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

Ségolène Riamon¹, Nicolas Tourment² & Antoine Louchart¹ ⊠

Passeriformes is the most diverse bird order. Nevertheless, passerines have a remarkably poor early fossil record. In addition, high osteological homoplasy across passerines makes partial specimens difficult to systematically assign precisely. Here we describe one of the few earliest fossil passerines, from the early Oligocene (ca 30 Ma) of southern France, and one of the best preserved and most complete. This fossil can be conservatively assigned to Tyrannida, a subclade of the New World Tyranni (Suboscines), i.e. of the 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 species¹. They comprise the basal Acantisittidae (two species), sister to the Eupasseres which in turn comprises the Tyranni (previously called Suboscines; 1,407 species), and the Passeri (previously called Oscines; 5,084 species). Molecular studies show that, as the sister clade to Psittaciformes (parrots and allies), Passeriformes originated in the earlier part of the Paleogene, and most of the extant families diverged near the Eocene-Oligocene-limit, i.e. some of them should be approximately as old as 30 million years (Ma)²⁻⁴. Nevertheless, the fossil record of passerine birds remains exceedingly poor prior to the middle Miocene, and increasingly toward earlier times. This taphonomic bias explains the difficulty in finding early specimens representing extant passerine clades. Among the few pre-Miocene published specimens, most are fragmentary⁵⁻¹¹, and even the three more complete specimens, on slab, are rather poorly preserved and prove difficult to identify with some precision. The latter specimens are all from the European early Oligocene: Wieslochia weissi (Germany^{12,13}), Jamna szybiaki and Resoviaornis jamrozi (Poland^{14,15}). This difficulty is also explained by (i) high apparent homoplasy observed on osteological characters within the Passeriformes^{12,13}, and (ii) the difficulty to compare fossils with a sufficiently large, representative sample of extant taxa, passerine clades being so rich at specific and generic levels. Some early fossils have been referred to Tyranni indet., others to Passeri indet., and the remaining to either the preceding taxa or possibly stem Eupasseres or stem passerines^{5–15}. All these fossils date to the Oligocene of France, Germany and Poland in Europe. In addition, late Oligocene fossils of logrunner (Oscines, Orthonychidae) are known from Australia¹⁶. As for the older, possible passerine remains from the lower Eocene of Australia^{17,18}, they are fragmentary (one proximal carpometacarpus and one distal tibiotarsus) and considered to be either not sufficiently diagnostic of the Passeriformes 12,19 or possibly Passeriformes outside Eupasseres20. Here we describe one of the earliest fossils on slab of a passerine bird, nearly complete, from the early Oligocene of the Luberon (Alpes-de-Haute-Provence, France). Its exceptional state of preservation allows for its identification as the oldest Passeriformes assignable to a modern subgroup of the 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.

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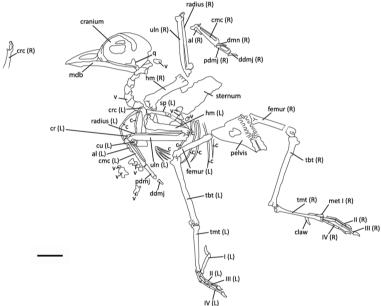


Figure 1. The fossil specimen NT-LBR-014 from Revest-des-Brousses, Luberon (France), and interpretative drawing. al, wing phalanx digiti alulae; c, costa; cmc, carpometacarpus; cr, os carpi radiale; crc, coracoid; cu, os carpi ulnare; ddmj, distal wing phalanx digiti majoris; dmn, wing phalanx digiti 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)¹⁸; and (iii) the processus intermetacarpalis and the os metacarpale minus are fused in the fossil, which is found only in Passeriformes²¹ and Piciformes²², 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.

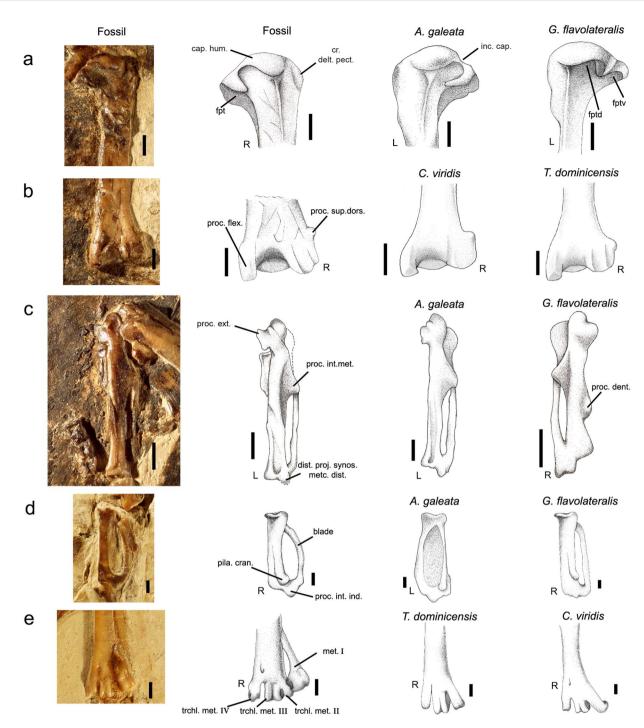


Figure 2. Selected bones of the Luberon fossil NT-LBR-014, compared with extant species (Acanthizidae, Calyptomenidae, Tyrannidae, Pipridae). Second column from the left, drawings of bones which photos are in the first column. Line a, proximal humeri in caudal view. Line b, distal humeri in caudal view. Line c, carpometacarpi 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

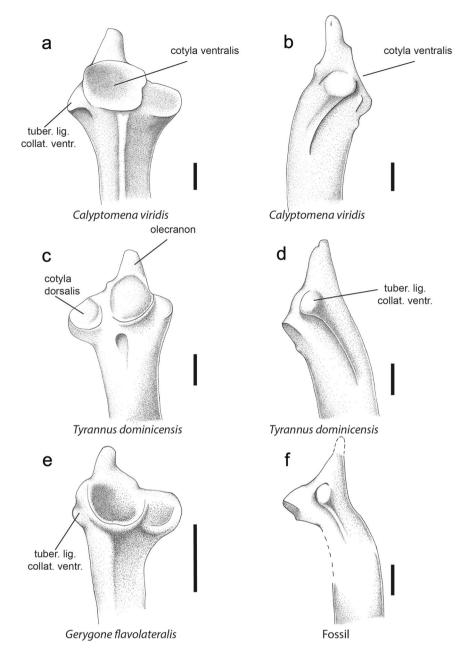


Figure 3. Drawings of right ulna of the Luberon fossil NT-LBR-014 and ulnas of extant species (Passeri, Acanthizidae; Tyranni, Calyptomenidae and Tyrannidae). (**a,b,e**), left ulnas; (**c,d,f**), right ulnas; (**a,c,e**), cranial views; (**b,d,f**), ventral views, tuber, lig. collat. ventr., tuberositas 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 Eupasseres, and does not possess a foramen situated medially at the base of the processus acrocoracoideus (present in the extant Eupasseres 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 Eupasseres.

