i>	<i>S. f. flavidorsalis</i>	<i>S. f. flavidorsalis</i>
—	<i>S. f. iterata</i>	<i>S. f. iterata</i>	<i>S. f. iterata</i>	<i>S. f. iterata</i>
<i>S. piurae</i>	<i>S. m. piurae</i>	<i>S. p. piurae</i>	<i>S. m. piurae</i>	<i>S. p. piurae</i>
<i>S. ochracea</i>	<i>S. m. ochracea</i>	<i>S. ochracea</i>	<i>S. m. ochracea</i>	<i>S. ochracea</i>
—	<i>S. m. berlepschi</i>	<i>S. m. berlepschi</i>	<i>S. m. berlepschi</i>	<i>S. m. berlepschi</i>
—	<i>S. m. macrophrys</i>	<i>S. p. macrophrys</i>	<i>S. m. macrophrys</i>	<i>S. p. macrophrys</i>

appeared (see Duncan 1937: 72). According to the Code (ICZN 1999), if a ‘slip to be inserted into the work’ is circulated, containing the correction of a spelling, the corrected name ‘is to be accepted as clear evidence of an inadvertent error’ (Art 32.5.1.1) and ‘the name thus corrected retains the authorship and date of the original spelling’ (Art. 33.2.2). Therefore, *contra* Dickinson & Christidis (2014), the correct genus and authority is *Sphenopsis* P. L. Sclater, 1861, referring to the ‘Catalogue’, not the ‘Proceedings’.

The range of *S. ochracea*, which some checklists classify as a subspecies of Black-eared Hemispingus *S. melanotis* (P. L. Sclater, 1855), is restricted to montane forest on the west slope of the Andes in Ecuador and Colombia. Chapman (1926: 688) ‘[saw] no specimens from western Ecuador’ and included *S. ochracea* on the authority of von Berlepsch & Taczanowski (1884), whose two type specimens (both females) were collected by Siemiradzki in 1882/83, at Cayandede and Chaguarpata, Ecuador, respectively. The types were later transferred from von Berlepsch’s private collection to the Senckenberg Gesellschaft für Naturforschung (SMF), Frankfurt am Main (Hellmayr 1936: 427), where only one now survives: SMF 58282, a ‘[female]?’ collected by Siemiradzki at ‘Chaguarpata’ (= Chaguarpata, Chimborazo, see Paynter 1993: 35) on 5 March 1883 (G. Mayr *in litt.* 2022). This study skin (Fig. 1), which is evidently the only surviving syntype of *S. ochracea* (von Berlepsch & Taczanowski), was not designated as such in the SMF collection prior to this study.

To my knowledge, expeditions in the 20th century yielded only nine more study skins of *S. ochracea*. In chronological order of collection, they are: (1) MLZ 7451, a male collected in 1929 near Pallatanga, Ecuador, housed at the Moore Laboratory of Zoology (MLZ), Occidental College, Los Angeles, CA; (2) ANSP 149722, a male collected in 1941 in Nariño, Colombia, housed at the Academy of Natural Sciences of Drexel University (ANSP), Philadelphia, PA; a toepad of this specimen was recently sampled for phylogenomic research (Price-Waldman 2019); (3–5) DMNH 59270, 85569 and 85570, two males and a female collected in 1976 in Chiriboga, Ecuador, which were unidentified prior to the

present study; (6–7) WFVZ 48203 and 48204, two females collected in 1989 near Chiriboga, Ecuador, housed at the Western Foundation of Vertebrate Zoology (WFVZ), Camarillo, CA; and (8–9) MECN 5265 and 5267, male and female juveniles, respectively, collected in 1991 at Molleturo, Azuay, Ecuador, housed at Museo Ecuatoriano de Ciencias Naturales (MECN), Quito; genetic samples of these specimens were (ostensibly) analysed by García-Moreno *et al.* (2001). It is possible that un-databased specimens exist in some South American museums, but the taxon is absent from the collections at the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Boyacá, Colombia (G. Bravo *in litt.* 2022) and Universidad Icesi, Cali, Colombia (G. Londoño *in litt.* 2022). To my knowledge, DMNH is the only collection with adult study skins of both sexes, and these were overlooked in the collection until June 2021.

Several points of confusion have arisen from the analyses of García-Moreno *et al.* (2001), which demand explanation. Rensen (2007) quoted this paper in SACC Proposal 284: ‘Within our limited sampling, we could not detect any differences to warrant separation of the east- and west-slope subspecies *melanotis* and *ochraceus*, neither at the molecular level nor based on the plumage characters’ (García-Moreno *et al.* 2001). However, this statement was unfounded because the *S. ochracea* samples in their study (MECN 5265 and 5267) were evidently not included in their morphological or phylogenetic analyses. Both vouchers were juveniles (i.e., unsuitable for analysis of plumage colour in adults) and deposited at MECN (N. Krabbe *in litt.* 2022); they were therefore unavailable to García-Moreno *et al.* (2001), whose morphology analysis was based on ‘[vouchered adult] specimens from the National Museum of Natural History (Stockholm) and [the Zoological Museum, Natural History Museum of Denmark] ZMUC’ (both of which lack specimens of *S. ochracea*). Furthermore, although the MECN samples were mentioned in the Methods and Discussion sections, they were absent from all phylogenetic analyses presented in the Results, including the table of genetic distances (see Figs. 2–4 and Table 1 in García-Moreno *et al.* 2001). Omission of these samples, and the ‘undescribed’ sample discussed below (ZMUC 104925), may also explain why they



