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Systematics of the Neopelminae (Aves: Passeriformes: Pipridae) with description of a new genus

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The genus *Neopelma* Sclater, 1860 contains five species of manakins found in humid tropical forests east of the Andes in South America. All five are cryptic in plumage and morphology. *Neopelma chrysolophum* Pinto, 1944 of SE Brazilian montane Atlantic Forests is so similar in appearance to the elevationally parapatric (Whitney *et al.* 1995) *N. aurifrons* Wied-Neuwied, 1831 occurring in lowland Atlantic Forest further north, that it was originally suggested to be a subspecies of the latter (Pinto 1944).

In an examination of vocal data and habitat preference as well as morphology, Whitney *et al.* (1995) proposed that the genus *Neopelma* as currently defined is not monophyletic and hypothesized that *N. aurifrons* would be most closely related to the two species in *Tyranneutes* Sclater & Salvin, 1881. Capurucho *et al.* (2018) investigated the relationships in *Neopelma* and *Tyranneutes* and found that *Neopelma* was indeed paraphyletic. Their phylogenetic analysis indicated that *Tyranneutes* is nested within *Neopelma*, and that *N. chrysolophum* is sister to a clade containing *Tyranneutes* and the remainder of *Neopelma*. However, Capurucho *et al.* (2018) did not include *N. aurifrons* in their study and were therefore unable to conclusively settle on a proper taxonomic arrangement of the group. Capurucho *et al.* (2018) hypothesized that *N. aurifrons* would be sister to *N. chrysolophum*, based on biogeographical patterns and elevational replacement of *N. aurifrons* by *N. chrysolophum*.

Harvey et al. (2020) included all species-level taxa of both Neopelma and Tyranneutes. Their topology was consistent with that of Capurucho et al. (2018), with Neopelma paraphyletic with respect to Tyranneutes. However, they found that Neopelma aurifrons is not sister to N. chrysolophum but instead represents the earliest divergence within the remaining Neopelma after the split with Tyranneutes.

The paraphyly of *Neopelma* combined with the availability of information on all members of the genus provides an opportunity to revise taxonomy to better reflect evolutionary history. *Tyranneutes* is characterized by diminutive size, proportionally short tails, and differently structured vocalizations relative to *Neopelma sensu lato* (see below). They also prefer taller, more mature and more humid forest in general than *Neopelma* (Whitney *et al.* 1995). The two species of *Tyranneutes* are a morphologically, vocally, and ecologically coherent group, so we prefer to maintain them in a genus separate from other members of the complex. Resolving paraphyly therefore requires placement of *Neopelma* in two genera. Because *aurifrons* is the type species of *Neopelma*, a new genus name is required for *N. chrysolophum*:

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Protopelma gen. nov.

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Type species. Neopelma aurifrons chrysolophum Pinto, 1944.

Included species. Protopelma chrysolophum (Pinto, 1944) comb. nov., Serra do Mar Tyrant-Manakin.

Diagnosis, morphology. Small bird of the family Pipridae (Table 2); 11.6–23.0 g and 12.2–14.5 cm long; tail 51–61 mm; wing chord 62–70 mm; tarsus 15.7–17.8 mm; bill length 10.11–12.03 mm (Kirwan & Green 2011; Tobias *et al.* 2022); bill width at nares 3.6–4.3 mm; bill depth at nares 3.0–3.8 mm (Whitney *et al.* 1995; Tobias *et al.* 2022). Sexually monomorphic in plumage.

Differs diagnostically from *Neopelma sensu stricto* in culmen length (10.11–12.03 mm versus 12.48–16.5 mm). Although other bill measures are diagnostic relative to most species of *Neopelma sensu stricto*, there is some overlap with *N. aurifrons* in culmen width, and the smallest individuals of *N. sulphureiventer* Hellmayr, 1903 have similar culmen depth to *Protopelma*. *Protopelma* differs most conspicuously from parapatric *N. aurifrons* in its well-developed yellow coronal patch, which is essentially lacking in *N. aurifrons* (Whitney *et al.* 1995). The remaining three species of *Neopelma* overlap with *Protopelma* in overall size and general coloration, having a hint of yellow on the venter, greenish dorsal and wing coloration and grayish heads with varying but generally similar degrees of yellow or orange in the crown (Kirwan & Green 2011).