Assignment to the tyranni. The wing elements are especially diagnostic for differentiation between the two sub-orders^{5,7,8,13} (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. ¹⁹: 136–137.); a prominent tuberculum ligamenti collateralis ventralis of the ulna (little prominent in the Passeri)¹³; 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);^{5,7,8,13} a distal extremity of the os metacarpale minus prominent and pointed (square-shaped, and more hollow in ventral view, in the Passeri);^{5,7,8,13} a blade of the wing phalanx 1 digiti majoris with a rounded, convex border (straight border in the Passeri);^{7,19} presence of a processus internus indicis on the distal extremity of the alar phalanx 1 digiti majoris (absent in the Passeri)^{7,19}. These and other diagnostic characters allow to identify NT-LBR-014 as belonging to the Tyranni (and exclude the Passeri).

Phylogenetic analyses. In order to precise the position of NT-LBR-014 within the Tyranni, phylogenetic analyses in parsimony were conducted based on the distribution of characters across the extant Tyranni examined and the fossil, transformed into a character matrix (Supplementary Methods; strict consensus, Supplementary Fig. 1; bootstrap analysis, Supplementary Fig. 2). The resulting trees show low robustness indices for most nodes (Supplementary Figs. 1, 2). We interpret the low robustness or poor resolution of the trees as the result of pervasive homoplasy in the distribution of osteological character states across the Tyranni (and probably across the whole Passeriformes). This had been observed in previous analyses involving fossil passerines, leading authors to refrain applying cladistic analyses (or other phylogenetic methods) to such osteological datasets^{12–14}. Results of our temptative phylogenetic analyses are not incongruent with our more qualitative results below, although they do not offer significant weight per se. *Sapayoa aenigma* is correctly placed in a clade exclusively with other Eurylaimides in the tree generated by bootstrap analysis (1000 replicates), although with poor support (Supplementary Fig. 2), as well as in the strict consensus tree (Supplementary Fig. 1). NT-LBR-014 is found distant from *Sapayoa* (and other Eurylaimides) in both analyses, and in addition it is found in a clade exclusively with piprid taxa in the strict consensus tree. The phylogenetic trees do not make it possible to ascertain which characters are plesiomorphic for the Tyrannida, for example, or synapomorphic for diverse subclades.

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

Assignment to the Tyrannides. The Tyranni comprises two infra-orders: the Eurylaimides ("Old World Tyranni") and the Tyrannides ("New World Tyranni"), based on molecular data 4,23-25. Few skeletal diagnostic characters make it possible to differentiate systematically between members of the two clades. Two of these characters apply to all the Eurylaimides and Tyrannides examined. As in the Tyrannides, the fossil exhibits: a straight processus flexorius of the distal humerus (partly produced, and somehow hooked more dorsally and caudally in the Eurylaimides); a cotyla ventralis of the proximal ulna slightly rounded and little developped ventrally (more rounded and developped 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 ¼ 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 gonys 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

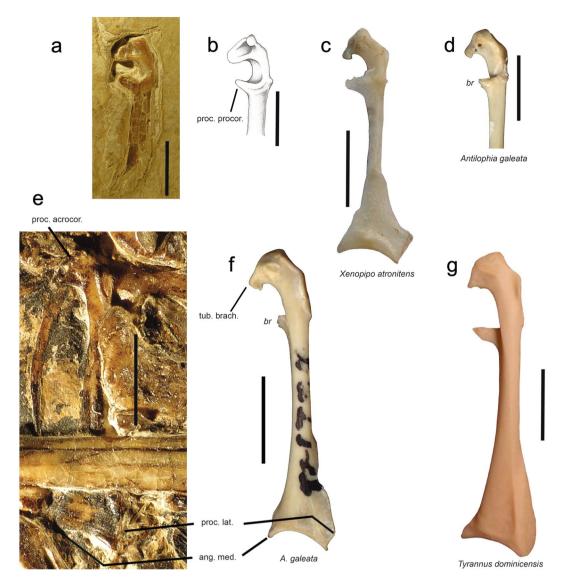


Figure 4. Coracoids of the Luberon fossil NT-LBR-014, compared with extant species (Tyrannida). (a,e), respectively right (dorsal view) and left (ventral view) coracoids of the fossil NT-LBR-014; b, drawing of (a,c), dorsal view, inverted left coracoid; (d), dorsal view; (f), ventral view; (g), ventral 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 capability²⁶. The fossil exhibits a processus supracondylaris dorsalis that is unique and well-developed (Fig. 2), a character shared with all the Pipridae, and Pitta sordida (Pittidae), Sapayoa aenigma (Sapayoidae), Scytalopus unicolor (Rhinocryptidae), Schiffornis turdina (Tityridae), and Pipreola arcuata (Cotingidae); the other extant species examined in the Tyrannides have a unique processus supracondylaris dorsalis, but which is reduced (or less prominent proximally).

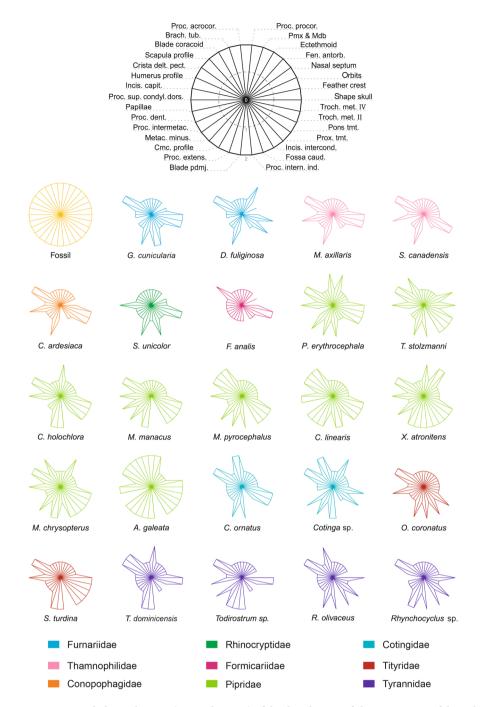


Figure 5. Radial visualisation (Kiviat diagram) of the distribution of character states of the Luberon fossil NT-LBR-014, across extant taxa of the Tyrannides for which all the characters were assessable. Top, position of the diagnostic characters considered here relative to each radius. In extant species,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