Figure 1. Lateral view of SMF 58282, the only surviving syntype of *Sphenopsis ochracea* (von Berlepsch & Taczanowski, 1884), collected by Siemiradzki at Chaguarpata, Chimborazo, Ecuador, on 5 March 1883. The original field label reads: ‘*Hemispingus?* / ♀ / Chaguarpata (5700’) [= 1,737 m] / 5/III 83 / Siemiradzki’. The identification on the secondary (Berlepsch) label reads: ‘*Chlorospingus* [in black ink] *ochraceus*, Berl. & Tacz. [in pencil]’, with ‘*Chloro*’ crossed out and replaced by ‘*Hemi*’ in pencil, and ‘*melanotis*’ in pencil (© Gerald Mayr)

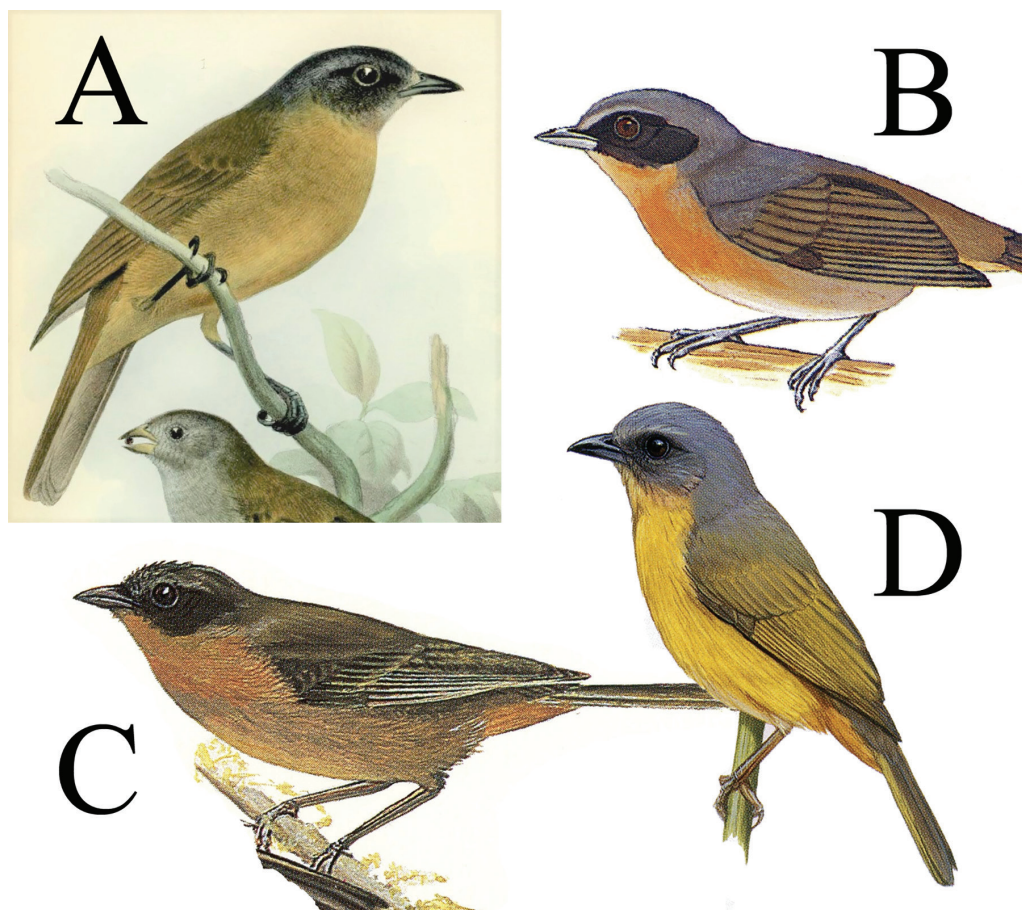


Figure 2. Four published illustrations of Western Hemispingus *Sphenopsis ochracea*: (A) lithograph by 'J. Smit', imprint by 'Hanhart', in von Berlepsch & Taczanowski (1884); (B) Ridgley & Greenfield (2001a); (C) Isler & Isler (1987); and (D) Hilty (2011).

were missing from DNA sequences deposited by García-Moreno *et al.* (2001) in GenBank (www.ncbi.nlm.nih.gov).

Another source of confusion arose from the questionable identity of ZMUC 104925 ('O2308' in Appendix 2 in García-Moreno *et al.* 2001). This sample was inadvertently mentioned twice in their Methods section, and once in Appendix 2, with three different identifications! First, it was listed as '*H. frontalis frontalis*...from Imbabura, Ecuador'; then, it was listed as 'an undescribed form from Imbabura'; finally, in Appendix 2, it was listed as '*H. melanotis?* (undescribed)' from Imbabura. Notably, no mention of the *S. f. frontalis* sample from Imbabura appeared in Appendix 2 (García-Moreno *et al.* 2001). My enquiry into the status of this specimen revealed that ZMUC 104925 was collected by N. Krabbe, who initially identified it as '*Hemispingus [frontalis] frontalis*' on the specimen label. However, N. Krabbe (*in litt.* 2022) later reidentified the specimen as '*Hemispingus melanotis ochraceus*' after misinterpreting the phylogenies in García-Moreno *et al.* (2001). With help from P. Hosner (*in litt.* 2022), I confirmed Krabbe's initial identification (*S. frontalis*) via digital photographs of ZMUC 104925, which is evidently the only existing *S. frontalis* specimen from western Ecuador (N. Krabbe *in litt.* 2022). It is an immature, based on gonad and skull data, which no doubt contributed to the confusion.