TABLE 1. Ingroup taxa used in this study with frozen tissue collection voucher number. Tissue collections: LSUMZ—Louisiana State University Museum of Natural Science, Baton Rouge; FMNH—Field Museum of Natural History, Chicago; AMNH—American Museum of Natural History, New York City; DZUFMG—*Coleção* Ornitológica do Departamento de Zoologia da Universidade Federal de Minas Gerais, Belo Horizonte.

Species	Tissue	Locality
Protopelma chrysolophum	FMNH 395453	Brazil: São Paulo, Boraceia
Tyranneutes stolzmanni	LSUMZ B-13803	Bolivia: Santa Cruz, Sa Huanchaca
Tyranneutes virescens	LSUMZ B-25483	Brazil: Pará, Rio Curuá
Neopelma aurifrons	DZUFMG 4027	Brazil: Minas Gerais, Leme do Prado
Neopelma pallescens	LSUMZ B-14646	Bolivia: Santa Cruz, Sa Huanchaca
Neopelma sulphureiventer	LSUMZ B-15218	Bolivia: Santa Cruz, Prov. Velasco
Neopelma chrysocephalum	AMNH DOT-13890	Venezuela: Amazonas, Río Negro

Protopelma and *Tyranneutes* are diagnosably distinct by several measures, including overall size (12.2–14.5 cm versus 7.0–9.0 cm), wing length (62–70 mm versus 45–52 mm), tail length (51–61 mm versus 17.0–28.0 mm), and tarsal length (15.7–17.8 mm versus 9.90–13.82 mm). Other features are useful but exhibit some overlap, such as body mass (11.6–23.0 g in *Protopelma* versus 6.0–13.0 g in *Tyranneutes*) and culmen length (10.11–12.03 mm in *Protopelma* versus 8.66–12.0 mm in *Tyranneutes*), whereas culmen depth and width overlap almost completely (Table 2; Hellmayr 1929; Kirwan & Green 2011; Tobias *et al.* 2022; Whitney *et al.* 1995).

Differs diagnostically from genera in Piprinae (Kirwan & Green 2011; Table 3) according to the following measures: in overall size (12.2–14.5 cm) from *Lepidothrix* Bonaparte, 1854 (7.5–11.2 cm); *Machaeropterus* Bonaparte, 1854 (8.0–12.4 cm); *Pseudopipra* Kirwan *et al.*, 2016 (8.5–11.8 cm); and *Corapipo* Bonaparte, 1854 (8.5–10.0 cm); in wing chord (62.0–70.0 mm) from *Manacus* Brisson, 1760 (46.0–61.5 mm); *Heterocercus* P. L. Sclater, 1862 (75.0–88.0 mm); *Corapipo* (49.5–61.5 mm); and *Antilophia* (72.0–82.5 mm); in tail length (51.0–61.0 mm) from *Lepidothrix* (23.0–34.0 mm); *Manacus* (25.5–41.0 mm); *Machaeropterus* (15.0–27.0 mm); *Pseudopipra* (23.5–34.0 mm); *Ilicura* Reichenbach, 1850 (29.0–42.0 mm); *Masius* Bonaparte, 1850 (39.0–46.8 mm); and *Corapipo* (26.0–32.0 mm). In tarsus length (15.7–17.8 mm) overlaps with all piprid genera, minus *Tyranneutes* (9.90–13.82 mm). For all of the aforementioned characters, *Protopelma* overlaps with *Pipra* Linnaeus, 1764, *Xenopipo* Cabanis, 1847, and *Chloropipo* Cabanis & F. Heine, Sr., 1860, and to distinguish the latter genera from *Protopelma*, vocalizations and coloration should be used.

