



**HAL**  
open science

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

Sécolène Riamon, Nicolas Tourment, Antoine Louchart

► **To cite this version:**

Sécolène Riamon, Nicolas Tourment, Antoine Louchart. The earliest Tyrannida (Aves, Passeriformes), from the Oligocene of France. *Scientific Reports*, 2020, 10 (1), 10.1038/s41598-020-66149-9 . hal-02909865

**HAL Id: hal-02909865**

**<https://hal.science/hal-02909865>**

Submitted on 21 Dec 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



OPEN

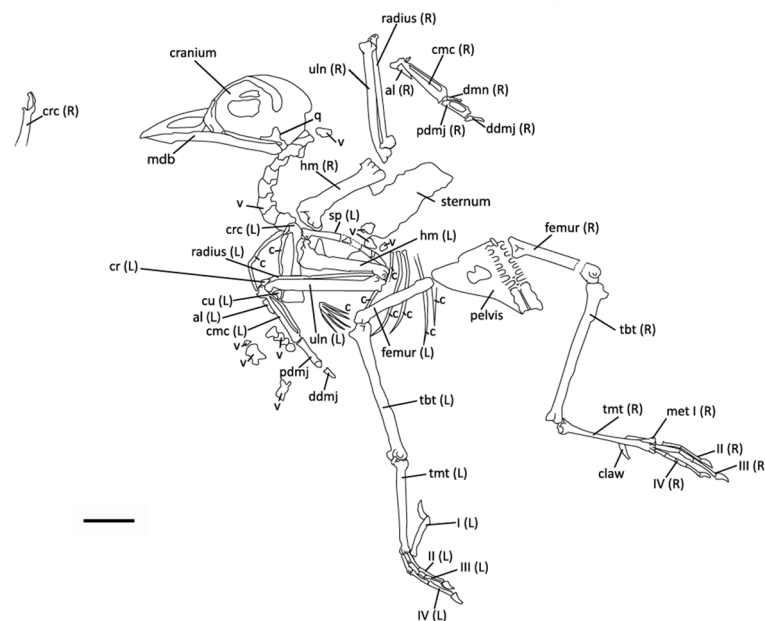
# The earliest Tyrannida (Aves, Passeriformes), from the Oligocene of France

Ségolène Riamon<sup>1</sup>, Nicolas Tourment<sup>2</sup> & Antoine Louchart<sup>1</sup>✉

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 Tyrannides. 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 Tyrannides, 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 Tyrannida 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 species<sup>1</sup>. 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 approximately as old as 30 million years (Ma)<sup>2–4</sup>. 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 fragmentary<sup>5–11</sup>, 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* (Germany<sup>12,13</sup>), *Jamna szybiaki* and *Resoviaornis jamrozi* (Poland<sup>14,15</sup>). This difficulty is also explained by (i) high apparent homoplasy observed on osteological characters within the Passeriformes<sup>12,13</sup>, 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 passerines<sup>5–15</sup>. 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 Australia<sup>16</sup>. As for the older, possible passerine remains from the lower Eocene of Australia<sup>17,18</sup>, they are fragmentary (one proximal carpometacarpus and one distal tibiotarsus) and considered to be either not sufficiently diagnostic of the Passeriformes<sup>12,19</sup> or possibly Passeriformes outside Eupasseres<sup>20</sup>. 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 Tyrannides (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.

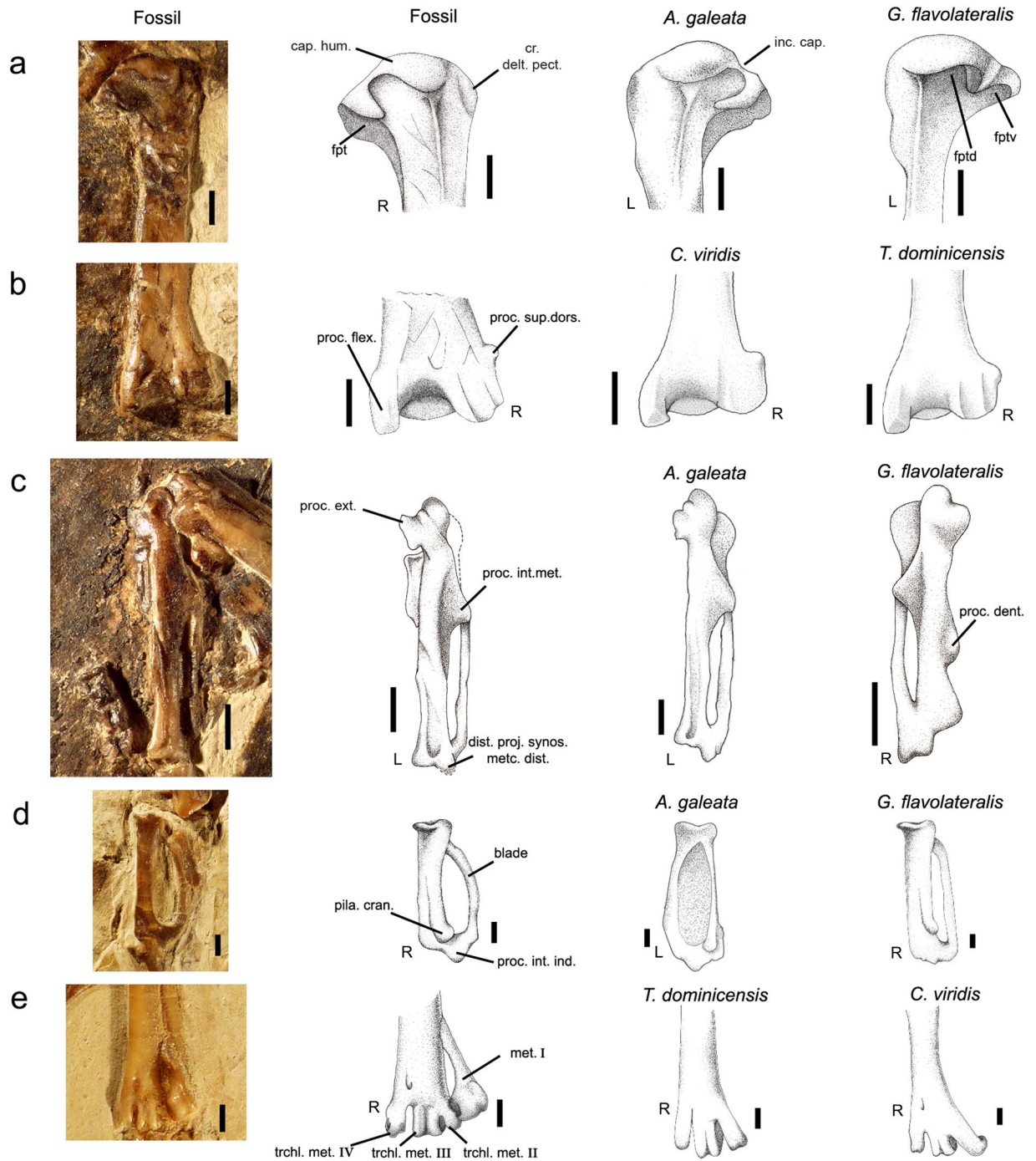
<sup>1</sup>Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, F-69622, Villeurbanne, France. <sup>2</sup>13012, Marseille, France. ✉e-mail: antoine.louchart@ens-lyon.fr



**Figure 1.** The fossil specimen NT-LBR-014 from Revest-des-Brousses, Luberon (France), and interpretative drawing. al, wing phalanx digiti alulae; c, costa; cmc, carpometacarpus; cr, os carpi radiale; crc, coracoid; cu, os carpi ulnare; ddmj, distal wing phalanx digiti majoris; dmn, wing phalanx digiti minoris; hm, humerus; mdb, mandible; met, metacarpal; pdmj, proximal wing phalanx digiti majoris; q, quadrate; sp, scapula; tbt, tibiotarsus; tmt, tarsometatarsus; uln, ulna; v, vertebra; II, III, IV, numbering of pedal digits. Scale bars, 10 mm.

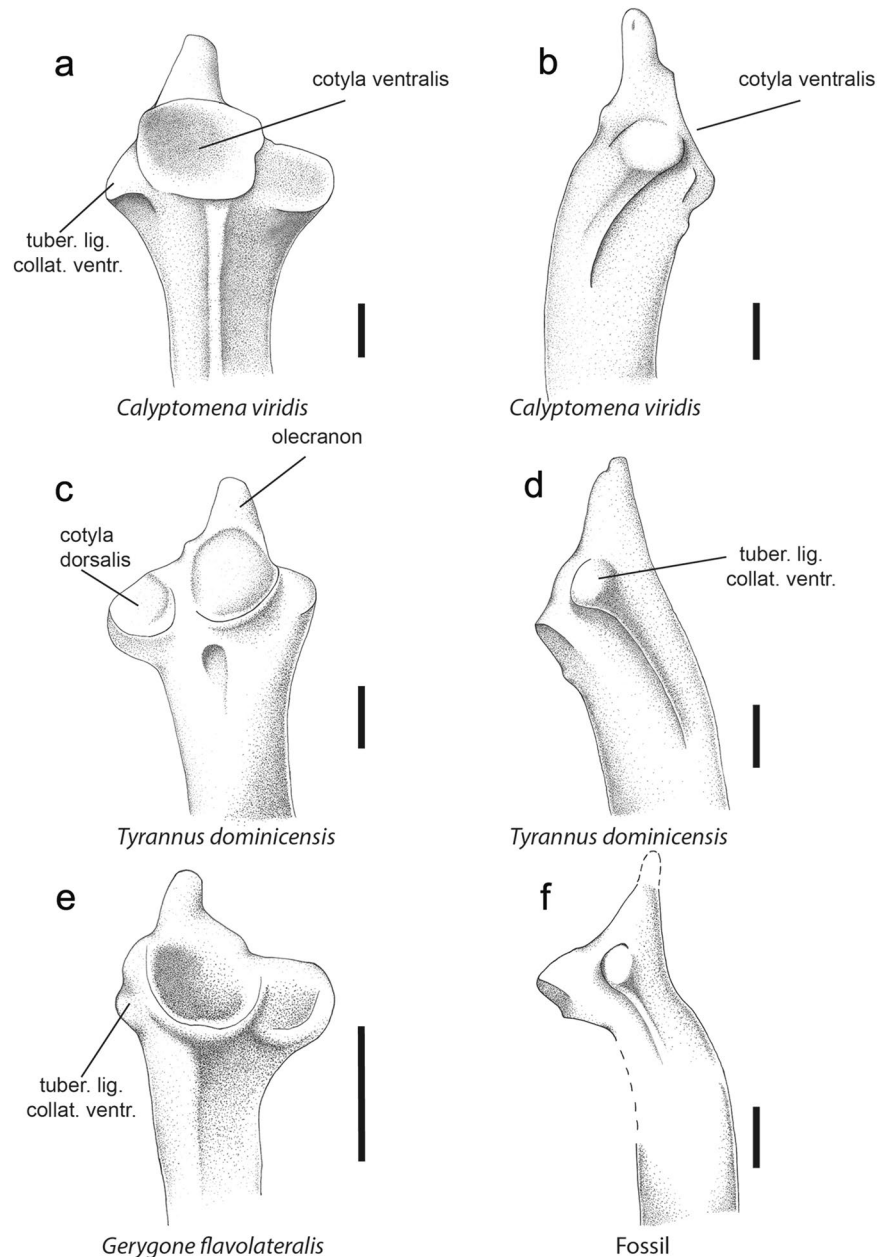
## Results

**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)<sup>18</sup>; and (iii) the processus intermetacarpalis and the os metacarpale minus are fused in the fossil, which is found only in Passeriformes<sup>21</sup> and Piciformes<sup>22</sup>, 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 2.** Selected bones of the Luberon fossil NT-LBR-014, compared with extant species (Acanthizidae, Calyptomenidae, Tyrannidae, Pipridae). Second column from the left, drawings of bones which photos are in the first column. Line a, proximal humeri in caudal view. Line b, distal humeri in caudal view. Line c, carpometacarpus in dorsal view. Line d, proximal wing phalanges digiti majoris in ventral view. Line e, distal tarsometatarsi in dorsal view. cap. hum., caput humeri; cr. delt. pect., crista deltopectoralis; dist. proj. synos. metc. dist., distal projection of synostosis metacarpalis distalis; fpt, fossa pneumotricipitalis; fptd, fossa pneumotricipitalis dorsalis; fptv, fossa pneumotricipitalis ventralis; inc. cap., incisura capitis; L, left side; met., metacarpal; pila cran., pila cranialis; proc. dent., processus dentiformis; proc. ext. processus extensorius; proc. flex., processus flexorius; proc. int. ind., processus internus indicis; proc. int. met., processus intermetacarpalis; proc. sup. dors., processus supracondylaris dorsalis; R, right side; trchl. met., trochlea metatarsi. Scale bars, 2 mm (a–c), 1 mm (d,e).

**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



**Figure 3.** Drawings of right ulna of the Luberon fossil NT-LBR-014 and ulnas of extant species (Passeri, Acanthizidae; Tyranni, Calyptomenidae and Tyrannidae). (a,b,e), left ulnas; (c,d,f), right ulnas; (a,c,e), cranial views; (b,d,f), ventral views. tuber. lig. collat. ventr., tuberositas ligamenti collateralis ventralis. Scale bars, 1 mm.

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 acroracoideus (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<sup>5,7,8,13</sup> (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-quadratojugal articulation of the suboscine type (see ref. <sup>19</sup>: 136–137.); a prominent tuberculum ligamenti collateralis ventralis of the ulna (little prominent in the Passeri)<sup>13</sup>; a tuberculum carpale more extended and spatulate (vs. shorter and obtuse in the Passeri; new described character); a processus dentiformis of the carpometacarpus poorly individualized (and moderately marked; less marked in some Tyranni; well individualized and strongly marked in the Passeri);<sup>5,7,8,13</sup> a distal extremity of the os metacarpale minus prominent and pointed (square-shaped, and more hollow in ventral view, in the Passeri);<sup>5,7,8,13</sup> a blade of the wing phalanx 1 digiti majoris with a rounded, convex border (straight border in the Passeri);<sup>7,19</sup> presence of a processus internus indicis on the distal extremity of the alar phalanx 1 digiti majoris (absent in the Passeri)<sup>7,19</sup>. 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 datasets<sup>12–14</sup>. Results of our tentative 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 subclasses.

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 Tyrannides.** The Tyranni comprises two infra-orders: the Eurylaimides (“Old World Tyranni”) and the Tyrannides (“New World Tyranni”), based on molecular data<sup>4,23–25</sup>. 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 cunicularia* (Furnariidae), *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 Tyrannides and differs from the Eurylaimides.

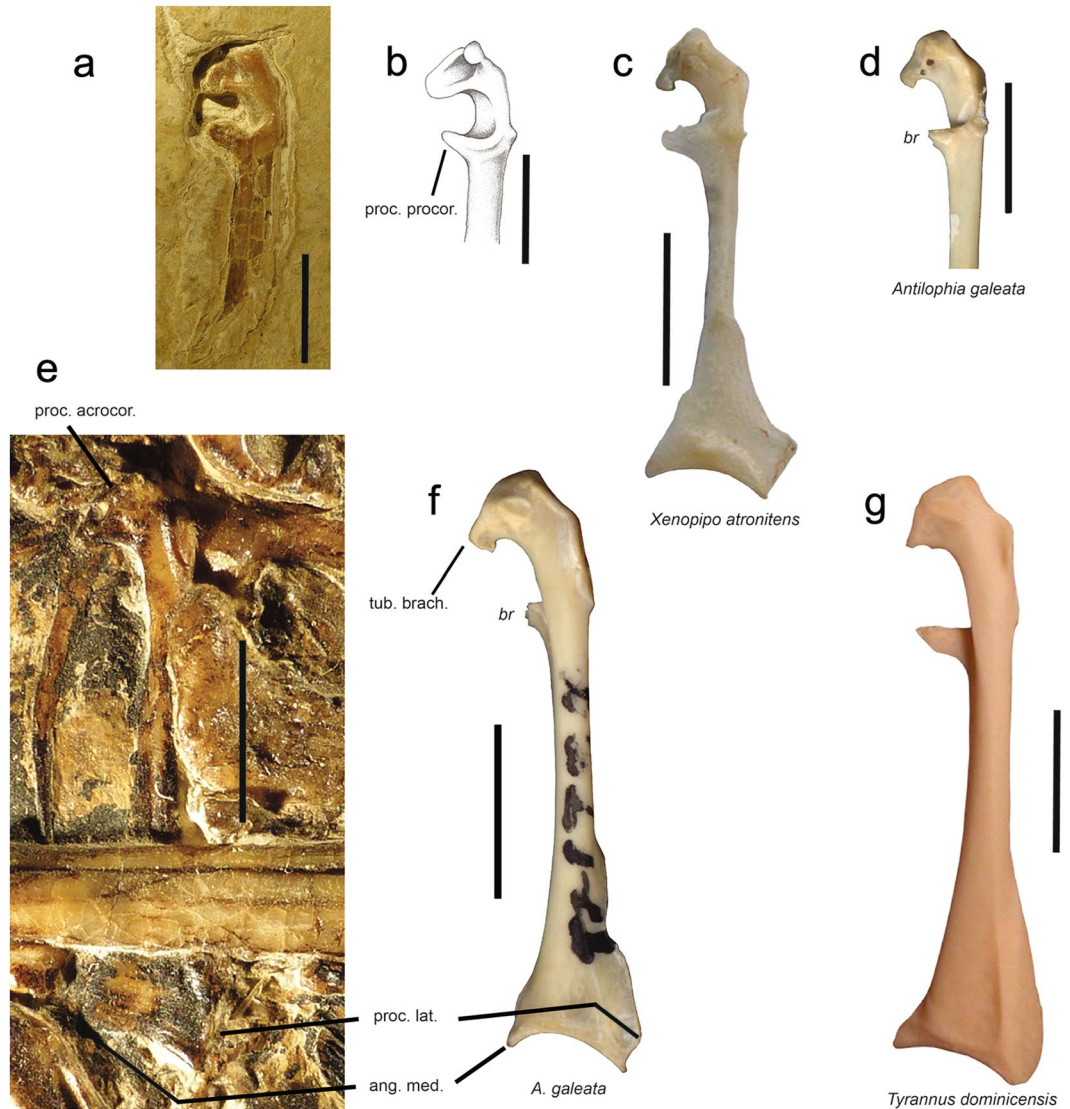
**Assignment within the Tyrannides.** Among all characters observed on the fossil, 53 are discriminant among the examined Tyranni, within which many are rather variable across the Tyrannides (Fig. 5, Supplementary Tables 1, 2) and do not help link the fossil with a particular family or genus. Nevertheless, 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  $\frac{1}{4}$  of the orbit length, like in the Pipridae.

