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The earliest Tyrannida (Aves, Passeriformes), from the Oligocene of France

Ségolène Riamon1, Nicolas Tourment2 & Antoine Louchart1✉

Passeriformes is the most diverse bird order. Nevertheless, passerines have a remarkably poor early fossil record. In addition, high osteological homoplasy across passerines makes partial specimens difficult to systematically assign precisely. Here we describe one of the few earliest fossil passerines, from the early Oligocene (ca 30 Ma) of southern France, and one of the best preserved and most complete. This fossil can be conservatively assigned to Tyrannida, a subclade of the New World Tyranni (Suboscines), i.e. of the Tyrannidae. A most probably stem-representative of Tyrannida, the new fossil bears strong resemblance with some manakins (Pipridae), possibly due to plesiomorphy. Furthermore, it yields a new point of calibration for molecular phylogenies, already consistent with the age of the fossil. Tyrannida, and the more inclusive Tyrannidae, are today confined to the New World. Therefore, the new fossil calls for scenarios of transatlantic crossing during or near the Oligocene. Later, the European part of the distribution of the Tyrannidae disappeared, leading to a relictual modern New World distribution of this clade, a pattern known in other avian clades. The history of Tyrannida somehow mirrors that of the enigmatic Sapayoa aenigma, sole New World representative of the Eurylaimides (Old World Tyranni), with transatlantic crossing probably caused by similar events.

The order Passeriformes (Aves) comprises 59% of the extant bird diversity, i.e. 6,493 over ca. 11,000 species1. They comprise the basal Acantisittidae (two species), sister to the Eupasseres which in turn comprises the Tyranni (previously called Suboscines; 1,407 species), and the Passeri (previously called Oscines; 5,084 species). Molecular studies show that, as the sister clade to Psittaciformes (parrots and allies), Passeriformes originated in the earlier part of the Paleogene, and most of the extant families diverged near the Eocene-Oligocene-limit, i.e. some of them should be as old as 30 million years (Ma)2–4. Nevertheless, the fossil record of passerine birds remains exceedingly poor prior to the middle Miocene, and increasingly toward earlier times. This taphonomic bias explains the difficulty in finding early specimens representing extant passerine clades. Among the few pre-Miocene published specimens, most are fragmentary5–11, and even the three more complete specimens, on slab, are rather poorly preserved and prove difficult to identify with some precision. The latter specimens are all from the European early Oligocene: Wieslochia weissi (Germany12,13), Jamna szybiaki and Resoviaornis jamrozi (Poland14,15). This difficulty is also explained by (i) high apparent homoplasy observed on osteological characters within the Passeriformes12,13, and (ii) the difficulty to compare fossils with a sufficiently large, representative sample of extant taxa, passerine clades being so rich at specific and generic levels. Some early fossils have been referred to Tyranni indet., others to Passeri indet., and the remaining to either the preceding taxa or possibly stem Eupasseres or stem passerines5–15. All these fossils date to the Oligocene of France, Germany and Poland in Europe. In addition, late Oligocene fossils of logrunner (Oscines, Orthonychidae) are known from Australia16. As for the older, possible passerine remains from the lower Eocene of Australia17,18, they are fragmentary (one proximal carpometacarpus and one distal tibiotarsus) and considered to be either not sufficiently diagnostic of the Passeriformes12,19 or possibly Passeriformes outside Eupasseres20. Here we describe one of the earliest fossils on slab of a passerine bird, nearly complete, from the early Oligocene of the Luberon (Alpes-de-Haute-Provence, France). Its exceptional state of preservation allows for its identification as the oldest Passeriformes assignable to a modern subgroup of the Tyrannidae (the latter being sometimes called “New World Tyranni”). This fossil provides the earliest calibration point for a subclade of the Tyranni. In addition, it yields evidence of an American passerine element in this locality, calling for several plausible paleobiogeographical scenarios.

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Results

Assignment to the Passeriformes. The whole morphology of the specimen NT-LBR-014 (Fig. 1), from the early Oligocene of Revest-des-Brousses (Luberon, Alpes-de-Haute-Provence, France), indicates that it belongs to the Passeriformes, to the exclusion of other birds. Among the more distinctive passerine characters, the fossil exhibits (i) trochleae II, III and IV of the tarsometatarsus situated in one plane, and the distal extremities of which are aligned (Figs. 1 and 2); (ii) a carpometacarpus with a wide processus intermetacarpalis (Fig. 2), a character found outside Passeriformes only in the Galliformes, Piciformes, Coliiformes and Coraciiformes (which differ from passerines by other characters)\textsuperscript{18}; and (iii) the processus intermetacarpalis and the os metacarpale minus are fused in the fossil, which is found only in Passeriformes\textsuperscript{21} and Piciformes\textsuperscript{22}, the latter differing in many other characters (among which zygodactylous type tarsometatarsus trochleae). Among numerous other passerine characters, the fossil also exhibits a tibiotarsus with two equally-sized and parallel condyles, not curved laterally or medially.

Figure 1. The fossil specimen NT-LBR-014 from Revest-des-Brousses, Luberon (France), and interpretative drawing. al, wing phalanx digitii alulae; c, costa; cmc, carpometacarpus; cr, os carpi radiale; crc, coracoid; cu, os carpi ulnare; ddmj, distal wing phalanx digitii majoris; dmn, wing phalanx digitii minoris; hm, humerus; mdb, mandible; met, metacarpal; pdmj, proximal wing phalanx digitii majoris; q, quadrate; sp, scapula; tbt, tibiotarsus; tmt, tarsometatarsus; uln, ulna; v, vertebra; II, III, IV, numbering of pedal digits. Scale bars, 10 mm.
Assignment to the Eupasseres (Passeri and Tyranni). Acanthisittids are osteologically very derived, probably owing to their long insular isolation without predators, which favoured characters associated with reduction of flight ability, apparent in certain species (some are or were even flightless). The fossil differs from
acanthisittids by numerous characters (Supplementary Table 1). Among these characters, the acanthisittid humerus is more curved (S-shaped), a shape approached by the Rhinocryptidae, also poorly flighted, contrary to the fossil which exhibits a straight humerus (Fig. 1). In addition, the fossa pneumotricipitalis is double in acanthisittids, as in most Passeri, whereas it is unique in the fossil (Fig. 2). The combination of those two characters is found only in acanthisittids.

In addition, among characters less susceptible to be associated with flight reduction (see also cranial characters in Supplementary Table 1), the coracoid in acanthisittids has a shape much different from that of the fossil and the extant Eupasserines, and does not possess a foramen situated medially at the base of the processus acrocoracoideus (present in the extant Eupasserines and the fossil). The acanthisittid carpometacarpus also exhibits differences, notably a more proximally situated processus intermetacarpalis, compared with the fossil and other passerines. The fossil therefore differs from the Acanthisittidae, and belongs to the Eupasserines.

**Assignment to the tyranni.** The wing elements are especially diagnostic for differentiation between the two sub-orders (Figs. 2 and 3, Supplementary Table 1), but other features are also helpful. These diagnostic features are confirmed, or one yielded, by the present comparative study. As in the Tyranni, the fossil exhibits:
a quadrate–quadrojugal articulation of the suboscine type (see ref. 19: 136–137.); a prominent tuberculum ligamenti collateralis ventralis of the ulna (little prominent in the Passeri)13; a tuberculum carpopedal more extended and spatiulate (vs. shorter and obtuse in the Passeri; new described character); a processus dentiformis of the carpo- metacarpus poorly individualized (and moderately marked; less marked in some Tyranni; well individualized and strongly marked in the Passeri);5,7,8,13 a distal extremity of the os metacarpale more prominent and pointed (square-shaped, and more hollow in ventral view, in the Passeri);5,7,8,13 a blade of the wing phalanx 1 digitus majoris with a rounded, convex border (straight border in the Passeri);2,19 presence of a processus internus indicis on the distal extremity of the alar phalanx 1 digitus majoris (absent in the Passeri).7,19 These and other diagnostic characters allow to identify NT-LBR-014 as belonging to the Tyranni (and exclude the Passeri).

Phylogenetic analyses. In order to precise the position of NT-LBR-014 within the Tyranni, phylogenetic analyses in parsimony were conducted based on the distribution of characters across the extant Tyranni examined and the fossil, transformed into a character matrix (Supplementary Methods; strict consensus, Supplementary Fig. 1; bootstrap analysis, Supplementary Fig. 2). The resulting trees show low robustness indices for most nodes (Supplementary Figs. 1, 2). We interpret the low robustness or poor resolution of the trees as the result of pervasive homoplasy in the distribution of osteological character states across the Tyranni (and probably across the whole Passeriformes). This had been observed in previous analyses involving fossil passerines, leading authors to refrain applying cladistic analyses (or other phylogenetic methods) to such osteological datasets12–14.

Results of our temptative phylogenetic analyses are not incongruent with our more qualitative results below, although they do not offer significant weight per se. Sapayoa aenigma is correctly placed in a clade exclusively with other Eurylaimides in the tree generated by bootstrap analysis (1000 replicates), although with poor support (Supplementary Fig. 2), as well as in the strict consensus tree (Supplementary Fig. 1). NT-LBR-014 is found distant from Sapayoa (and other Eurylaimides) in both analyses, and in addition it is found in a clade exclusively with piprid taxa in the strict consensus tree. The phylogenetic trees do not make it possible to ascertain which characters are plesiomorphic for the Tyrannida, for example, or synapomorphic for diverse subclades.

In spite of the limitations of phylogenetic analyses based on a character matrix, the distribution of characteristics observed makes it possible, nevertheless, to identify sets of characters that successively exclude taxa in the assignment of NT-LBR-014, and restrain the clade to which it belongs, starting again at the level of the Tyranni.

Assignment to the Tyranni. The Tyranni comprises two infra-orders: the Eurylaimides ("Old World Tyranni") and the Tyrannides ("New World Tyranni"), based on molecular data14,23–25. Few skeletal diagnostic characters make it possible to differentiate systematically between members of the two clades. Two of these characters apply to all the Eurylaimides and Tyrannides examined. As in the Tyrannides, the fossil exhibits: a straight processus flexorius of the distal humerus (partly produced, and somehow hooked more dorsally and caudally in the Eurylaimides); a cotyla ventralis of the proximal ulna slightly rounded and little developed ventrally (more rounded and developed ventrally in the Eurylaimides) (Figs. 2 and 3, Supplementary Table 1).

In addition, most of the Tyrannides, as well as the fossil, exhibit other characters distinct from the Eurylaimides: more rounded orbits; a brachial tuberosity of coracoid (tuberculum brachiale; Fig. 4) more developed medially; and a processus extensorius of carpometacarpus (Fig. 2) less deported ventrally and slightly laterally. Species in the Tyrannides that exhibit intermediate states for these characters (between Eurylaimides and typical Tyrannides) are: Geositta cupularis Carvalho, Scytalopus unicolor (Rhinocryptidae), Formicarius analis (Formicariidae), Cotinga sp. (Cotingidae), Tyrannus dominicensis (Tyrannidae). These few intermediate cases do not affect the observation that for all these characters NT-LBR-014 corresponds to the Tyrannida and differs from the Eurylaimides.

Assignment within the Tyrannidae. Among all characters observed on the fossil, 53 are discriminant among the examined Tyranni, within which many are rather variable across the Tyrannidae (Fig. 5, Supplementary Tables 1, 2) and do not help link the fossil with a particular family or genus. Nevertheless, a number of other characters on each skeletal element appear diagnostic for one or several families (Supplementary Table 1); the more prominent ones are detailed below.