Diagnosis, voice. Differs from all other members of Neopelminae in at least two conspicuous characters. Firstly, full songs comprise three distinct, multi-syllabic elements, not single elements (Fig. 1A versus Fig. 1B–G). Secondly, all of the notes of the song and calls are sharp and clear, audible at much greater distance than those of any of the other taxa. Aside from some alarm calls, other Neopelminae share a "harsh" or "burry" or "scratchy" quality of notes of songs and calls, visible as harmonic blotching, especially conspicuous in e.g. Fig. 1G. As far as we know, *Protopelma* is the only member of Neopelminae that has a call type that is a single sharp note without harmonics (Fig. 1O versus Fig. 1H–N).

TABLE 2. Morphometric measurements of all species in Neopelminae, taken from Kirwan & Green (2011), the AVONET database (Tobias *et al.* 2022), Whitney *et al.* (1995) and Hellmayr (1929).

Kirwan & Green 2011	wing	n	tail	n	tarsus	n	culmen length	n				
pallescens	67–80	25	55–66	24	16–19	6	12.68-16.08	25				
sulphureiventer	66–79	39	49–62	3	14–16.49	2	13.42-15	2				
aurifrons	65–77	24	47–58	24	14.8–17.2	13	12.58-14.39	13				
chrysocephalum	64–74	23	45–56	24	13–17	14	12.48-15.00	24				
chrysolophum	63-68.5	22	54-61	22	16.4–17.8	9	10.11-12.03	13				
stolzmanni	46–52	14	18-25	13	10.0-12.0	8	9.42-12	10				
virescens	45-52	15	17.5–22.5	10	9.01-13.82	13	8.66-11.4	15				
Tobias et al. 2022	wing	n	tail	n	tarsus	n	culmen length	n	culmen width	n	culmen depth	n
pallescens	69.9–81.0	14	49.7–65.4	16	14.5–18.0	15	12.7-14.8	16	4.5-4.8	5	3.8-5.5	15
sulphureiventer	65.5-75.0	8	51-61	8	14.3–17.6	8	13.3–16.5	8	4.4-4.8	4	3.7-4.1	3
aurifrons	71	1	50	1	15.7	1	12.7	1	4.2	1	4.3	1
chrysocephalum	61-72	4	43-51	4	14.0-16.3	4	14.0-15.8	4	4.8-5.1	4	3.8-4.3	4
chrysolophum	62-70	4	51-61	4	15.7-17.2	4	10.5-12.0	4	4.1-4.2	4	3.0-3.7	3
stolzmanni	46-49	6	20–28	6	9.9-13.1	6	9.5-11.4	6	3.1-4.3	6	2.8-3.6	6
virescens	49–52	5	17–23	5	11.1-13.0	5	10.5-12.0	5	3.6-4.4	5	3.0-3.9	5
Whitney et al. 1995	wing	n	tail	n	tarsus	n	culmen length	n	culmen width	n	culmen depth	n
aurifrons	66.8–71.3	11	48.3–53.4	11	14.8–16.0	8	NA		3.7-4.7	17	3.7-4.3	13
chrysolophum	62.8-66.1	8	53.7-60.6	8	16.8-17.8	8	NA		3.6-4.3	16	3.3-3.8	13
stolzmanni	47.7–52.0	12	20.1-22.7	12	NA		NA		3.3-3.9	12	3.0-3.6	11
virescens	47.1	1	22.6	1	NA		NA		3.5	1	2.8	1
Hellmayr 1929												
virescens	47–51	14	19–23	14	NA		NA		NA		NA	

TABLE 3. Select morphometric measurements of *Protopelma*, compared to genera in Piprinae, taken from Kirwan & Green (2011). A few measurements were omitted, because these represented different measurement methods (Kirwan & Green 2011) and deviated from the measures represented here.