The outline of the cranium, orbits, (and beak) of the fossil, in comparison with extant Tyrannides, 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* (Sapayoidae), 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, *Neopelma*, is in contrast similar to the fossil in most cranial characters (including the marked gonyes of mandible), and less so in postcranial 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



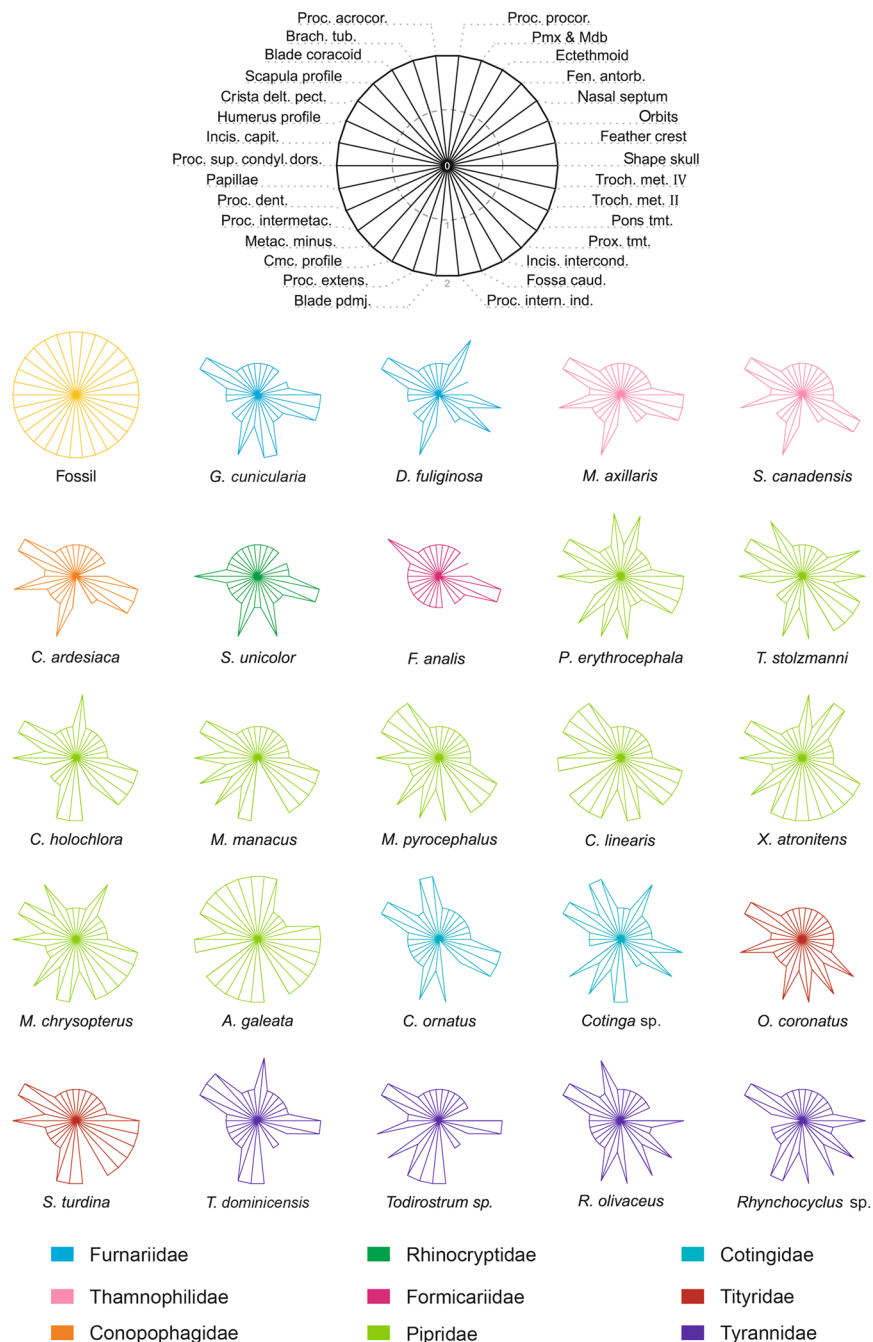
**Figure 4.** Coracoids of the Luberon fossil NT-LBR-014, compared with extant species (Tyrannida). (a,e), respectively right (dorsal view) and left (ventral view) coracoids of the fossil NT-LBR-014; b, drawing of (a,c), dorsal view, inverted left coracoid; (d), dorsal view; (f), ventral view; (g), ventral view, inverted right coracoid. ang. med., angulus medialis; proc. acrocor., processus acrocoracoideus; proc. lat., processus lateralis; proc. procor., processus procoracoideus; tub. brach., tuberculum brachiale; br, broken. Scale bars, 5 mm.

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 capability<sup>26</sup>. 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 arcuata* (Cotingidae); the other extant species examined in the Tyrannides have a unique processus supracondylaris dorsalis, but which is reduced (or less prominent proximally).

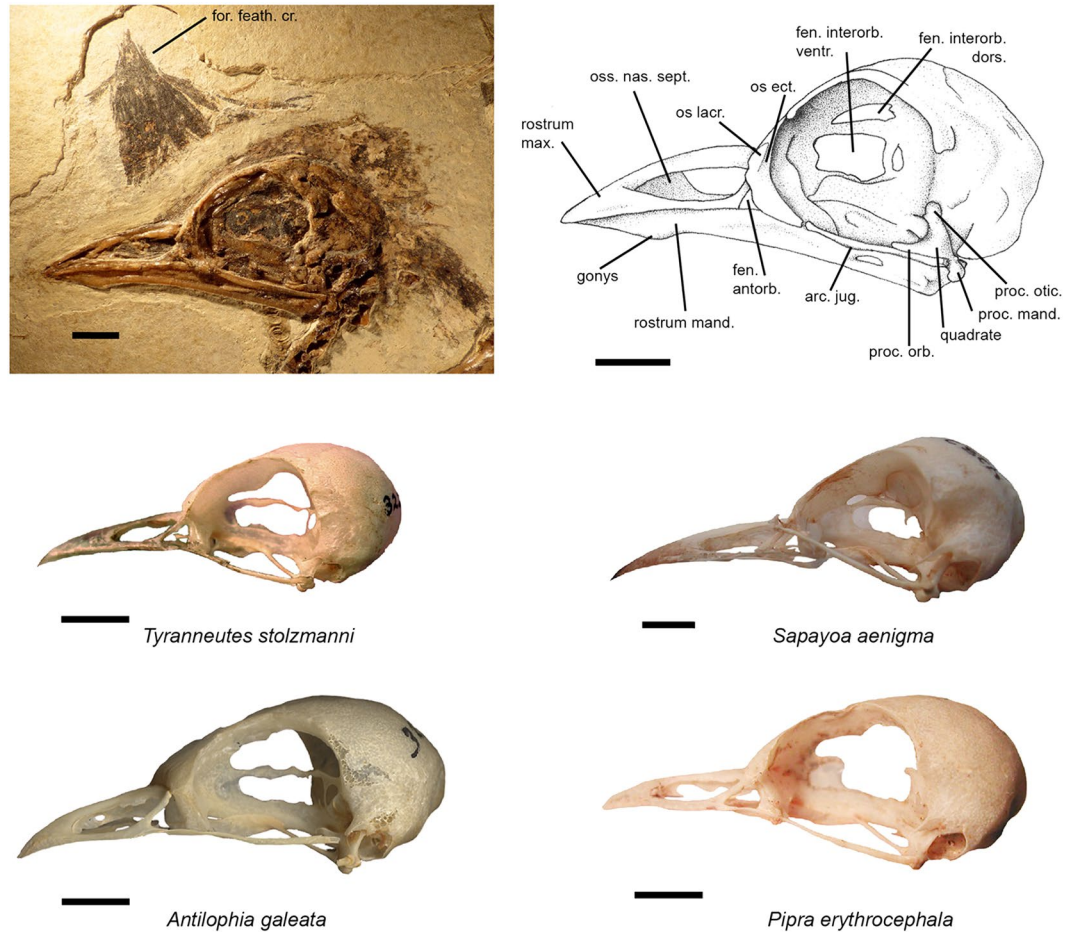


**Figure 5.** Radial visualisation (Kiviat diagram) of the distribution of character states of the Luberon fossil NT-LBR-014, across extant taxa of the Tyrannidae for which all the characters were assessable. Top, position of the diagnostic characters considered here relative to each radius. In extant 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).

**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, Formicariidae 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 6.** Skull of the Luberon fossil NT-LBR-014, compared with extant species (Pipridae, Sapayoidae). All left lateral views. Top left, fossil NT-LBR-014; top right, drawing of the preceding. NB: the part below the os lacrimale is collapsed, and seems to have been developed as in, e.g., *Sapayoa*. arc. jug., arcus jugalis; fen. antorb., fenestra antorbitalis; fen. interorb. dors., fenestra interorbitalis dorsalis; fen. interorb. ventr., fenestra interorbitalis ventralis; for. feath. cr., forehead feather crest; os ect., os ecthymoidale; os lacr., os lacrimale; oss. nas. sept., osseous nasal septum; proc. orb., processus orbitalis of quadrate; proc. otic., processus oticus of quadrate; proc. mand., processus mandibularis of quadrate; rostrum mand., rostrum mandibulare; rostrum max., rostrum maxillare. Scale bars, 5 mm.

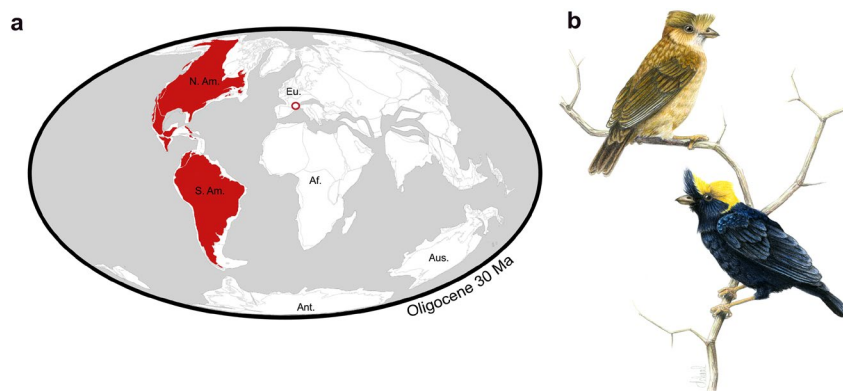
**Wing phalanx digiti majoris 1.** Among the Tyrannides, certain families exhibit a processus internus indicis that is only faint, or even absent: the Furnariidae, Thamnophilidae, Conopophagidae, Rhinocryptidae, Formicariidae, Dendrocolaptidae. In addition, in these families the shape of the blade is 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<sup>19</sup>. 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).

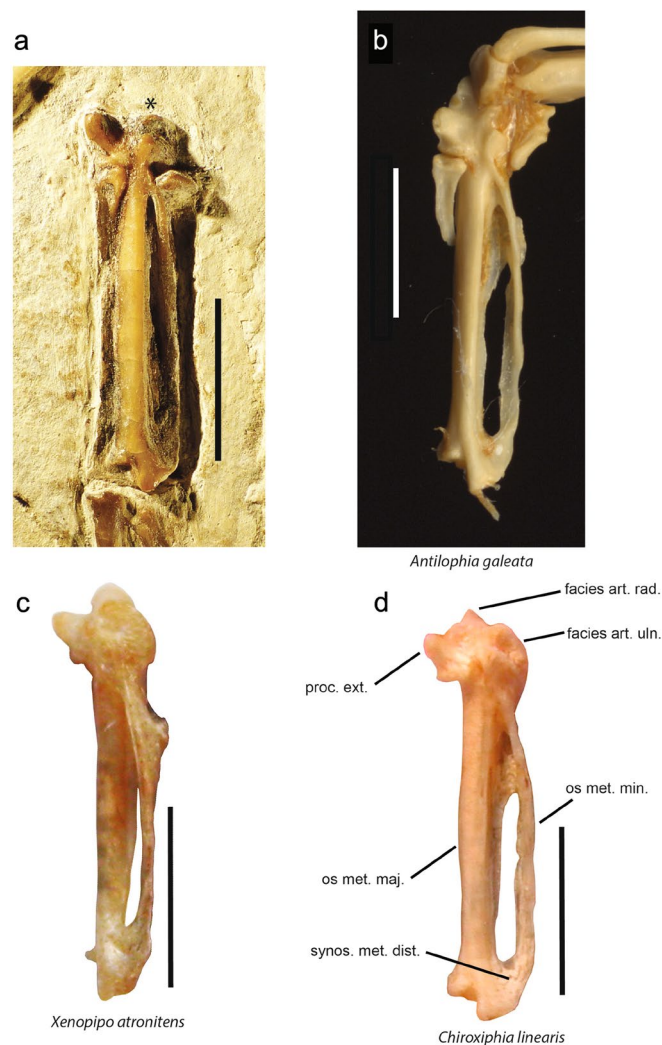
**Tibiotarsus.** A medial crest on the proximal end is absent, contrary to *Scytalopus unicolor* (Rhinocryptidae), *Phytotoma rara* (Cotingidae), *Rhynchocyclus olivaceus* (Tyrannidae), and most of the Tityridae examined, which exhibit a marked crest.

**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 *Todirostrum* sp. (both Tyrannidae), and at least no other Tyranni (Fig. 9, Supplementary Table 1).

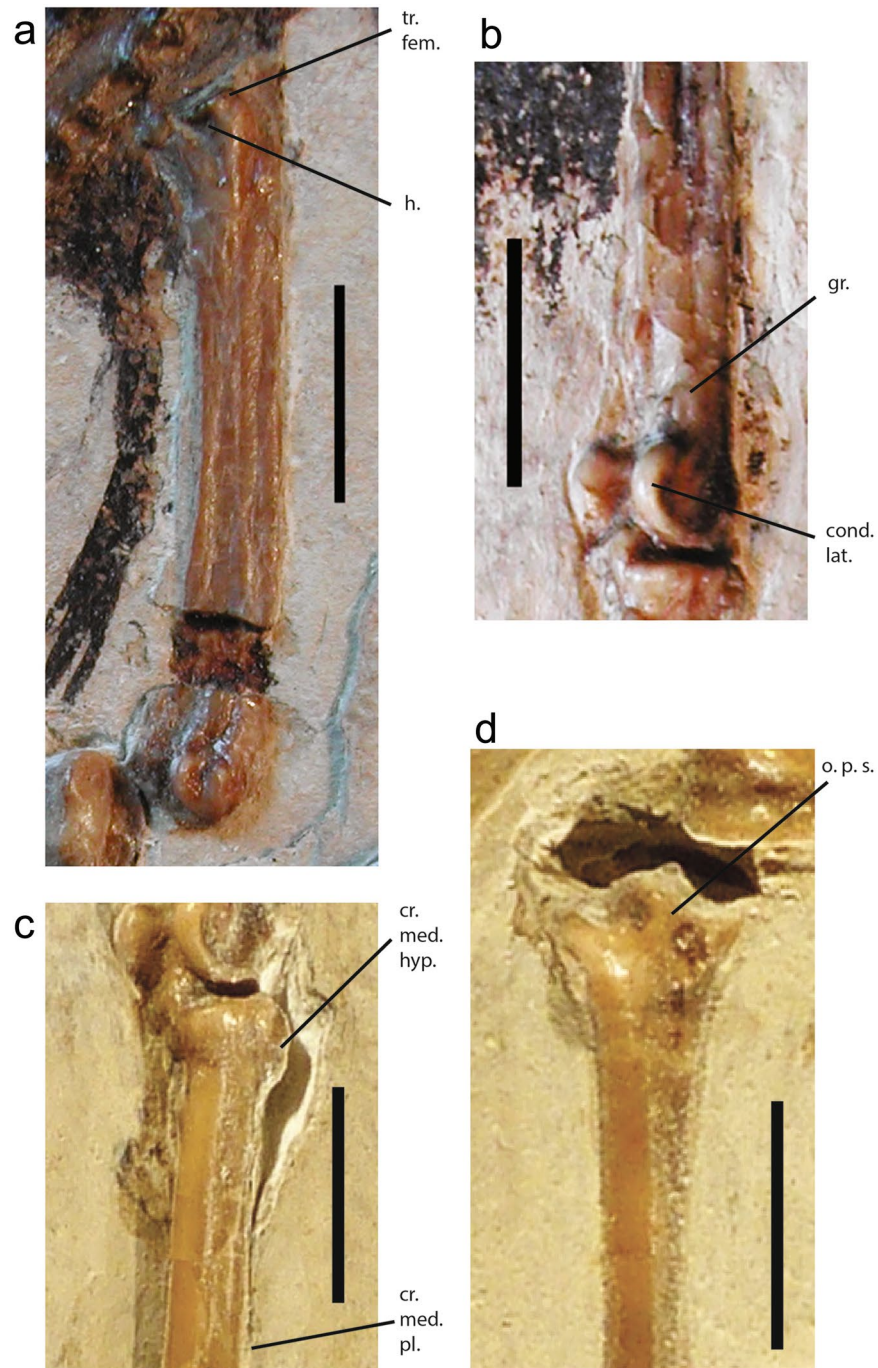
**Combinations and distributions of characters.** A Kiviat diagram allows visualization of the distribution of the states of the characters that show heterogeneity across extant Tyrannides, and the states observed in the fossil (Fig. 5). The families in the Tyrannides are grouped into two clades: the 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.