Figure 3 (left). Lateral view of (Northern) Black-eared Hemispingus *Sphenopsis melanotis melanotis* (P. L. Sclater, 1855). From left to right, (1) ANSP 154444, adult female prepared by Kjell von Sneider on 25 April 1942 at 'Toche, Tolima, Colombia'. (2) ANSP 154443, adult male, prepared by Kjell von Sneider on 28 April 1942 at 'Toche, Tolima, Colombia'. (3) ANSP 165629, adult male, collected on 30 November 1950 on the 'Rio Rumiayaco, [Nariño] Colombia' (Matthew R. Halley)

Figure 4 (right). Lateral view of (Southern) Black-eared Hemispingus *Sphenopsis melanotis castaneicollis* (P. L. Sclater, 1858). From left to right, (1) ANSP 102295, adult female collected on 30 May 1931 at 'Oconeque, [Puno] Peru'. (2) ANSP 102285, adult male collected on 30 May 1931 at 'Oconeque, [Puno] Peru'. (3) ANSP 119323, adult male collected on 15 September 1922 at 'Sandillani, Yungas', La Paz, Bolivia. (4) ANSP 119336, adult incubating female collected on 9 December 1934 at 'Sandillani, Yungas', La Paz, Bolivia (Matthew R. Halley)

Finally, confusion as to the morphology of *S. ochracea* has also proliferated in part because of the variability and inaccuracy of published illustrations (Fig. 2). Unfamiliar with this taxon in the field, I initially suspected the DMNH study skins were undescribed, when I was unable to find a matching illustration. Subsequent research in the DMNH Archives revealed that their collectors also suspected them to be undescribed (see below). At that time (1976), the only published illustration of *S. ochracea* was the original plate in von Berlepsch & Taczanowski (1884), which inaccurately portrayed the taxon (Fig. 2). Correct identification of the DMNH specimens did not become clear until I carried them on loan to ANSP and compared them to ANSP 149722, a male *S. ochracea* from Nariño, Colombia, and a more representative sample of *Sphenopsis* taxa.

A recent phylogenetic analysis of ultraconserved elements (Price-Waldman 2019) indicates that *S. ochracea* (based on DNA from a toepad of ANSP 149722) is the sister group of Piura Hemispingus *S. piurae* (Chapman, 1923); this clade is the sister group of Oleaginous Hemispingus *S. frontalis* (von Tschudi, 1844), based on a sample of *S. f. frontalis* from Amazonas, Peru (MSB 31856); and these three taxa form a clade that is sister to Black-

eared Hemispingus *S. melanotis castaneicollis* (P. L. Sclater, 1858). The sample of '*S. melanotis*' in Price-Waldman's (2019) study was collected in Cuzco, Peru, within the range of *S. m. castaneicollis*. Therefore, the phylogenetic position of *S. m. melanotis* (*sensu stricto*) remains uncertain. These four species, and some other distinctive subspecies, including *S. frontalis hanieli* (Hellmayr & Seilern, 1914), were formerly placed in the genus *Hemispingus* Cabanis, 1851, before genetic data became available. To reassess the morphological characters of *Sphenopsis* species, in light of Price-Waldman's (2019) phylogenetic hypothesis, I assembled study skins under a single light source, to take digital photographs and compare plumage characters to published colour standards. I also quantified and analysed morphometric variation. Here, before explaining my comparative analysis, I briefly recount the history of the DMNH specimens, without which this study would have been impossible.

History of the DMNH specimens

The overlooked skins of *S. ochracea* at DMNH were collected and prepared by researchers from the Yale Peabody Museum (YPM) in June and August 1976, during field work for the groundbreaking 'tapestry' research of Charles G. Sibley and Jon E. Ahlquist (Sibley & Ahlquist 1990). The expedition was financed by John E. duPont, founder of the DMNH, under an agreement wherein YPM (Sibley) would get the tissues (blood) for molecular research, and DMNH (duPont) the study skins and pickles. A total of US\$60,000 sent by duPont in support of YPM field work in South America, Africa and Asia is documented in correspondence between Sibley and Harold K. Light, Associate Director of DMNH, during April 1975–May 1977 (DMNH Archives). On 14 February 1977, just prior to receiving the last US\$10,000 check, Sibley wrote to duPont: 'I am most grateful to you for your generous help which has resulted in a DNA collection that otherwise never could have been made.' A list prepared at YPM, which includes two skins and one pickle of 'unknown tanagers', bears the following note in the margin: 'skins, skeletons, and pickles arrived as of 8/5/76 [5 August] All sent to Dupont' (DMNH Archives).

Fred C. Sibley (no relation), the YPM collections manager and expedition leader, was accompanied in the field by his teenage sons (David A. & Steven C. Sibley), a professor from Southern Connecticut University (Noble S. Proctor) and two graduate students (Keith B. Aubry and Carol A. Apruzzese). Hereafter, for simplicity, the surname 'Sibley' refers to Fred Sibley. The YPM team collected four specimens of *S. ochracea* in subtropical montane forest (2,000 m elevation) near the small village of Chiriboga, on an old and seldom-travelled road that descends the west slope of the Andes between Quito and Santo Domingo de los Colorados (Paynter 1993: 42, Ridgley & Greenfield 2001b: 41). The first specimen, collected on 12 June 1976, was a female (YPM field catalogue C-184). Sibley was uncertain of its identity and simply wrote 'Tanager' in the field catalogue (DMNH Archives). Later the same day, he caught and prepared two more specimens (C-202, C-203), which were identified as the 'same as C-184'. The second specimen (C-202) was a male with 1 mm testes, prepared as a study skin. The third (C-203) was pickled and sex was therefore not determined. To my knowledge, this is the only pickled specimen of *S. ochracea* ever collected. It was catalogued as DMNH 64739 in 1978, without any taxonomic identification in the ledger, and the DMNH pickle collection was transferred to ANSP in 2013. Finally, when the YPM team returned to the same road on 14 August 1976, they collected a fourth specimen (N-604, '*Tachyphonus* sp. nov.?'), a male with enlarged testes ('5 mm') that Aubry prepared as a study skin (DMNH Archives). After returning to the USA, Sibley shipped the field catalogues and specimens to David M. Niles, Associate Curator of birds at DMNH, with the following note:

'Ecuador — Fred Sibley *et al.* — all specimens from July 17 on are included in this shipment...Specimens prior to July 17 have already been sent to you. Missing skins were left in Ecuador. No pickles or skeletons should be missing...We have noted a *Synallaxis*¹ and *Tachyphonus* as sp. nov. just to make us feel good — we have not checked out either of these very well. Will of course be interested to know what they come out as.' (DMNH Archives)

Niles and Gene K. Hess, the DMNH Collections Manager, catalogued and databased nearly 5,000 study skins that arrived at the DMNH in the 1976 accession from YPM, of which >1,500 skins were from Ecuador. They were evidently (and understandably) puzzled by the tanagers. On a list of corrections to the YPM catalogue, Niles wrote 'C-184, 202, N-604, the mystery tanagers, may be *Hemispingus* sp.? or *Tachyphonus* sp.?; they'll be intensively checked at AMNH'. Niles did not realise that the American Museum of Natural History, New York (AMNH) collection lacks specimens of *S. ochracea*, despite its extensive holdings of South American tanagers, so a trip there would have been insufficient to resolve the problem. On 30 September 1977, Sibley wrote again to Niles: 'Did anything ever come out of that one Ecuador tanager we were hoping was a new species? Would love to go back to Ecuador before O'Neil [*sic*]² collects all the undiscovered birds of South America.' Niles responded on 30 January 1980: 'I did finally get up to AMNH for a short day, and ran all of our South American suboscine problems through their collections (the Tanagers await, still)' (DMNH Archives).

The tanager problem was still unresolved in 1986, when Niles left DMNH, and in 2007, when Hess retired. By this time, only one of the unidentified study skins had been catalogued, on 27 January 1977, under the uncertain identity '*Tachyphonus* sp.' (DMNH 59270). None was entered into the DMNH collections database, which caused the specimens to remain 'hidden' from outside researchers. In 2001, Jean L. Woods was hired as curator of birds. For various reasons, the collections manager position remained vacant until 2021, when I was hired and found the rare specimens in a 'hold-up' cabinet, where they had apparently been stored since the 1970s. When asked about the skins, Woods did not have any information about their identity or history (J. Woods pers. comm. 2021). After her departure, in December 2021, I was promoted to interim curator of birds and completed the present study.

Methods

I catalogued, databased and pest-treated the novel *S. ochracea* skins at DMNH, then hand-carried them on loan to ANSP, for direct comparison with ANSP 149722 (*S. ochracea* male) and study skins of *S. melanotis*, *S. m. castaneicollis*, *S. f. frontalis*, *S. f. hanieli* and *S. piurae*. For each specimen, I used colour standards in Smithe (1975) to score the plumage colour on eight body parts (dorsal: crown, back, tail; ventral: throat, breast, belly, vent, tail). I also scored the ventral plumage of *S. ochracea* in published illustrations to assess their accuracy. To assess morphometric variation, I recorded the following five measurements from every specimen, unless the body part was damaged: (1) wing length (WG), measured with a ruler from the carpal joint to the tip of the longest primary; (2) tarsometatarsus (tarsus) length (TR), measured with callipers from the intertarsal joint to the distal end of the final leg

¹ After visiting the American Museum of Natural History (AMNH), Niles identified the '*Synallaxis*' specimen as *Cranioleuca curtata griseipectus* Chapman, 1924, which is a junior synonym of *C. c. cisandina* (Taczanowski, 1882) (see Bond 1945).

² John P. O'Neill, former director of the Louisiana State University Museum of Natural Science, Baton Rouge, described 15 new species and one subspecies from South America during his career.

TABLE 2

Plumage colour of species in the genus *Sphenopsis*, scored using study skins ($n = 43$) in the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP) and Delaware Museum of Nature & Science, Greenville (DMNH) collections (see Appendix for lists of specimens examined). The codes ‘tail-D’ and ‘tail-V’ denote the dorsal and ventral surface of the tail, respectively. Numbers are taken from Smithe (1975): (18) Orange Yellow; (23) Raw Umber; (28) Olive-Brown; (49) Greenish Olive; (51) Citrine; (82) Blackish Neutral Gray; (83) Dark Neutral Gray; (89) Jet Black; (119A) Hair Brown; (121) Vandyke Brown; (121A) Prout’s Brown; (123A) Cinnamon; (123B) Clay Color; (123C) Yellow Ocher; (124) Buff; (129) Dark Brownish Olive; (136) Raw Sienna; (223D) Tawny Olive.

Species	Crown	Back	Tail-D	Tail-V	Throat	Breast	Belly	Vent
<i>S. melanotis melanotis</i>	83 ³	83 ⁷	28 ³	23	123A	123A	124	123A
<i>S. m. castaneicollis</i>	82	83 ⁷	28 ³	28	89 ³	136	124	136 ⁴
<i>S. frontalis frontalis</i>	49 ^{1,3,5}	49 ³	28 ³	28	18 ⁶	51 ⁵	51 ⁵	51 ⁵
<i>S. f. hanieli</i>	49 ³	49 ^{1,3}	28 ³	28	123C ⁴	123B	123B	123A
<i>S. piurae</i>	89 ³	119A	28 ³	28 ⁴	89 ³	136	136 ⁴	136 ⁴
<i>S. ochracea</i>	83 ¹	129 ²	28 ³	28	223D	123B ³	223D	123A

¹slightly browner

²slightly lighter and more olive

³slightly darker

⁴slightly lighter

⁵slightly more yellow

⁶slightly duller, less bright

⁷slightly more olive

scale; (3) tail length (TL), measured with a ruler from the insertion point of the two central rectrices to the tip of the longest rectrix; (4) bill length (BL), measured with callipers from the anterior edge of the right nare to the tip; and (5) bill width (BW), measured with callipers at the anterior edge of the nares. Finally, I chose 3–4 exemplary specimens of each species for digital reference photographs, which I took under diffuse natural light passing through a large laboratory window.