Skull. The fossil, as well as Xenopipo atronitens (Pipridae), exhibit a reduced and triangular anteorbital fenestra (Fig. 6, Supplementary Table 1). The other species exhibit a fenestra generally more developed proportionally, and less neatly triangular.

The dorsal interorbital fenestra is smaller than the ventral, and the separation between them is thin, in the fossil (Fig. 6, Supplementary Table 1). The relative size of these fenestrae shows great variability across extant species and families. However, there are certain trends in the position of these fenestrae, relative to the orbit, between families. The fenestrae generally start rostrally at the same level relative to the orbit, in species of a given family. In the fossil, the rostral extremity of the fenestrae lies at the rostral ⅔ of the orbit length, like in the Pipridae.

The outline of the cranium, orbits, (and beak) of the fossil, in comparison with extant Tyrannidae, also helps delimiting close similarities of several characters with different taxa: one genus in the Tityridae and two in the Tyrannidae, but several in the Pipridae, and also Sapayoa (Sapayoidea), different suites of characters being involved for every of these taxa (Supplementary Table 1, Fig. 6). Incidentally, among piprid taxa, for Antilophia, which otherwise shares a number of similarities with NT-LBR-014, differences mainly concern a few cranial characters (Fig. 5); another piprid, Neopodmo, is in contrast similar to the fossil in most cranial characters (including the marked gonys of mandible), and less so in postcranical ones.

The feather crest erected above the rostrum basis of NT-LBR-014, in close examination, is clearly in exact life position and shape, and has been unaffected by taphonomic processes. It is triangular, well-developed, directed rostrally but with the tip slightly recurved caudally (Figs. 1 and 6, Supplementary Table 1). Several families
comprise species that exhibit a crest (or crests) on the head, but different in shape and/or in precise position (Tyrannidae, Tityridae, Cotingidae, Thamnophilidae, Rhinocryptidae, Furnariidae). Only in certain Pipridae a crest above the beak exhibits a shape approaching (Chiroxiphia, Masius) or being identical (Antilophia) to that of the fossil. The crest of the fossil is only slightly larger proportionally (18.6 mm length) than that of A. galeata (13.0–14.5 mm), with a coefficient of proportionality of ca. 4/3 (see Fig. 7B).

**Coracoid.** The fossil coracoid exhibits a prominent processus acrocoracoideus (Fig. 4), with a shape similar to that of A. galeata (Pipridae).

The processus procoracoideus of the fossil is well-developed medially (Fig. 4), and is similar to that of Tyrannus dominicensis (Tyrannidae). This process has a shape approaching that of the piprid species C. holochlora and X. atronitens at least (broken in the available specimen of A. galeata, also suggesting prominent shape).

**Humerus.** Scytalopus unicolor (Rhinocryptidae) differs from other extant taxa examined and the fossil by the reduced crista deltopectoralis, a character linked with reduced flight capability26. The fossil exhibits a processus supracondylaris dorsalis that is unique and well-developed (Fig. 2), a character shared with all the Pipridae, and Pitta sordida (Pittidae), Sapayoa aenigma (Sapayoidae), Scytalopus unicolor (Rhinocryptidae), Schiffornis turdina (Tityridae), and Pipreola arciata (Cotingidae); the other extant species examined in the Tyrannidae have a unique processus supracondylaris dorsalis, but which is reduced (or less prominent proximally).
Ulna. The fossil exhibits relatively reduced papillae remigales caudales, similar to the condition in *Myrmotherula axillaris* (Thamnophilidae), *Conopophaga ardesiaca* (Conopophagidae), *Oxyuncus cristatus* (Tityridae), *Todirostrum* sp. (Tyrannidae), and most of the Pipridae.

Carpometacarpus. The shape and position of the processus intermetacarpalis in the fossil are similar to those observed in *C. linearis, X. atronitens, A. galeata* (Pipridae), and *Cotinga* sp. (Cotingidae) (Fig. 2). The processus dentiformis in NT-LBR-014 is well marked, as is observed in some taxa of the Eurylaimides (including *Sapayoa*), as well as some Conopophagidae, Rhinocryptidae, Formicaridae and Pipridae in the Tyrannidae. In the Pipridae, a marked processus dentiformis is seen in *Manacus* and *Xenopipo*. The outline of the bone is otherwise similar to that in several piprid species (Fig. 8).

Figure 5. Radial visualisation (Kiviat diagram) of the distribution of character states of the Luberon fossil NT-LBR-014, across extant taxa of the Tyrannidae for which all the characters were assessable. Top, position of the diagnostic characters considered here relative to each radius. In extant species, character state can be 0 (centre; character absent), 1 (mid-radius; character present but state still different from fossil), or 2 (state identical or similar to fossil) (see Supplementary Table 4).
Wing phalanx digiti majoris 1. Among the Tyrannides, certain families exhibit a processus internus indicis that is only faint, or even absent: the Furnariidae, Thamnophilidae, Conopophagidae, Rhinocryptidae, Formicariidae, Dendrocolaptidae. In addition, in these families the shape of the blade is intermediate between the typical Passeri state (straight border) and the typical Tyranni state (convex border), a character directly linked with the development of the processus internus indicis\(^1\). These six families can therefore be differentiated from the other Tyrannides and the fossil NT-LBR-014 (Fig. 2) based on these characters.

**Femur.** The proximal end of the fossil femur exhibits a rather deep caudal fossa (Fig. 9), a character observed in *Geositta cunicularia* (Furnariidae), *Scytalopus unicolor* (Rhinocryptidae), and *Masius chrysopterus*, *C. linearis* and *X. atronitens* (Pipridae).

**Tibiotarsus.** A medial crest on the proximal end is absent, contrary to *Scytalopus unicolor* (Rhinocryptidae), *Phytotoma rara* (Cotingidae), *Rhynchocyclus olivaceus* (Tyrannidae), and most of the Tityridae examined, which exhibit a marked crest.

**Tarsometatarsus.** The fossil exhibits an ossified pons supratendineus on the proximal part of the dorsal face, positioned rather proximally. A pons is positively absent in only two of the examined extant passerines, *Tyrannus dominicensis* and *Toadrostrum* sp. (both Tyrannidae), and at least no other Tyranni (Fig. 9, Supplementary Table 1).

**Combinations and distributions of characters.** A Kiviat diagram allows visualization of the distribution of the states of the characters that show heterogeneity across extant Tyrannides, and the states observed in the fossil (Fig. 5). The families in the Tyrannides are grouped into two clades: the Tyrannida and the Furnariida. A
Figure 7. Geographic location, and reconstruction of the Luberon early Oligocene Tyrannida. In (a), the geographic location of the Luberon Tyrannida NT-LBR-014 is represented (red circle), together with the extant distribution of Tyrannida (red area), superimposed on a paleogeographic map of landmasses in the early Oligocene (map background modified after The Paleobiology Database). In (b), reconstruction of the Luberon Oligocene manakin-like Tyrannida in life; drawing copyright Manon Delval.

Figure 8. Right carpometacarpus of the Luberon fossil NT-LBR-014, compared with extant species (Pipridae). (b,c), inverted left carpometacarpi. In (c), the angle of view (ventral) is slightly different from that in (a,b,d) (slightly cranio-ventral, in (b) more than in (a,d)). *The facies articularis radiocarpalis is masked under the matrix. facies art. rad., facies articularis radialis; facies art. uln., facies articularis ulnaris; os met. maj., os metacarpale majus; os met. min., os metacarpale minus; proc. ext., processus extensorius; synos. met. dist., synostosis metacarpalis distalis. The angles of view prevent from seeing the processus dentiformis when present. Scale bars, 5 mm.
number of characters are shared between the fossil and the Tyrannidae, Cotingidae, Tityridae and Pipridae—these four families forming the Tyrannida—and differ from those in the Furnariida. In addition, all the characters of the fossil are similar to those of at least one of the examined species of Pipridae. And last, the fossil shows a greater resemblance overall with *C. linearis* and *X. atronitens*, and above all a maximum of similar/identical characters with *A. galeata*.

NT-LBR-014 exhibits a mosaic of characters present in one or more families of Tyrannidae, and systematically in some or all of the examined Pipridae, contrary to other families (Fig. 5, Supplementary Table 1, and also

Figure 9. Leg bones of the Luberon fossil NT-LBR-014. a, right femur, latero-caudal view; b, left distal tibiotarsus, latero-cranial view; c, left proximal tarsometatarsus, latero-dorsal view; d, right proximal tarsometatarsus, dorsal view. cond. lat., condylus lateralis; cr. med. hyp., crista medialis hypotarsi; cr. med. pl., crista medialis plantaris; gr., tiny groove between the tuberositas retinaculi extensorius lateralis and the tuberculum retinaculi m. fibularis, proximal to the condylus lateralis (see Supplementary Table 1); h., hollow just distal to the facies articularis antitrochanterica; o. p. s., ossified pons supratendineus; tr. fem., trochanter femoris. Scale bars, 5 mm.
Supplementary Table 2 showing six additional characters that are discriminant for certain genera and species across the Tyrannidae).

**Discussion**  

**Systematic assignment of the Oligocene fossil.**  

NT-LBR-014, unambiguously assignable to the Tyrannidae within the Passeriformes, can also be firmly placed more precisely in the Tyrannidae. All the character states of NT-LBR-014 are systematically present in members of the Tyrannidae and they include the diagnostic characters of Tyrannidae, to the exclusion of the Eurylaimidae, that we highlighted. Even though with poor support, our tentative phylogenetic analyses are concordant with this result, placing the fossil outside the Eurylaimidae, the latter comprising *Sapayoa* in agreement with molecular works (see below). Within the Tyrannidae, several characters exclude the infra-order Furnariida (composed of the Furnariidae – this family including the former Dendrocolaptidae, the Thamnophilidae, Conopophagidae, Formicariidae, and Rhinocryptidae) and, no character state is shared only between the fossil and one or more members of these six families to the exclusion of other Tyrannidae – the Tyrannida. Not all the extant genera (not to mention species) could be examined in the Furnariida, but a sample that we consider sufficiently well-distributed phylogenetically, to allow for some extrapolation of the character states that were observed, and which differ systematically from NT-LBR-014. The most genus and species-rich families in the Furnariida are the Thamnophilidae and the Furnariidae. The representatives examined (or for which data are available in the literature) are considered sufficiently different from the fossil to be confident in our conclusions. Conversely, most characters are shared between the fossil and the other infra-order, the Tyrannida (composed of the families Cotingidae, Tityridae, Tyrannidae, and Pipridae). Specimens of Cotingidae, Tityridae and Tyrannidae differ from NT-LBR-014 mostly in characters of the skull and the coracoid. The fossil shares a maximum of characters with the Pipridae, and every character is in common with at least one, or all of the genera examined in the Pipridae. Similarity is greater with the Pipinae (Chloropipo, Antilophia, Chiroxipha, Masius, Xenopipo, Manacus, Pipra, Machaeropitrus) on postcranial characters, and with the Neopelminae (Neopelma et Typannus; the more basal subfamily of Pipridae) on cranial characters (particularly with *Neopelma*). Within the Pipinae, the fossil shares a greater number of postcranial characters with *Chiroxipha and Xenopipo*, and an even greater number with *Antilophia* (26 of 30 characters, excluding those diagnostic for Passeriformes and for Tyranni). However, NT-LBR-014 exhibits a mosaic of characters present in several different piprid genera (Pipinae or Neopelminae; Supplementary Table 1). But moreover, it is possible that osteological characters are also shared with at least one other Tyrannida outside the Pipidae. This is especially possible in the family Tyrannidae since a number of extant genera and species could not be examined among the 449 species in 101 genera of this extremely rich family. Among the 67 species in 24 genera of Cotingidae, or the 49 species in 11 genera of Tityridae, most could not be seen either. As a consequence, some characters here found in common exclusively with some piprid taxa could possibly be plesiomorphic for the Pipidae, or even plesiomorphic for the Tyrannida as a whole, and present also in other families. Some of the Tyrannidae examined already show a number of shared characteristics with the fossil, although less than the piprid taxa. Even rare features such as the particular feather crest could be found in an Oligocene fossil through plesiomorphy or convergence outside crown Pipridae, or even in another family. Therefore, even if more extant species of Tyrannida were examined and considered here than in all previous literature on an early fossil passerine, we suggest, pending a more thorough survey of other taxa in the Tyrannida, to conservatively assign NT-LBR-014 to the Tyrannida, more probably as a stem representative.