**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.

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 Tyrannides, and systematically in some or all of the examined Pipridae, contrary to other families (Fig. 5, Supplementary Table 1, and also

Supplementary Table 2 showing six additional characters that are discriminant for certain genera and species across the Tyrannida).

## Discussion

**Systematic assignment of the Oligocene fossil.** NT-LBR-014, unambiguously assignable to the Tyranni within the Passeriformes, can also be firmly placed more precisely in the Tyrannides. All the character states of NT-LBR-014 are systematically present in members of the Tyrannides and they include the diagnostic characters of Tyrannides, to the exclusion of the Eurylaimides, that we highlighted. Eventhough with poor support, our tentative phylogenetic analyses are concordant with this result, placing the fossil outside the Eurylaimides, the latter comprising *Sapayoa* in agreement with molecular works (see below). Within the Tyrannides, several characters exclude the infra-order Furnariida (composed of the Furnariidae –this family including the former Dendrocolaptidae<sup>1</sup>, the Thamnophilidae, Conopophagidae, Formicariidae, and Rhinocryptidae<sup>1,2,27</sup>), and no character state is shared only between the fossil and one or more members of these six families to the exclusion of other Tyrannides –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<sup>1,2,27</sup>). 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 Piprinae (*Chloropipo*, *Antilophia*, *Chiroxiphia*, *Masius*, *Xenopipo*, *Manacus*, *Pipra*, *Machaeropterus*) on postcranial characters, and with the Neopelminae (*Neopelma* et *Tyrannetes*; the more basal subfamily of Pipridae<sup>28</sup>) on cranial characters (principally with *Neopelma*). Within the Piprinae, the fossil shares a greater number of postcranial characters with *Chiroxiphia* 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 (Piprinae or Neopelminae; Supplementary Table 1). But moreover, it is possible that osteological characters are also shared with at least one other Tyrannida outside the Pipridae. 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 Pipridae, 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 Tyranni<sup>29</sup>. 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<sup>29</sup>, 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 Eurylaimides, of which it is the only New World representative<sup>2,3,30</sup>. 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<sup>5–15,31</sup>, including a nearly completely represented taxon from the early Oligocene of Germany, *Wieslochia weissi*<sup>12,13</sup> (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 Tyranni, or Eupasseres, or even Passeriformes as a whole<sup>13</sup>. 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.*<sup>31</sup>, to consider them outside crown Passeriformes<sup>32</sup>.

**Paleoecology.** With a length of 15 cm, the fossil NT-LBR-014 is a medium-sized Tyrannida; 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 Tyrannida, and are compatible with a rather generalist diet, comprising insects and small fruits, as in most extant manakins, tyrant-flycatchers and allies. Extant Tyrannida live in the Americas, with most diversity in the neotropical ecozone<sup>1</sup>. NT-LBR-014 derives

from a near-coastal lagunar, freshwater depositional setting, surrounded by forests, under a subtropical to tropical paleoclimate<sup>33–35</sup>, consistent with the ecological requirements of the vast majority of present-day members of the Tyrannida; only the Tyrannidae expand across entire North America in the breeding season, in addition to the Neotropics.

**Early passerines and molecular ages.** Recent molecular studies have determined the age of divergence between Acanthisittidae and Eupasseres (Passeri and Tyranni) as around the Paleocene-Eocene limit (ca. 56 Ma)<sup>3</sup>, or later in the early Eocene, near 48 Ma<sup>4</sup>. The earliest ascertained fossil passerines are from the early Oligocene of Europe. They comprise Passeri, Tyranni and possibly more basal lineage(s)<sup>5–15</sup>. 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<sup>2,27</sup> or near 24 Ma<sup>4</sup>, and the divergence between Tyrannida and Furnariida at 38.9 Ma<sup>3</sup> or near 36 Ma<sup>4</sup>. 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 several different scenarios, as for two other stem-representatives of New World clades found in the same area: the stem hummingbird *Eurotrochilus* sp.<sup>34</sup> and the stem Galbulae *Jacamatia*<sup>36</sup>. 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<sup>4</sup> based only on extant distributions. As is the case for the stem hummingbirds<sup>34</sup> and stem Galbulae<sup>36</sup> 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<sup>37</sup>. 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<sup>38</sup>. 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<sup>39</sup> 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<sup>37,38</sup>. 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<sup>36,40,41</sup>. 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<sup>3</sup>.

## Methods

**Fossil material.** The fossil NT-LBR-014 (collection Nicolas Tourment, Marseille<sup>34,35</sup>) 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<sup>42–45</sup>) 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<sup>34–36</sup>.

**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 Acanthiittidae 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<sup>46</sup>, unless stated otherwise. Systematic arrangement follows Del Hoyo *et al.*<sup>1</sup>.

**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.

Received: 25 February 2020; Accepted: 12 May 2020;

Published online: 17 June 2020

### References

- 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).
- Ericson, P. G., Klopstein, 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).
- 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).
- Oliveros, C. H. *et al.* Earth history and the passerine superradiation. *Proc. Natl. Acad. Sci. USA* **116**, 7916–7925 (2019).
- Mourer-Chauviré, C., Huguéney, M. & Jonet, P. Découverte de Passeriformes dans l'Oligocène supérieur de France. *C. R. Acad. Sci. Paris Série 2* **309**, 843–849 (1989).
- Mourer-Chauviré, C., Berthet, D. & Huguéney, M. The late Oligocene birds of the Créchy quarry (Allier, France), with a description of two new genera (Aves: Pelecaniformes: Phalacrocoracidae, and Anseriformes: Anseranatidae). *Senckenbergiana lethaea* **84**, 303–315 (2004).
- Mayr, G. & Manegold, A. A small suboscine-like passeriform bird from the early Oligocene of France. *The Condor* **108**, 717–720 (2006).
- 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).
- Bochenski, Z. M., Tomek, T. & Swidnicka, E. The first complete leg of a passerine bird from the early Oligocene of Poland. *Acta Palaeont. Polon.* **59**, 281–285 (2014).
- Bochenski, Z. M., Tomek, T. & Swidnicka, E. A complete passerine foot from the late Oligocene of Poland. *Palaeontologia Electronica* **17.1.6A**, 1–7 (2014).
- Bochenski, 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).
- Mayr, G. & Manegold, A. The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften* **91**, 173–177 (2004).
- Mayr, G. & Manegold, A. New specimens of the earliest European passeriform bird. *Acta Palaeontol. Polon.* **51**, 315–323 (2006).
- Bochenski, Z. M., Tomek, T., Bujoczek, M. & Wertz, K. A new passerine bird from the early Oligocene of Poland. *J. Ornithol.* **152**, 1045–1053 (2011).
- Bochenski, 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).
- 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 (2014).
- Boles, W. E. The world's oldest songbird. *Nature* **374**, 21–22 (1995).
- Boles, W. E. Fossil songbirds (Passeriformes) from the early Eocene of Australia. *Emu* **97**, 43–50 (1997).
- Manegold, A. Zur Phylogenie und Evolution der "Racken"-, Specht- und Sperlingsvögel ("Coraciiformes", Piciformes und Passeriformes: Aves). Ph.D Dissertation. Freie Universität Berlin (2005).
- Mayr, G. The origins of crown group birds: molecules and fossils. *Palaeontology* **57**, 231–242 (2014).
- Kakegawa, Y. A Miocene passeriform bird from the Iwami Formation, Tottori Group, Tottori, Japan. *Bull. Natl. Sci. Mus. Series C* **49**, 33–37 (2003).
- Smith, N. A., de Bee, A. M. & Clarke, J. A. Systematics and phylogeny of the Zygodactylidae (Aves, Neognathae) with description of a new species from the early Eocene of Wyoming, USA. *PeerJ* **6**, e4950, <https://doi.org/10.7717/peerj.4950> (2018).
- Chesser, R. T. Molecular systematics of New World suboscine birds. *Mol. Phylogenet. Evol.* **32**, 11–24 (2004).
- Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. Phylogeny and diversification of the largest avian radiation. *Proc. Natl. Acad. Sci. USA* **101**, 11040–11045 (2004).
- 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).
- Feduccia, A. & Olson, S. L. Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the southern hemisphere. *Smithson. Contrib. Zool.* **366**, 1–22 (1982).
- 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).
- Ohlson, J. I., Fjeldså, J. & Ericson, P. G. Molecular phylogeny of the manakins (Aves: Passeriformes: Pipridae), with a new classification and the description of a new genus. *Mol. Phylogenet. Evol.* **69**, 796–804 (2013).
- 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).
- 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. Vertebr. Paleontol.* **30**, 479–498 (2010).
33. Roux, T. Deux fossiles d'oiseaux de l'Oligocène inférieur du Lubéron. *Courrier scientifique du Parc naturel régional du Lubéron* **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., Riamon, 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/auk/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 “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 in *Synthèse Géologique du Sud-Est de la France* (ed S. Debrand-Passard) 389–468 (*Mémoires BRGM France* **125**, 1984).
43. Ducreux, J. L., Hugué, 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 dépôts. *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. Sigé, B. & Hugué, M. Les micromammifères des gisements à phosphate du Quercy (SW France). *Strata Sér. I* **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) 45–132 (*Publ. Nuttall Ornithol. Club* **23**, 1993).

## Acknowledgements

We thank the following curators and institutions for providing extant comparative specimens: C. Lefèvre (MNHN, Paris, France), S. W. Cardiff and J. V. Remsen (MZLSU, Baton Rouge, USA), D. Willard (FMNH, Chicago, USA), J. Cooper and J. White (NHM, Tring, UK), A. Tennyson (NMNZ Te Papa Tongarewa, Wellington, New Zealand), J. Dean (NMNH, Washington, D.C., USA). We also thank C. Mourer-Chauviré and T. Roux for early initiation of the study, E. Robert (UCBL) for taking care of casts, M. Makou for revising English, and M. Delval for drawing the reconstruction in life of the Luberon Oligocene Tyrannida.

## 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

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41598-020-66149-9>.

**Correspondence** and requests for materials should be addressed to A.L.

**Reprints and permissions information** is available at [www.nature.com/reprints](http://www.nature.com/reprints).

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2020

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15

## **Supplementary Information**

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

Ségolène 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)**



## 16 **Supplementary Methods**

17 List of extant specimens examined, and their collection acronyms

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

21 Acanthisittidae, *Acanthisitta chloris chloris*, MNZ 26466; Pittidae, *Pitta sordida*, LAC  
22 1884.2469; Philepittidae, *Philepitta castanea*, F, FMNH 384764; Eurylaimidae,  
23 *Cymbirhynchus macrorhynchus*, LAC 1884.256; Calyptomenidae, *Calyptomena viridis*, LAC  
24 1997.830; Sapayoidae, *Sapayoa aenigma*, M, USNM 428203; Furnariidae, *Geositta*  
25 *cunicularia*, M, USNM 614657; *Dendrocincla fuliginosus*, M, FMNH 321160;  
26 *Thamnophilidae*, *Myrmotherula axillaris*, M, FMNH 319192; *Sakesphorus canadensis*  
27 *loretoyacuensis*, M, FMNH 389206; *Thamnophilus doliatus*, (skull) LAC 1997.556;  
28 *Thamnophilus coecus*, (skull) LAC 1884.1557; *Conopophagidae*, *Conopophaga ardesiaca*  
29 *saturata*, M, FMNH 322380; *Rhinocryptidae*, *Scytalopus unicolor*, M, USNM 559977;  
30 *Formicariidae*, *Formicarius analis*, M, USNM 612383; *Pipridae*, *Ceratopipra erythrocephala*,  
31 LAC 1880.125; *Neopelma sulphureiventer*, M, MZLSU 101474; *Tyranneutes stolzmanni*, F,  
32 FMNH 322555; *Chloropipo holochlora viridior*, M, FMNH 322514; *Manacus manacus*  
33 *trinitatis*, FMNH 394500; *Machaeropterus pyrocephalus pyrocephalus*, M, FMNH 322563;  
34 *Chiroxiphia linearis fastuosa*, F, FMNH 434065; *Xenopipo atronitens*, M, USNM 622077;  
35 *Masius chrysopterus*, M, MZLSU 89991; *Antilophia galeata*, USNM 321704; *Cotingidae*,  
36 *Pipreola arcuata*, F, MZLSU 104416; *P. intermedia signata*, (skull) LAC 1884.1554;  
37 *Cephalopterus ornatus*, LAC 1986.37; *Cotinga* sp., LAC n° 2278; *Procnias* sp., (skull) LAC  
38 1884.1583; *Rupicola rupicola*, LAC 2004.635; *Rupicola* sp., (skull) LAC 1884.1574  
39 (=111/711); *Phytotoma rara*, NHM 1891.7.20.273; *Tityridae*, *Oxyruncus cristatus*, M,  
40 MZLSU 108942; *Onychorhynchus coronatus*, NHM 1891.7.20.143; *Tityra semifasciata*,

41 NHM 1891.7.20.16; *Schiffornis turdinus amazonus*, F, FMNH 322490; Tyrannidae, *Tyrannus*  
42 *dominicensis*, LAC 1996.60; *Tyrannus* sp., LAC; *Todirostrum* sp., LAC 2000.556; *Contopus*  
43 *latirostris*, (skull) LAC; *Rhynchocyclus olivaceus*, NHM S/1974.11.83; *Rhynchocyclus* sp.,  
44 LAC 2000.459; Menuridae, *Menura novaeohollandiae*, LAC 1883.2208; Ptilonorhynchidae,  
45 *Sericulus* sp. LAC 1845.92, *Ptilonorhynchus violaceus* LAC A 4307 = BVI/417;  
46 Meliphagidae, *Meliphaga lewini* LAC 1883.2127 = IV/342, *Philemon corniculatus* LAC A  
47 4319 = BVI/370, *Manorina melanocephala* LAC A 4468 = BVI/364; Pardalotidae,  
48 *Pardalotus punctatus* LAC 1860.96; Acanthizidae, *Gerygone flavolateralis*, LAC 1997.535;  
49 Pomatostomatidae, *Pomatostomus temporalis trivirgatus*, LAC A 4467 = BVI/373;  
50 Paradisaeidae, *Ptiloris paradiseus* LAC 1860.102 = A 4291 = BVI/360, LAC A 4295 =  
51 BVI/359, *Paradisaea minor* LAC 1878.620.

52

53 Institutions acronyms

54 FMNH, Field Museum of Natural History (Chicago, USA); LAC, Laboratoire d'Anatomie  
55 Comparée (Muséum National d'Histoire Naturelle, Paris, France); NHM, Natural History  
56 Museum (Tring, UK); MNZ, Museum of New Zealand Te Papa Tongarewa (Wellington,  
57 New-Zealand); MZLSU, Museum of Zoology, Louisiana State University (Baton Rouge,  
58 USA); UCBL, Université Claude Bernard Lyon 1 (Villeurbanne, France); USNM, National  
59 Museum of Natural History (Smithsonian Institution, Washington, D.C., USA).

60

61 Methods for phylogenetic analyses

62 The phylogenetic analyses were realized using 36 characters, which were discriminant for at  
63 least one among the Tyranni examined, and 34 taxa of the Tyranni (including the fossil). The  
64 character matrix (Supplementary Table 5), is derived from the characters observed

65 (Supplementary Tables 1, 2). *Gerygone flavolateralis* (Passeri, Acanthizidae) and *Acanthisitta*  
66 *chloris* (Acanthisittidae) were chosen as respective outgroup taxa to the Tyranni.

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

75

76 Osteological characters used in the phylogenetic analysis.

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

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

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

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

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

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

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

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

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

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

89 Processus procoracoideus: 0, little developed; 1, well developed.

- 90 Processus acrocoracoideus: 0, little developed; 1, well developed.
- 91 Brachial tuberosity (tuberculum brachiale): 0, little developed; 1, developed; 2, well  
92 developed.
- 93 Sulcus medialis supracoracoidei: 0, straight; 1, rounded; 2, almost circular.
- 94 Fossa pneumotricipitalis: 0, single fossa; 1, double fossa: present of an additional fossa.
- 95 Crista deltopectoralis: 0, developed; 1, reduced.
- 96 Crus ventralis fossae: 0, little developed; 1, well developed.
- 97 Crus dorsalis fossae: 0, little developed; 1, well developed.
- 98 Shaft shape: 0, curved; 1, not curved.
- 99 Depth of incisura capitis: 0, shallow; 1, moderately deep; 2, deep.
- 100 Processus flexorius: 0, dorso-caudally deflected edge; 1, straight edge.
- 101 Processus supracondylaris dorsalis: 0, double; 1, single.
- 102 Processus supracondylaris dorsalis: 0, little developed; 1, developed; 2, well developed.
- 103 Tuberculum ligamenti collateralis ventralis: 0, projecting; 1, not projecting.
- 104 Cotyla ventralis: 0, ventral edge developed and almost circular; 1, convex ventral edge.
- 105 Cotyla dorsalis: 0, little developed; 1, large.
- 106 Position of the dorso-proximal edge of the incisura tendinosa (for mm extensor metacarpi  
107 ulnaris and extensor digitorum communis), distal ulna: 0, proximal; 1, distal.
- 108 Papillae remigales caudales: 0, almost absent; 1, little developed; 2, developed; 3, well  
109 developed.
- 110 Processus dentiformis: 0, absent; 1, little developed: edge with a slightly wavy; 2, developed;  
111 3, well developed.
- 112 Position of processus intermetacarpalis: 0, proximal; 1, more proximal.
- 113 Distal symphysis of os metacarpale minus: 0, the os metacarpale minus is lightly protruding,  
114 and forms a marked square projection; 1, the distal end of os metacarpale minus is moderately

115 protruding and its cranial portions forms a projection that reaches farther distally than the  
116 *facies ricularis digitalis minor* (Mourer-Chauviré et al., 1989; Mayr and Manegold 2006).