Genus	min size	max size	min wing	max wing	min tail	max tail	min	max	min	max	
						max tan	culmen	culmen	tarsus	tarsus	
Protopelma	12.2	14.5	62	70	51	61	10.11	12.03	15.7	17.8	
Pipra	7.5	12.7	51	71	17	98	9.85	14.54	12.64	18.9	
Lepidothrix	7.5	11.2	47	64	23	34	8.66	12.97	12.6	17.22	
Manacus	9.3	14.4	46	61.5	25.5	41	10.66	14.8	16.85	26.3	
Heterocercus	13.8	16.3	75	88	43	61	12.5	16.56	12.94	15.95	
Machaeropterus	8	10.4	48	66	15	27	8.01	12	12.68	16.18	
Dixiphia	8.5	11.8	57	69	23.5	34	9.3	12.91	11.25	16.3	
Xenopipo	12	13.9	64.5	74	40	52.5	11.94	14.02	12.69	16.64	
Chloropipo	11	14	54	83	39	55	9.2	15.01	12.7	18	
Ilicura	11	14	58	66	29	42	8.14	9.95	17.28	19.25	
Masius	10	12.5	54	67	39	46.8	8.3	11.6	16.47	18.7	
Corapipo	8.5	10	49.5	61.5	26	32	8.14	11.1	13.45	18.2	
Chiroxiphia	10.7	17.3	62.5	80.5	27	56	9.48	14.5	15.91	21.71	
Antilophia	13.9	17.5	72	82.5	54	70	10.86	13.6	17	19.6	

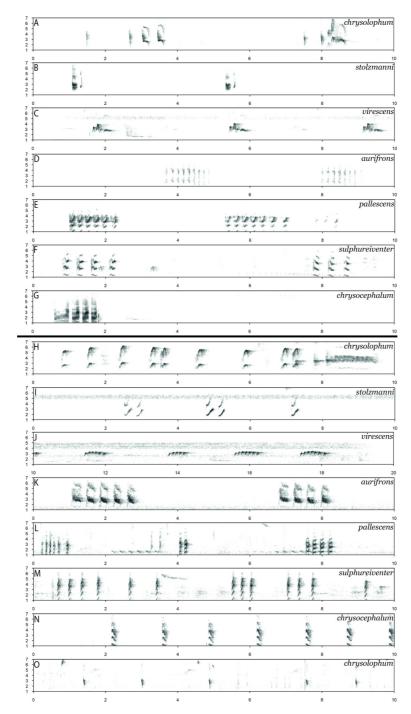


FIGURE 1. Representative songs of all species in Neopelminae: A. *P. chrysolophum* XC82303, São Paulo, Brazil, Jeremy Minns, 9-10-2003, showing harmonics particularly in second song bout; B. *T. stolzmanni* XC69825, Andrew Spencer, Orellana, Ecuador, 7-1-2011; C. *T. virescens* XC44177, Alexandre Renaudier, French Guiana, 8-2-2010, both with short repetitive songs; D. *N. aurifrons* XC330630, Roney Souza, Minas Gerais, Brazil, 9-8-2016; E. *N. pallescens* XC708083, Jayrson Araujo de Oliveira, Goiás, Brazil, 11-3-2022; F. *N. sulphureiventer* XC514867, Jacob Wijpkema, Santa Cruz, Bolivia, 1-1-2020; and G. *N. chrysocephalum* XC41926, Andrew Spencer, Loreto, Peru, 29-12-2009, and characterized by quickly, repeated, harsh notes. Representative calls of all Neopelminae: H. typical call of *P. chrysolophum* including harmonics, XC494958, Marcelo J Feliti, São Paulo, Brazil, 10-8-2019; I. *T. stolzmanni* call, XC81860, Andrew Spencer, Vaupés, Colombia, 13-6-2011; J. *T. virescens* call XC395133, Phil Stouffer, Amazonas, Brazil, unknown date; K. *N. aurifrons* call, XC36735, Ciro Albano, Espírito Santo, Brazil, 30-6-2009; L. *N. pallescens* call, XC38082, Nick Athanas, Minas Gerais, Brazil, 20-8-2009; M. *N. sulphureiventer* call, XC673872, Jacob Wijpkema, Beni, Bolivia, 11-8-2021; N. *N. chrysocephalum* call, XC66427, Alexandre Renaudier, Bolívar, Venezuela, 5-12-2010; O. call type of *P. chrysolophum* lacking harmonics, XC291062, Jeremy Minns, Rio de Janeiro, Brazil, 26-6-1998.