Interestingly, a synapomorphy of Pipridae has been known since the 19th century, namely the syndactyly of the outer toes (III and IV); and this character also evolved convergently in some members of other clades in the Tyrannida. Aware of this character, we nevertheless found no indication of fusion between phalangeal bones themselves, in any extant piprid, nor in any other extant specimen examined (Supplementary Fig. 3). The syndactyly of toes III and IV in Pipridae, as well as other forms of syndactyly, were observed exclusively on naturalized specimens, and obviously they concern only the soft tissues surrounded the bones. Therefore, the absence of fusion of toe bones in the fossil (Supplementary Fig. 3), as well as on all extant specimens examined, has no bearing on reported syndactyly, which rests on soft tissues, and the latter is a character out of reach on the fossil.

The early assignment of *Sapayoa* to the Pipridae in the history of classification, on the basis of morphology, is consistent with the osteological partial resemblance on some characters noticed here between these two taxa. More recently, molecular phylogenetic analyses revealed that *Sapayoa* belonged in the Eurylaimidae, of which it is the only New World representative. The characters of *Sapayoa* showing similarity with the Pipridae, as well as with the fossil, are therefore interpretable as the result of convergences.

NT-LBR-014 shows no close similarity with the few incomplete passeriform fossils found in the Oligocene or early Miocene of France, Germany and Poland, including a nearly completely represented taxon from the early Oligocene of Germany, *Wieslochia weissi* (Supplementary Table 1), which displays a greater number of assessable characters than others. Although disarticulated and with moderately well preserved detail, *W. weissi* exhibited features leading to consideration of its position as probably basal in the Tyrannini, or Eupasserines, or even Passeriformes as a whole. Incidentally, a range of comparable phylogenetic positions (including within crown passerines) is indeed plausible for some European Miocene tarsometatarsi, the hypotarsus of which had initially led Manegold et al., to consider them outside crown Passeriformes.

**Paleoecology.**  

With a length of 15 cm, the fossil NT-LBR-014 is a medium-sized Tyrannina; its legs are of medium length proportionally, as well as the wings (Supplementary Table 3, Supplementary Fig. 4). The beak and claw shapes are also unspecialized compared with modern Tyrannina, and are compatible with a rather generalist diet, comprising insects and small fruits, as in most extant manakins, tyrant-flycatchers and allies. Extant Tyrrannina live in the Americas, with most diversity in the neotropical ecozone. NT-LBR-014 derives from a medium-sized passerine, possibly from a more ancient time period, suggesting that the modern diversity of the family has evolved over a long period of time.
Early passerines and molecular ages. Recent molecular studies have determined the age of divergence between Acanthisitidae and Eupasseres (Passeri and Tyranni) as around the Paleocene-Eocene limit (ca. 56 Ma)\(^3\), or later in the early Eocene, near 48 Ma\(^4\). The earliest ascertained fossil passerines are from the early Oligocene of Europe. They comprise Passeri, Tyranni and possibly more basal lineage(s)\(^5\)–\(^15\). NT-LBR-014 is the first to be assignable to a more precise, extant passerine clade, the Tyrannida, at ca 30 Ma. A molecular age of diversification for the Tyrannida was proposed at 32–33 Ma\(^2\)\(^,\)\(^27\) or near 24 Ma\(^4\), and the divergence between Tyrannida and Furnariida at 38.9 Ma\(^3\) or near 36 Ma\(^4\). The identification of NT-LBR-014 as a stem Tyrannida, or possibly situated at the start of the diversification of the Tyrannida, is congruent, at ca 30 Ma, with these molecular results. Furthermore, this fossil will now offer a new calibration point for a minimal age of stem Tyrannida (prior to crown diversification), for future molecular studies, which would presumably tend to slightly increase the diversification ages cited above.

Paleobiogeography of the Tyranni. The early Oligocene presence in Europe of a Tyrannida, a clade today exclusively American (Fig. 7), might be explained by different scenarios, as for two other stem-representatives of New World clades found in the same area: the stem hummingbird Eurotrochilus sp.\(^3\) and the stem Galbulae Jacamaria\(^36\). The stem Tyrannida may have originated in the New World, and then the presence of a Tyrannida in southern France in the Oligocene implies that they rapidly colonized Europe in the early Oligocene. This passage might have taken the route of landmasses and straits between northern North America and Europe. Fossil records of Tyrannida (and other Tyranni) are lacking in Oligo-Miocene or older strata of northern America to support this hypothesis, but this apparent absence does not rule out the hypothesis since sufficiently diagnostic fossil passerines are extremely rare worldwide in these periods in general. The passage might alternatively have been from southern America to Europe, directly or via Africa, where the avian fossil record is extremely scarce for these periods. Alternatively, the stem Tyrannida may have originated in the Old World. A new fossil such as NT-LBR-014 can disrupt models that are inferred\(^4\) based only on extant distributions. As is the case for the stem hummingbirds\(^3\)\(^,\)\(^34\) and stem Galbulae\(^36\) found in Europe in the early Oligocene, the new fossil Tyrannida calls for the possibility of a much more complex history of past distributions. In the hypothesis of an Old World origin of stem Tyrannida (and hence, probably also the stem Tyrannides, from the Old World stem of its sister clade Eurylaimides), they must have colonized the Americas at some point between the early Oligocene and the middle Miocene. Again, the passage could have occurred north of the northern Atlantic via northern America, or from Europe to southern America. In the latter case, an additional scenario might be envisioned as colonisation of southern America by European populations becoming medium-distance or long-distance seasonal migrants, in a context of increased seasonality during these periods\(^37\). Such populations would have been progressively wintering in southern America where descendents would have become more resident later in evolution. In both scenarios of family origin, transatlantic crossing by the northern route was rendered possible by the tropical to subtropical climate up to high latitudes, but preferentially early in the Oligocene, owing to later global cooling stages\(^38\). And in both scenarios, crossing between northwest Africa and South America would have required a transit of “only” 1,000 km across the ocean, and progressively more with continental drift. Paleo-islands in the southern Atlantic in the Oligocene\(^39\) would have helped this crossing. A last possibility of passage would have been via the Bering Strait which benefited from a mild climate, but the absence of fossil evidence added to the much greater distance, make this scenario much less likely.

In every hypothesis, after the Oligocene the European distribution of Tyrannida would have become reduced and eventually disappeared at latest in the upper Miocene, owing to global cooling and a decrease in winter temperatures among other factors\(^37\)\(^,\)\(^38\). This led to a relictual distribution in the southern hemisphere, tropical regions, in this case neotropical zones, as was the case for several other bird groups\(^6\)\(^,\)\(^40\)\(^,\)\(^41\). Concomitant with this retreat towards the equator in America, some lineages could become progressively long-distance migrants (including members of the Tyrannidae today breeding in North America and wintering in the Neotropics). Interestingly, Sapayoa aenigma, “Old World” Tyranni (Eurylaimides) living in South America, also illustrates a transatlantic crossing of an ancestor, leaving descendents on both sides (this species is neotropical, and all other Eurylaimides are paleotropical). It is not possible to favour a northern or a southern passage in the case of Sapayoa, but it must have occurred between the latest Oligocene and middle Miocene\(^4\).

Methods
Fossil material. The fossil NT-LBR-014 (collection Nicolas Tourment, Marseille\(^33\)\(^,\)\(^35\)) is a nearly complete articulated skeleton on slab, embedded in fine limestone laminites. A cast is deposited in the Collections of the Université Lyon 1-Claude Bernard (Villeurbanne, France, collection n° UCBL-FSL-444666). The depositional setting was calm; only a few bones are disarticulated (e.g., the right coracoid is slightly displaced). Parts of the feathering are preserved as a thin layer of dark organic matter, showing among other features the shape of a typical frontal crest, in place and undisturbed. The laminites were deposited in a coastal freshwater to slightly brackish lagoon, and date to the early Oligocene (“Vachères limestones”, Rupelian strata, biozone MP24, 33–28.25 Ma\(^42\)–\(^45\)) of Revest-des-Brousses (Apt Basin, Luberon, Alpes-de-Haute-Provence, southeastern France). These levels locally comprise elements of a tropical to subtropical fauna and flora, essentially of continental origin, and including birds of a dozen families\(^34\)–\(^36\).
Comparative material. Comparisons were made with representatives of the families osteologically close to passerines, and within passerines with a representative sample of most families in the Passeri, as well as with Acanthisitidae and members of all families of Tyranni (41 species), and also with the literature (extant and fossil taxa) (Supplementary Methods, Supplementary Table 1).

Comparative anatomy, osteological nomenclature, and systematics. Observations of the fossil and extant specimens were realized using a binocular microscope at various magnifications. Drawings were additionally realized using a camera lucida with binocular microscope. Osteological nomenclature follows primarily Baumel and Witmer, unless stated otherwise. Systematic arrangement follows Del Hoyo et al.

Phylogenetic analyses. Methods used for phylogenetic analyses in parsimony are in Supplementary Methods.

Data availability. Data analysed during this study are included as Supplementary Information files. The fossil NT-LBR-014 is deposited in the Collection Nicolas Tourment, Marseille, and is accessible upon request. The cast UCBL-FSL-444666 is deposited in the Collections of Paleontology, Université Lyon 1, Villeurbanne. Any additional data are available from the author upon reasonable request.