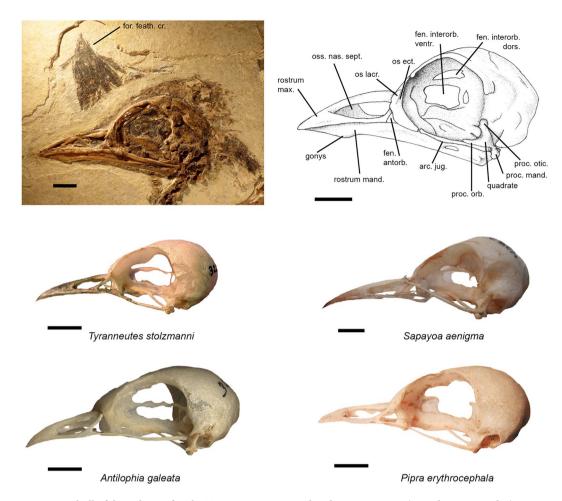


Figure 6. Skull of the Luberon fossil NT-LBR-014, compared with extant species (Pipridae, Sapayoidae). All left lateral views. Top left, fossil NT-LBR-014; top right, drawing of the preceding. NB: the part below the os lacrimale is collapsed, and seems to have been developed as in, e.g., *Sapayoa*. arc. 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 ectethmoidale; 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 indicis¹⁹. 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

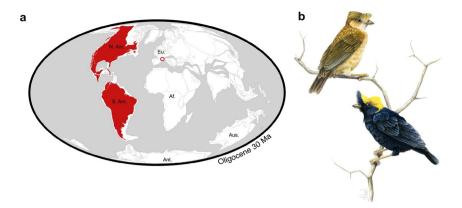


Figure 7. Geographic location, and reconstruction of the Luberon early Oligocene Tyrannida. In (a), the geographic location of the Luberon Tyrannida NT-LBR-014 is represented (red circle), together with the extant distribution of Tyrannida (red area), superimposed on a paleogeographic map of landmasses 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.

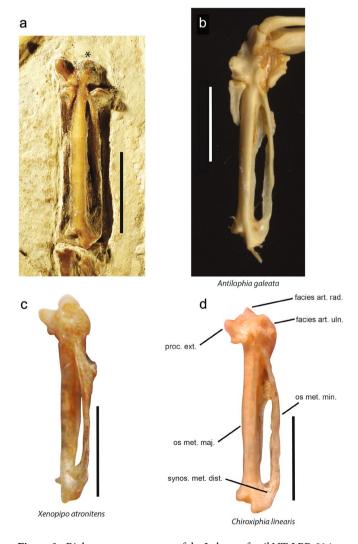


Figure 8. Right carpometacarpus of the Luberon fossil NT-LBR-014, compared with extant species (Pipridae). (**b,c**), inverted left carpometacarpi. In (**c**), the angle of view (ventral) is slightly different from that in (**a,b,d**) (slightly cranio-ventral, in (**b**) more than in (**a,d**)). *The 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.

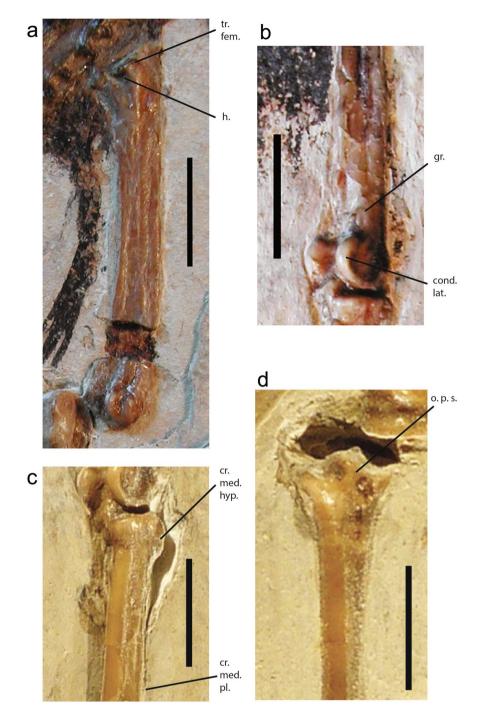


Figure 9. Leg bones of the Luberon fossil NT-LBR-014. a, right femur, latero-caudal view; b, left distal tibiotarsus, latero-cranial view; c, left proximal tarsometatarsus, latero-dorsal view; d, right proximal tarsometatarsus, dorsal view. cond. lat., condylus lateralis; cr. med. hyp., crista medialis 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, unambigously 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 temptative 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 Dendrocolaptidae¹, the Thamnophilidae, Conopophagidae, Formicariidae, and Rhinocryptidae)^{1,2,27}, 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^{1,2,27}). 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 Tyranneutes; the more basal subfamily of Pipridae²⁸) 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

Interestingly, a synamoporphy 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 Tyranni²⁹. 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 specimens²⁹, 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, wich 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^{2,3,30}. 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 $^{5-15,31}$, including a nearly completely represented taxon from the early Oligocene of Germany, *Wieslochia weissi* 12,13 (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 13 . 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* 31 , to consider them outside crown Passeriformes 32 .

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 ecozone¹. NT-LBR-014 derives

from a near-coastal lagunar, freshwater depositional setting, surrounded by forests, under a subtropical to tropical paleoclimate^{33–35}, 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)³, or later in the early Eocene, near 48 Ma⁴. The earliest ascertained fossil passerines are from the early Oligocene of Europe. They comprise Passeri, Tyranni and possibly more basal lineage(s)^{5–15}. NT-LBR-014 is the first to be assignable to a more precise, extant passerine clade, the Tyrannida, at ca 30 Ma. A molecular age of diversification for the Tyrannida was proposed at 32–33 Ma^{2,27} or near 24 Ma⁴, and the divergence between Tyrannida and Furnariida at 38.9 Ma³ or near 36 Ma⁴. 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. 34 and the stem Galbulae Jacamatia³⁶. 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 inferred⁴ based only on extant distributions. As is the case for the stem hummingbirds³⁴ and stem Galbulae³⁶ 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 periods³⁷. 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 stages³⁸. 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 Oligocene³⁹ would have helped this crossing. A last possibility of passage would have been via the Bering Strait which benefited from a mild climate, but the absence of fossil evidence added to the much greater distance, make this scenario much less likely.

In every hypothesis, after the Oligocene the European distribution of Tyrannida would have become reduced and eventually disappeared at latest in the upper Miocene, owing to global cooling and a decrease in winter temperatures among other factors^{37,38}. This led to a relictual distribution in the southern hemisphere, tropical regions, in this case neotropical zones, as was the case for several other bird groups^{36,40,41}. Concomitant with this retreat towards the equator in America, some lineages could become progressively long-distance migrants (including members of the Tyrannidae today breeding in North America and wintering in the Neotropics). Interestingly, *Sapayoa aenigma*, "Old World" Tyranni (Eurylaimides) living in South America, also illustrates a transatlantic crossing of an ancestor, leaving descendents on both sides (this species is neotropical, and all other Eurylaimides are paleotropical). It is not possible to favour a northern or a southern passage in the case of *Sapayoa*, but it must have occurred between the latest Oligocene and middle Miocene³.