Results

The four *Sphenopsis* species, including *S. ochracea*, and two taxa currently classified as subspecies (*S. m. castaneicollis*, *S. f. hanieli*), have unique and diagnosable plumage phenotypes, with negligible individual variation within each taxon (Table 2, Figs. 3–7). The only plumage trait with no discernible differences among *Sphenopsis* taxa was the colour of the uppertail, which was slightly darker than Olive-Brown (Color 28).

Some distantly related *Sphenopsis* taxa share ventral colour characters to the exclusion of more closely related taxa. For example, *S. piurae* and *S. m. castaneicollis* have the same colour throat (Jet Black, Color 89), breast, and vent (Raw Sienna, Color 136), although they are not sister taxa (see Price-Waldman 2019). Similarly, the colour of the vent is identical in *S. ochracea*, *S. m. melanotis* and *S. f. hanieli* (Cinnamon, Color 123A), and also in females of the distantly related Flame-crested Tanager *Loriotus cristatus* (Linnaeus, 1766), which was formerly placed in *Tachyphonus* (Burns *et al.* 2014). The colour of the vent is also similar in females of Fulvous-crested Tanager *Tachyphonus surinamus* (Linnaeus, 1766). This may explain Sibley’s initial suspicion that the DMNH skins were an undescribed species of *Tachyphonus*.

Published illustrations of *S. ochracea* varied greatly in ventral coloration, from slightly darker than Spectrum Yellow (Color 55) in Hilty (2011), to slightly darker than Flesh Ocher (Color 132D) in Isler & Isler (1987). In contrast, specimens of *S. ochracea* were invariably Tawny Olive (Color 223D) on the throat and belly, and slightly darker than Clay Color (Color 123B) on the breast. Published illustrations have also typically shown some black on the cheeks, and a faint gray supercilium (see Fig. 2), but the three *S. ochracea* skins





Figure 5 (left). Lateral view of Oleaginous Hemispingus *Sphenopsis frontalis* (Chapman, 1923). From left to right, (1) ANSP 141983, adult female *S. f. frontalis* prepared by Kjell von Sneidern on 20 March 1939 at 'La Costa, Huila, Colombia'. (2) ANSP 185826, adult male *S. f. frontalis*, prepared by Tristan J. Davis on 22 July 1992 at 'Panguri; ca. 12 km NE San Francisco del Vergel', Zamora Chinchipe, Ecuador. (3) ANSP 83780, adult male *S. f. frontalis*, collected on 15 September 1922 at 'Baeza, Ecuador'. (4) ANSP 67191, adult male *S. f. hanieli*, collected on 3 March 1914 at 'Galeparo; Curro Del Avito, Venezuela' (Matthew R. Halley)

Figure 6 (right). Lateral view of Piura Hemispingus *Sphenopsis piurae* (Chapman, 1923). From left to right, (1) ANSP 116357, adult female prepared by M. A. Carriker, Jr., on 21 June 1933 at 'Palambra, D. Piura', Peru. (2) ANSP 116352, adult male, prepared by M. A. Carriker, Jr., on 22 June 1933 at 'Palambra, D. Piura', Peru. (3) ANSP 116358, adult male, prepared by M. A. Carriker, Jr., on 24 August 1933 at 'Chira, D. Cajamarca', Peru (Matthew R. Halley)

from Chiriboga, Ecuador (one female, two males) possess no trace of these characters; and they are faint in ANSP 149722 (Fig. 7) and SMF 58282 (Fig. 1). In photos, the plumage of SMF 58282 appears slightly foxed after nearly 140 years, but its warm brown plumage and greyish crown (like modern specimens of *S. ochracea*, Fig. 7) lack the greenish tinge of *S. frontalis* (Fig. 5) and ZMUC 104925, the formerly misidentified *S. frontalis* skin from Imbabura discussed above (P. Hosner *in litt.* 2022).

There were subtle differences in size among taxa, all of which exhibited a general pattern of male-biased sexual size dimorphism in the length of the wings and tail, which was not evident in other morphometric traits (Table 3). However, although these data are generally informative about size variation in the genus, sample sizes were too small for a more robust statistical analysis.

Discussion

The scarcity of specimens of *S. ochracea* in major collections, and problems stemming from the analyses of García-Moreno *et al.* (2001), have caused much confusion. Most illustrated works portray the external phenotype of *S. ochracea* inaccurately (e.g., Isler &



Figure 7. Lateral view of Western Hemispingus *Sphenopsis ochracea* (von Berlepsch & Taczanowski, 1884). From left to right, (1) DMNH 85570, adult female prepared by Fred C. Sibley on 12 June 1976 at ‘Chiriboga, km. 45, Quito-Santo Domingo (Old Rd.) 2000 m, Pichincha, Ecuador’. YPM field series = C 184. (2) DMNH 59270 (YPM N-604), adult male, prepared by Keith B. Aubry on 15 August 1976 at ‘Chiraborga [= Chiriboga], 2000 m, Old Quito-Santo Domingo Rd., Pichincha, Ecuador’. At the time it was prepared, the bird weighed 21.5 g and had enlarged testes (‘5 mm’). (3) DMNH 85569, adult male, prepared by Fred C. Sibley on 12 June 1976 at ‘Chiriboza [= Chiriboga], km. 45, Quito-Santo Domingo (Old Road) 2000 m, Pichincha, Ecuador’. YPM field series = C 202. When prepared, the bird weighed 16 g and testes were not enlarged (‘1 mm’). (4) ANSP 149722, adult male, prepared by Kjell von Sneidern on 3 April 1941 at ‘Mayasquer, Nariño, Colombia, Pac[ific] side / 7800 ft.’ [=2,377 m] (Matthew R. Halley)

TABLE 3

Morphometrics of taxa in the genus *Sphenopsis*, recorded from adult male ($n = 21$) and female ($n = 15$) study skins in the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP) and Delaware Museum of Nature & Science, Greenville (DMNH) collections. Sample sizes and means ($\pm$ SD) are given for each taxon, within each sex class (female, male), for the following variables: (WG) wing length, (TR) tarsometatarsus length, (TL) tail length, (BL) bill length, and (BW) bill width. All measurements in mm.