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References
1. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds) Handbook of the Birds of the World Alive ( Lynx Edicions, Barcelona, 2019). (retrieved from https://www.hbw.com/ on 13 March 2019).
2. Ericson, P. G., Klopfstein, S., Irestedt, M., Nguyen, J. M. & Nylander, J. A. Dating the diversification of the major lineages of Passeriformes (Aves). BMC Evol. Biol. 14, 8 (2014).
3. Selvatti, A. P. & Gonzaga, L. P. & de Moraes Russo, C. A. A Paleogene origin for crown passerines and the diversification of the Oscines in the New World. Mol. Phylogenet. Evol. 88, 1–15 (2015).
4. Oliveros, C. H. & et al. Earth history and the passerine superradiation. Proc. Natl. Acad. Sci. USA 116, 7916–7925 (2019).
5. Mourer-Chauviré, C., Hugueney, M. & Jouet, P. Découverte de Passeriformes dans l'Oligocène supérieur de France. C. R. Acad. Sci. Paris Série 2 309, 843–849 (1989).
6. Mourer-Chauviré, C., Berthet, D. & Hugueney, M. The late Oligocene birds of the Crédy quarry (Allier, France), with a description of two new genera (Aves: Pelecaniformes: Phalacrocoracidae, and Anseriformes: Anseranatidae). Senckenbergiana lethaea 84, 303–315 (2004).
7. Mayr, G. & Manegold, A. A small suboscine-like passeriform bird from the early Oligocene of France. The Condor 108, 717–720 (2006).
8. Manegold, A. Passerine diversity in the late Oligocene of Germany: earliest evidence for the sympatric coexistence of Suboscines and Oscines. Ibis 150, 377–387 (2008).
9. Bochenksi, Z. M., Tomek, T. & Swidnicka, E. The first complete leg of a passerine bird from the early Oligocene of Poland. Acta Palaeontol. Polon. 59, 281–285 (2014).
10. Bochenksi, Z. M., Tomek, T. & Swidnicka, E. A complete passerine foot from the late Oligocene of Poland. Palaeontologia Electronica 17.1.6A, 1–7 (2014).
11. Bochenksi, Z. M. et al. Articulated avian remains from the early Oligocene of Poland add to our understanding of passerine evolution. Palaeontologia Electronica 21.2.32A (2018).
12. Mayr, G. & Manegold, A. The oldest European fossil songbird from the early Oligocene of Germany. Naturwissenschaften 91, 173–177 (2004).
13. Mayr, G. & Manegold, A. New specimens of the earliest European passeriform bird. Acta Palaeontol. Polon. 51, 315–323 (2006).
14. Bochenksi, Z. M., Tomek, T., Bujoczek, M. & Wertz, K. A new passerine bird from the early Oligocene of Poland. J. Ornithol. 152, 1045–1053 (2011).
15. Bochenksi, Z. M., Tomek, T., Wertz, K. & Swidnicka, E. The third nearly complete passerine bird from the early Oligocene of Europe. J. Ornithol. 154, 923–931 (2013).
16. Nguyen, J. M. T., Boles, W. E., Worthy, T. H., Hand, S. J. & Archer, M. New specimens of the logrunner Orthonyx kaldowinyeri (Passeriformes: Orthonychidae) from the Oligo-Miocene of Australia. Alcheringa 38, 245–255 (2015).
17. Boles, W. E. The world’s oldest songbird. Nature 374, 21–22 (1995).
18. Boles, W. E. Fossil songbirds (Passeriformes) from the early Eocene of Australia. Emu 97, 43–50 (1997).
19. Manegold, A. Zur Phylogenie und Evolution der "Racken"-, Specht- und Sperlingsvögel ("Coraciiformes", Piciformes und Passeriformes: Aves). Ph.D Dissertation. Freie Universität Berlin (2005).
20. Mayr, G. The origins of crown group birds: molecules and fossils. Palaeontology 57, 231–242 (2014).
21. Kakegawa, V. Kioscian passeriform bird from the Iwami Formation, Tottori Group, Tottori, Japan. Bull. Natl. Sci. Mus. Series C 49, 33–37 (2003).
22. Smith, N. A., de Bee, A. M. & Clarke, I. A. Systematics and phylogeny of the Zygodyactylidae (Aves, Neognathae) with description of a new species from the early Eocene of Wyoming, USA. PeerJ 6, e5950, https://doi.org/10.7717/peerj.6950 (2018).
23. Chesser, R. T. Molecular systematics of New World suboscine birds. Mol. Phylogenet. Evol. 32, 11–24 (2004).
24. Barker, F. K., Cássio, A., Schikler, P., Feinstein, J. & Cracraft, J. Phylogeny and diversification of the largest avian radiation. Proc. Natl. Acad. Sci. USA 101, 11040–11045 (2004).
25. Irestedt, M., Ohlson, J. I., Zuccon, D., Källersjö, M. & Ericson, P. G. Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). Zoologica Scripta 35, 567–580 (2006).
26. Feduccia, A. & Olson, S. L. Morphological similarities between the Menuridae and Rhinocryptidae, relict passerine birds of the southern hemisphere. Smithson. Contrib. Zool. 366, 1–22 (1982).
27. Ohlson, J. I., Irestedt, M., Ericson, P. G. & Fjeldså, J. Phylogeny and classification of the New World suboscines (Aves, Passeriformes). Zootaxa 3613, 1–35 (2013).
28. Ohlson, J. I., Fjeldså, J. & Ericson, P. G. Phylogeny of the manakins (Aves: Pipridae), with a new classification and the description of a new genus. Mol. Phylogenet. Evol. 69, 796–804 (2013).
29. Prum, R. O. A test of the monophyly of the manakins (Pipridae) and of the cotingas (Cotingidae) based on morphology. Occasional Papers of the Museum of Zoology, the University of Michigan 723, 1–44 (1990).
30. Fjeldså, J., Zuccon, D., Irestedt, M., Johansson, U. S. & Ericson, P. G. Sapayoa aenigma: a New World representative of “Old World suboscines. Proc. Royal Soc. London B 270, S238–S241 (2003).
31. Manegold, A., Mayr, G., Mourer-Chauviré, C. & Nelson, D. A. Miocene songbirds and the composition of the European passeriform avifauna. *The Auk* **121**, 1155–1160 (2004).

32. Worthy, T. H. *et al.* Biogeographical and phylogenetic implications of an early Miocene wren (Aves: Passeriformes: Acanthisittidae) from New Zealand. *J. Vert. Paleont.* **30**, 479–498 (2010).

33. Roux, T. Deux fossiles d’oiseaux de l’oligocène inférieur du Luberon. *Courrier scientifique du Parc naturel régional du Luberon* **6**, 38–57 (2002).

34. Louchart, A., Tourment, N., Carrier, J., Roux, T. & Mourer-Chauviré, C. Hummingbird with modern feathering: an exceptionally well-preserved Oligocene fossil from southern France. *Naturwissenschaften* **95**, 171–175 (2008).

35. Louchart, A., Tourment, N. & Carrier, J. The earliest known pelican reveals 30 million years of evolutionary stasis in beak morphology. *J. Ornithol.* **152**, 15–20 (2011).

36. Duhamel, A., Balme, C., Legal, S., Rivaron, S. & Louchart, A. An early Oligocene stem Galbulae (jacamars and puffbirds) from southern France, and the position of the Paleogene family Sylphornithidae. *The Auk: Ornithological Advances* **137** (2020). doi: 10.1093/aou/ukaa023.

37. Louchart, A. Emergence of long distance bird migrations: a new model integrating global climate changes. *Naturwissenschaften* **95**, 1109–1119 (2008).

38. Zachos, J. C., Dickens, G. R. & Zeebe, R. E. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–283 (2008).

39. De Oliveira, F. B., Molina, E. C. & Marroig, G. Paleogeography of the south Atlantic: a route for primates and rodents into the New World? in *South American Primates, Developments in Primatology: Progress and Prospects* (eds. P. A. Garber *et al.*) 55–68 (Springer Science, New York, 2009).

40. Blondel, J. & Mourer-Chauviré, C. Evolution and history of the western Palaearctic avifauna. *Trends Ecol. Evol.* **13**, 488–492 (1998).

41. Mayr, G. Two-phase extinction of of “Southern Hemispheric” birds in the Cenozoic of Europe and the origin of the Neotropical avifauna. *Palaeobiodiversity and Palaeoenvironments* **91**, 325–333 (2011).

42. Cavelier, C. Paléogène en *Synthèse Géologique du Sud-Est de la France* (ed S. Debrand-Passard) 389–468 (*Mémoires BRGM France* **125**, 1984).

43. Ducreux, J. L., Hugueney, M. & Truc, G. La formation des Calcaires et Lignites de Sigonce (Oligocène moyen, bassin de Forcalquier, Alpes-de-Haute-Provence): datation à l’aide des mammifères; reconstitution des milieux de dépôt. *Geobios* **18**, 109–114 (1985).

44. Escarguel, G., Marandat, B. & Legendre, S. On the numerical ages of the Paleogene mammalian faunas from Western Europe, particularly of the lower and middle Eocene. *Mém. Trav. EPHE Inst. Montpellier* **21**, 443–460 (1997).

45. Ségé, B. & Hugueney, M. Les micromammifères des gisements à phosphate du Quercy (SW France). *Strata Sér.* **13**, 207–226 (2006).

46. Baumel, J. J. & Witmer, L. M. Osteologia. I in *Handbook of avian anatomy: nomina anatomica avium* (eds J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans & J. C. Vanden Berge) 45–152 (*Publ. Nuttall Ornithol. Club* **23**, 1993).

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**Author contributions**

A.L. conceived the study. N.T. provided the fossil material. S.R. and A.L. performed the analyses and realised the figures, for which S.R. made the drawings. S.R. and A.L. developed and discussed interpretations, and prepared the manuscript. All authors read and modified the manuscript.

**Competing interests**

The authors declare no competing interests.

**Additional information**

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Supplementary Information

The earliest Tyrannida (Aves, Passeriformes), from the Oligocene of France

Ségalène Riamon, Nicolas Tourment & Antoine Louchart

This PDF file includes:

Supplementary Methods

Supplementary Figures 1 to 4

Supplementary Tables 1 to 5

References (for Supplementary Table 1)
Supplementary Methods

List of extant specimens examined, and their collection acronyms

In addition to preliminary comparisons with representatives of almost all other avian families, including a number of derived Oscine passerines (UCBL), skeletal specimens of the following extant species were examined for comparison. (F, female; M, male).

Acanthisittidae, *Acanthisitta chloris chloris*, MNZ 26466; Pittidae, *Pitta sordida*, LAC 1884.2469; Philepittidae, *Philepitta castanea*, F, FMNH 384764; Eurylaimidae, *Cymbirhynchus macrorhynchos*, LAC 1884.256; Calyptomenidae, *Calyptomena viridis*, LAC 1997.830; Sapayoidae, *Sapayoa aenigma*, M, USNM 428203; Furnariidae, *Geositta cunicularia*, M, USNM 614657; *Dendrocincla fuliginosus*, M, FMNH 321160;

Thamnophilidae, *Myrmotherula axillaris*, M, FMNH 319192; *Sakesphorus canadensis loretoyacensis*, M, FMNH 389206; *Thamnophilus doliatus*, (skull) LAC 1997.556; *Thamnophilus coecus*, (skull) LAC 1884.1557; Conopophagidae, *Conopophaga ardesiacasaturata*, M, FMNH 322380; Rhinocryptidae, *Scytalopus unicolor*, M, USNM 559977;

Formicariidae, *Formicarius analis*, M, USNM 612383; Pipridae, *Ceratopipra erythrocephala*, LAC 1880.125; *Neopelma sulphureiventer*, M, MZLSU 101474; *Tyranneutes stolzmanni*, F, FMNH 322555; *Chloropipo holochlora viridior*, M, FMNH 322514; *Manacus manacus trinitatis*, FMNH 394500; *Machaeropetala pyrocephalus pyrocephalus*, M, FMNH 322563;

*Chiroxiphia linearis fastuosa*, F, FMNH 434065; *Xenopipo atronitens*, M, USNM 622077; *Masius chrysopterus*, M, MZLSU 89991; *Antilophia galeata*, USNM 321704; *Cotinga sp.*, LAC n° 2278; *Procnias sp.*, (skull) LAC 1884.1583; *Rupicola rupicola*, LAC 2004.635; *Rupicola sp.*, (skull) LAC 1884.1574; (=111/711); *Phytotoma rara*, NHM 1891.7.20.273; *Tityra semifasciata*, M, MZLSU 108942; *Onychorhynchus coronatus*, NHM 1891.7.20.143;
NHM 1891.7.20.16; Schiffrinis turdinus amazonus, F, FMNH 322490; Tyrannidae, Tyrannus dominicensis, LAC 1996.60; Tyrannus sp., LAC; Todirostrum sp., LAC 2000.556; Contopus latirostris, (skull) LAC; Rhynchocyclus olivaceus, NHM S/1974.11.83; Rhynchocyclus sp., LAC 2000.459; Menuridae, Menura novaeohollandiae, LAC 1883.2208; Ptilonorhynchidae, Sericulus sp. LAC 1845.92, Ptilonorhynchus violaceus LAC A 4307 = BVI/417; Meliphagidae, Meliphaga lewini LAC 1883.2127 = IV/342, Philemon corniculatus LAC A 4319 = BVI/370, Manorina melanocephala LAC A 4468 = BVI/364; Pardalotidae, Pardalotus punctatus LAC 1860.96; Acanthizidae, Gerygone flavolateralis, LAC 1997.535; Pomatostomatidae, Pomatostomus temporalis trivirgatus, LAC A 4467 = BVI/373; Paradisaeidae, Ptiloris paradiseus LAC 1860.102 = A 4291 = BVI/360, LAC A 4295 = BVI/359, Paradisaea minor LAC 1878.620.