Methods

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

Comparative material. Comparisons were made with representatives of the families osteologically close to passerines, and within passerines with a representative sample of most families in the Passeri, as well as with Acanthisittidae 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 Witmer⁴⁶, unless stated otherwise. Systematic arrangement follows Del Hoyo *et al*¹..

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

Data availability

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

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References

- 1. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds) *Handbook of the Birds of the World Alive* (Lynx Edicions, Barcelona, 2019). (retrieved from https://www.hbw.com/ on 13 March 2019).
- Ericson, P. G., Klopfstein, S., Irestedt, M., Nguyen, J. M. & Nylander, J. A. Dating the diversification of the major lineages of Passeriformes (Aves). BMC Evol. Biol. 14, 8 (2014).
- 3. Selvatti, A. P. & Gonzaga, L. P. & de Moraes Russo, C. A. A Paleogene origin for crown passerines and the diversification of the Oscines in the New World. *Mol. Phylogenet. Evol.* 88, 1–15 (2015).
- 4. Oliveros, C. H. et al. Earth history and the passerine superradiation. Proc. Natl. Acad. Sci. USA 116, 7916-7925 (2019).
- 5. Mourer-Chauviré, C., Hugueney, M. & 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. & Hugueney, 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).
- 7. 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).
- 9. 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).
- 10. 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).
- 12. Mayr, G. & Manegold, A. The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften* 91, 173-177 (2004).
- 13. Mayr, G. & Manegold, A. New specimens of the earliest European passeriform bird. Acta Palaeontol. Polon. 51, 315-323 (2006).
- 14. 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).
- 15. 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).
- 16. Nguyen, J. M. T., Boles, W. E., Worthy, T. H., Hand, S. J. & Archer, M. New specimens of the logrunner *Orthonyx kaldowinyeri* (Passeriformes: Orthonychidae) from the Oligo-Miocene of Australia. *Alcheringa* 38, 245–255 (2014).
- 17. Boles, W. E. The world's oldest songbird. Nature 374, 21-22 (1995).
- 18. Boles, W. E. Fossil songbirds (Passeriformes) from the early Eocene of Australia. *Emu* **97**, 43–50 (1997).
- 19. Manegold, A. Zur Phylogenie und Evolution der "Racken"-, Specht- und Sperlingsvögel ("Coraciiformes", Piciformes und Passeriformes: Aves). Ph.D Dissertation. Freie Universität Berlin (2005).
- 20. Mayr, G. The origins of crown group birds: molecules and fossils. Palaeontology 57, 231-242 (2014).
- 21. Kakegawa, Y. A Miocene passeriform bird from the Iwami Formation, Tottori Group, Tottori, Japan. Bull. Natl. Sci. Mus. Series C 49, 33–37 (2003).
- 22. Smith, N. A., de Bee, A. M. & Clarke, 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).
- 23. Chesser, R. T. Molecular systematics of New World suboscine birds. Mol. Phylogenet. Evol. 32, 11-24 (2004).
- 24. 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).
- 25. Irestedt, M., Ohlson, J. I., Zuccon, D., Källersjö, M. & Ericson, P. G. Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). *Zoologica Scripta* 35, 567–580 (2006).
- 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).
- 27. Ohlson, J. I., Irestedt, M., Ericson, P. G. & Fjeldså, J. Phylogeny and classification of the New World suboscines (Aves, Passeriformes). *Zootaxa* 3613, 1–35 (2013).
- 28. Ohlson, J. I., Fjeldså, J. & Ericson, P. G. 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).
- 29. Prum, R. O. A test of the monophyly of the manakins (Pipridae) and of the cotingas (Cotingidae) based on morphology. Occasional Papers of the Museum of Zoology, the University of Michigan 723, 1–44 (1990).
- 30. Fjeldså, J., Zuccon, D., Irestedt, M., Johansson, U. S. & Ēricson, 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 Luberon. Courrier scientifique du Parc naturel régional du Lubéron 6, 38-57 (2002).
- 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).
- 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).
- De Oliveira, F. B., Molina, E. C. & Marroig, G. Paleogeography of the south Atlantic: a route for primates and rodents into the New World? in South American Primates, Developments in Primatology: Progress and Prospects (eds. P. A. Garber et al.) 55–68 (Springer Science, New York, 2009).
- 40. Blondel, J. & Mourer-Chauviré, C. Evolution and history of the western Palaearctic avifauna. Trends Ecol. Evol. 13, 488–492 (1998).
- 41. Mayr, G. Two-phase extinction of of "Southern Hemispheric" birds in the Cenozoic of Europe and the origin of the Neotropic 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., Hugueney, M. & Truc, G. La formation des Calcaires et Lignites de Sigonce (Oligocène moyen, bassin de Forcalquier, Alpes-de-Haute-Provence): datation à l'aide des mammifères; reconstitution des milieux de 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. & Hugueney, M. Les micromammifères des gisements à phosphate du Quercy (SW France). Strata Sér. I 13, 207-226 (2006).
- 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).

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Author contributions

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

Competing interests

The authors declare no competing interests.

Additional information

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1	Supplementary Information
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3	The earliest Tyrannida (Aves, Passeriformes), from the Oligocene of France
4	
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6	
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9	Supplementary Methods
10	Supplementary Figures 1 to 4
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12	References (for Supplementary Table 1)
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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,
- 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 macrorhynchos, LAC 1884.256; Calyptomenidae, Calyptomena viridis, LAC
- 24 1997.830; Sapayoidae, Sapayoa aenigma, M, USNM 428203; Furnariidae, Geositta
- cunicularia, M, USNM 614657; Dendrocincla fuliginosus, M, FMNH 321160;
- Thamnophilidae, Myrmotherula axillaris, M, FMNH 319192; Sakesphorus canadensis
- 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,

- 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.,
- 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;
- Paradisaeidae, *Ptiloris paradiseus* LAC 1860.102 = A 4291 = BVI/360, LAC A 4295 =
- 51 BVI/359, Paradisaea minor LAC 1878.620.
- 53 Institutions acronyms