Etymology. In light of the old stem age of the branch leading to *Protopelma* relative to other extant related species, we name the genus from ancient Greek *prôtos* for 'first', and (retaining the stem from the name *Neopelma*) Ancient Greek *pélma* for 'the under surface of the foot'.

Molecular analyses. Here, we present a subset of taxa from a densely sampled molecular phylogeny of the suboscine passerines (Harvey *et al.* 2020) to show that *Neopelma* as currently defined is paraphyletic. Taxon sampling for this subset (Table 1) includes the following species in Neopelminae: *Protopelma chrysolophum* (type species); *Tyranneutes stolzmanni* Hellmayr, 1906; *T. virescens* von Pelzeln, 1868 (type species); *Neopelma aurifrons* (type species); *N. pallescens* Lafresnaye, 1853; *N. sulphureiventer*; *N. chrysocephalum* von Pelzeln, 1868.

We briefly summarize molecular analyses here. For details, see Harvey *et al.* (2020). Whole genomic DNA were extracted from frozen tissues using a standard protocol and kit (Qiagen, Valencia, CA). DNA extracts were quantified using a Qubit fluorometer (ThermoFisher, Waltham, MA) and sent to Rapid Genomics (Gainesville, FL) for library preparation, sequence capture, and Illumina sequencing following the general protocol of Faircloth *et al.* (2012). Loci targeted were a set of 2,321 ultraconserved elements (UCEs) and 96 exons. Reads were assembled into multiple sequence alignments using a pipeline adapted from the Phyluce assembly pipeline (Faircloth 2016). Species trees were estimated from concatenated datasets using ExaML (Kozlov *et al.* 2015), a method for maximum likelihood inference of phylogenies on supercomputers using MPI. Branch-length evaluation ("-f E") was conducted under GAMMA (equivalent to GTRGAMMA in RAxML) and a penalized likelihood approach in TreePL (Smith & O'Meara 2012) with prior fossil information (see Harvey *et al.* 2020 for details) to time calibrate the tree. A bootstrapping procedure was completed using RAxML and 100 final bootstrap trees were summarized on primary tree for evaluation of support. This method produces a robust phylogeny and we did not adjust parameters to subset the phylogeny of Neopelminae.

The resulting phylogeny indicates that *Protopelma* is the sole extant representative of a relatively old lineage that is sister to a clade containing both *Tyranneutes* (sister to each other) and the remaining members of *Neopelma* (Fig. 2). All relationships in Neopelminae are perfectly supported across bootstrap replicates. These patterns suggest that *P. chrysolophum* is sister to a lineage that gave rise to the Amazonian *Tyranneutes* and subsequently another forest-based isolate in the Atlantic lowlands, *N. aurifrons*, before diversifying into three species across isolated Neotropical short-stature forests. It is possible that *N. aurifrons* also merits treatment as a separate genus from other *Neopelma* species due to its distinct vocalization structure and some ecological attributes, but more detailed study of intrageneric differentiation is warranted before revision of that group.

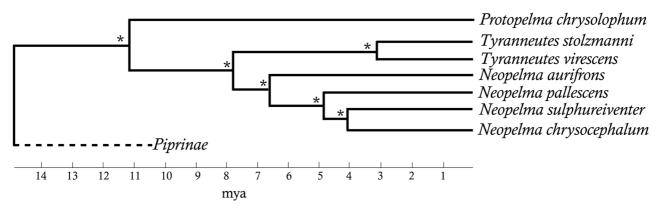


FIGURE 2. Subsection of suboscine phylogenetic tree from Harvey *et al.* (2020) containing Neopelminae. The highly distinctive genus *Tyranneutes* is embedded within *Neopelma*, thus requiring taxonomic revision. Asterisks indicate 100% bootstrap support and time scale is in millions of years (mya).

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