Methods for phylogenetic analyses

The phylogenetic analyses were realized using 36 characters, which were discriminant for at least one among the Tyranni examined, and 34 taxa of the Tyranni (including the fossil). The character matrix (Supplementary Table 5), is derived from the characters observed...
(Supplementary Tables 1, 2). *Gerygone flavolateralis* (Passeri, Acanthizidae) and *Acanthisitta chloris* (Acanthisittidae) were chosen as respective outgroup taxa to the Tyranni.

The taxon-character matrix was analysed with parsimony using PAUP*4.a166. The executable data matrix with PAUP commands is appended as Nexus File (in Supplementary information). Both parsimony analyses were performed with characters ordered. Gaps were treated as missing data. Parsimony analyses treated all changes as equal (“unweighted”) and used heuristic searches with tree-bisection-reconnection (TBR) branch swapping and other default settings, and 1000 random addition replicates per search. Strict consensus trees were computed from the set of most parsimonious trees, and clade support was assessed by bootstrapping using the same settings and 1000 replicates.

Osteological characters used in the phylogenetic analysis.

Feather crest: 0, absent; 1, present but different of fossil; 2, present and similar of fossil.

Relative size of orbits: 0, more than half of the skull; 1, less than half of the skull.

Shape of orbits: 0, the dorsal part is flatter, 1, rounded; 2, almost circular.

Size of nasal opening: 0, wide opening; 1, intermediate size, 2, small opening.

*Fenestra antorbitalis* (proportion): the proportional size of the fenestra antorbitalis compared to that of the skull. 0, developed; 1, reduced.

*Os lacrimale*: 0, free; 1, present and more or less individualized.

Latero-dorsal part of ectethmoid: 0, little developed; 1, developed; 2, well developed; 3, highly developed.

Lateral parts of ectethmoid: 0, reduced gap; 1, intermediate gap; 2, large gap.

Crest/ridge on culmen: 0, absent; 1, present.

*Foramen* (foramina) of coracoid omal end: 0, present, 1, absent.

*Processus procoracoideus*: 0, little developed; 1, well developed.
Processus acrocoracoideus: 0, little developed; 1, well developed.

Brachial tuberosity (tuberculum brachiale): 0, little developed; 1, developed; 2, well developed.

Sulcus medialis supracoracoidei: 0, straight; 1, rounded; 2, almost circular.

Fossa pneumotricipitalis: 0, single fossa; 1, double fossa: present of an additional fossa.

Crista deltopectoralis: 0, developed; 1, reduced.

Crus ventralis fossae: 0, little developed; 1, well developed.

Crus dorsalis fossae: 0, little developed; 1, well developed.

Shaft shape: 0, curved; 1, not curved.

Depth of incisura capitis: 0, shallow; 1, moderately deep; 2, deep.

Processus flexorius: 0, dorso-caudally deflected edge; 1, straight edge.

Processus supracondylaris dorsalis: 0, double; 1, single.

Processus supracondylaris dorsalis: 0, little developed; 1, developed; 2, well developed.

Tuberculum ligamenti collateralis ventralis: 0, projecting; 1, not projecting.

Cotyla ventralis: 0, ventral edge developed and almost circular; 1, convex ventral edge.

Cotyla dorsalis: 0, little developed; 1, large.

Position of the dorso-proximal edge of the incisura tendinosa (for mm extensor metacarpul
ulnaris and extensor digitorum communis), distal ulna: 0, proximal; 1, distal.

Papillae remigales caudales: 0, almost absent; 1, little developed; 2, developed; 3, well developed.

Processus dentiformis: 0, absent; 1, little developed: edge with a slightly wavy; 2, developed;
3, well developed.

Position of processus intermetacarpalis: 0, proximal; 1, more proximal.

Distal symphysis of os metacarpale minus: 0, the os metacarpale minus is lightly protruding,
and forms a marked square projection; 1, the distal end of os metacarpale minus is moderately
protruding and its cranial portions forms a projection that reaches farther distally than the facies rticularis digitalis minor (Mourer-Chauviré et al., 1989; Mayr and Manegold 2006).

Processus extensorius: 0, not ventrally deflected; 1, ventrally deflected; 2, slightly ventrally dejected.

Blade of Phx 1 digiti majoris: 0, straight edge; 1, slightly rounded edge; 2, rounded edge (Manegold, 2005).

Processus internus indicis: 0, present; 1, absent.

Femur: hollow just distal to proximal articular surface, caudal side: 0, absent; 1, shallow; 2, marked.

Medial crest (tibiotarsis proximal most shaft): 0, absent; 1, present.

Tiny proximo-distal groove between the tuberositas retinaculi extensorius lateralis and the tuberculum retinaculi m fibularis, lateral side of distal end, proximal to the lateral condyle, rostral aspect: 0, absent; 1, it is located relatively distally; 2, it is located more proximally.

Fusion (continuity) between crista med plantaris and crista med hypotarsi: 0, absent; 1, present.

Ossified pons supratendineus: 0, not ossified, 1, ossified.

Position of pons supratendineus: 0, not ossified, 1, located proximally; 2, located proximally; 3, located less proximally; 4, located in an intermediate position.

Trochlea metatarsi II: 0, as distal as trochlea metatarsi III; 1, shorter than trochlea metatarsi III; 2, longer than trochlea metatarsi III.

Trochlea metatarsi IV: 0, as distal as trochlea metatarsi III; 1, shorter than trochlea metatarsi III; 2, longer than trochlea metatarsi III.
Supplementary Figures

Supplementary Fig. 1 Strict consensus tree, hardly resolved. As for the bootstrap analysis (Supplementary Fig. 2), the poor resolution and support convey pervasive homoplasy. The fossil is associated in a clade with five members of the Pipridae, although five other extant piprids are more basally misplaced in a wide unresolved polytomy with many Tyrannides. The fossil is, as in the bootstrap analysis, distant from \textit{Sapayoa aenigma}, which is correctly placed within the Eurylaimides.
Supplementary Fig. 2 Bootstrap analysis, with 1000 replicates. Only four nodes are supported by the bootstrap, but with a very low value (between 37 and 40%). As for the strict consensus (Supplementary Fig. 1), the poor resolution and support convey pervasive homoplasy. The fossil is however, as in the strict consensus, distant from *Sapayoa aenigma*, which is correctly placed within the Eurylaimides.
Pitta sordida
Philepitta castanea
Cymbirhynchus macrorhynchos
Calyptomena viridis
Sapayoa aenigma
Geositta cunicularia
Myrmotherula axillaris
Sakesphorus canadensis loretoyacensis
Conopophaga ardesiaca saturata
Scytalopus unicolor
Formicarius analis
Dendrocincia fuliginosa
Pipra erythrocephala
Neopelma sulphureiventer
Tyranneutes stolzmanni
Chloropipo holochlora viridior
Manacus manacus trinitatis
Machaeropterus pyrocephalus pyrocephalus
Chiroxiphia linearis
Xenopipo atronitens
Masius chrysopterus
Antilophia galeata
Pipreola arcuata
Cephalopterus ornatus
Cotinga sp
Phytotoma rara
Onychorynchus coronatus
Tityra semifasciata
Schiffornis turdina amazonum
Tyrannus dominicensis
Todirostrum sp
Rhynchocyclus olivaceus
Rhynchocyclus sp
Fossil
Acanthisitta chloris
Gerygone flavolateralis
Supplementary Fig. 3 Distal part of the tarsometatarsus and toe bones (both right side, in dorsal view) in (A) *Antilophia galeata* (Pipridae) and (B) the fossil NT-LBR-014. There is no fusion at the level of pedal phalanges bones, despite *A. galeata* exhibiting syndactyly of toes III and IV in life, and this is because syndactyly affects only the soft tissues surrounding the bones. I, first digit, positioned in distal extension in (A), in proximal extension in (B); II, second digit –only the first phalanx was preserved attached in the preparation of specimen (A); III, third digit; IV, fourth digit –only the first two phalanges were preserved attached in the preparation of specimen (A); mtI, first metatarsal; tmt, tarsometatarsus. In the fossil (B) the first phalanx of digit II presents proximally a sort of bulb that seems to be pathological. Scale bar, 1 cm.
**Supplementary Fig. 4** Simpson’s diagram of intersegment proportions of the Luberon fossil NT-LBR-014, compared with extant species of the Tyranni. The differences in Log10 of length of the main elements are expressed for the fossil and ten species of Tyranni.

**Supplementary Tables**

**Supplementary Table 1** Osteological characters as observed in the fossil passerine NT-LBR-014, and extant representatives of Tyranni families, Acanthisittidae, basal and other Passeri, and *Wieslochia weissi*, passerine from the Oligocene of Germany.