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

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

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

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

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

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

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

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

131 Position of *pons supratendineus*: 0, not ossified, 1, located proximally; 2, located proximally;  
132 3, located less proximally; 4, located in an intermediate position.

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

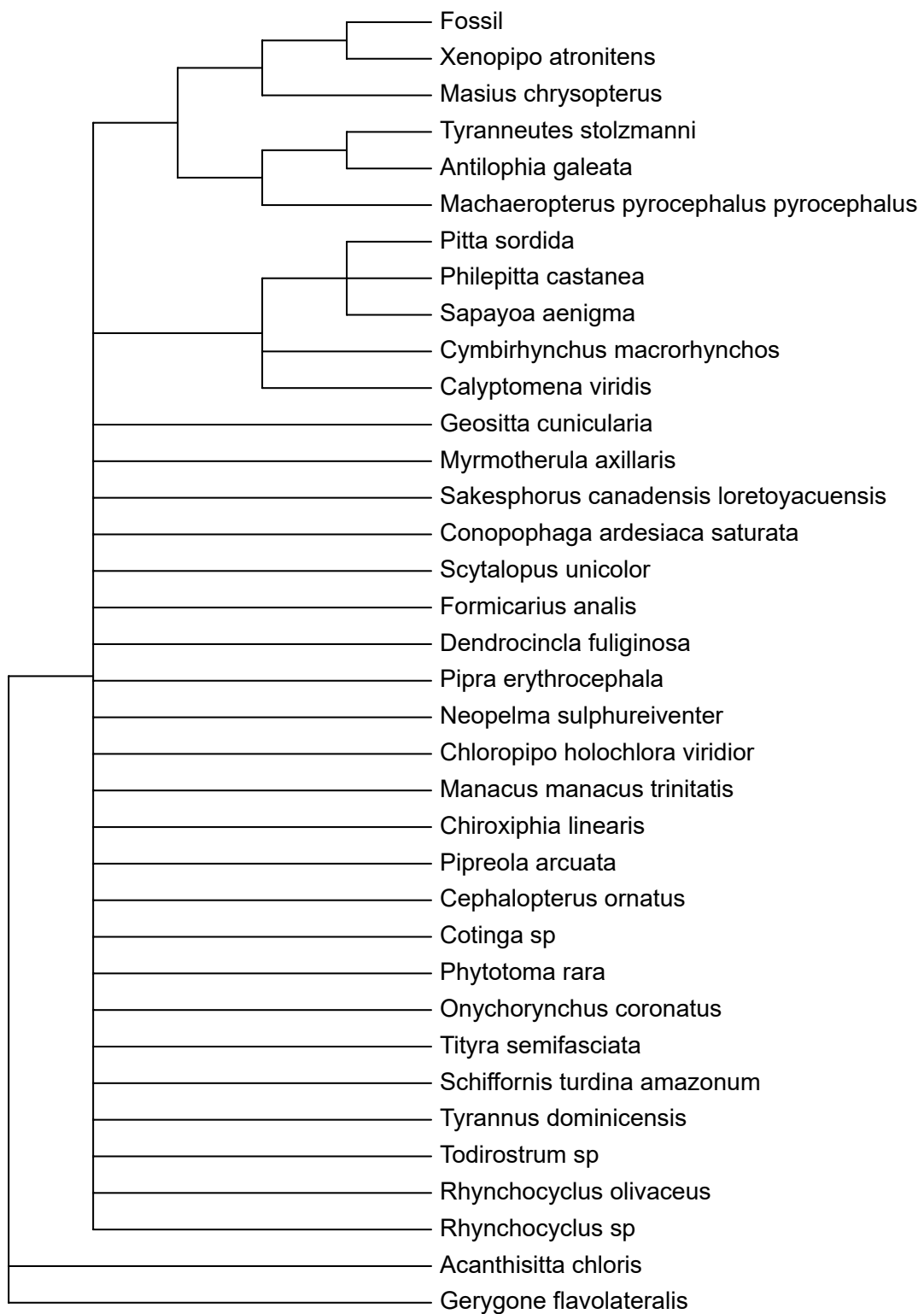
135 *Trochlea metatarsi IV*: 0, as distal as *trochlea metatarsi III*; 1, shorter than *trochlea metatarsi*  
136 *III*; 2, longer than *trochlea metatarsi III*.

137

138

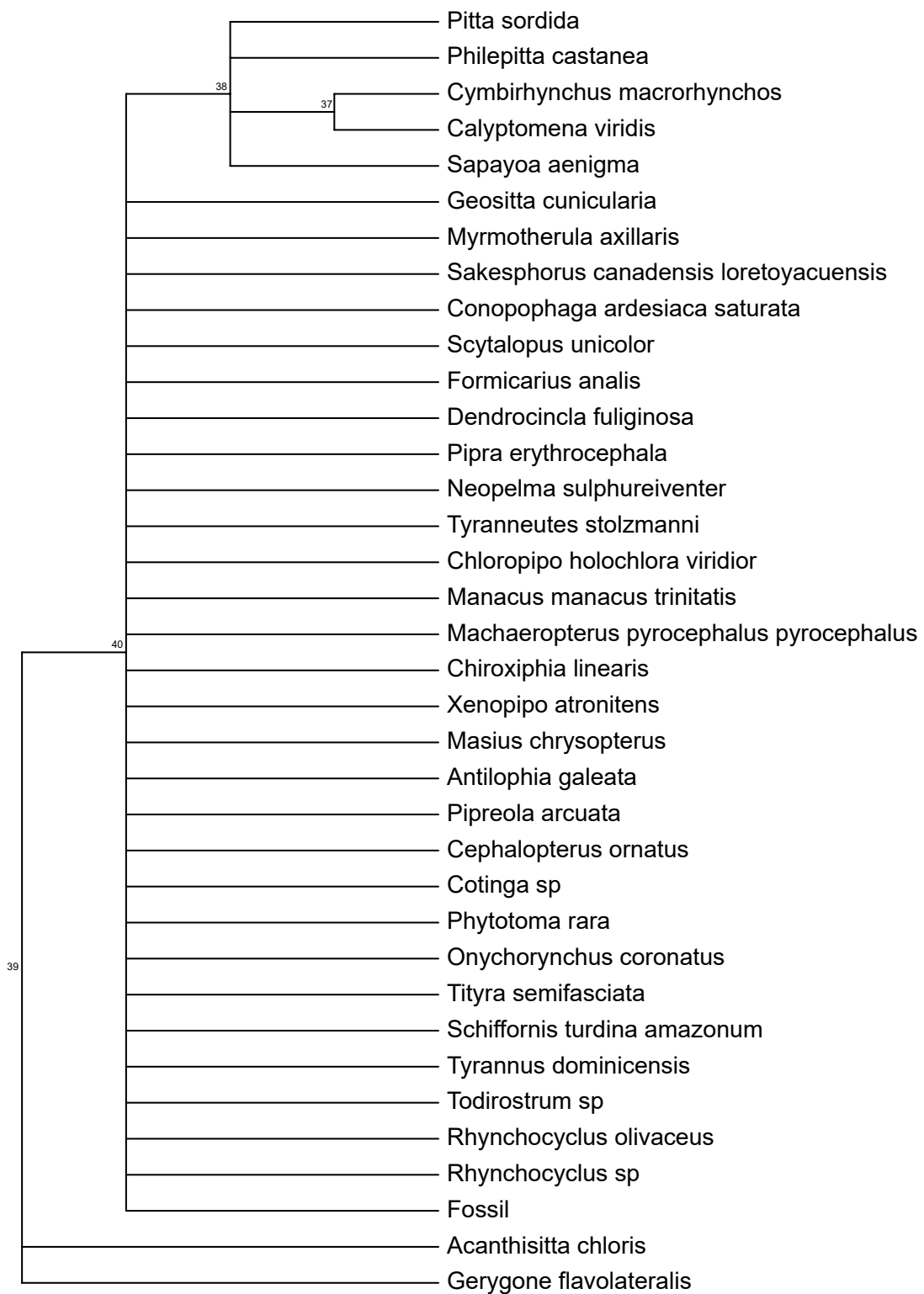
139 **Supplementary Figures**

140 **Supplementary Fig. 1** Strict consensus tree, hardly resolved. As for the bootstrap  
141 analysis (Supplementary Fig. 2), the poor resolution and support convey pervasive  
142 homoplasy. The fossil is associated in a clade with five members of the Pipridae,  
143 although five other extant piprids are more basally misplaced in a wide unresolved  
144 polytomy with many Tyrannides. The fossil is, as in the bootstrap analysis, distant from  
145 *Sapayoa aenigma*, which is correctly placed within the Eurylaimides  
146



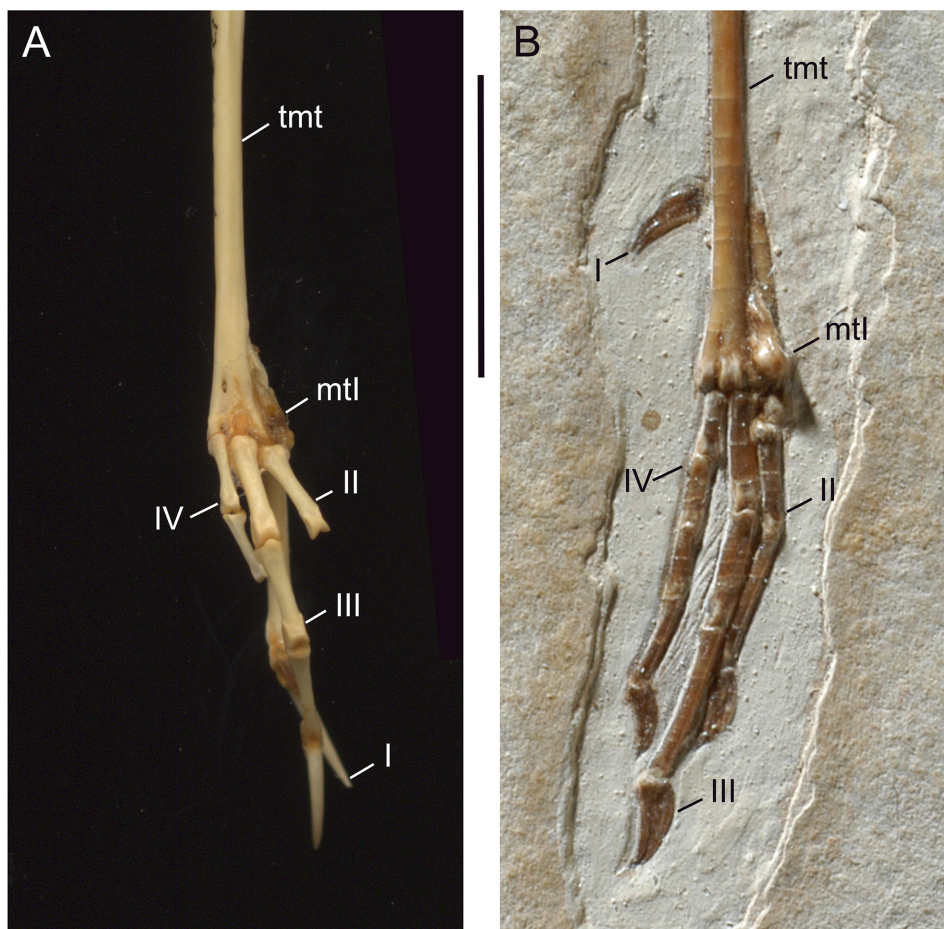
148 **Supplementary Fig. 2** Bootstrap analysis, with 1000 replicates. Only four nodes are  
149 supported by the bootstrap, but with a very low value (between 37 and 40%). As for the  
150 strict consensus (Supplementary Fig. 1), the poor resolution and support convey  
151 pervasive homoplasy. The fossil is however, as in the strict consensus, distant from  
152 *Sapayoa aenigma*, which is correctly placed within the Eurylaimides  
153





156 **Supplementary Fig. 3** Distal part of the tarsometatarsus and toe bones (both right side, in  
157 dorsal view) in (A) *Antilophia galeata* (Pipridae) and (B) the fossil NT-LBR-014. There is no  
158 fusion at the level of pedal phalanges bones, despite *A. galeata* exhibiting syndactyly of toes  
159 III and IV in life, and this is because syndactyly affects only the soft tissues surrounding the  
160 bones. I, first digit, positioned in distal extension in (A), in proximal extension in (B); II,  
161 second digit –only the first phalanx was preserved attached in the preparation of specimen  
162 (A); III, third digit; IV, fourth digit –only the first two phalanges were preserved attached in  
163 the preparation of specimen (A); mtI, first metatarsal; tmt, tarsometatarsus. In the fossil (B)  
164 the first phalanx of digit II presents proximally a sort of bulb that seems to be pathological.  
165 Scale bar, 1 cm

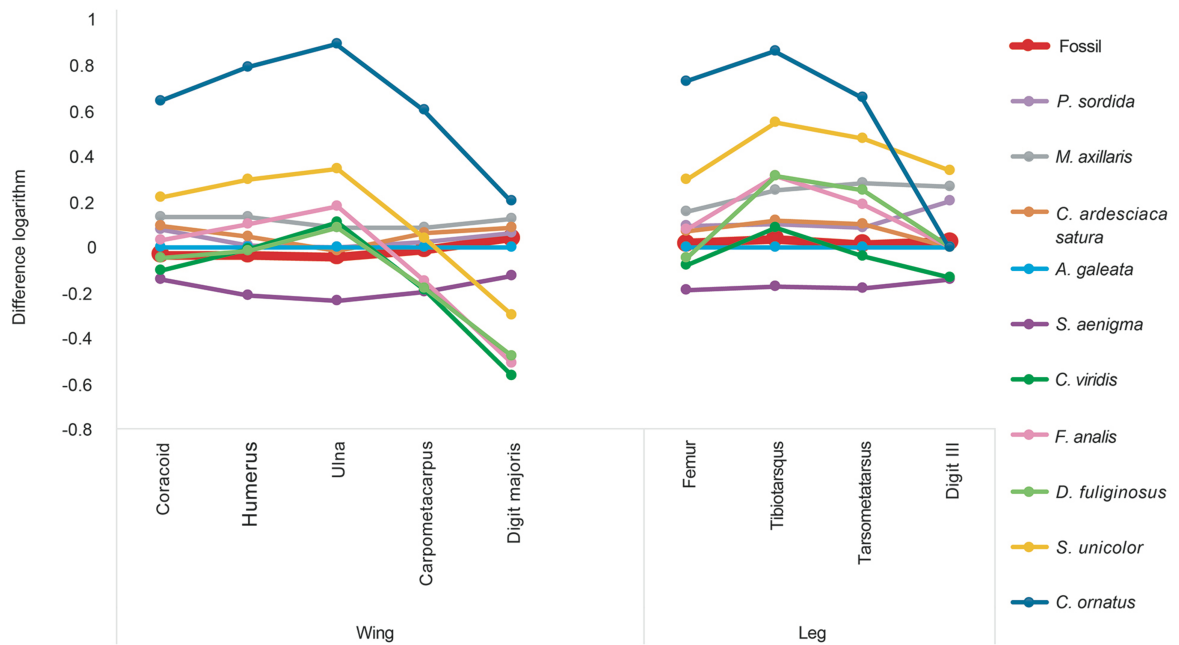
166



167

168

169 **Supplementary Fig. 4** Simpson's diagram of intersegment proportions of the Luberon fossil  
 170 NT-LBR-014, compared with extant species of the Tyranni. The differences in Log10 of  
 171 length of the main elements are expressed for the fossil and ten species of Tyranni  
 172



173

174

## 175 **Supplementary Tables**

176 **Supplementary Table 1** Osteological characters as observed in the fossil passerine NT-LBR-  
 177 014, and extant representatives of Tyranni families, Acanthisittidae, basal and other Passeri,  
 178 and *Wieslochia weissi*, passerine from the Oligocene of Germany.