Sex	Species	<i>n</i>	WG	TR	TL	BL	BW
female	<i>S. melanotis melanotis</i>	5	73.2 $\pm$ 1.6	19.9 $\pm$ 0.3	62.8 $\pm$ 2.4	8.2 $\pm$ 0.3	3.9 $\pm$ 0.1
	<i>S. m. castaneicollis</i>	3	61.7 $\pm$ 1.5	21.3 $\pm$ 2.1	55.0 $\pm$ 2.8	7.6 $\pm$ 0.4	3.7 $\pm$ 0.3
	<i>S. frontalis frontalis</i>	5	69.5 $\pm$ 2.8	19.4 $\pm$ 0.8	61.0 $\pm$ 4.0	8.3 $\pm$ 0.1	3.5 $\pm$ 0.0
	<i>S. f. hanieli</i>	0	–	–	–	–	–
	<i>S. piurae</i>	1	68	21.7	61	8.8	3.2
	<i>S. ochracea</i>	1	67	23.5	56	8.4	4.1
male	<i>S. m. melanotis</i>	2	75.0 $\pm$ 2.8	19.5 $\pm$ 0.1	63.0 $\pm$ 5.7	8.4 $\pm$ 0.4	4.1 $\pm$ 0.4
	<i>S. m. castaneicollis</i>	6	69.3 $\pm$ 1.5	21.1 $\pm$ 1.4	60.0 $\pm$ 1.8	7.8 $\pm$ 0.5	3.7 $\pm$ 0.2
	<i>S. f. frontalis</i>	6	73.7 $\pm$ 3.4	19.4 $\pm$ 1.4	62.7 $\pm$ 2.4	8.5 $\pm$ 0.1	3.5 $\pm$ 0.1
	<i>S. f. hanieli</i>	1	70	19.9	–	8.5	3.5
	<i>S. piurae</i>	3	70.0 $\pm$ 0.0	21.9 $\pm$ 1.5	63.3 $\pm$ 5.8	8.7 $\pm$ 0.0	3.4 $\pm$ 0.1
	<i>S. ochracea</i>	3	72.5 $\pm$ 0.7	22.2 $\pm$ 0.1	60.5 $\pm$ 0.7	9.1 $\pm$ 0.0	4.2 $\pm$ 0.0

Isler 1987, Ridgley & Greenfield 2001a, Hilty 2011). The data presented here, including digital photographs of males and females taken under natural light (Figs. 3–7), serve to clarify the distinctiveness of the external morphology of *S. ochracea* and its closest relatives. Hopefully, this will be sufficient to prevent future researchers from erroneously concluding that overlooked specimens of *S. ochracea* in collections are undescribed. For clarity of

reference, the synonyms and nomenclatural combinations of *S. melanotis*, *S. frontalis*, *S. piuræ* and *S. ochracea*, with lists of specimens examined and brief commentaries under each taxon, are provided in the Appendix.

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Appendix

SACC Proposal 284 (Remsen 2007), which sought to 'Recognize *Hemispingus piurae* as a species' by splitting it from *H. melanotis*, failed to garner enough votes to pass (two yes, seven no). At the time, most committee members were unconvinced by 'weak' genetic data (i.e., too few base pairs) published by García-Moreno *et al.* (2001) and García-Moreno & Fjeldså (2003), which suggested that *S. piurae* was sister to *S. melanotis* + *S. frontalis*. Recently, a different and fully supported topology—((*ochracea*, *piurae*), *frontalis*), *melanotis*)—was reconstructed with UCE data, bolstering the case for treating *S. piurae* and *S. ochracea* at species rank (Price-Waldman 2019).

Remsen (2007) contended that *S. piurae* and *S. m. castaneicollis* were 'much more similar to each other than either is to nominate *melanotis* (no superciliary, pale throat) of e. Ecuador', but this depends on whether one prioritises some plumage characters (e.g., throat colour, supercilium) over others (e.g., back and/or belly): *S. m. melanotis* and *S. m. castaneicollis* are the same colour on the back (slightly more olive than Dark Neutral Gray, Color 83) and belly (Buff, Color 124), to the exclusion of *S. piurae* and other *Sphenopsis* taxa. Furthermore, genomic data suggest that plumage characters shared by *S. piurae* and *S. m. castaneicollis* are homoplastic, which bolsters the case for species rank (Price-Waldman 2019). Nevertheless, until the phylogenetic relationship of *S. melanotis* (*sensu stricto*) is resolved, I recommend following Hilty (2011) and Gill *et al.* (2021) in recognising *S. piurae* and *S. melanotis* at species rank, and retaining *S. m. castaneicollis* as a subspecies of *S. melanotis*.

Therefore, in the following taxonomy, I recognise four species arranged according to a 'linearised' phylogeny following Price-Waldman (2019). Synonyms, taxonomic combinations and principal citations of *S. melanotis*, *S. frontalis*, *S. piurae* and *S. ochracea* are followed by lists of specimens examined and general comments. Type localities and whereabouts of type specimens are provided for each taxon.

Sphenopsis melanotis (P. L. Sclater) Black-eared Hemispingus (Figs. 3–4)

Chlorospingus melanotis P. L. Sclater, 1855.