All character states of species compared to the fossil are given relative to state of the fossil. Only characters that discriminate at least one species among the Tyranni and Acanthisittidae examined have been selected here. *On occasions, character states are given not only for the extant species examined here for comparison, but for more species in the family (in such instances references are given via number in parentheses). (1) it is mentioned if other extant taxa in every genus or family concerned exhibit a crest approaching the fossil’s (after del
from this work, and characters 22 and 55 in James et al., 2003. (3) from this work and Mourer-Chauviré et al., 1989; NB: C. Mourer-Chauviré (pers. comm.) noticed (in Smithsonian Institution collections) that among 21 extant species of Furnariidae, only one exhibited a slight undulation, the others none (straight edge of major metacarpal), and among 30 species of Formicariidae, only four possessed a proc. dentiformis (the others nothing: straight edge of major metacarpal). (4) from Boles, 2006. (5) from this work, Millener, 1988, and Millener and Worthy, 1991. (6) sensu del Hoyo et al., 2019, i.e. comprising taxa earlier in the former Dendrocolaptidae. (7) also from Fjeldsa et al., 2005. (8) a few genera and species exhibit a crest that is different from that of NT-LBR-014, triangular, often acute, pointing upwards over the head, and spread caudally (some Leptasthenura spp., Furnarius cristatus, Coryphistera alaudina, and more or less in the different species of Pseudoseisura). (9) same in Pseudoseisura. (10) a few genera and species exhibit a crest that is different from that of NT-LBR-014, triangular, often acute, pointing dorso-caudally over the head, and spread caudally. Pithys albifrons exhibits original long, upright white tufts on both sides of forehead, shorter tufts below chin. (11) from this work and Feduca and Olson, 1982. (12) In Rhinocrypta a crest extends from the back of the head, that can be spread upwards, making an acute triangle. In Merulaxis feathers above the base of rostrum make a « crest » resembling that of Calyptomena but sparser. (13) An ossified bridge exists in Melanopareia (recently placed in own family). (14) Quadrato even more different in Melanopareia. (15) Apart from Masius, Antilophia and Chiroxiphia (see Table), feather ornaments over the head in the Pipridae exist also in Ilicura militaris (where it consists of short, round feather fluffy crest over rostrum base; more developed in male). (16) Apart from Cephalopterus and Rupicola (see Table), in the Cotingidae only Phytotoma exhibits feather head ornament, especially P. raimondii (rear head, spreading upward). (17) In the Tyrannidae, in addition to some species of Contopus (short, slight crest back to top of
head; see Table), crests exist in several genera and species, where always at the back of head, forming when spread a crest with longest feathers toward the top of head (extent of crest variable among genera and species concerned). (For instance also the crest of Comptostoma is more on top of head and shorter (and still toward back)). An exception consists in Anairetes (variable among species) of a prominent frontal crest of long feathers implanted over the rostrum base, and pointing upwards and backwards; they form either a fan or a bifurcated crest (like horns) of long, thin feathers. (18) from this work, Feduccia and Olson, 19829 and Rich et al., 198510. (19) from Feduccia and Olson, 19829, and Rich et al., 198510. (20) data also from Bock, 196311 and Olson et al., 198312 (NB: Turnagra now known to be in the Oriolidae13). (21) data also from Bock, 196311. (22) The fossa is simple in all the Passeriformes except most of the the Oscines Passerida - and a few Oscines Corvoidea - where derived states of a double fossa occur polyphyletically; pneumatic in Corvoidea, either pneumatic or non-pneumatic in Passerida2,3,14. (23) A processus dentiformis is present in most of the Passerida, while within the Corvoidea it is either absent or present3,15,16. (24) Oligocene, Wiesloch-Frauenweiler (Germany); assigned to stem Passeriformes or stem Tyranni17,18. NB: for several modern specimens, character states are absent due to the lack of the element or element part, or the incomplete specimen preparation, obscuring detail by ligaments for instance. It is specified for which specimens the skull only could be examined.
| Taxon | Beak | Forehead | Variations |
|-------|------|----------|------------|
| Machaeropterus pyrocephalus | Flare | Flare, Elongated | Similar |
| Thamnophilus doliatus | Flare | Flare, Flare, Flare | Similar |
| Onychorhynchus coronatus | Flare | Flare, Flare, Flare | Similar |
| Tyranneutes stolzmanni | Flare | Flare, Flare, Flare | Similar |
| Dendrocincla fuliginosa | Flare | Flare, Flare, Flare | Similar |
| Acanthisia chloris | Flare | Flare, Flare, Flare | Similar |
| Xenopipo atronitens | Flare | Flare, Flare, Flare | Similar |
| Manacus manacus | Flare | Flare, Flare, Flare | Similar |
| Schiffornis | Flare | Flare, Flare, Flare | Similar |
| Procnias sp. | Flare | Flare, Flare, Flare | Similar |
Atrichornithidae

Phalonorhynchidae

Climacteridae

Meliphagidae

Pardalothidae

Acanthizidae

Pomatostomidae

Paradisaeidae

Other oscines

Many Corvoidea: free lacrimal present; most Passerida: free lacrimal absent

Many Corvoidea: dorsal fenestra absent; many Passerida: dorsal fenestra present

Corvidae: proc. orbitalis shorter, slightly narrower, expanded

Corvidae: yes

Corvidae: very much developed, much more developed laterally

Wieslochia weissi †
| Taxon                        | Cymbirhynchus macrorhynchos | Tyrannidae      | Calyptomenidae | Furnariidae | Tityridae | Sapayoa taenigma | Phytotoma rara | Todirostrum sp. | CoEnga sp. |
|-----------------------------|-----------------------------|-----------------|----------------|-------------|-----------|-----------------|---------------|----------------|-------------|

**Note:**
- More curved distally.
- Maximal curvature.
- Rather similar but more curved and distally (except wider; area of Scapula).
- Two similar fossae, unique, pneumonia.
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| Family            | Genus                | Species                  | Blade       | Lamina     | Pneuma     | Prominent | Division | Dorsal | Ventral | Symphysis | Special Features                                      |
|-------------------|----------------------|--------------------------|-------------|------------|------------|-----------|----------|--------|---------|-----------|-------------------------------------------------------|
| Seriophagidae     | Atrichornis          | sp.                      | curved      | more       | non-prominent | flat      | slight   | double | more     |            |                                                      |
|                   |                      | Great Spotted Cuckoo     | curved      | more       | non-prominent | flat      | slight   | double | more     |            |                                                      |
|                   |                      | Spotted Cuckoo           | curved      | more       | non-prominent | flat      | slight   | double | more     |            |                                                      |
| Meliphagidae      |                      | Philemon corniculatus    | straight    | wider      | non-prominent | flat      | slight   | double | more     |            |                                                      |
|                   |                      | Meliphaga lewini         | straight    | wider      | non-prominent | flat      | slight   | double | more     |            |                                                      |
|                   |                      | Manorina melanocephala  | straight    | wider      | non-prominent | flat      | slight   | double | more     |            |                                                      |
| Pardalidae        |                      | Pardalotus punctatus    | more curved and angular | distally | unique, | very well marked |            |          |        |          | more curved and angular, symphysis poorly developed |
| Acanthizidae      |                      | Gerygone flavolateralis  | rather similar | double | dorsal fossa | prominent |            |        |          | double    | more angular, symphysis poorly developed |
| Pomatostomidae    |                      | Pomatostomus temporalis | more curved and angular | distally | unique, | very well marked |            |          |        |          | more curved and angular, symphysis poorly developed |
| Paradisaeidae     |                      | Ptilinopus paradiseus   | more curved and angular | distally | unique, | very well marked |            |          |        |          | more curved and angular, symphysis poorly developed |
| Other oscines     |                      | Cephalopterus dominus    |            |            |            |            |          |        |          |            | more curved and angular, symphysis poorly developed |
|                   |                      | Cephalopterus decipiens |            |            |            |            |          |        |          |            | more curved and angular, symphysis poorly developed |
|                   |                      | Cephalopterus neglectus |            |            |            |            |          |        |          |            | more curved and angular, symphysis poorly developed |

**Note:** The table includes various bird species belonging to different families, with columns indicating the presence or absence of certain features such as blade, lamina, pneuma, prominent, division, and special features like symphysis and dorsal fossa.
| Taxon       | Suborder to Family | Comments |
|------------|-------------------|----------|
| Tyrannides | Thamnophilidae    |          |
| Eurylaimides | Rhinocryptidae |          |
| Acanthisioidae | Philepidae |          |
| Pipreola intermedia signata | |          |
| Conopophaga ardensia saturata | |          |
| Chloropipo holochlora viridior | |          |
| Thamnophilus coecus | |          |
| Onychorhynchus coronatus | |          |
| Neopelma sulphureiventer | |          |
| Contopus lepidus | |          |
| Dendrocincla fuliginosa | |          |
| Tyrannus dominicensis | |          |
| Acanthisia chloris | |          |
| Xenopipo treronitens | |          |
| Geosia cunicularia | |          |
| Chiroxiphia linearis | |          |
| Schiffornis | |          |
| Formicarius analis | |          |
| Tibiotarsus plantaris | |          |
| Tarsometatarsus | |          |
| Ossified pons (flapped) | |          |
| Shape of claws | |          |
| Length of legs | |          |
| Fused tarsometatarsi | |          |
| Family: yes/no | |          |
| Family               | Genus                        | Species            | Present? | Marked? | Rather | Similar? | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |
|---------------------|-----------------------------|--------------------|----------|---------|---------|----------|-----|-------------------------------|------------------------------------|--------------------|----------------------|-----|------------------------|
| Passeridae           | Passer          | Passeridae          | Present; | Marked; | Rather; | Similar; | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |
| Menuridae            | Menura         | novaehollandiae    | Absent;  | Marked; | Rather; | Similar; | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |
| Atrichornithidae     | Atrichornis     |                  |          |         |        |          |    |                                |                                    | Yes                |                      |     |                        |
| Ploniornithidae      | Ploniornis      | violaceus          | Absent;  | Almost absent; | Hardly visible; | Yes; | Extension slightly less distal |                                    | Yes                |                      |     |                        |
| Climacteridae        | Climacteris     |                  |          |         |        |          |    |                                |                                    | Yes                |                      |     |                        |
| Meliphagidae         | Meliphaga       | flavolateralis     | Absent;  | Present; | Marked; | Missing; | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |
| Pardalidae           | Pardalopsis     | punctatus          | Absent;  | Present; | Marked; | Missing; | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |
| Acanthizidae         | Acanthiza       | flavolateralis     | Absent;  | Present; | Marked; | Missing; | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |
| Pomatistomidae       | Pomatostomus    | temporalis trivirgatus | Absent;  | Very light; | Very light; | Yes; | Extension slightly less distal |                                    | Yes                |                      |     |                        |
| Paradisaeidae        | Paradisaea      | minor              | Absent;  | Almost absent; | Small; | Almost absent; | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |
| Other oscines        |                  |                   | Absent;  | Almost absent; | Small; | Almost absent; | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |
| Corvidae             |                    |                   | Present; | Less distal; | Absent to very light; | Generally present; | Yes; | Extension slightly more distal |                                    | Yes                |                      |     |                        |
| Corvidae             |                    |                   | Present; | More distal; | No (or extremely plantarly); | Generally present; | Yes; | Extension slightly less distal than III |                                    | Yes                |                      |     |                        |
| Corvidae             |                    |                   | Present; | Very slightly less distal extension than the III | No |                     |     |                                |                                    | Yes                |                      |     |                        |
| Wieslochia weissi    | Wieslochia      | weissi             | Absent;  | Almost absent; | Small; | Almost absent; | No; | Wide gap between the two crests | Crista plantaris very likely developed | Present as fossil | Extension less distal | No; | More curved and tapering |

Note: “Present” indicates the presence of the species. “Absent” indicates the absence of the species. “Marked” indicates a marked presence. “Rather” indicates a rather similar presence. “Similar” indicates a similar presence. “No” indicates no presence. “Wide gap” indicates a wide gap between the two crests. “Crista plantaris” indicates the development of the crista plantaris. “Extension” indicates the extension of the species. “More curved and tapering” indicates a more curved and tapering presence.
**Supplementary Table 2** Additional characters in the fossil NT-LBR-014 and extant Tyrannida (i.e., Pipridae, Cotingidae, Tityridae and Tyrannidae).

All character states of species compared to the fossil are given relative to state of the fossil.