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

180 Only characters that discriminate at least one species among the Tyranni and Acanthisittidae

181 examined have been selected here. \*On occasions, character states are given not only for the

182 extant species examined here for comparison, but for more species in the family (in such

183 instances references are given via number in parentheses). (1) it is mentioned if other extant

184 taxa in every genus or family concerned exhibit a crest approaching the fossil's (after del

185 Hoyo et al., 2019<sup>1</sup>). (2) from this work, and characters 22 and 55 in James et al., 2003<sup>2</sup>. (3)  
186 from this work and Mourer-Chauviré et al., 1989<sup>3</sup>; NB: C. Mourer-Chauviré (pers. comm.)  
187 noticed (in Smithsonian Institution collections) that among 21 extant species of Furnariidae,  
188 only one exhibited a slight undulation, the others none (straight edge of major metacarpal),  
189 and among 30 species of Formicariidae, only four possessed a proc. dentiformis (the others  
190 nothing: straight edge of major metacarpal). (4) from Boles, 2006<sup>4</sup>. (5) from this work,  
191 Millener, 1988<sup>5</sup>, and Millener and Worthy, 1991<sup>6</sup>. (6) sensu del Hoyo et al., 2019<sup>1</sup>, i.e.  
192 comprising taxa earlier in the former Dendrocolaptidae. (7) also from Fjeldsa et al., 2005<sup>7</sup>.  
193 (8) a few genera and species exhibit a crest that is different from that of NT-LBR-014,  
194 triangular, often acute, pointing upwards over the head, and spread caudally (some  
195 *Leptasthenura* spp., *Furnarius cristatus*, *Coryphistera alaudina*, and more or less in the  
196 different species of *Pseudoseisura*). (9) same in *Pseudoseisura*<sup>8</sup>. (10) a few genera and  
197 species exhibit a crest that is different from that of NT-LBR-014, triangular, often acute,  
198 pointing dorso-caudally over the head, and spread caudally. *Pithys albifrons* exhibits original  
199 long, upright white tufts on both sides of forehead, shorter tufts below chin. (11) from this  
200 work and Feduccia and Olson, 1982<sup>9</sup>. (12) In *Rhinocrypta* a crest extends from the back of the  
201 head, that can be spread upwards, making an acute triangle. In *Merulaxis* feathers above the  
202 base of rostrum make a « crest » resembling that of *Calypdomena* but sparser. (13) An ossified  
203 bridge exists in *Melanopareia* (recently placed in own family<sup>1</sup>)<sup>9</sup>. (14) Quadrate even more  
204 different in *Melanopareia*<sup>9</sup>. (15) Apart from *Masius*, *Antilophia* and *Chiroxiphia* (see Table),  
205 feather ornaments over the head in the Pipridae exist also in *Ilicura militaris* (where it  
206 consists of short, round feather fluffy crest over rostrum base ; more developed in male). (16)  
207 Apart from *Cephalopterus* and *Rupicola* (see Table), in the Cotingidae only *Phytotoma*  
208 exhibits feather head ornament, especially *P. raimondii* (rear head, spreading upward). (17) In  
209 the Tyrannidae, in addition to some species of *Contopus* (short, slight crest back to top of

210 head ; see Table), crests exist in several genera and species, where always at the back of head,  
211 forming when spread a crest with longest feathers toward the top of head (extent of crest  
212 variable among genera and species concerned). (For instance also the crest of *Comptostoma* is  
213 more on top of head and shorter (and still toward back)). An exception consists in *Anairetes*  
214 (variable among species) of a prominent frontal crest of long feathers implanted over the  
215 rostrum base, and pointing upwards and backwards ; they form either a fan or a bifurcated  
216 crest (like horns) of long, thin feathers. (18) from this work, Feduccia and Olson, 1982<sup>9</sup> and  
217 Rich et al., 1985<sup>10</sup>. (19) from Feduccia and Olson, 1982<sup>9</sup>, and Rich et al., 1985<sup>10</sup>. (20) data  
218 also from Bock, 1963<sup>11</sup> and Olson et al., 1983<sup>12</sup> (NB: *Turnagra* now known to be in the  
219 Oriolidae<sup>13</sup>). (21) data also from Bock, 1963<sup>11</sup>. (22) The fossa is simple in all the  
220 Passeriformes except most of the the Oscines Passerida - and a few Oscines Corvoidea -  
221 where derived states of a double fossa occur polyphyletically; pneumatic in Corvoidea, either  
222 pneumatic or non-pneumatic in Passerida<sup>2,3,14</sup>. (23) A processus dentiformis is present in most  
223 of the Passerida, while within the Corvoidea it is either absent or present<sup>3,15,16</sup>. (24)  
224 Oligocene, Wiesloch-Frauenweiler (Germany); assigned to stem Passeriformes or stem  
225 Tyranni<sup>17,18</sup>. NB: for several modern specimens, character states are absent due to the lack of  
226 the element or element part, or the incomplete specimen preparation, obscuring detail by  
227 ligaments for instance. It is specified for which specimens the skull only could be examined.  
228

Taxon		Skull										Cranium								
Suborder to Family	Series (series used for comparison are listed, but see *)	Cranium shape (broad poles)	Rostrum crest (R)	Relative size of orbits	Shape of orbits	Omnivora rostr. upturn	Mensura orbitorbitalis (proportion)	Ox. Isometric	Intern. dorsal part of orbitals	Internorbital fenestrae (I)	Quadrata shape	Cerebellar cerebellum	Rostrum and mandible (incl.)	Ferream (Dorsum of rostrum area)	Process precondylo	Process retrocondylo	Basal tuberosity (Subtubercle)	Sulcus medialis suprastomatoid	Cranial blade shape	
Revest-des-Brouesses fossil (early Oligocene) NT-LBR-014		see illustration	over base of rostrum; crest "triangular", directed forward, with five recurved slight teeth	large (3.5 times more than half orbit)	much rounded	present over most of rostral aperture (broadly)	reduced, equilateral triangle	present and indistinct	well developed	dorsal smaller than ventral, separation narrow	see illustration	no	relatively straight, rostral opening 2/3 of rostrum, with small rounded gony	yes	developed	developed	very developed, straight	relatively circular edge	see illustration	
Acanthitidae		Acanthitina chloris (R)	variable	none	generally more rounded	none	larger (variable)	free?	very slightly developed	dorsal fenestrae proportionally larger, separation very thin	processus orbitalis much reduced and obscure; promaxilla wider	no	beak on average longer and thicker	no	poorly developed, "forn" SP	not developed medially	?	?	similar	
Eurylamidae	Pittidae	Pitta sorabide	similar	none	similar	dorsal edge flatter	present over most of rostral aperture except ventral edge	similar	free?	developed	ventral fenestrae slightly larger	rather similar	no	rostral opening only 1/2 of rostrum (1); rostrum straight; rostr. without gony	yes	developed, pointed distally	very slightly less developed medially, more hooked	less developed	relatively straight edge	processus lateralis much more elevated
	Phalipotidae	Phalipitocastoreo	hooked flatter	none	similar	dorsal edge flatter	present over dorsal and ventral border of rostral aperture	similar	free?	slightly developed	dorsal fenestrae larger and separation thicker	slightly different	no	beak thinner, longer, decurved and pointed	yes	developed, but elongation more proximal than in the basal	less developed medially	?	?	similar
	Eurylamidae	Cymbisthynchus macrophyllus	rather similar (broadly slightly flatter)	none	similar	dorsal edge flatter	?	more extended distally, shape more elongated and narrow	free?	moderately developed	both fenestrae much larger, separation thicker	processus orbitalis shorter; processus mandibularis and obtus more curved	no	beak more curved, hooked and robust	yes, smaller but deep	not much developed	less developed medially, more hooked	much less developed	straight edge	similar
	Calyptomidae	Calyptomax viridis	rather similar (broadly slightly flatter)	none reduced, rounded, directed forward	similar	dorsal edge flatter	present only over dorsal and ventral border of the rostral aperture	more extended distally, more rounded	free?	moderately developed	ventral fenestrae slightly reduced, dorsal slightly larger	different	yes, small	beak more curved and hooked	yes	developed, same shape as fossil, shorter	less developed medially	less developed	relatively straight edge	processus lateralis more developed distally
	Sapayoidae	Sapayoc ornaiemo	identical	none	identical	dorsal edge flatter	almost complete (starting from dorsal edge)	similar	free?	slightly developed	ventral fenestrae reduced, separation slightly thicker	similar	no	rostrum similar, rostr. without gony	yes	developed, same shape as fossil	very slightly less developed medially and pointed	?	?	rather similar
Furnariidae (6)	Geothlyta canicularis	rather similar (?)	none (R)	similar (?)	dorsal edge slightly flatter	none / oblique bar	generally wider	absent or fused	moderately developed	rather similar to fossil; however not on fossil (no separation)	very similar	no	beak thinner, longer, decurved and pointed; rostral opening reduced; rostr. with gony less marked (2)	yes	moderately developed, pointed rather acute	highly less developed medially	no much developed	more rounded edge	processus lateralis more elevated latero-distally	
	Dendroica fuliginea	forward slightly flatter	none	similar	rounded	none	larger	absent or fused	well developed	ventral fenestrae much smaller	proc. orbitalis narrower	no	beak much longer; rostral opening reduced	yes	developed, thinner, and shape different	very slightly less developed medially	developed	rounded edge	processus lateralis much more elevated latero-distally	
Thamnotrogonidae	Myrmotherula axillaris	rather similar	none (2)	smaller	dorsal edge slightly less rounded	almost complete (except rostral part)	slightly larger	absent or fused	developed	dorsal fenestrae larger and separation much thicker	proc. orbitalis narrower	no	beak thinner, straighter, no gony	?	moderately developed, pointed rather acute	highly less developed medially	developed	rounded edge	processus lateralis more elevated distally	
	Sakspeles condensis	rather similar (broadly slightly flatter)	crest on the back of head (can be spread upwards)	similar	rounded	complete	highly larger	absent or fused	well developed	dorsal fenestrae slightly larger, separation thicker	proc. orbitalis proportionally longer	no	beak longer - rostral opening reduced; gony slightly reduced	?	slightly less developed	point slightly less shifted medially	?	?	processus lateralis developed slightly more distally	
	Thamnotrogon albitarsis (skull)	hooked flatter	present, directed distally	similar	rounded	almost complete	larger more rounded	absent or fused	developed	similar to fossil; separation thin	proc. orbitalis narrower	no	beak longer and more hooked	?	?	?	?	?	?	
	Thamnotrogon curvica (skull)	hooked flatter	none	similar	much rounded	almost complete	more rounded	absent or fused	very slightly developed	?	?	?	no	beak longer and more hooked	?	?	?	?	?	?
Conopophagidae	Conopophaga andicola satorata	similar	none	similar	rounded	over 1/2 dorsal	1/4	slightly larger	absent or fused	slightly developed	dorsal fenestrae larger, separation thicker	proc. orbitalis narrower	no	beak longer beyond rostral opening	?	not much / moderately developed, obtuse corner shaped and	highly less developed medially	much less developed	very rounded edge	similar
Bibacoidae	Synalipus urucator	slightly flatter	none (2)	smaller (1)	dorsal edge flatter	none / narrow oblique bar	variable	absent or fused	very slightly developed	single large fenestra (no dorsal)	rather similar (1)	yes / no (1)	rostrum shorter and more hooked; rostr. straighter and gony almost absent	?	very little developed	not much developed	much less developed	very rounded edge	less developed	
Formicidae	Formicivora analis	hooked more angular	none	very slightly smaller	rounded	none	larger	absent or fused	developed	ventral fenestrae more developed, separation thicker	similar	no	beak longer - rostral opening reduced; gony reduced	yes	not much / moderately developed, wider corner shaped and	less developed medially	much less developed	very rounded edge	processus lateralis more developed distally	
Tyrannidae (Suboscines)	Certhopygia erythrocephala	similar	none (2)	similar	much rounded	beak rostral and dorsal border	dorsal and slightly more rounded	present and more or less individualized	developed	dorsal fenestrae more developed; separation thicker	very similar	no	similar to fossil; gony reduced	yes	developed, slightly more anterior	developed	?	?	?	
	Neotoma subphalaenator	rather similar (broadly slightly flatter)	none	slightly smaller	rounded	narrow over dorsal edge	much larger, more rounded, and more developed rostrally	?	developed	dorsal fenestrae more reduced; ventral fenestrae more reduced	proc. orbitalis less developed	no	similar	yes, smaller	developed, straighter and more massive	developed; more hooked; thicker	slightly less developed	rounded edge	processus lateralis more developed distally	
	Tyrannetes stolonator	similar	none	similar	much rounded	narrow over dorsal edge	slightly larger	?	developed	dorsal fenestrae more developed, ventral fenestrae smaller	proc. orbitalis more ventral	no	beak thicker; rostral opening reduced; gony reduced	yes	developed, slightly more anterior	slightly less shifted medially	highly less developed	very rounded edge	similar	
	Chlorophanes holochlorus viridor	forward slightly flatter	none	similar	rounded	narrow over dorsal and rostral edge	similar	?	developed	dorsal fenestrae larger, ventral fenestrae smaller	?	no	beak straighter, with slight more curved gony reduced	yes	similar, slightly more anterior	highly less developed	highly less developed	rounded edge	rather similar	
	Manacus sutorius	forward slightly flatter	none	similar	rounded	over rostral half, and also over rostral dorsal inflection	slightly larger	?	moderately developed	dorsal fenestrae larger, ventral fenestrae smaller	proc. orbitalis more ventral	no	beak more decurved; rostral opening reduced	?	more squarer, very slightly less pointed	highly less pointed	highly less developed	very rounded edge	slightly more developed distally	
Pipridae	Microeruptus pyrrochloa	hooked flatter, rostrum flatter	none	similar	rounded	oblique narrow central extension	slightly larger	?	developed	dorsal fenestrae larger, ventral fenestrae smaller	proc. orbitalis more ventral	no	beak slightly decurved with an angle	?	wider and more obtuse, rostr.	point less shifted medially	much less developed	very rounded edge	similar	
	Chlorophanes linearis	forward slightly flatter	short, round feather tufts over rostral base	similar	rounded	over 1/2 rostral part, with narrow caudal ventral extension	slightly larger	rostrum visible	developed, rostral part indistinct	dorsal fenestrae larger, ventral fenestrae smaller	proc. orbitalis slightly more ventral	no	beak smaller, thinner and much more curved, rostral opening reduced	?	more tapering	slightly less pointed	highly less developed	rounded edge	similar	
	Xenopipa atrifrons	forward slightly flatter	none	similar	rounded	over dorsal half	identical	present, individualized; fusion with rostrum visible	well developed, similar to fossil	ventral fenestrae smaller, dorsal fenestrae larger, separation slightly thicker	proc. orbitalis slightly more ventral	no	beak shorter, decurved, gony absent	yes	similar, slightly more anterior	developed slightly less	slightly less developed	relatively circular edge	more developed laterally	
	Micropus chrysorrhopus	forward slightly flatter	crest over rostrum base; present, directed forward and rostrum slightly	similar	rounded	over dorsal caudal half	slightly larger	present and more or less individualized	well developed, similar to fossil	ventral fenestrae smaller, dorsal fenestrae larger, separation slightly thicker	proc. orbitalis slightly more ventral	no	beak shorter; rostr. much more decurved, and gony slightly reduced	yes	only slightly wider	less developed medially	highly less developed, hooked	relatively circular edge	similar	
Tyrannidae	Atalapha galata	similar	crest over rostrum base directed to back	similar	rounded	over more than 1/4 dorsal	slightly larger	present and more or less individualized	developed	dorsal fenestrae larger, ventral fenestrae smaller	similar	no	similar, but gony less marked	yes	as fossil	developed; shape similar	similarly very developed; slightly more hooked	very rounded edge	similar	
	Pipilo arcuatus	forward flatter; rostrum more elongated	none	similar	rounded	over 1/2 rostral	shape similar but larger	present and more or less individualized	well developed	dorsal fenestrae much larger, ventral fenestrae smaller	proc. orbitalis less developed	no	beak more hooked and robust; rostr. with more curved gony less developed	yes, fenestrae	developed; more developed anteriorly	slightly less developed	highly less developed	very rounded edge	more developed distally	
	Cathartes aura	flatter	increase crest over head, rostral forward and reaching level of beak tip	similar	similar	over 1/2 rostral	more extended distally	present and more or less individualized	developed	both fenestrae much smaller, separation wider	proc. orbitalis wider and more ventral	no	beak more developed; rostr. more hooked; gony almost absent	yes	not much developed	developed	similarly very developed	relatively rounded edge	much more developed distally	
	Cotinga sp.	flatter	none (2)	similar	dorsal edge slightly flatter	over more than 1/4 caudal	rather similar	present and more or less individualized	well developed	both fenestrae much smaller, dorsal fenestrae larger than the ventral	proc. orbitalis more ventral	no	rostrum slightly longer and more hooked; much more straight, rostral opening reduced	yes	slightly less developed	highly less pointed medially	similarly very developed	relatively rounded edge	similar	
	Procinax sp. (skull)	similar	none	similar	rounded	slit - almost complete ventrally	more comma-shaped; pointed ventro-caudally	present and more or less individualized	well developed	One single larger	?	?	no	beak shorter, rostral opening smaller	?	?	?	?	?	?
	Pipilo intermedia signatus (skull)	hooked flatter	none	similar	rounded	slit - almost complete ventrally	similar	present and fused	well developed	One single larger fenestrae, no caudal septum	?	?	no	rostr. slightly more tapered	?	?	?	?	?	?
Rupicola rupicola	hooked flatter	present; fan-shaped	similar	rounded	slit - almost complete along the rostral aperture, viewed in dorsal aspect; dorsal fenestrae present (this ventral fenestra)	more rounded, and comma-shaped; pointed ventro-caudally	present and more or less individualized	slightly developed	One single larger fenestrae, no caudal septum	?	?	no	beak more hooked, rostr. more tapered	yes	very little developed	much less developed	highly less developed	rounded edge	rather similar	
Phytoloma rora	hooked flatter	none (2)	similar	rounded	almost complete distally	larger, more rectangular	present and more or less individualized	developed	dorsal fenestrae larger	processus orbitalis much narrower; processus mandibularis wider	no	no	beak more hooked, rostral opening reduced; absence of gony	yes	less developed	highly less developed	highly less developed	relatively rounded edge	processus lateralis more developed distally	
Tyrannidae	Oryzopsis cristatus	forward flatter; rostrum more elongated	none	similar	rounded	dorsal, thin rostrum more developed distally	similar	present and more or less individualized	developed	dorsal fenestrae much reduced, ventral fenestrae more reduced	?	no	beak thinner	yes	developed, as fossil	less developed, weaker	similarly very developed; more hooked	rounded edge	processus lateralis more developed distally	
	Oryzopsis coronatus	forward flatter; rostrum more elongated	large, semi-circular crest fan-shaped; rostrally - same for other species in the genus	similar	rounded	over 1/2 rostral	larger, more developed distally	present and more or less individualized	developed	both fenestrae much smaller	processus mandibularis more developed laterally	no	beak larger and more hooked, rostral opening more reduced; gony very reduced	yes	slightly less developed, longer than fossil	highly less developed	rounded edge	processus lateralis more developed distally		
	Tyrus similis	hooked flatter	none	similar	rounded	semi-circular small before central open area	larger	free?	well developed	both fenestrae larger	processus orbitalis much more developed distally	no	rostral opening reduced; absence of gony	yes	much thinner	less developed	highly less developed	relatively straight edge	processus lateralis more developed medially and distally	
	Schiffornis turdina	similar	none	similar	rounded	fan-like ridge central, flat, derived from rostral dorsal caudal part	larger	well individualized; reaches the ectotympanum	well developed	ventral fenestrae slightly reduced, dorsal fenestrae larger	proc. orbitalis more ventral	no	similar, but gony less marked and less slightly decurved	yes, fenestrae	wider and more elongated	less pointed	highly less developed	rounded edge	more developed latero-distally	
	Tyrannus dominicensis	rather similar	none (1)	rather smaller	?	over 1/2 rostral	?	present and more or less individualized	developed	ventral fenestrae much reduced, dorsal fenestrae larger	?	?	no	beak longer; gony less marked	yes	developed, same shape as fossil	much less developed	relatively straight edge	rather similar	
Tyrannidae	Tyrannus sp.	hooked much flatter	right crest in dorsal position	similar	dorsal edge flatter	over rostral dorsal half	larger	?	slightly developed; pointed	ventral fenestrae larger, ventral fenestrae smaller	proc. orbitalis shorter and more circular wider	?	beak much longer; gony less marked	yes	markedly less developed; point in dorsal position	less developed medially	highly less developed	relatively straight edge	developed more latero-distally	
	Rodrostrum sp.	similar	none	similar	rounded	over rostral dorsal half, very thin	more extended distally	free?	slightly developed; pointed	dorsal fenestrae larger, separation thicker	?	?	beak thinner and more hooked; rostral opening reduced; gony less marked	yes	markedly less developed	less developed medially	highly less developed	rounded edge	processus lateralis more developed distally; more elevated latero-distally	
	Cotopaxus leucotis (skull)	hooked much flatter	right crest in rostral position (short in this species)	similar	rounded	over large part	rather similar	?	moderately developed	?	?	?	beak much larger, with edges parallel	?	?	?	?	?	?	
	Rhyncocyclus olivaceus	similar	none (1)	rather smaller	?	dorsal half and 1/4 rostral	larger	free?	more developed	ventral fenestrae more reduced, dorsal fenestrae larger	processus mandibularis more elevated laterally	no	beak slightly thinner; slightly more decurved; rostral opening more reduced; gony less marked	yes	less developed than in the fossil; with an individualized elongation opening more rostrally	less developed	similarly very developed; slightly more hooked	relatively circular edge	more developed medially and laterally	
Rhyncocyclus sp.	similar	right crest in dorsal position	similar	rounded	dorsal half and 1/4 rostral	larger	free?	more developed	ventral fenestrae more reduced, dorsal fenestrae larger	?	?	no	beak slightly thinner; slightly more decurved; rostral opening more reduced; gony less marked	yes	even more developed than fossil; with an individualized elongation opening more rostrally; oblique area at the ectotympanum, ventral side	less developed	highly less developed	rounded edge	more developed medially and laterally	
Passer (Oscines)	Melospiza (R)	Melospiza coronata	?	none	?	?	present and reduced (but not in skull)	developed	dorsal fenestrae much reduced, ventral fenestrae more reduced	proc. orbitalis reduced, and more robust	no	?	yes	undifferentiated	?	?	?	?	?	