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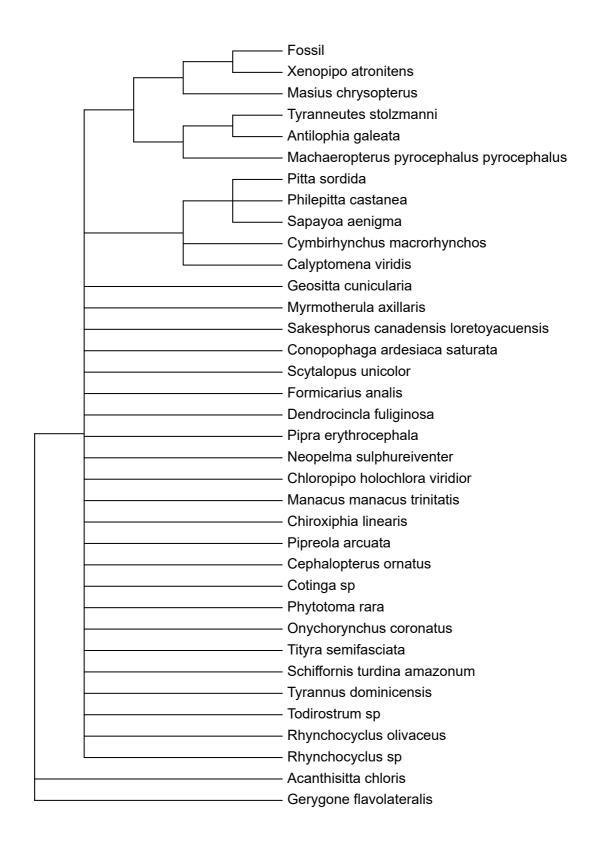
- 54 FMNH, Field Museum of Natural History (Chicago, USA); LAC, Laboratoire d'Anatomie
- Comparée (Muséum National d'Histoire Naturelle, Paris, France); NHM, Natural History
- Museum (Tring, UK); MNZ, Museum of New Zealand Te Papa Tongarewa (Wellington,
- New-Zealand); MZLSU, Museum of Zoology, Louisiana State University (Baton Rouge,
- 58 USA); UCBL, Université Claude Bernard Lyon 1 (Villeurbanne, France); USNM, National
- Museum of Natural History (Smithsonian Institution, Washington, D.C., USA).
- 61 Methods for phylogenetic analyses
- The phylogenetic analyses were realized using 36 characters, which were discriminant for at
- least one among the Tyranni examined, and 34 taxa of the Tyranni (including the fossil). The
- 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.
- The taxon-character matrix was analysed with parsimony using PAUP*4.a166. The
- executable data matrix with PAUP commands is appended as Nexus File (in Supplementary
- 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
- used heuristic searches with tree-bisection-reconnection (TBR) branch swapping and other
- default settings, and 1000 random addition replicates per search. Strict consensus trees were
- 73 computed from the set of most parsimonious trees, and clade support was assessed by
- bootstrapping using the same settings and 1000 replicates.
- 75
- 76 Osteological characters used in the phylogenetic analysis.
- Feather crest: 0, absent; 1, present but different of fossil; 2, present and similar of fossil.
- Relative size of orbits: 0, more than half of the skull; 1, less than half of the skull.
- 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.
- Latero-dorsal part of ectethmoid: 0, little developed; 1, developed; 2, well developed; 3,
- highly developed.
- Lateral parts of etecthmoid: 0, reduced gap; 1, intermediate gap; 2, large gap.
- 87 Crest/ridge on culmen: 0, absent; 1, present.
- Foramen (foramina) of coracoid omal end: 0, present, 1, absent.
- 89 Processus procoracoideus: 0, little developed; 1, well developed.

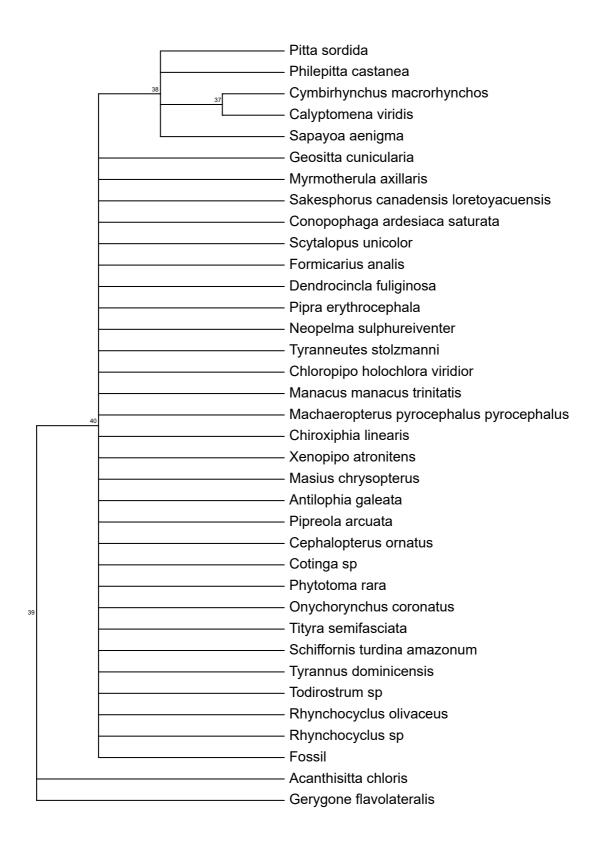
- Processus acrocoracoideus: 0, little developed; 1, well developed.
- 91 Brachial tuberosity (tuberculum brachiale): 0, little developed; 1, developed; 2, well
- 92 developed.
- 93 Sulcus medialis supracoracoidei: 0, straight; 1, rounded; 2, almost circular.
- Fossa pneumotricipitalis: 0, single fossa; 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.
- Processus flexorius: 0, dorso-caudally deflected edge; 1, straight edge.
- 101 Processus supracondylaris dorsalis: 0, double; 1, single.
- Processus supracondylaris dorsalis: 0, little developed; 1, developed; 2, well developed.
- Tuberculum ligamenti collateralis ventralis: 0, projecting; 1, not projecting.
- 104 Cotyla ventralis: 0, ventral edge developed and almost circular; 1, convex ventral edge.
- 105 Cotyla dorsalis: 0, little developed; 1, large.
- Position of the dorso-proximal edge of the incisura tendinosa (for mm extensor metacarpi
- ulnaris and extensor digitorum communis), distal ulna: 0, proximal; 1, distal.
- Papillae remigales caudales: 0, almost absent; 1, little developed; 2, developed; 3, well
- developed.
- Processus dentiformis: 0, absent; 1, little developed: edge with a slightly wavy; 2, developed;
- 3, well developed.
- Position of processus intermetacarpalis: 0, proximal; 1, more proximal.
- Distal symphysis of os metacarpale minus: 0, the os metacarpale minus is lightly protruding,
- and forms a marked square projection; 1, the distal end of os metacrpale minus is moderately

- protruding and its cranial portions forms a projection that reaches farther distally than the
- facies rticularis digitalis minor (Mourer-Chauviré et al., 1989; Mayr and Manegold 2006).
- Processus extensorius: 0, not ventrally deflected; 1, ventrally deflected; 2, slightly ventrally
- dejected.
- Blade of Phx 1 digiti majoris: 0, straight edge; 1, slightly rounded edge; 2, rounded edge
- 120 (Manegold, 2005).
- Processus internus indicis: 0, present; 1, absent.
- Femur: hollow just distal to proximal articular surface, caudal side: 0, absent; 1, shallow; 2,
- marked.
- Medial crest (tibiotarsis proximal most shaft): 0, absent; 1, present.
- 125 Tiny proximo-distal groove between the tuberositas retinaculi extensorius lateralis and the
- tuberculum retinaculi m fibularis, lateral side of distal end, proximal to the lateral condyle,
- rostral aspect: 0, absent; 1, it is located relatively distally; 2, it is located more proximally.
- Fusion (continuity) between crista med plantaris and crista med hypotarsi: 0, absent; 1,
- 129 present.
- Ossified pons supratendineus: 0, not ossified, 1, ossified.
- Position of pons supratendineus: 0, not ossified, 1, located proximally; 2, located proximally;
- 3, located less proximally; 4, located in an intermediate position.
- 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.