NB: for several modern specimens, character states are absent due to the lack of the element or element part, or the incomplete specimen preparation, obscuring detail by ligaments for instance. It is specified for which specimens the skull only could be examined.
| Family          | Species                      | Size of nasal opening | Lateral parts of ectethmoid | Crus ventralis fossa | Crus dorsalis fossa | Cotyla dorsalis | Position of the dorso-proximal edge of the incisura tendinosa (for mm. extensor digitorum communis), distal ulna |
|----------------|------------------------------|-----------------------|-----------------------------|----------------------|---------------------|----------------|-----------------------------------------------------------|
| Pipridae       | Pipra erythrocephala         | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
|                | Neopelma sulphureventer      | large; more than half rostrum length | gap reduced | ? | ? | hollow; little developed | proximal |
|                | Tyrannus stolzmanni          | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
|                | Chloropipo halochiora viridior | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
|                | Manacus manacus              | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
|                | Machaeropterus pyrocephalus  | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
|                | Chiraxphix linearis          | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
|                | Xenopipo atrtonitis          | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
|                | Masius chrysopterus          | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
|                | Antilophia galeatae          | large; more than half rostrum length | gap reduced | little developed | well developed | hollow; little developed | proximal |
| Cotingidae     | Pipreola arcuata             | medium-sized          | gap larger | well developed | well developed | flat; wide | proximal |
|                | Cephalopterus ornatus        | medium-sized          | gap larger | well developed | well developed | flat; wide | proximal |
|                | Cotinga sp.                  | medium-sized          | gap larger | well developed | well developed | flat; wide | proximal |
|                | Procnias sp. (skull)         | medium-sized          | gap larger | ? | ? | ? | ? |
| Tyridae        | Pipreola intermedi signata (skull) | medium-sized          | gap larger | ? | ? | ? | ? |
|                | Phytoptoma rara              | medium-sized          | gap larger | well developed | well developed | flat; wide | proximal |
|                | Oxyrunax cristatus           | small                 | gap larger | ? | ? | flat; wide | proximal |
|                | Omophorhynchus coronatus     | small                 | gap larger | well developed | well developed | flat; wide | proximal |
|                | Tyrrha semifasciata          | small                 | gap larger | well developed | well developed | flat; wide | proximal |
|                | Schiffonis turdina           | small                 | gap larger | well developed | well developed | flat; wide | proximal |
|                | Tyrannus dominicensis        | large; more than half rostrum length | gap moderate but larger than fossi | well developed | little developed | hollow; wide | distal |
|                | Tyrannus sp.                 | large; more than half rostrum length | gap moderate but larger than fossi | well developed | little developed | hollow; wide | distal |
|                | Todirostrum sp.              | large; more than half rostrum length | gap moderate but larger than fossi | well developed | little developed | hollow; wide | distal |
|                | Contopus latirstris          | large; more than half rostrum length | gap moderate but larger than fossi | ? | ? | hollow; wide | distal |
|                | Rhynchocyclus olivaceus      | large; more than half rostrum length | gap moderate but larger than fossi | well developed | little developed | hollow; wide | distal |
|                | Rhynchocyclus sp.            | large; more than half rostrum length | gap moderate but larger than fossi | well developed | little developed | hollow; wide | distal |
**Supplementary Table 3** Measurements (lengths) of the main bones of the Luberon fossil NT-LBR-014 (mm).

| Skull | Wing | Leg |
|-------|------|-----|
| Cranium | Humerus | 19.4 | Femur | 18.6 |
| Beak | Ulna | 25.2 | Tibiotarsus | 28.7 |
| | Carpometacarpus | 13.6 | Tarsometatarsus | 20.4 |
| Scapular belt | Wing Phalanx 1 of major digit | 6.5 | Digit III | 16.8 |
| Coracoid | Total length of wing bones | 64.7 | Total length of leg bones | 84.5 |
| Scapula | 19.6 | |

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**Supplementary Table 4** States of characters selected and coded for the radial visualisation in Fig. 5. The character states are coded in order to categorize observations in Supplementary Tables 1 and 2, as follows. State (0) corresponds to absence of the character, state (1) to presence of the character but state different from the fossil’s, and state (2) to presence of character and state similar or identical to the fossil’s. The extant species of comparison are limited here to the Tyrannides for which all characters were assessable, and the characters are those exhibiting heterogeneous states across the Tyrannides.
| Content (shape, dental profiles) | Feather crest | Skull | Coracoid | Scapula | Humerus | Ulna | Carpal-metacarpus | Proximal wing phalange of major digit | Femur | Tibiotarsus | Tarsometatarsus | Prognathism (angle of superciliary processes) | Medial wing phalange of major digit |
|----------------------------------|--------------|-------|----------|---------|---------|-----|-----------------|--------------------------------------|-------|-----------|--------------|--------------------------------|-------------------------------|
| Fossil                           |              |       |          |         |         |     |                 |                                       |       |           |              |                                 |                                |
| Geositta cunicularia             | 2             | 2     | 2        | 2       | 2       | 2   |                 |                                       |       |           |              |                                 |                                |
| Dendrocincla filignosa           | 1             | 0     | 0        | 1       | 2       | 1   |                 |                                       |       |           |              |                                 |                                |
| Myrmotherula axillaris           | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Sterophasia caripensis           | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Conopophagidae ardiaca          | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Bispallidum unicolor             | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| fremeliodes euriale             | 2             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Tyrannus albicaudatus            | 1             | 2     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Oliphante albilatera             | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Monarchus melas                | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Macrochelidae punctulata         | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Chrysophorus cristatus           | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Anaplectes attochae             | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Mecistopterus cyaneus            | 1             | 1     | 1        | 1       | 2       | 1   |                 |                                       |       |           |              |                                 |                                |
| Archaeopteryx sp.                | 2             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Caprimulgus rufus                | 1             | 1     | 1        | 1       | 1       | 2   |                 |                                       |       |           |              |                                 |                                |
| Chalinoptilus sp.                | 1             | 1     | 1        | 1       | 2       | 1   |                 |                                       |       |           |              |                                 |                                |
| Dacelo montanus                  | 2             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Leptonycteris curasoae           | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Rhinopoma megaloureum           | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Tadaridae sp.                    | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Aegostoma confusum              | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Hylomyidae sp.                   | 2             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Geositta cunicularia             | 2             | 2     | 2        | 2       | 2       | 2   |                 |                                       |       |           |              |                                 |                                |
| Dendrocincla filignosa           | 1             | 0     | 0        | 1       | 2       | 1   |                 |                                       |       |           |              |                                 |                                |
| Myrmotherula axillaris           | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Sterophasia caripensis           | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Conopophagidae ardiaca          | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Bispallidum unicolor             | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| fremeliodes euriale             | 2             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| tyrannus albicaudatus            | 1             | 2     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Oliphante albilatera             | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Monarchus melas                | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Macrochelidae punctulata         | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Chrysophorus cristatus           | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Anaplectes attochae             | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Mecistopterus cyaneus            | 1             | 1     | 1        | 1       | 2       | 1   |                 |                                       |       |           |              |                                 |                                |
| Archaeopteryx sp.                | 2             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Caprimulgus rufus                | 1             | 1     | 1        | 1       | 1       | 2   |                 |                                       |       |           |              |                                 |                                |
| Chalinoptilus sp.                | 1             | 1     | 1        | 1       | 2       | 1   |                 |                                       |       |           |              |                                 |                                |
| Dacelo montanus                  | 2             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Leptonycteris curasoae           | 1             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Rhinopoma megaloureum           | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Tadaridae sp.                    | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Aegostoma confusum              | 1             | 0     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
| Hylomyidae sp.                   | 2             | 1     | 1        | 1       | 1       | 1   |                 |                                       |       |           |              |                                 |                                |
1 Supplementary Table 5 Character matrix used for the phylogenetic analyses.

2
| Trait | S. philadelphia | S. olivaceus | S. stolzmanni | C. ardesiaca | G. flavolateralis | C. holochlora | P. terythrocephala | X. atronitens | C. viridis | A. chloris | C. linearis | P. pyrocephalus | N. coronatus | N. viridior |
|-------|----------------|-------------|---------------|-------------|----------------|-------------|----------------|-------------|-----------|---------|----------|--------------|----------|-----------|
| Size of nasal process | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Os lacrimale | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Foramen incisura capitis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Processus flexorius | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Processus supracondylaris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of processus indicis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of pons | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of os retinaculi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of crista medialis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of foramen remigales | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of processus tuberculum ulnare | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of processus tuberculum capitatum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of tuberculum Brachial | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of crus ventralis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of fossae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of brachial trench | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of canal femoris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of processus coracoideus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of processus metacarpi ulnaris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of processus metacarpi digitales | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of cotyla dorsi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of tuberculum capitale | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Position of retinaculi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
References (for Supplementary Table 1)

1. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds) *Handbook of the Birds of the World Alive* (Lynx Edicions, Barcelona, 2019). (retrieved from https://www.hbw.com/ on 13 March 2019).

2. James, H. F., Ericson, P. G. P., Slikas, B., Lei, F. M., Gill, F. B. & Olson, S. L.

   *Pseudopodoces humilis*, a misclassified terrestrial tit (Paridae) of the Tibetan Plateau: evolutionary consequences of shifting adaptive zones. *Ibis* **145**, 185–202 (2003).

3. Mourer-Chauviré, C., Hugueney, M. & Jonet, P. Découverte de Passeriformes dans l'Oligocène supérieur de France. *C. R. Acad. Sci. Paris, Série II* **309**, 843–849 (1989).

4. Boles, W. E. A new songbird (Aves: Passeriformes) from the mid-Cenozoic of Riversleigh, northwestern Queensland. *Alcheringa* Special Issue 1, 31–37 (2006).

5. Millener, P. R. Contributions to New Zealand's Late Quaternary avifauna. 1: *Pachyplichas*, a new genus of wren (Aves: Acanthisittidae), with two new species. *Journal of the Royal Society of New Zealand* **18**, 383–406 (1988).

6. Millener, P. R. & Worthy, T. H. Contributions to New Zealand's Late Quaternary avifauna. 2: *Dendroscansor decurvirostris*, a new genus and species of wren (Aves: Acanthisittidae). *Journal of the Royal Society of New Zealand* **21**, 179–200 (1991).

7. Fjeldsa, J., Irestedt, M. & Ericson, P. G. P. Molecular data reveal some major adaptational shifts in the early evolution of the most diverse avian family, the Furnariidae. *J. Ornithol.* **146**, 1–13 (2005).

8. Tonni, E. P. & Noriega, J. I. Una especie extinta de *Pseudoseisura* Reichenbach 1853 (Passeriformes: Furnariidae) del Pleistoceno de la Argentina: comentarios filogeneticos. *Ornitologia Neotropical* **12**, 29–44 (2001).
9. Feduccia, A. & Olson, S. L. Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the Southern Hemisphere. *Smithsonian Contributions to Zoology* **366**, 1–22 (1982).

10. Rich, P. V., McEvey, A. R. & Baird, R. F. Osteological comparison of the scrub-birds, *Atrichornis*, and Lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae). *Records of the Australian Museum* **37**, 165–191 (1985).

11. Bock, W. J. Relationships between the birds of paradise and the bower birds. *The Condor* **65**, 91–125 (1963).

12. Olson, S. L., Parkes, K. C., Clench, M. H. & Borecky, S. R. The affinities of the New Zealand passerine genus *Turnagra*. *Notornis* **30**, 319–336 (1983).

13. Zuccon, D. & Ericson, P. G. P. Molecular and morphological evidences place the extinct New Zealand endemic *Turnagra capensis* in the Oriolidae. *Mol. Phylogen. Evol.* **62**, 414–426 (2012).

14. Bock, W. J. The pneumatic fossa of the humerus in the Passeres. *The Auk* **79**, 425–443 (1962).

15. Pocock, T. N. Osteology. Contributions to the osteology of African birds. *Proceedings of the Second Pan African Ornithological Congress*, 83–94 (1966).

16. Harrison, C. J. O. Additional information on the carpometacarpal process as a taxonomic character. *Bulletin B.O.C.* **89**, 27–29 (1969).

17. Mayr, G. & Manegold, A. The oldest european fossil songbird from the Early Oligocene of Germany. *Naturwissenschaften* **91**, 173–177 (2004).