	Arctomorphidae (18)		?	none	reduced		none	?	present, free and small	(developed)	One single large seleniza, no modified septum	pterosau orbitals reduced and more robust	yes	?	?	very little developed	?	?	?	?
	Pleurophryneidae (13)	<i>Sirivola</i> sp., <i>Pleurophryne albivitta</i>	?	none	large (25)	?	none		present and individualized large	?	ventral and dorsal fenestrae reduced	proc. oticus proportionally absent	no	?	yes	obscure to highly acute	?	?	?	?
	Climacoptera (2)		?	none	?	?	?	?	free lacrimal absent (2)	?	One single large seleniza, no modified septum (2)		?	?	?	?	?	?	?	?
	Meliphagidae	<i>Ptilopus corvulinus</i> , <i>Meliphaga</i> sp., <i>Meliphaga melanogaster</i>	?	none	large	?	none	?	free lacrimal absent (2)	?	ventral and dorsal fenestrae reduced, a third ventral ones smaller (2)	proc. orbitals developed more distally	no	?	?	very little developed	?	?	?	?
	Parabellidae	<i>Parabellus punctatus</i>	?	none	large	?	none	?	?	?	One single large seleniza, no modified septum	?	no	?	?	undveloped	?	?	?	?
	Acetabidae	<i>Geogaster pavostris</i>	lowhead fatter and longer	none	large	dorsal edge fatter	almost complete	larger	fused or absent	highly developed	Dorsal fenestrae more developed, ventral fenestrae more reduced, separation thinner	?	no	rostrum longer and thicker, sub-gonys less reduced	no	less developed	much less developed	ventrally very developed, much more hooked	rounded edge	more developed latero-distally
	Pomatorhinidae	<i>Pomatorhinus temporalis</i> <i>trivittatus</i>	?	none	?	?	?	?	?	?	?	?	?	?	?	very little developed	?	?	?	?
	Parabellidae	<i>Pleurophryne</i> , <i>Parabellus</i> <i>nostris</i>	?	present, directed distally	large (21)	?	complete	?	present	?	One single large seleniza, no modified septum	pterosau orbitals distinct, slightly narrower top expanded	no	?	?	very little developed	?	?	?	?
	Other oases								many Corvidae: free lacrimal present; most Phoenicidae: free lacrimal absent (2)	Corvidae very much developed	many Corvidae: dorsal fenestrae absent; most Phoenicidae: dorsal fenestrae present (2)	Corvidae: proc. orbitals proportionally distinct	no	?	Corvidae: yes	absent or very little developed (in Corvidae absent)	Corvidae: developed	?	?	?
	<i>Mitrochus</i> <i>serius</i> ? (24)		?	?	more reduced (less than half of the cranium length)	?	absent	?	?	?	?	?	no	?	no	developed	not much developed	?	?	much more developed laterally

Taxon			Mandible							Ulna						Carpometacarpus				Proximal wing phalanges of major digit	
Suborder to Family	Species (species seen for comparison are listed, but see *)	Outline	Fossa pneumatica/triangular	Crista deltopectoralis	Shaft shape	Depth of notches caudally	Processus flexorius	Processus supraepiphyseal/dorsalis	Tuberculum ligamentum/collare/ventral	Caudal ventral	Papilla sesamoidea	Processus dorsalis (D)	Processus intermetacarpalis	Dorsal angulation of C1	Carpometacarpus outline	Processus extensorius	Blade	Processus internus indicis			
Revest-des-Brousses fossil (early Oligocene) NT-LBR-014			see illustrations	unique	see illustrations	straight	Rather deep	Straight edge	unique, well marked	prominent	rather gross (see distal to the distal border of the carpal wedge. Plane of cut. vert. forms an angle with oblique axis, ventral view)	rather little marked	present, rather well marked	see illustrations	see illustrations	in dorsal aspect, the proximal border of the C1 processes forms a right angle with the radial border of the dorsal edge of the trochlear carpal, without a notch in the angle.	"subcuneiform" in shape and rounded caudally, and forming a notched distal pointed protuberance extending more distally. NB pointed protuberance slight	present			
Acanthisittidae			<i>Acanthisitta chloris</i> (S)	Two similar fossae, moderate non-pneumatic	reduced	curved (S-shaped)	shallow	?	very little marked to absent	prominent	?	marked to very well marked	absent, or marked undulation	more proximal	rather similar	variable between genera (S)	"cuneiform", in caudal edge straight	reduced to absent			
Eurylaimides	Pittidae	<i>Pitta sordida</i>	slender proximally	unique, pneumatic	similar	straight	rather deep	edge deflected dorso-caudally	unique, well marked	prominent	distal edge of cunya well marked, no groove distal to S. Plane of cut. vert. forms an angle with oblique axis.	very well marked	present, rather well marked	similar	"subcuneiform" type, with pointed protuberance	slightly less elongated	there is a distinct notch in the angle between the proc. ext. and the dorsal edge of trochlear carpal.	intermediate between typical subcuneiform and typical cuneiform types	present		
	Philipidae	<i>Philippia castanea</i>	rather similar	unique, pneumatic	similar	straight	rather deep	?	unique, well marked	prominent	?	very well marked	absent	similar	intermediate between subcuneiform and cuneiform types, with pointed protuberance	slightly less elongated	there is a distinct notch in the angle between the proc. ext. and the dorsal edge of trochlear carpal.	intermediate between typical subcuneiform and typical cuneiform types	present		
	Eurylaimidae	<i>Cymbalychnus macrochrysalis</i>	rather similar but wider	unique, pneumatic	similar	straight	moderately deep	edge deflected dorso-caudally	unique, little marked	prominent	distal edge of cunya well marked, no groove distal to S. Plane of cut. vert. forms an angle with oblique axis.	very well marked	present, rather well marked, situated more proximally	similar but less pointed	subcuneiform type, pointed protuberance more developed	slightly more robust	there is a distinct notch in the angle between the proc. ext. and the dorsal edge of trochlear carpal.	subcuneiform type, blade edge slightly more rounded	present		
	Calystonidae	<i>Calystonia viridis</i>	rather similar but more curved distally	unique, pneumatic	similar	straight	rather deep	edge deflected dorso-caudally	unique, little marked	prominent	distal edge of cunya well marked, no groove distal to S. Plane of cut. vert. forms an angle with oblique axis.	very well marked	absent to rather well marked	similar but less pointed	rather more similar to cuneiform type (in shape), but with a pointed protuberance	slightly more robust	there is a distinct notch in the angle between the proc. ext. and the dorsal edge of trochlear carpal.	subcuneiform type, blade edge slightly more rounded	present		
	Sapayoidae	<i>Sapayoa onymus</i>	similar	unique, pneumatic	similar	straight	shallow	edge deflected dorso-caudally	unique, well marked	prominent	distal edge of cunya well marked, no groove distal to S. Plane of cut. vert. forms an angle with oblique axis.	moderately better marked	present	more distal	subcuneiform type, with pointed protuberance	less elongated	there is a distinct notch in the angle between the proc. ext. and the dorsal edge of trochlear carpal.	similar	present		
	Fumaridae (S)	<i>Groenitella curvicularis</i>	NB: cranial eminence slightly rounded	unique, pneumatic	similar	straight	shallow	straight edge	unique, very little marked	prominent	?	very little marked	absent to very slight undulation	similar	subcuneiform type, with pointed protuberance	similar	intermediate between typical subcuneiform and typical cuneiform types (closer to the latter)	present			
		<i>Dendrocincla fuliginosa</i>	rather similar	unique, pneumatic	similar	straight	rather deep	?	unique, very little marked, and an even less marked second one	prominent	?	slightly better marked	absent to very slight undulation	similar	subcuneiform type	slightly less elongated	similar	rather cuneiform type	almost absent		
		<i>Myrmotherula ovalis</i>	more curved and more angled distally	unique, pneumatic	similar	straight	?	?	?	unique, very little marked	very prominent	?	similar	slight undulation	more square	rather more similar to cuneiform type (in shape), but with a very slight pointed protuberance	processus extensorius more the shape of an isosceles triangle	?	rather cuneiform type	absent	
	Thamnotrochidae	<i>Subospizus comobensis</i>	more curved distally	unique, pneumatic	similar	straight	?	?	unique, little marked	prominent	?	?	similar	rather similar	intermediate between subcuneiform and cuneiform types, close to subcuneiform type with a very slight pointed protuberance	rather similar	intermediate between typical subcuneiform and typical cuneiform types	rather similar	absent		
		<i>Thamnotrochus dolosus</i> (skull)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
		<i>Thamnotrochus conicus</i> (skull)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	Conopophagidae	<i>Conopophaga andresaca saturata</i>	much more curved distally	unique, pneumatic	similar	very slightly S-shaped	?	?	unique, well marked, with a very little marked second one	prominent	?	similar	present, very well marked	slightly more developed	rather more similar to cuneiform type (in shape), but with a pointed protuberance	(slightly more robust)	similar	intermediate between typical subcuneiform and typical cuneiform types; rather similar to the subcuneiform but narrower	absent		
Rhinocryptidae	<i>Scytalopus unicolor</i>	more curved distally	unique, less pneumatic	reduced	S-shaped	rather deep; (all rhinocryptids have a deep as in leaf) (S)	straight edge	unique, well marked	very prominent	?	very little marked	present, very well marked (S)	rather developed	subcuneiform type	more robust	similar	rather cuneiform type	almost absent			
Formicariidae	<i>Formicarius analis</i>	more curved distally	unique, pneumatic	similar	straight; (all formicariids straight to S-shaped) (S)	shallow; (all formicariids more or deep as in leaf) (S)	straight edge	unique, rather marked	prominent	?	moderately better marked	very well marked in this species, but its frequency absent in this family.	slightly more developed	subcuneiform type, with pointed protuberance	similar	somewhat intermediate	intermediate between typical subcuneiform and typical cuneiform types (closer to the latter)	very slight			
Tyranni (Subocines)	<i>Centropus erythrogalax</i>	slightly more curved	unique, pneumatic	similar	straight	rather deep	straight edge	unique, well marked	prominent	similar	unique, very little marked	absent	similar	subcuneiform type, with very slight pointed protuberance	similar	similar	subcuneiform type, very slightly narrower	present			
	<i>Neopelma sulphureiventer</i>	?	?	?	?	?	?	?	prominent	similar	unmarked	absent	less developed; straighter	subcuneiform type, with slight pointed protuberance	similar	similar	similar	?	?		
	<i>Tyrannus abbotsoni</i>	slightly more curved distally	unique, pneumatic	similar	straight	moderately deep	straight edge	unique, well marked	prominent	?	very little marked	absent	similar	subcuneiform type, with pointed protuberance	similar	similar	subcuneiform type, but narrower	present			
	<i>Chlorospiza holochroa viridis</i>	rather similar	unique, pneumatic	similar	straight	shallow	straight edge	unique, well marked	prominent	?	rather marked	absent	rather similar	subcuneiform type, with pointed protuberance	rather similar	similar	identical	present			
	Pipridae	<i>Mniotiltus melanax</i>	distal two-thirds much wider	unique, pneumatic	similar; slightly shorter (more distally)	straight	shallow	straight edge	unique, very well marked	prominent	?	similar	present	much more developed	subcuneiform type, with slight pointed protuberance	more robust	similar	similar	absent		
		<i>Macharopipra pyrocephala</i>	similar	unique, pneumatic	similar; slight less developed; slightly shorter (more distally)	straight	rather deep	straight edge	unique, well marked	prominent	?	very well marked	slight undulation	slightly more developed	subcuneiform type, with very slight pointed protuberance	similar	similar	subcuneiform type, but narrower	present		
		<i>Chirogalia linearis</i>	similar	unique, pneumatic	similar	straight	rather deep	straight edge	unique, very well marked	prominent	?	similar	absent	similar	subcuneiform type, with very slight pointed protuberance	similar	similar	subcuneiform type, but the most caudal extremity of the blade is present	present		
	<i>Xenospiza atronotus</i>	more curved distally	unique, pneumatic	similar	straight	shallow	straight edge	unique, very well marked	prominent	?	very little marked	present	similar	subcuneiform type, with pointed protuberance	similar	similar	similar	present			
	<i>Mniotiltus chrysotus</i>	rather similar	unique, pneumatic	similar	straight	shallow	straight edge	unique, very well marked	prominent	similar	very little marked	very slight	similar	subcuneiform type, with very slight pointed protuberance	similar	similar	similar	similar	present		
	<i>Amphispiza bilineata</i>	similar	unique, pneumatic	similar	straight	rather deep	straight edge	unique, well marked	prominent	similar	similar	absent	similar	subcuneiform type, with very slight pointed protuberance	similar	similar	subcuneiform type, but narrower	present			
	Tyrannidae	<i>Pipilo maculatus</i>	?	unique, pneumatic	similar	straight	moderately deep	straight edge	unique, well marked	prominent	similar	?	undulation	more pointed	subcuneiform type, with slight pointed protuberance	shorter, straighter, intermetacarpals less developed	similar	subcuneiform type, but narrower	present		
<i>Cyhalopterus ornatus</i>		slender proximally	unique, pneumatic	similar	straight	shallow	edge relatively straight	unique, very little marked	prominent	similar	very well marked	absent or slight undulation	more developed	subcuneiform type, with pointed protuberance	similar	similar	subcuneiform type; blade more pronounced caudally	present			
<i>Cottage sp.</i>		area of maximal curvature wider	unique, pneumatic	similar	straight	shallow	straight edge	unique, very little marked, and an even less marked second one	prominent	similar	moderately better marked	undulation	similar	subcuneiform type, with pointed protuberance	similar	somewhat intermediate but closer to fossil	similar	present			
<i>Procinus sp. (skull)</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Pipilo intermedium signatus</i> (skull)		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Rupicola rupicola</i>		wider, area of maximal curvature more proximal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Phylloscopus borealis</i>		wider and more curved distally	unique, pneumatic	similar	straight	rather deep	straight edge	unique, very little marked	prominent	similar	very little marked	very slight	more pointed and narrower	subcuneiform type, with pointed protuberance	similar	?	very similar	present			
Tityridae	<i>Oxyechus cristatus</i>	?	?	?	?	?	?	?	prominent	similar	similar	?	?	?	?	?	?	?	?	?	
	<i>Oxyechus coronatus</i>	wider and more curved distally	unique, pneumatic	similar	straight	rather deep	straight edge	unique, rather marked	prominent	similar	similar	slight undulation	more developed laterally	subcuneiform type, with pointed protuberance	similar	intermetacarpals more developed	similar	slight middle; pile cranial more individualized and protruding in relation to the blade plane	present		
	<i>Tityro semifasciata</i>	wider	unique, non-pneumatic	similar	straight	rather deep	straight edge	unique, well marked	prominent	similar	very little marked	absent	slightly more developed	subcuneiform type, with pointed protuberance	trochlear capsule more developed	similar; proc. ext. more developed	similar	slight middle; pile cranial more individualized and protruding in relation to the blade plane	present		
	<i>Schiffornis taurina</i>	more curved distally	unique, pneumatic	similar	straight	rather deep	straight edge	unique, well marked	prominent	?	(very little marked)	slight undulation	similar	subcuneiform type, with pointed protuberance	similar	similar	very similar	present			
Tyrannidae	<i>Tyrannus dominicensis</i>	similar	unique, pneumatic	similar	straight	rather deep	straight edge	unique, rather little marked	prominent	similar	moderately better marked	slight undulation	slightly less developed	subcuneiform type, with pointed protuberance	similar	similar	very similar	present			
	<i>Tyrannus sp.</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
	<i>Tadornistrum sp.</i>	much wider and more curved	unique, pneumatic	similar	straight	shallow	straight edge	unique, very little marked	prominent	similar	similar	absent	similar	subcuneiform type, with pointed protuberance	similar	similar	very similar	present			
	<i>Centropus fuscatus</i> (skull)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
	<i>Athyya olivacea</i>	more curved distally	unique, pneumatic	similar	straight	shallow	straight edge	unique, rather marked, wider	prominent	similar	very little marked	undulation	less pointed medially; narrower	subcuneiform type, with pointed protuberance	similar	similar	slight middle; pile cranial more individualized and protruding in relation to the blade plane	present			
<i>Rhythidion sp.</i>	more curved	unique, pneumatic	similar	straight	shallow	straight edge	unique, very little marked, and beginning of a second	prominent	similar	absent	slight undulation	slightly more pointed medially	subcuneiform type, with pointed protuberance	similar	similar	slight middle; pile cranial more individualized and protruding in relation to the blade plane	present				