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



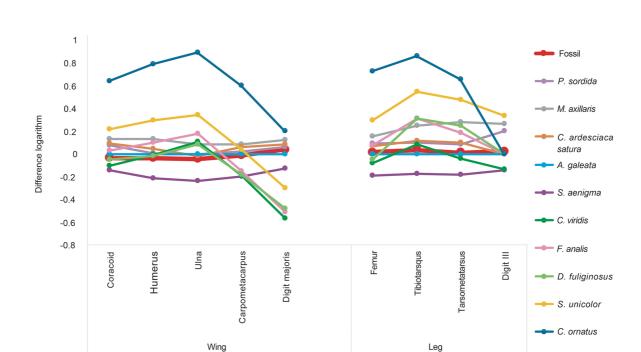
Supplementary Fig. 2 Bootstrap analysis, with 1000 replicates. Only four nodes are supported by the bootstrap, but with a very low value (between 37 and 40%). As for the strict consensus (Supplementary Fig. 1), the poor resolution and support convey pervasive homoplasy. The fossil is however, as in the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



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

A tmt mtl mtl

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



175 Supplementary Tables

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

All character states of species compared to the fossil are given relative to state of the fossil. Only characters that discriminate at least one species among the Tyranni and Acanthisittidae examined have been selected here. *On occasions, character states are given not only for the extant species examined here for comparison, but for more species in the family (in such instances references are given via number in parentheses). (1) it is mentioned if other extant taxa in every genus or family concerned exhibit a crest approaching the fossil's (after del

Hoyo et al., 2019¹). (2) from this work, and characters 22 and 55 in James et al., 2003². (3) 185 from this work and Mourer-Chauviré et al., 1989³; NB: C. Mourer-Chauviré (pers. comm.) 186 187 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, 2006⁴. (5) from this work, Millener, 1988⁵, and Millener and Worthy, 1991⁶. (6) sensu del Hoyo et al., 2019¹, i.e. 191 192 comprising taxa earlier in the former Dendrocolaptidae. (7) also from Fieldsa et al., 2005⁷. 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 Leptasthenura spp., Furnarius cristatus, Coryphistera alaudina, and more or less in the 195 different species of *Pseudoseisura*). (9) same in *Pseudoseisura*⁸. (10) a few genera and 196 197 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 work and Feduccia and Olson, 1982⁹. (12) In *Rhinocrypta* a crest extends from the back of the 200 201 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 Calyptomena but sparser. (13) An ossified bridge exists in *Melanopareia* (recently placed in own family¹)⁹. (14) Quadrate even more 203 different in Melanopareia⁹. (15) Apart from Masius, Antilophia and Chiroxiphia (see Table), 204 205 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

head; see Table), crests exist in several genera and species, where always at the back of head, forming when spread a crest with longest feathers toward the top of head (extent of crest variable among genera and species concerned). (For instance also the crest of *Comptostoma* is more on top of head and shorter (and still toward back)). An exception consists in Anairetes (variable among species) of a prominent frontal crest of long feathers implanted over the rostrum base, and pointing upwards and backwards; they form either a fan or a bifurcated crest (like horns) of long, thin feathers. (18) from this work, Feduccia and Olson, 1982⁹ and Rich et al., 1985¹⁰. (19) from Feduccia and Olson, 1982⁹, and Rich et al., 1985¹⁰. (20) data also from Bock, 1963¹¹ and Olson et al., 1983¹² (NB: *Turnagra* now known to be in the Oriolidae¹³). (21) data also from Bock, 1963¹¹. (22) The fossa is simple in all the Passeriformes except most of the the Oscines Passerida - and a few Oscines Corvoidea where derived states of a double fossa occur polyphyletically; pneumatic in Corvoidea, either pneumatic or non-pneumatic in Passerida^{2,3,14}. (23) A processus dentiformis is present in most of the Passerida, while within the Corvoidea it is either absent or present^{3,15,16}. (24) Oligocene, Wiesloch-Frauenweiler (Germany); assigned to stem Passeriformes or stem Tyranni^{17,18}. NB: for several modern specimens, character states are absent due to the lack of the element or element part, or the incomplete specimen preparation, obscuring detail by ligaments for instance. It is specified for which specimens the skull only could be examined.