Syntype: NHMUK 1844.12.29.19, in Natural History Museum, Tring: 'Bogotá', Colombia (see Warren & Harrison 1971: 343).

Chlorospingus castaneicollis P. L. Sclater, 1858, Sclater 1861: 90, Taczanowski 1884: 520.

Holotype: NHMUK 1885.6.12.883: 'Interior of Peru...bordering on Bolivia' (see Warren & Harrison 1971: 96).

Chlorospingus berlepschi Taczanowski, 1880, Taczanowski 1884: 521.

Holotype: Lost, formerly in Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw (MIZ): 'Ropaybamba', Junín, Peru (see Mlíkovský 2009: 148).

Hemispingus castaneicollis von Berlepsch 1912: 1094 (in part).

Hemispingus melanotis von Berlepsch 1912: 1095, Isler & Isler 1987: 78.

Hemispingus berlepschi von Berlepsch 1912: 1095.

Hemispingus melanotis stresemanni Sztolcman & Domaniewski, 1927: 190.

Holotype: MIZ 34227: 'Baños sur Rio Pastaza' (= Baños), Ambato, Ecuador (see Mlíkovský 2009: 154).

Hemispingus melanotis melanotis Hellmayr 1936: 426, Isler & Isler 1987: 78, Hilty 2011: 167.

Hemispingus melanotis berlepschi Hellmayr 1936: 428, Zimmer 1947: 17, Isler & Isler 1987: 78, Hilty 2011: 167.

Hemispingus melanotis castaneicollis Hellmayr 1936: 428, Zimmer 1947: 17, Hilty 2011: 167.

SPECIMENS EXAMINED: *S. m. melanotis* (two males, five females, one unsexed): Colombia: Tolima: Toche (male: ANSP 154443; female: ANSP 154445, 154447–449; unsexed: ANSP 154444); Nariño: río Rumiayaco (male: ANSP 165629); 'N. Grenada' (female: ANSP 7731). *S. m. castaneicollis* (six males, five females, one unsexed): Peru: Puno: Sto. Domingo mine (male: ANSP 102288, 102290, 102294; female: ANSP 102289, 102292); Oconeque (male: ANSP 102285); Bolivia: Cochabamba: San Jacinto (unsexed: ANSP 133555); La Paz: Calabatea (male: ANSP 119327); Sandillani (male: ANSP 119323; female: ANSP 119324, 119325, 119328).

COMMENTS: The phylogenetic placement of the nominate subspecies *S. m. melanotis* within the genus *Sphenopsis*, and its relationship to *S. m. castaneicollis*, remain unresolved because the '*S. melanotis*' sample analysed by Price-Waldman (2019) was collected in Cuzco, Peru, within the range of *S. m. castaneicollis*, and no sample of *S. m. melanotis* from the eastern Andes of Colombia or Ecuador was included. Notwithstanding, the data in Price-Waldman (2019) at least confirm the distant relationship of *S. m. castaneicollis* and *S. piurae*, the phenotypic similarity of which has been emphasised in debates over species rank (see Remsen 2007). Here, following tradition, I treat *S. m. castaneicollis* as a subspecies of *S. melanotis* and, following Hilty (2011) and Gill *et al.* (2021), elevate *S. ochracea* and *S. piurae* to species rank, removing them from the synonymy of *S. melanotis*. Nevertheless, further study may yet indicate that *S. m. castaneicollis* also deserves species rank, as suggested by homoplastic patterns of plumage colour revealed by phylogenomic analysis (Price-Waldman 2019).

Sphenopsis frontalis (von Tschudi)
Oleaginous Hemispingus
(Fig. 5)

Hylophilus frontalis von Tschudi, 1844.

Lectotype: MHNN 92.8817, in Muséum d'Histoire Naturelle de Neuchâtel, Switzerland (*vide* Hellmayr 1936: 423); eastern slope of Andes, Junín, Peru (Desfayes 1994: 90).

Sphenops [sic] ***ignobilis*** Sclater 1861: 160 (see Coues 1879: 278 for publication date).³

Sphenopsis ignobilis P. L. Sclater, 1862a: 379 (see Duncan 1937: 72 for publication date).

Holotype: NHMUK 1885.6.12.876: 'in Brasilia' = Mérida, Venezuela (see Paynter & Storer 1970: 265).⁴

Chlorospingus oleagineus P. L. Sclater, 1862b: 110, Taczanowski 1884: 516.

Holotype: NHMUK 1885.6.12.877: 'In Nov. Granada int.' = Bogotá, Colombia (see Warren & Harrison 1971: 402).

Chlorospingus ignobilis Sclater & Salvin 1871: 784 (see Dickinson 2005 for publication date), Sclater & Salvin 1879: 504.

Chlorospingus frontalis Taczanowski 1884: 517, von Berlepsch & Hellmayr 1905: 8.

Chlorospingus frontalis ignobilis von Berlepsch & Hellmayr 1905: 9.

Hemispingus frontalis von Berlepsch 1912: 1094, Isler & Isler 1987: 77, Hilty 2011: 167.

Hemispingus frontalis oleagineus von Berlepsch 1912: 1094.

Hemispingus frontalis ignobilis von Berlepsch 1912: 1094, Chapman 1925: 13, Hellmayr 1936: 424, Hilty 2011: 167.

Hemispingus hanieli Hellmayr & von Seilern, 1914: 87.

Holotype: ZSM 13925, in Zoologische Staatssammlung, Munich (*vide* Hellmayr 1936): Galipán, Cerro del Ávila, Distrito Federal, Venezuela (see Hellmayr & von Seilern 1914: 87, Paynter & Storer 1970: 266).

Hemispingus frontalis frontalis Chapman 1921: 122, Chapman 1925: 13, Zimmer 1947: 17, Isler & Isler 1987: 77, Hellmayr 1936: 423.