																			ventrally, relative to the black plate		
Passer (Oscines)	Mniotiltidae (2)	Mniotilta maculirostris	curved, more homogeneously	unique, pneumatic	reduced	straight	?	?	unique, little marked	non- prominent flap	?	moderately marked	present, very well marked	developed	ocine type	more robust	?	?	?		
	Alcedinidae (1)		curved, more homogeneously	unique, pneumatic	reduced	S-shaped	?	?	absent	non- prominent flap	?	rather marked	slight	?	ocine type	?	?	?	ocine type (blade caudal edge straight)	?	
	Ptilinopus (1)	Sericornis sp., Ptilinopus albertus	curved, more homogeneously	unique, pneumatic	similar	straight	?	?	marked, sometimes beginning of a wave	non- prominent flap	?	little marked	absent	similar	ocine type	similar	?	?	ocine type	absent	
	Climacteridae (2)		?	unique, non-pneumatic (2)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	Meliphagidae	Ptilinopus corollatus, Meliphaga lewis Melospiza melanocorypha	straighter and wider proximally	unique, pneumatic (2) (beginning of a second sometimes rather marked)	similar	straight	?	?	double, little developed	non- prominent flap	?	?	extremely slight undulation	?	ocine type	?	?	?	?	ocine type	absent
	Pardalipidae	Pardalipus punctatus	more curved and more angular distally	unique, pneumatic	similar	straight	?	?	unique, very well marked	?	?	?	?	?	?	?	?	?	?	?	?
	Acrididae	Gerygone olivacea	rather similar	double, dorsal lobe pronounced	similar	straight	rather deep, very narrow	straight edge	pronounced (double but with very shallow divert)	non- prominent flap	?	?	distal edge of carina well marked, no groove distal to it. Flare of carina wide. In ventral view more in continuity with abdomen area.	moderately marked	very well marked	more proximal, less developed	ocine type	similar	similar	?	?
	Fananiidae	Fananius tenuis	more curved and more angular distally	unique, pneumatic	[similar]	straight	?	?	unique, little marked	non- prominent flap	?	?	?	slight undulation	?	ocine type	?	?	?	ocine type	very reduced
	Rendulidae	Rendulca parvulus, Rendulca minor	more curved and more angular distally	unique, pneumatic	similar	straight	?	?	double, rather little marked	non- prominent flap	?	?	?	extremely slight undulation	similar	ocine type	similar	?	?	ocine type	absent
	Other oscines		?	unique or double (2) (in Corvidae unique, pneumatic)	similar	straight	?	?	Generally double (in Corvidae double, well marked)	non- prominent flap				absent or present (2) (in Corvidae absent)		ocine type				ocine type	absent
Wattlebird wren T (2)		?	unique	?	straight	?	?	?	?	?	?	marked	more rounded	symphysis poorly developed; presents a pointed protuberance	similar	?	?	?	?	?	



		<i>Rhycolocycylus olivaceus</i>	absent	marked	rather similar		no, wide gap between the two cristae, cristae plantaris very little developed	present	as fossil	no	extension less distal	?	no	more curved and tapering
		<i>Rhycolocycylus</i> sp.	absent	marked	rather similar		no, wide gap between the two cristae, cristae plantaris very little developed	present	as fossil	no	as fossil	extension less distal	no	similar
Passer (Oscines)	Mniotiltidae (18)	<i>Mniotilta maculirostris</i>	absent	marked, and more proximal	?	marked	no, crista plantaris little developed	present	rather proximal	yes	extension slightly more distal	extension slightly less distal	yes	?
	Archonotidae (18)		absent	marked	?	little to moderately marked	no, crista plantaris little developed	present	intermediate / proximal	yes	extension slightly more distal	extension slightly less distal	yes	?
	Ptilonotidae (12)	<i>Sericornis sp.</i> , <i>Ptilonotus ruber</i>	absent	almost absent	hardly visible	almost absent	yes	present	?	no	extension slightly less distal	extension slightly less distal	no	?
	Climacteridae (2)		?	?	?		yes (2)	?	?	?	?	?	?	?
	Meliphagidae	<i>Ptilinopus coronatus</i> , <i>Meliphaga lewinii</i> , <i>Meliphaga melanocapilla</i>	absent	present, moderately marked	little marked	little marked	variable: no fusion to almost fusion (figure very fusion in <i>Ptilinopus</i> ) (2)	present	?	no	slightly less distal	?	no	
	Paridae	<i>Paridae punctata</i>	absent	present, moderately marked	absent (or hardly visible)	very little marked	no	?	?	no	?	?	?	?
	Acanthidae	<i>Gerygone olivacea</i>	?	present, marked	absent		yes	absent?	?	?	no, IV slightly as fossil	extension slightly less distal	?	more curved and tapering
	Parastomatidae	<i>Parastotanus temporei</i> , <i>misgonyx</i>	absent	?	very slight	very slight	no, small gap between the two cristae	present	?	?	?	?	no	?
	Paridae	<i>Ptilinopus parvulus</i> , <i>Paridae minor</i>	absent	almost absent	small	almost absent	no, wide gap between the two cristae	present	?	no	oriented more proximally	?	slightly	?
	Other oscines		?	absent or almost absent	Consider: present, less distal	absent to very slight	no (2)	generally present	Consider: more distal	no (or extremely slightly plantaris)	Consider: slightly less distal extension than in	Consider: very slight less distal extension than the III.	no	Consider: generalist
<i>Mniotilta arvensis</i> ? (2)		?	?	?		?	absent	?	?	?	?	?	slightly more robust	

1 **Supplementary Table 2** Additional characters in the fossil NT-LBR-014 and extant  
2 Tyrannida (i.e., Pipridae, Cotingidae, Tityridae and Tyrannidae).  
3 All character states of species compared to the fossil are given relative to state of the fossil.  
4 NB: for several modern specimens, character states are absent due to the lack of the element  
5 or element part, or the incomplete specimen preparation, obscuring detail by ligaments for  
6 instance. It is specified for which specimens the skull only could be examined.  
7

Taxon		Skull		Humerus		Ulna	
Family	Species	Size of nasal opening	Lateral parts of etectmoid	Crus ventralis fossae	Crus dorsalis fossae	Cotyla dorsalis	Position of the dorso-proximal edge of the incisura tendinosa (for mm. extensor metacarpi ulnaris and extensor digitorum communis), distal ulna
Revest-des-Brousses fossil (early Oligocene) NT-LBR-014		large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
Pipridae	<i>Pipra erythrocephala</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	<i>Neopelma sulphureiventer</i>	large; more than half rostrum length	gap reduced	?	?	hollow; little developed	proximal
	<i>Tyrannetes stolzmanni</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	<i>Chloropipo holochlora viridior</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	<i>Manacus manacus</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	<i>Machaeropterus pyrocephalus</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	<i>Chiroxiphia linearis</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	<i>Xenopipo atronitens</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	<i>Masius chrysopterus</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	<i>Antilophia galeata</i>	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
Cotingidae	<i>Pipreola arcuata</i>	medium-sized	gap larger	well developed	well developed	flat; wide	proximal
	<i>Cephalopterus ornatus</i>	medium-sized	gap larger	well developed	well developed	flat; wide	proximal
	<i>Cotinga</i> sp.	medium-sized	gap larger	well developed	well developed	flat; wide	proximal
	<i>Procnias</i> sp. (skull)	medium-sized	gap larger	?	?	?	?
	<i>Pipreola intermedia signata</i> (skull)	medium-sized	gap larger	?	?	?	?
	<i>Rupicola rupicola</i>	medium-sized	gap larger	?	?	?	?
	<i>Phytotoma rara</i>	medium-sized	gap larger	well developed	well developed	flat; wide	proximal
Tityridae	<i>Oxyruncus cristatus</i>	small	gap larger	?	?	flat; wide	proximal
	<i>Onychorhynchus coronatus</i>	small	gap larger	well developed	well developed	flat; wide	proximal
	<i>Tityra semifasciata</i>	small	gap larger	well developed	well developed	flat; wide	proximal
	<i>Schiffornis turdina</i>	small	gap larger	well developed	well developed	flat; wide	proximal
Tyrannidae	<i>Tyrannus dominicensis</i>	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal
	<i>Tyrannus</i> sp.	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal
	<i>Todirostrum</i> sp.	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal
	<i>Contopus latirostris</i>	large; more than half rostrum length	gap moderate but larger than fossil	?	?	hollow; wide	distal
	<i>Rhynchocyclus olivaceus</i>	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal
	<i>Rhynchocyclus</i> sp.	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal

1 **Supplementary Table 3** Measurements (lengths) of the main bones of the Luberon fossil  
 2 NT-LBR-014 (mm).

Skull		Wing		Leg	
Cranium	21.5	Humerus	19.4	Femur	18.6
Beak	15.1	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	15.7	Total length of wing bones	64.7	Total length of leg bones	84.5
Scapula	19.6				

3

4

5 **Supplementary Table 4** States of characters selected and coded for the radial visualisation in  
 6 Fig. 5. The character states are coded in order to categorize observations in Supplementary  
 7 Tables 1 and 2, as follows. State (0) corresponds to absence of the character, state (1) to  
 8 presence of the character but state different from the fossil's, and state (2) to presence of  
 9 character and state similar or identical to the fossil's. The extant species of comparison are  
 10 limited here to the Tyrannides for which all characters were assessable, and the characters are  
 11 those exhibiting heterogeneous states across the Tyrannides.

12

	Skull							Coracoid			Scapula		Humerus		Ulna		Carpometacarpus					Proximal wing phalanx of major digit			Femur		Tibiotarsus		Tarsometatarsus			
	Cranium shape (lateral profile)	Feather crest	Relative size of orbits	Osseous nasal septum	Fenestra antorbitalis (proportion)	latero-dorsal part of ectethmoid	Rostrum and mandible (mdb)	Processus procoracoides	Processus acrocoracoides	Brachial tuberosity (tuberculum brachiale)	Coracoid blade shape	Outline	Crista deltopectoralis	Shaft shape	Depth of incisura capitis	Processus supracondylaris dorsalis	Papillae laminae caudalis	Processus dentiformis	Processus intermetacarpalis	Distal symphysis of os carpale minus	carpometacarpus outline	Processus extensorius	Blade	Processus internus indicis	Hollow just distal to proximal articular surface, caudal side	Incisura intercondylaris	Proximal tarsometatarsus	Position of pons supratendineus	Trochlea metatarsus II	Trochlea metatarsus IV		
<i>Fossil</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>Geositta cunicularia</i>	2	1	1	0	1	1	1	1	1	1	1	2	2	1	1	1	0	1	1	1	1	2	1	2	2	1	1	1	2	2	2	
<i>Dendrocincla fuliginosa</i>	1	0	1	0	1	2	1	1	1	1	1	2	2	1	1	1	0	1	1	1	2	1	0	0	1	1	2	1	2	1	2	
<i>Myrmotherula axillaris</i>	2	1	1	1	1	1	1	1	1	1	1	2	2	1	1	2	1	1	1	1	2	1	0	0	1	1	1	2	2	1	2	
<i>Sakesphorus canadensis</i>	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	2	0	1	1	1	2	1	0	0	1	1	2	2	1	2	1	
<i>Conopophagidae ardesiaca</i>	1	0	1	1	1	1	1	1	1	1	1	2	2		1	2	1	1	1	1	2	1	0	0	1	1	2	2	2	2	2	
<i>Scytalopus unicolor</i>	1	1	1	0	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	1	2	1	1	1	2	2	1	2	2
<i>Formicarius analis</i>	1	0	1	0	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	2	2	1	2	2
<i>Pipra erythrocephala</i>	2	1	1	1	1	1	2	1	2	1	1	2	2	1	2	1	0	1	2	1	2	1	2	1	1	1	2	2	2	2	2	2
<i>Tyrannetes stolzmanni</i>	2	1	2	1	1	1	1	1	1	2	1	2	2	1	2	1	0	1	1	1	2	1	2	0	2	2	2	2	2	2	2	1
<i>Chloropipo holochlora</i>	1	1	1	1	1	1	2	1	1	1	1	2	2	1	2	1	0	1	1	1	2	2	2	0	1	2	2	2	2	2	2	2
<i>Manacus manacus</i>	1	1	1	1	1	1	1	1	1	1	1	2	2	1	2	1	2	1	2	1	2	2	0	0	2	2	2	2	2	2	2	2
<i>Machaeropterus pyrocephalus</i>	1	1	1	1	1	1	1	1	1	2	2	2	2	1	2	1	1	1	2	1	2	1	2	0	2	2	2	2	2	2	2	1
<i>Chiroxiphia linearis</i>	1	1	1	1	1	1	1	1	1	2	2	2	2	1	2	2	0	2	2	2	2	1	2	2	1	2	2	2	2	2	2	2
<i>Xenopipo atronitens</i>	1	1	1	1	2	2	1	2	1	1	1	2	2	1	2	1	1	2	1	2	2	2	2	2	2	2	2	2	2	2	2	1
<i>Masius chrysopterus</i>	1	1	1	1	1	2	1	1	1	2	1	2	2	1	2	1	1	1	2	1	2	2	1	2	2	2	2	2	2	2	2	2
<i>Antilophia galeata</i>	2	2	1	1	1	1	2	2	2	2	2	2	2	1	2	2	0	2	2	2	2	2	2	0	2	2	2	2	2	2	2	2
<i>Cephalopterus ornatus</i>	1	1	1	1	1	1	1	2	2	1	1	2	2	1	1	1	1	1	1	1	2	1	2	0	0	1	2	2	2	2	2	2
<i>Cotinga sp.</i>	1	1	1	1	1	2	1	1	2	2	1	2	2	1	1	1	0	2	1	2	1	2	2	0	1	1	2	1	2	1	2	2
<i>Onychorhynchus coronatus</i>	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	2	1	1	1	1	2	1	2	1	2	1	2	1	2	1	2	1
<i>Schiffornis turdina</i>	2	1	1	1	1	1	1	1	1	1	1	2	2	1	2	1	1	1	1	1	2	2	2	0	2	2	2	2	2	2	2	2
<i>Tyrannus dominicensis</i>	2	1	1	1	1	1	2	1	1	1	2	2	2	1	1	1	1	1	1	1	2	2	2	0	1	1	0	1	2	1	2	2
<i>Todirostrum sp.</i>	2	0	1	1	1	1	1	1	1	1	1	2	2	1	1	2	0	2	1	2	2	2	2	0	1	1	0	1	2	1	2	2
<i>Rhynchocyclus olivaceus</i>	2	0	1	1	1	1	1	1	2	1	1	2	2	1	1	1	1	1	1	1	2	1	2	0	2	1	2	1	1	1	1	1
<i>Rhynchocyclus sp.</i>	2	1	1	1	1	1	1	1	1	1	1	2	2	1	0	1	1	1	1	1	2	2	2	0	2	1	2	1	1	1	1	1

1 **Supplementary Table 5** Character matrix used for the phylogenetic analyses.