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		Taxon								Skull								Coracoid			
			Species (species seen for comparison	Cranium shape		Relative size			Fenestra antorbitalis		latero-dorsal part	Intercribital fenestrae		Crest/rides	Rostrum and	Foramen	Processus	Processus	Brachial tuberosity (tuberculum	Sukus medialis	Coracold blade
	Sub	border to Family	Species (species seen for comparison are listed, but see *)	Cranium shape (lateral profile)	Feather crest (1)	Relative size of orbits	Shape of orbits	Osseous nasal septum	Fenestra antorbitalis (proportion)	Os lacrimale	latero-dorsal part of ectethmoid	(2)	Quadrate shape	on culmen	Rostrum and mandible (mdb)	Foramen (foramina) of coracold omal end	Processus procoracoideus	acrocoracoldeus	(tuberculum brachiale)	supracoracoidei	Coracold blade shape
					over base of rostrum; crest	large (11.5mm: more than		present over most of	neduced equilateral	present and		donal smaller than ventral; separation			relatively straight;				uny deselorant		
	Revest-des-l	Brousses fossil (early Oligo	ocene) NT-LBR-014	see illustrations	'triangular', directed forward, with tip recurved slightly backwards	more than half of the cranium)	much rounded	nasal aperture (rostrally)	triangle	Individualized	well developed	ventral; separation rather narrow	see Bustrations	no	relatively straight; nasal opening 2/3 of rostnam; mdb with marked gonys	yes	developed	developed	straight	relatively circular edge	e see Bustrations
	Aca	ınthisittidae	Acanthisitta chloris (5)	variable	none	(generally more reduced)	rounded	none	larger (variable)	free?	very slightly developed	dorsal fenestra proportionally larger; separation very thin	processus orbitalis much reduced and obtuse; proc. oticus wider	no	beak on average longer and thinner	no	poorly developed, turned 90°	not developed medially	2	?	similar
				similar			donal edge	present over most of	similar	free?		ventral fenestra slightly		no	nasal opening only 1/2of rostrum;		developed, pointed	very slightly less		relatively straight	processus lateralis
		Pittidae	Pitta sordida	unar	none	similar	dorsal edge flatter	nasal aperture escept ventral edge	unur	****	developed	larger	rather similar	no	rostrum straighter; mdb without gonys	yes	developed, pointed distally developed, but	developed medially	less developed	edge	processus lateralis more obtuse
		Philepittidae	Philepitta castanea	forehead flatter	none	similar	donal edge flatter	present over dorsal and nostral large border of the nasal aperture	similar	free?	slightly developed	dorsal fenestra larger, and separation thinner	slightly different	no	beak thinner, longer, decurved and pointed	yes	elongation more proximal than in the fossil	less developed medially	2	?	similar
		Eurylaimidae	Cymbirhynchus macrorhynchas	rather similar (forehead slightly flatter)	none	similar	donal edge flatter	2	more extended donally, shape more elongated and narrow	free?	moderately developed	both fenestrae much larger, separation much	processus orbitals shorter, processi mandibularis and oticus more curved	no	beak more curved,	yes; smaller but deep	not much developed	less developed medially, more hooked	much less developed	straight edge	similar
	Eurylaimide	s	, , , , , , , , , , , , , , , , , , , ,	flatter)			flatter		elongated and narrow		developed	larger, separation much thinner	oticus more curved		hooked and robust	deep		more hooked	developed		
		Calyptomenidae	Colyptomena viridis	rather similar (forehead slightly flatter)	more reduced, rounded, directed forward	similar	donal edge flatter	present only over dorsal and rostral border of the rusual aperture	more extended donally, more rounded	free?	moderately developed	wentral fenestra slightly reduced, dorsal slightly larger	different	yes, small	beak more curved and hooked	yes	developed, same shape as fossil; shorter	less developed medially	far less developed	relatively straight edge	processus lateralis more developed laterally
								almost complete				ventral fenestra						very slightly less			
		Sapayoidae	Sopayoa aenigma	Identical	none	identical	donal edge flatter	(starting from donsal edge)	similar	free ?	slightly developed	reduced, separation slightly thinner	similar	no	rostrum similar; mdb without gonys	yes	developed, same shape as fossil	very slightly less developed medially and pointed	?	7	rather similar
			Geositta cunicularia	rather similar (7)	none (1)	similar (7)	dorsal edge slightly flatter	none / oblique bar	generally wider	absent or fused	moderately developed	rather similar to fossil; fenestrae can be fused (no separation)	very similar	no	beak thinner, longer, decurved and pointed; rasal opening reduced;	yes	moderately developed, pointed rather acutely	slightly less developed medially	not much developed	more rounded edge	processus lateralis more extended latero-distally
		Furnariidae (6)													mdb gonys less marked (1) beak much longer;						processus lateralis
			Dendrocincla fuliginasa	forehead slightly flatter	none	similar	rounded	none	larger	absent or fused	well developed	ventral fenestra much smaller	proc. orbitalis narrower	no	nasal opening reduced	yes	developed, thinner, and shape different	very slightly less developed medially	developed	rounded edge	much more extended latero- distally
			Myrmotherula axillaris	rather similar	none (10)	smaller	dorsal edge slightly less rounded	almost complete (except rostralmost part)	slightly larger	absent or fused	developed	dorsal fenestra larger and separation much thinner	proc. orbitalis narrower	no	beak thinner, straighter; no gonys	7	moderately developed, pointed rather acutely	slightly less developed and pointed medially	developed	rounded edge	processus lateralis more obtuse
		Thamnophilidae	Sakesphorus canadensis	rather similar (forehead slightly flatter)	crest on the back of head (can be spread upwards)	similar	rounded	complete	slightly larger	absent or fused	well developed	dorsal fenestra slightly larger, and separation thinner	proc. orbitalis proportionally longer	no	beak longer; nasal opening reduced; gonys slightly reduced	7	slightly less developed	point slightly less shifted medially	2	,	processus lateralis developed slightly more distally
			Thamnophilus doliatus (skull)	forehead flatter	present; directed donally	smaller	rounded	almost complete	larger, more rounded	absent or fused	developed	similar to fossil; separation thin	proc. orbitals namower	no	beak longer and more curved	2	?	?	2	?	?
			Thamnophilus coecus (skull)	forehead flatter	none	similar	much rounded	almost complete	more rounded	absent or fused	very slightly developed	no dorsal fenestra dorsal fenestra larger,	7	no	more hooked beak longer beyond	7	not much / moderately	?	? much less	7	7
		Conopophagidae	Conopophaga ordesiaca saturata	similar	none	similar	rounded	over the caudal 3/4	slightly larger	absent or fused	slightly developed	separation thinner	proc. orbitalls narrower	no	nasal opening	no; (and NB:	developed; obtuse corner shaped end	slightly less developed medially	developed	very rounded edge	similar
		Rhinocryptidae	Scytalopus unicolor	slightly flatter	none (12)	smaller (11)	dorsal edge flatter	none / narrow oblique bar	variable	absent or fused	very slightly - to developed	single large fenestra (no ossified septum/separation) (13)	rather similar (14)	yes / no (11)	rostrum thinner and more hooked; mdb thinner, decurved, and gonys almost	triosseal canal closed, by junction between processi procoracolideus and	very little developed	not much developed medially	much less developed	very rounded edge	less developed
												ventral fenestra more			absent beak longer; nasal	acrocoracoldeus)	not much / moderately				processus lateralis
		Formicariidae	Formicarius analis	forehead more angular	none	very slightly smaller	rounded	none	larger	absent or fused	developed	developed, separation thinner	similar	no	opening reduced; gonys reduced	yes	developed; acute corner shaped end	less developed medially	much less developed	very rounded edge	developed more distally
			Ceratopipra erythrocephala	similar	none (15)	similar	much rounded	over rostnal and domail border	larger and slightly more rounded	present and more or less individualized	developed	dorsal fenestra more developed, ventral fenestra more reduced, separation thinner	very similar	no	similar to fossil; gonys reduced	yes	developed, slightly more external	developed	2	,	7