18. Mayr, G. & Manegold, A. New specimens of the earliest European passeriform bird. *Acta Palaeontologica Polonica* **51**, 315–323 (2006).
#NEXUS
BEGIN TAXA;
    DIMENSIONS NTAX=36;
    taxlabels
Fossil
Pitta_sordida
Philepitta_castanea
Cymbirhynchus_macrorhynchos
Calyptomena_viridis
Sapayoa_aenigma
Geositta_cunicularia
Myrmotherula_axillaris
Sakesphorus_canadensis_loretoyacuensis
Conopophaga_ardesiaca_saturata
Scytalopus_unicolor
Formicarius_analis
Dendrocincla_fuliginosa
Pipra_erythrocephala
Neopelma_sulphureiventer
Tyranneutes_stolzmanni
Chloropipo_holochlora_virdior
Manacus_manacus_trinitatis
Machaeropeterus_pyrocephalus_pyrocephalus
Chiroxiphia_linearis
Xenopipo_atronitens
Masius_chrysopterus
Antilophia_galeata
Pipreola_arculata
Cephalopterus_ornatus
Cotinga_sp
Phytotoma_rara
Onychorhynchus_coronatus
Tityra_semifasciata
Schiffornis_turdina_amazonum
Tyrannus_dominicensis
Todirostrum_sp
Rhynchoecyclus_olivaceus
Rhynchoecyclus_sp
Acanthisitta_chloris
Gerygone_flavolateralis
;
end;
BEGIN CHARACTERS;
    DIMENSIONS NCHAR=42;
    FORMAT SYMBOLS = "0 1 2 3 4" GAP=- MISSING = ?;
    Charlabels
Feathercrest
Sizeorbits
Formorbits
Taillenarine
Fenestraantorb
Lacrimal
LatDorsEctethmoid
LatEtectmoid
Crestculmen
Foramencor
Procoracorideus
Acrocoracoideus
Tubbrachiale
Sulsupracoracoidei
Fossapneum
Cristadeltpect
Crusventral
Crusdorsal
Curvedhum
Profcapitis
Procflexorius
Procsupcondylords
Procsupcondylords
Ulna
Cotylavent
Cotyldors
Tubcondords
Papillae
Procdent
Positionprocintrcarm
Osmetacminus
Procexentens
Lameborder
Procindicis
Fosscaud
Medcrest
Incintcondy
Hypotarsi
Ponttmt
Positionponttmt
Trochlint
Trochlext
;

MATRIX

Fossile 3 1 3 1 2 3 4
1 1 1 2 2 3 3 2
1 1 2 2 3 2 2 3
2 2 1 1 2 3 1 2
1 1 1 3 1 3 1 2
2 1 2

Pitta_sordida 1 1 1 ? 2 1
2 ? 1 1 2 2 1 1
2 1 ? ? 2 2 1 2
3 2 1 ? ? 4 3 1
2 2 2 1 2 1 2 1
2 2 1 3

Philepitta_castanea 1 1 1 ? 2
| Species                                      | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---------------------------------------------|---|---|---|---|---|---|---|---|---|
| Cymbirhynchus_macrorhynchos                  | 1 | 1 | 1 | 1 | ? |   |   |   |   |
| Calyptomena_viridis                         | 2 | 1 | 1 | ? | 1 |   |   |   |   |
| Sapayoa_aenigma                              | 1 | 1 | 1 | ? | 2 | 1 |   |   |   |
| Geositta_cunicularia                         | 2 | 3 | ? | 1 | 1 | 1 | 2 | 1 |   |
| Myrmotherula_axillaris                       | 2 | 2 | 1 | ? | ? | 2 | 1 | 2 |   |
| Sakesphorus_canadensis_loretoyacuensis       | 4 | 3 | 1 | 2 |   |   |   |   |   |
| Conopophaga_ardeziaca_saturata               | 1 | 1 | 1 | 2 | ? |   |   |   |   |
| Scytalopus_unicolor                           | 2 | 2 | ? | 2 | 2 | 1 | 1 | 1 | 1|
|                                             | 3 | 2 | ? | ? | ? | 1 | 2 | 2 |   |
|                                             | 2 | 3 | ? | ? | ? | 1 | 4 |   |   |
| # | 1  | 2  | 1  | 2  | 2  | 3  | 1  | 2  |
|---|---|---|---|---|---|---|---|---|
| 1 | 4 | 3 | 1 | 2 |
| Formicarius_analis | 1 | 1 | 2 | ? | 1 |
| 2 | 2 | ? | 1 | 1 | 1 | 1 | 1 |
| 2 | 2 | 1 | ? | ? | 2 | 2 | 2 |
| 2 | 3 | 2 | ? | ? | ? | 3 | 3 |
| 1 | 2 | 3 | 2 | 2 | 1 | 1 | 2 |
| 1 | 3 | 1 | 1 | ? |
| Dendrocincla_fuliginosus | 1 | 1 | 2 | ? | 1 |
| 2 | 4 | ? | 1 | 1 | 2 | 2 | 2 |
| 2 | 2 | 1 | ? | ? | 2 | 2 | ? |
| 2 | 2 | 2 | ? | ? | ? | 2 | 2 |
| 1 | 2 | 1 | 2 | 2 | 1 | 2 | 2 |
| 1 | 2 | 2 | 2 | 2 |
| Pipra_erythrocephala | 2 | 1 | 3 | 1 | 1 |
| 3 | 2 | 1 | 1 | 1 | 2 |
| 2 | ? | ? | 2 | 1 | 1 | 2 | 2 |
| 2 | 2 | 2 | 3 | 2 | 2 | 1 | 1 |
| 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 |
| 1 | 2 | 1 | 2 | 2 | 1 | 2 |
| Neopelma_sulphureiventer | 1 | 2 | 2 | 1 |
| 1 | ? | 2 | 1 | 1 | 1 | 2 | 2 |
| 2 | 2 | ? | ? | 1 |
| 2 | ? | ? | ? | ? | 2 | 2 |
| 1 | 1 | 1 | 1 | 1 | 2 |
| 1 | ? | ? | ? | ? | ? | ? |
| ? | ? | ? |
| Tyranneutes_stolzmanni | 1 | 1 | 3 | 1 |
| 1 | ? | 2 | 1 | 1 | 1 | 2 | 2 |
| 2 | 3 | 2 | 1 | 1 | 2 | 2 | 2 |
| 2 | 2 | 3 | 2 | ? | 1 | 1 | 1 |
| 1 | 1 | 2 | 1 | 1 | 1 | 1 |
| 3 | 1 | 2 | 2 | 1 | 1 |
| Chloropipo_holochlora_viridior | 1 | 1 | 2 | 1 |
| 2 | ? | 2 | 1 | 1 | 1 | 2 | 2 |
| 2 | 2 | 2 | 1 | 1 | 2 | 2 | 1 |
| 2 | 2 | 3 | 2 | ? | 1 | 1 | 2 |
| 1 | 1 | 2 | 1 | 1 | 1 | 1 |
| 2 | 1 | 2 | 2 | 1 | 2 |
| Manacus_manacus_trinitatis | 1 | 1 | 2 | 1 |
| 1 | ? | 3 | 1 | 1 | ? | 2 | 2 |
| 2 | 2 | 2 | 1 | 1 | 2 | 2 | 1 |
| 2 | 2 | 3 | 2 | ? | 1 | 1 | 2 |
| 3 | 1 | 2 | 1 | 1 | 2 | 1 |
| 1 | ? | 1 | ? | ? | 1 | 2 |
| Machaeropterus_pyrocephalus_pyrocephalus | 1 | 1 | 2 |
| 1 | 1 | ? | 2 | 1 | 1 | ? | 2 |
| 2 | 1 | 3 | 2 | 1 | 1 | 2 | 2 |
| 2 | 2 | 2 | 3 | 2 | ? | 1 | 1 |
| 4 | 2 | 1 | 2 | 1 | 1 | 1 |
| 1 | ? | 1 | 2 | 2 | 1 | 1 |
| Species                          | 1 | 1 | 2 | 1 | 1 |
|---------------------------------|--|--|--|--|--|
| Chiroxiphia_linearis            | 3 | 2 | 1 | 1 | ? |
| Xenopipo_atronitens             | 2 | 1 | 2 | 1 | 1 |
| Masius_chrysopterus             | 3 | 4 | 1 | 1 | 1 |
| Antilophia_galeata              | 2 | 1 | 1 | 2 | 1 |
| Pipreola_arcurata               | 1 | 2 | 2 | 1 | ? |
| Cephalopterus_ornatus           | 2 | 2 | 1 | 2 | 1 |
| Cotinga_sp                     | 1 | 3 | 1 | 1 | ? |
| Phytotoma_rara                  | 2 | 3 | 1 | 1 | ? |
| Onychorynchus_coronatus         | 2 | 1 | 1 | 1 | 1 |
|   |   |   |   |   |   |
|---|---|---|---|---|---|
| 1 | 2 | 2 | 2 | 3 |   |
| **Tityra semifasciata** | 1 | 1 | 2 | 3 | 1 |
| 1 | 2 | 3 | 1 | 1 | 2 |
| 1 | 2 | 1 | 2 | 2 | 2 |
| 2 | 3 | 2 | 2 | 2 | 1 |
| 1 | 2 | 1 | 1 | 1 | 2 |
| 1 | ? | ? | 1 | 1 |   |
| **Schiffornis turdinus amazonus** | 1 | 1 | 2 | 3 |   |
| 1 | 3 | 2 | 3 | 1 | 2 |
| 2 | 2 | 1 | 2 | 2 | 2 |
| 2 | 2 | 3 | 2 | ? | 1 |
| 2 | 1 | 2 | 1 | 1 | 1 |
| 3 | 1 | 2 | 2 | 1 | 2 |
| **Tyrannus dominicensis** | 1 | 1 | ? | 1 |   |
| 3 | 2 | 2 | 1 | 2 | 1 |
| 1 | 2 | 1 | 2 | 1 | 2 |
| 2 | 2 | 2 | 2 | 2 | 3 |
| 1 | 2 | 1 | 1 | 1 | 1 |
| 1 | 1 | 0 | 2 | 2 |   |
| **Todirostrum sp** | 1 | 1 | 2 | 1 | 1 |
| 1 | 2 | 1 | 1 | 1 | 2 |
| 2 | 1 | 2 | 1 | 2 | 2 |
| 2 | 2 | 2 | 2 | 1 | 1 |
| 2 | 1 | 1 | 1 | 2 | 3 |
| 1 | 0 | 2 | 2 |   |
| **Rhynchocyclus olivaceus** | 1 | 1 | 2 | 1 | 1 |
| 1 | 2 | 1 | 1 | 1 | 3 |
| 2 | 2 | 1 | 2 | 1 | 2 |
| 2 | 2 | 2 | 2 | 1 | 2 |
| 1 | 2 | 1 | 1 | 1 | 2 |
| 1 | 2 | 2 | 2 | ? |   |
| **Rhynchocyclus sp** | 2 | 1 | 2 | 1 | 1 |
| 2 | 2 | 1 | 2 | 1 | 2 |
| 2 | 1 | 2 | 1 | 2 | 2 |
| 2 | 1 | 1 | 1 | 2 | 3 |
| 2 | 2 | 2 | 3 |   |
| **Acanthisitta chloris** | 1 | 2 | 2 | ? | 2 |
| 1 | 1 | ? | 1 | 2 | 1 |
| 1 | ? | ? | 1 | 1 | ? |
| 1 | ? | 2 | 1 | ? | ? |
| 3 | 1 | 2 | 2 | ? | 3 |
| 2 | 1 | 2 | 1 | 2 | ? |
| **Gerygone flavolateralis** | 1 | 1 | 1 | ? | 1 |
| 2 | 1 | ? | 1 | 2 | 1 |
| 2 | 1 | 1 | ? | ? | 2 |
| 1 | 3 | 1 | 1 | ? | 3 |
| 2 | 1 | 1 | ? | ? | 2 |
| 2 | 1 | 0 | 2 | 1 |   |

END;

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roottrees/root=outgroup;
savetrees/file=tree2.tre;
describetrees/fvalue apolist;
end;