2



Species name	Relative size of orbit	Shape of orbit	Size of nasal opening	Femora antero-lateral (proportion)	On lacrimal	Lateral-dorsal part of ectotympan	Lateral parts of ectotympan	Crest of supra-orbital margin	Forearm (presence of concave distal end)	Processus procarpalis	Processus acrocarpalis	Basal tubercle (tuberculum basale)	Sulcus medialis supra-carpalis	Fossa pneumonostriata	Crista deltopectoralis	Crua ventralis foveae	Crua dorsalis foveae	Depth of supra-carpal fossa	Processus flexorius	Processus supra-carpalis dorsalis	Processus supra-carpalis ventralis	Tuberculum ligamentis collateralibus ventralis	Capula ventralis	Capula dorsalis	Position of the dorso-proximal edge of the radius between PIV and anterior metacarpal ulna and anterior ulnar condyle, distal side	Capula caudalis	Processus dentiformis	Position of processus osseus/articularis	Distal depth of os metacarpale distale	Processus osseus	Metacarpal distal to proximal articular surface	Metacarpal distal to proximal articular surface	They protrude distal groove between the scapular and the tuberculum carpalis distal, proximal to the lateral condyle, medial aspect	Trochlea humeralis	Position of carpi	Position of panni	Trochlea metatarsi II	Trochlea metatarsi IV				
Fossil	2	0	2	0	1	2	3	0	0	1	1	2	2	1	0	0	1	1	2	1	1	1	0	0	1	2	0	1	0	0	2	0	2	0	1	2	0	1				
Felis concolor	0	0	0	7	1	0	1	7	0	0	1	1	0	0	1	0	7	7	1	1	0	1	2	1	0	7	7	7	2	1	1	1	0	1	1	2	0	2				
Philopelta castanea	0	0	0	7	1	0	0	7	0	0	1	1	0	7	0	7	7	1	1	7	1	2	1	0	7	7	7	2	1	1	1	0	1	1	0	1	2	0	7			
Erythronchus megarhynchus	0	0	0	7	0	0	2	7	0	0	0	0	0	1	0	7	7	1	1	0	1	1	1	0	7	7	2	0	1	1	0	0	1	0	1	0	1	2	1	2		
Colaptes auratus	1	0	0	7	0	0	2	7	1	0	1	0	0	1	0	7	7	1	1	0	1	1	1	0	7	7	2	1	0	1	1	0	0	0	1	0	1	2	1	2		
Sayornis nigricans	0	0	0	7	1	0	0	7	0	0	1	1	7	7	1	0	7	7	1	0	1	2	1	0	7	7	2	0	1	1	0	0	0	0	1	0	1	2	2	7		
Geothlypis trichas	0	0	0	7	0	1	2	7	0	0	1	0	2	1	0	7	7	1	0	1	1	1	1	7	7	7	0	1	0	1	0	2	1	1	0	1	4	0	7			
Melanerpes formicivorus	0	1	1	7	0	1	1	7	0	7	0	1	1	1	0	7	7	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1	3	0	1			
Sialia mexicanus	0	0	1	7	0	1	2	7	0	7	0	1	7	7	1	0	7	7	1	7	7	1	1	1	1	1	1	0	1	7	1	1	0	1	1	0	1	2	0	0		
Coccyzus erythrophthalmus	0	0	1	7	0	1	0	7	0	7	0	1	0	2	1	0	7	7	1	7	7	1	2	1	7	7	7	1	3	0	1	0	1	1	0	0	1	0	1			
Sialia arctica	0	1	0	7	0	1	1	7	1	1	0	0	0	2	1	1	7	7	0	1	1	1	1	2	1	7	7	7	0	2	0	1	0	1	1	2	0	1	0	1		
Empidonax griseus	0	0	1	7	0	1	1	7	0	0	0	0	1	1	0	7	7	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	1	0	1		
Dendroica fulvica	0	0	1	7	0	1	1	7	0	0	1	1	1	1	1	0	7	7	1	1	7	1	1	1	7	7	7	1	1	0	1	0	1	1	0	1	1	0	1	1		
Pipilo erythrophthalmus	1	0	2	0	0	2	1	0	0	0	1	1	7	7	1	0	0	1	1	1	1	1	1	2	1	1	0	0	0	0	0	0	1	0	0	1	0	1	2	0	1	
Regulus satrapa	0	1	1	0	0	7	1	0	0	0	1	1	1	1	7	7	0	1	7	7	7	7	7	7	1	1	0	0	0	0	0	0	1	0	7	7	7	7	7	7		
Tyrannus carolinensis	0	0	2	0	0	7	1	0	0	0	1	1	1	2	1	0	0	1	1	1	1	1	1	2	1	7	0	0	0	0	0	0	0	0	2	0	1	2	0	0		
Chondestes motacilla	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	1	2	0	1	
Melanerpes formicivorus	0	0	1	0	0	7	1	0	0	7	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	0	1	2	0	1	0	0	1	0	1	1	0	1		
Melanerpes formicivorus	0	0	1	0	0	7	1	0	0	7	1	1	0	2	1	0	0	1	1	1	1	1	1	2	1	7	0	0	3	1	0	1	0	0	0	0	7	0	1	2	0	0
Empidonax griseus	0	0	1	0	0	2	1	0	0	7	1	1	1	1	1	0	0	1	1	1	1	1	2	1	7	0	0	1	0	0	1	0	0	0	2	0	0	1	2	0	1	
Empidonax griseus	0	0	1	0	0	2	1	0	0	7	1	1	1	1	1	0	0	1	1	0	1	1	1	2	1	7	0	0	0	2	0	1	0	0	0	2	0	1	1	0	0	
Empidonax griseus	1	0	1	0	0	2	1	0	0	1	0	1	2	1	0	0	0	1	1	0	1	1	1	2	1	1	0	0	0	1	0	0	0	2	0	0	1	2	0	1		
Artibeus lituratus	2	0	1	0	0	2	1	0	0	0	1	1	2	2	1	0	0	1	1	1	1	1	2	1	1	0	0	1	0	0	1	0	0	1	0	0	1	2	0	7		
Pipilo maculatus	0	0	1	1	0	2	1	2	0	0	1	1	1	1	1	0	1	1	1	1	1	1	2	1	1	1	0	7	1	0	1	0	0	0	7	7	7	7	7	7		
Cephalopterus curvipennis	1	0	1	1	0	2	1	2	0	0	0	1	2	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	2	0	0	1	0	0	0	0	0	0	1	2	0	1
Colaptes auratus	0	0	1	1	1	1	2	2	0	0	1	2	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	0	2	0	0	1	2	0	0	0	1	2	0	1		
Rhyacionia caryocarpae	0	0	1	1	0	2	1	2	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1	2	0	1	7	7	
Dryobates pubescens	1	0	1	2	0	2	1	2	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1	1	2	0	1	2	
Tyrus semifasciatus	0	0	1	2	0	0	1	2	0	0	0	0	1	0	1	0	1	1	1	1	1	1	2	1	1	1	0	0	0	0	1	0	0	0	0	1	2	0	7	7	0	7
Sialia mexicanus	0	0	1	2	0	2	1	2	0	0	1	0	1	1	1	0	1	1	1	1	1	1	2	1	7	1	0	0	1	0	1	0	0	0	0	0	2	0	1	2	0	1
Tyrannus dominicensis	0	0	7	0	7	2	1	1	0	0	1	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	
Troglodytes aedon	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	
Rhyacionia caryocarpae	0	0	1	0	0	0	1	0	0	0	0	0	2	1	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	2	0	0	1	1	7
Rhyacionia caryocarpae	1	0	1	0	0	0	1	1	0	0	1	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	1	2	0	1	2	1	2
Acridothera tristis	0	1	1	7	1	0	0	7	0	1	0	0	7	7	0	7	7	0	0	7	1	0	1	7	7	7	2	0	1	1	7	2	1	0	1	1	0	1	1	1	7	
Ceryle alcyon	0	0	0	7	0	1	0	7	0	1	0	0	2	1	0	0	7	7	1	1	1	0	0	2	0	0	7	7	2	1	1	0	0	7	7	7	1	0	1	0	0	

## 1 **References (for Supplementary Table 1)**

- 2 1. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds) *Handbook of the*  
3 *Birds of the World Alive* (Lynx Edicions, Barcelona, 2019). (retrieved from  
4 <https://www.hbw.com/> on 13 March 2019).
- 5 2. James, H. F., Ericson, P. G. P., Slikas, B., Lei, F. M., Gill, F. B. & Olson, S. L.  
6 *Pseudopodoces humilis*, a misclassified terrestrial tit (Paridae) of the Tibetan Plateau:  
7 evolutionary consequences of shifting adaptive zones. *Ibis* **145**, 185–202 (2003).
- 8 3. Mourer-Chauviré, C., Hugué, M. & Jonet, P. Découverte de Passeriformes dans  
9 l'Oligocène supérieur de France. *C. R. Acad. Sci. Paris, Série II* **309**, 843–849 (1989).
- 10 4. Boles, W. E. A new songbird (Aves: Passeriformes) from the mid-Cenozoic of Riversleigh,  
11 northwestern Queensland. *Alcheringa* Special Issue **1**, 31–37 (2006).
- 12 5. Millener, P. R. Contributions to New Zealand's Late Quaternary avifauna. 1: *Pachyplichas*,  
13 a new genus of wren (Aves: Acanthisittidae), with two new species. *Journal of the*  
14 *Royal Society of New Zealand* **18**, 383–406 (1988).
- 15 6. Millener, P. R. & Worthy, T. H. Contributions to New Zealand's Late Quaternary avifauna.  
16 2: *Dendroscansor decurvirostris*, a new genus and species of wren (Aves:  
17 Acanthisittidae). *Journal of the Royal Society of New Zealand* **21**, 179–200 (1991).
- 18 7. Fjeldsa, J., Irestedt, M. & Ericson, P. G. P. Molecular data reveal some major adaptational  
19 shifts in the early evolution of the most diverse avian family, the Furnariidae. *J.*  
20 *Ornithol.* **146**, 1–13 (2005).
- 21 8. Tonni, E. P. & Noriega, J. I. Una especie extinta de *Pseudoseisura* Reichenbach 1853  
22 (Passeriformes: Furnariidae) del Pleistoceno de la Argentina: comentarios  
23 filogeneticos. *Ornitología Neotropical* **12**, 29–44 (2001).

- 24 9. Feduccia, A. & Olson, S. L. Morphological similarities between the Menurae and the  
25 Rhinocryptidae, relict passerine birds of the Southern Hemisphere. *Smithsonian*  
26 *Contributions to Zoology* **366**, 1–22 (1982).
- 27 10. Rich, P. V., McEvey, A. R. & Baird, R. F. Osteological comparison of the scrub-birds,  
28 *Atrichornis*, and Lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae).  
29 *Records of the Australian Museum* **37**, 165–191 (1985).
- 30 11. Bock, W. J. Relationships between the birds of paradise and the bower birds. *The Condor*  
31 **65**, 91–125 (1963).
- 32 12. Olson, S. L., Parkes, K. C., Clench, M. H. & Borecky, S. R. The affinities of the New  
33 Zealand passerine genus *Turnagra*. *Notornis* **30**, 319–336 (1983).
- 34 13. Zuccon, D. & Ericson, P. G. P. Molecular and morphological evidences place the extinct  
35 New Zealand endemic *Turnagra capensis* in the Oriolidae. *Mol. Phylogen. Evol.* **62**,  
36 414–426 (2012).
- 37 14. Bock, W. J. The pneumatic fossa of the humerus in the Passeres. *The Auk* **79**, 425–443  
38 (1962).
- 39 15. Pocock, T. N. Osteology. Contributions to the osteology of African birds. *Proceedings of*  
40 *the Second Pan African Ornithological Congress*, 83–94 (1966).
- 41 16. Harrison, C. J. O. Additional information on the carpometacarpal process as a taxonomic  
42 character. *Bulletin B.O.C.* **89**, 27–29 (1969).
- 43 17. Mayr, G. & Manegold, A. The oldest european fossil songbird from the Early Oligocene  
44 of Germany. *Naturwissenschaften* **91**, 173–177 (2004).
- 45 18. Mayr, G. & Manegold, A. New specimens of the earliest European passeriform bird. *Acta*  
46 *Palaeontologica Polonica* **51**, 315–323 (2006).
- 47

```

#NEXUS
BEGIN TAXA;
    DIMENSIONS NTAX=36;
    taxlabels

Fossil
Pitta_sordida
Philepitta_castanea
Cymbirhynchus_macrorhynchus
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_viridior
Manacus_manacus_trinitatis
Machaeropterus_pyrocephalus_pyrocephalus
Chiroxiphia_linearis
Xenopipo_atronitens
Masius_chrysopterus
Antilophia_galeata
Pipreola_arcuata
Cephalopterus_ornatus
Cotinga_sp
Phytotoma_rara
Onychorhynchus_coronatus
Tityra_semifasciata
Schiffornis_turdina_amazonum
Tyrannus_dominicensis
Todirostrum_sp
Rhynchocyclus_olivaceus
Rhynchocyclus_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  
 LatEctethmoid  
 Crestculmen  
 Foramen  
 Procoracoroideus  
 Acrocoracoideus  
 Tubbrachiale  
 Sulsupracoracoidei  
 Fossapneum  
 Cristadeltopect  
 Crusventral  
 Crusdorsal  
 Curvedhum  
 Profcapitis  
 Procflexorius  
 Procsupcondyldors  
 Procsupcondyldors  
 Ulna  
 Cotylavent  
 Cotyladors  
 Tubcondors  
 Papillae  
 Procdent  
 Positionprocintcarp  
 Osmetacminus  
 Procextens  
 Lamaborder  
 Procindicis  
 Fossacaud  
 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

1	1	?	1	1	2		
1	?	?	2	1	?	?	2
2	?	2	3	2	?	?	?
4	2	1	2	2	2	1	1
2	2	1	2	2	1	?	
Cymbirhynchus_macrorhynchos				1	1	1	?
1	1	3	?	1	1	1	1
1	1	2	1	?	?	2	2
1	2	2	2	1	?	?	4
3	1	2	2	1	1	2	1
2	1	2	2	2	3		
Calyptromena_viridis				2	1	1	?
1	3	?	2	1	2	1	1
1	2	1	?	?	2	2	1
2	2	2	1	?	?	4	2
1	2	2	1	1	1	1	2
1	2	2	2	3			
Sapayoa_aenigma				1	?	2	1
1	?	1	1	2	2	?	?
2	1	?	?	2	1	1	2
3	2	1	?	?	3	3	1
2	2	1	1	1	1	2	1
2	2	3	?				
Geositta_cunicularia				1	1	?	1
2	3	?	1	1	1	2	1
3	2	1	?	?	2	1	2
2	2	2	?	?	?	1	2
1	2	1	2	1	3	2	2
1	3	4	1	?			
Myrmotherula_axillaris				1	2	?	1
2	2	?	1	?	1	2	2
2	2	1	?	?	2	?	?
2	2	2	?	?	?	2	2
1	2	?	3	2	2	1	2
1	4	3	1	2			
Sakesphorus_canadensis_loretoyacuensis					1	1	
2	?	1	2	3	?	1	?
1	2	?	?	2	1	?	?
2	?	?	2	2			
2	?	?	?	2	1	1	
2	?	2	2	1	2	2	1
2	2	1	1				
Conopophaga_ardesiaca_saturata				1	1	2	?
1	2	1	?	1	?	1	2
1	3	2	1	?	?		
2	?	?	2	3			
2	?	?	?	2	4	1	2
1	2	2	1	1	2	1	2
2	1	2					
Scytalopus_unicolor				1	2	?	1
2	2	?	2	2	1	1	1
3	2	2	?	?	1	2	2
2	3	2	?	?	?	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	1	
3	1	2	2	1	1			
Chloropipo_holochlora_viridior				1	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	1	
2	1	2	2	1	2			
Manacus_manacus_trinitatis				1	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	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	?	1	2	2	1	1		

Chiroxiphia_linearis	1	1	2	1	1
3	2	1	1	?	2
2	2	1	1	2	2
2	3	2	?	1	1
1	2	1	1	1	3
1	2	2	1	2	
Xenopipo_atronitens	1	1	2	1	2
3	4	1	1	1	2
3	2	1	1	2	2
2	3	2	?	1	1
1	2	1	1	1	3
1	2	1	1	1	
Masius_chrysopterus	2	1	2	1	1
3	4	1	1	1	2
3	2	1	1	2	2
2	3	2	2	1	1
1	2	1	1	1	3
1	2	2	1	2	
Antilophia_galeata	3	1	2	1	1
3	2	1	1	1	2
3	2	1	1	2	2
2	3	2	2	1	1
1	2	1	1	1	2
1	2	2	1	?	
Pipreola_arcuata	1	1	2	2	1
2	3	1	1	2	2
2	1	2	2	2	2
3	2	2	2	1	?
2	1	1			
1	?	?	?	?	?
?					
Cephalopterus_ornatus	2	1	2	2	1
3	2	3	1	1	1
2	2	1	2	2	2
2	2	2	2	2	1
1	2	1	1	1	1
1	2	2	1	2	
Cotinga_sp	1	1	1	2	2
3	3	1	1	1	2
2	1	2	2	2	1
2	2	2	2	1	3
2	3	1	1	1	1
2	2	2	2		
Phytotoma_rara	1	1	2	2	1
2	3	1	1	1	2
2	1	2	2	2	2
2	2	2	2	1	1
2	?	1	1	2	2
2	2	?	?		
Onychorhynchus_coronatus	2	1	2	3	1
3	2	3	1	1	1
2	2	1	2	2	2
2	2	2	2	2	1
1	2	1	1	1	2



1	2	2	2	3				
Tityra_semifasciata			1	1	2	3	1	
1	2	3	1	1	1	1	2	
1	2	1	2	2	2	2	2	
2	3	2	2	2	1	1	1	
1	2	1	1	1	1	2	3	
1	?	?	1	?				
Schiffornis_turdinus_amazonus			1	1	1	2	3	
1	3	2	3	1	1	2	1	
2	2	2	1	2	2	2	2	
2	2	3	2	?	2	1	1	
2	1	2	1	1	1	1	1	
3	1	2	2	1	2			
Tyrannus_dominicensis			1	1	?	1	?	
3	2	2	1	1	2	1	1	
1	2	1	2	1	2	2	2	
2	2	2	2	2	2	3	2	
1	2	1	1	1	1	1	1	
1	1	0	2	2				
Todirostrum_sp		1	1	2	1	1	1	
1	2	1	1	1	1	2	2	
2	1	2	1	2	1	2	2	
2	2	2	2	2	2	1	1	
2	1	1	1	1	2	3	1	
1	0	2	2					
Rhynchocyclus_olivaceus			1	1	2	1	1	
1	2	2	1	1	1	1	3	
2	2	1	2	1	2	1	2	
2	2	2	2	2	2	1	2	
1	2	1	1	1	1	2	3	
1	2	2	2	?				
Rhynchocyclus_sp		2	1	2	1	1	1	
2	2	1	1	2	1	2	2	
2	1	2	1	2	1	2	2	
1	2	2	2	2	1	2	1	
2	1	1	1	1	2	3	1	
2	2	2	3					
Acanthisitta_chloris			1	2	2	?	2	
1	1	?	1	2	1			
1	?	?	1	1	?	?	1	
1	?	2	1	2	?	?	?	
3	1	2	2	?	3	2	1	
2	2	1	2	1	2	?		
Gerygone_flavolateralis			1	1	1	?	1	
2	1	?	1	2	1	1	3	
2	1	1	?	?	2	2	2	
1	3	1	1	?	?	3	4	
2	1	1	?	?	?	2	1	
2	1	0	2	1	;			

END;  
log/file=resultats-2.txt;  
Begin paup;

```
    outgroup Acanthisitta_chloris Gerygone_flavolateralis;  
    hsearch swap=tbr addseq=random;  
    roottrees/root=outgroup;  
    savetrees/file=tree2.tre;  
    describetrees/fvalue apolist;  
end;
```