Hemispingus frontalis iteratus Chapman, 1925: 13, Hellmayr 1936: 425, Isler & Isler 1987: 77.

Holotype: AMNH 188022, in American Museum of Natural History, New York: Carapas, Mt. Turumiquire, Sucre, Venezuela (see LeCroy 2012: 68).

Hemispingus frontalis hanieli Chapman 1925: 13, Hellmayr 1936: 425, Isler & Isler 1987: 77, Hilty 2011: 167.

Hemispingus [sic] ***frontalis flavidorsalis*** Phelps & Phelps, Jr., 1953: 140.

Holotype: Colección Ornitológica Phelps, Caracas (COP 55625, 'on deposit' at AMNH according to Phelps & Phelps 1953): Cerro Jurustaca, upper río Negro, Sierra de Perijá, Zulía, Venezuela (see Paynter & Storer 1970: 265).

Hemispingus frontalis flavidorsalis Isler & Isler 1987: 77, Hilty 2011: 167.

SPECIMENS EXAMINED: *S. f. frontalis* (six males, five females, one unsexed): Colombia: Caldas: Salento (female: ANSP 154474); Cauca: El Tambo (male: ANSP 141981); San Antonio (female: ANSP 141982); Huila: La Candela (male: ANSP 155593, 155594; unsexed: 155591); La Costa (female: ANSP 141983); Tolima: Toche (female: ANSP 154472). Ecuador: Napo: Baeza (male: ANSP 83779, 83780). Peru: Junín (female: ANSP 91539). *S. f. hanieli* (one male): Venezuela: 'Galeparo, Curro del Avito' (ANSP 67191).

COMMENTS: In addition to rectifying the identity of ZMUC 104925 (see introduction), which was a source of confusion for García-Moreno *et al.* (2001), my study confirms that *S. f. frontalis* and *S. f. hanieli* are divergent and diagnosable, relative to other *Sphenopsis* species, and from each other. The adult plumage of *S. f. hanieli* differs from *S. f. frontalis* in colour, especially on the ventral surface, and has 'a sharply defined superciliary stripe' as emphasised in the original description ('Ein scharf abgesetzter Superciliarstreif', Hellmayr & von Seilern 1914: 87). Given the surprising degree of homoplasy in plumage colour uncovered by phylogenomic analysis (Price-Waldman 2019), re-evaluating the taxonomic status of *S. f. hanieli*, and other *S. frontalis* subspecies not included in this study, should be prioritised by future researchers. Here, following tradition, I have treated *S. f. hanieli* as a subspecies of *S. f. frontalis*, although additional data may support classifying it at species rank.

Sphenopsis piurae (Chapman)
Piura Hemispingus
(Fig. 6)

Hemispingus castaneicollis von Berlepsch 1912: 1094 (in part).

Hemispingus piurae Chapman, 1923, Hilty 2011: 167.

Holotype: AMNH 174541, Palambla, Piura, Peru (see LeCroy 2012: 69).

Hemispingus castaneicollis chapmani Sztolcman & Domaniewski, 1927.

³ Spelling corrected in 'Errata et Emendanda' slip (see introduction).

⁴ The registration number of this specimen was mis-transcribed in Warren & Harrison (1971) and has now been corrected in the NHMUK digital catalogue (A. L. Bond *in litt.* 2022).

Holotype: lost, formerly in the Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw (MIZ): Tambillo, Cajamarca, Peru (see Mlíkovský 2009: 154).

Hemispingus melanotis piurae Hellmayr 1936: 427, Zimmer 1947: 17, Isler & Isler 1987: 78.

Hemispingus melanotis macrophrys Koepcke, 1961: 22, Isler & Isler 1987: 78.

Holotype: UNMSM 0630, in Museo de Historia Natural 'Javier Prado', Lima: Sunchubamba, Otuzco, La Libertad Department, Peru (see Plenge 1979: 7).

SPECIMENS EXAMINED: (four males, one female): Peru: Piura: Palambla (male: ANSP 116350, 116353, 116354, 116357; female: ANSP 116352).

COMMENTS: As explained above, I consider the morphological and molecular data reviewed here to be sufficient to alleviate concerns of data deficiency that arose during debate of SACC Proposal 284 (Remsen 2007), bolstering the case for recognizing *S. piurae* at species rank.

Sphenopsis ochracea (von Berlepsch & Taczanowski)
Western Hemispingus
(Fig. 7)

Chlorospingus ochraceus von Berlepsch and Taczanowski, 1884.

Syntype: SMF 58282, in Senckenberg Gesellschaft für Naturforschung (SMF), Frankfurt am Main (Hellmayr 1936: 427): Chaguarpata, Chimborazo, Ecuador (see Paynter 1993: 35).⁵ The original field label reads: '*Hemispingus?* / ♀? / Chaguarpata (5,700') [= 1,737 m] / 5/III 83 / Siemiradzki'.

Hemispingus ochraceus von Berlepsch 1912: 1095, Hilty 2011: 168.

Hemispingus melanotis ochraceus Hellmayr 1936: 427, Isler & Isler 1987: 78.

SPECIMENS EXAMINED: (three males, one female): Colombia: Nariño: Mayasquer (male: ANSP 149722); Ecuador: Pichincha: Chiriboga (male: DMNH 59270, 85569; female: DMNH 85570).

COMMENTS: Evidence presented here confirms that *S. ochracea* and *S. melanotis* are diagnosable by plumage colour (Table 2), *contra* García-Moreno *et al.* (2001), whose conclusions were unfounded (see above). Furthermore, Price-Waldman (2019) has demonstrated the genetic diagnosability of *S. ochracea* and its surprising sister relationship to *S. piurae*, which further bolsters the case for species rank for these taxa.

⁵ The type status of this specimen was not recognised in the SMF collection prior to this study (G. Mayr *in litt.* 2022).