			Neopelma sulphureiventer	rather similar (forehead slightly	none	slightly	rounded	narrow over dorsal edge	much larger, more rounded, and more developed rostrally	,	developed	dament franches arrange	more robust; processus orbitalis less developed	no	similar	yes; smaller	developed; straighter and more massive	developed; more	slightly less	rounded edge	processus lateralis more developed
				(forehead slightly flatter)		smaller			developed rostrally			developed; ventral fenestra more reduced donal fenestra more	orbitalis less developed	-	beak thinner; nasal	,		hooked; thinner	Servingeo		more developed distally
			Tyranneutes stolzmanni	similar	none	similar	much rounded	narrow over dorsal edge	slightly larger	7	developed	developed; ventral fenestra more reduced	proc. orbitalis more ventral	no	opening reduced; gonys reduced	yes	developed, slightly more external	slightly less shifted medially	slightly less developed	very rounded edge	similar
			Chloropipo holochlora viridior	forehead slightly flatter	none	similar	rounded	narrow over dorsal and rostral edge	similar	7	developed	dorsal fenestra larger, ventral fenestra smaller	7	no	beak straighter, with edges more 'parallel'; gonys reduced	yes	similar, slightly more external	slightly less pointed medially	slightly less developed	rounded edge	rather similar
		Pipridae	Manacus manacus	forehead slightly flatter	none	similar	rounded	over rostral half, and also a narrow central caudal extension	slightly larger	7	moderately developed	dorsal fenestra larger, ventral fenestra smaller	proc. orbitalis more ventral	no	beak more decurved; gonys slightly reduced mdb slightly more	7	more squarish; very slightly more external	slightly less pointed	slightly less developed	very rounded edge	slightly more developed distally
			Machaeropterus pyrocephalus	forehead flatter, cranium flatter forehead slightly	none	similar	rounded	oblique narrow central extension over 4/5 rostro-donal	slightly larger	7	developed developed, round	dorsal fenestra larger, ventral fenestra smaller dorsal fenestra larger.	proc. orbitalis more ventral proc. orbitalis slightly more	no	mdb slightly more decurved with an angle beak smaller, shorter and much more	?	wider and more obtuse; square	point les shifted medially	much less developed slightly less	very rounded edge	similar
Tyran (Subc	ni scines)		Chiroxiphia linearis	flatter	crest over rostrum base	similar	rounded	part, with namow caudo- ventral extension	slightly larger	suture visible	and obtuse	ventral fenestra smaller	ventral	no	curved; nasal opening reduced	7	more tapering	slightly less pointed	developed	rounded edge	similar
			Xenopipo atronitens	forehead slightly flatter	none	similar	rounded	over dorsal half	identical	present, individualized, fusion with suture visible	well developed, similar to fossil	ventral fenestra smaller, dorsal fenestra larger; separation slightly thinner	proc. orbitalis slightly more ventral	no	beak shorter, decurved; gonys absent	yes	similar, slightly more external	developed slightly less medially	slightly less developed; hooked	relatively circular edge	more developed laterally
			Masius chrysopterus	forehead slightly concave	crest over rostnum base: ponted, directed forward and recurved forward	similar	rounded	over donso-caudal half	(shape similar but) slightly larger	present and more or less individualized	well developed, similar to fossil	ventral fenestra smaller, dorsal fenestra	proc. orbitalis slightly more ventral	no	beak shorter; mdb much more decurved, and gonys slightly reduced	yes	only slightly wider	less developed medially	slightly less developed; hooked	relatively circular edge	e similar
			Antilophia galeata	similar	crest over rostrum base identical to fossil's	similar	rounded	over more than 3/4 donal	slightly larger	present and more or less	developed	larger; separation slightly thinner dorsal fenestra larger, ventral fenestra smaller	similar	no	slightly reduced similar; but gonys less marked	yes	as fossil	developed; shape similar	similarly very developed; slightly	very rounded edge	similar
	Tyrannides			forehead flatter;					shape similar but	Individualized present and more		donal fenestra much	more robust; processus		beak more hooked and robust; mdb		developed; more		more hooked		more developed
			Pipreola arcuata	cranium more elongated	none	similar	rounded	over 1/3 rostral	larger	or less Individualized	well developed	larger, vectral fenestra smaller	orbitalis less developed	no	more curved; gonys less developed	yes: fenestra	developed anteriorly	slightly less developed	developed	very rounded edge	distally
			Cephalopterus omatus	flatter	Immense crest over head, recurved forward and reaching level of beak tip	similar	rounded	ower 1/3 rostro-donsal	more extended donally	present and more or less individualized	developed	both fenestrae much smaller; separation wider	proc. orbitalis wider and more ventral	no	beak more developed rostralmost; more hooked; gonys almost absent	yes	not much developed	developed	similarly very developed	relatively rounded edge	much more developed distally
										present and more		both fenestrae much			rostrum sliehtly						
		Cotingidae	Cotinga sp	flatter	none (16)	similar	dorsal edge slightly flatter	over more than 3/4 caudal	rather similar	present and more or less individualized	well developed	both fenestrae much smaller, (donal fenestra larger than the ventral)	proc. orbitalis more ventral	no	longer and more hooked; mdb much thinner and straighter, without gonys	yes	slightly less developed	slightly less pointed medially	similarly very developed	relatively rounded edge	similar
			Procnias sp. (skull)	similar	none	similar	rounded	thin ; almost complete ventrally	more comma- shaped, pointed ventro-caudally	present and more or less individualized	well developed	One single large fenestra	7	no	beak shorter; nasal opening smaller	2	7	7	7	7	7
			Pipreola intermedia signata (skull)	forehead flatter	none	similar	rounded	thin ; almost complete ventrally	similar	present and fused	well developed	One single large fenestra, no ossified septum	7	no	mdb slightly more curved	?	7	7	2	7	7
			Rupicola rupicala	forehead flatter	present; fan-shaped	similar	rounded	almost completely closing the nasal aperture, viewed in lateral aspect (except thin westral limit)	more rounded, and comma-shaped, pointed ventro- caudally	present and more or less individualized	slightly developed	One single large fenestra, no ossified septum	7	no	beak more hooked; mdb thinner	yes	very little developed	much less developed	slightly less developed	rounded edge	rather similar
			Phytotoma rara	forehead flatter	none (16)	similar	rounded	thin ventral limit) almost complete dorsally	larger, more rectangular	present and more	developed	dorsal fenestra larger,	processus orbitalis much narrower, processus	no	beak more hooked, nasal opening more reduced, absence of	yes	less developed	slightly less developed	slightly less	relatively rounded	processus lateralis more developed
			,,,,,,	forehead flatter;				docul thin sentum		or less individualized present and more		ventral fenestra much reduced, and round donal fenestra much	narrower, processus mandibularis wider		gonys				developed similarly very	edge	more developed medially processus lateralls
			Oxyruncus cristotus	cranium more elongated	none	similar	rounded	more developed (high) rostrally	similar	or less Individualized	developed	reduced; ventral fenestra even more reduced	7	no	beak thinner beak longer	yes	developed, as fossil	less developed; smaller	developed; more hooked	rounded edge	thinner and more curved
			Onychorbynchus coronatus	forehead flatter ; cranium more elongated	large, semi-circular crest, fan-shaped; nuchally; same for other species in the genus	similar	rounded	over 1/3 ventral	larger, more developed donally	present and more or less individualized	developed	both fenestrae much smaller	processus mandibularis more developed laterally	no	rostralmost, and more hooked; nasal opening more reduced; gonys very slight	yes	slightly less developed, thinner than fossil	much less developed	slightly less developed	rounded edge	processus lateralis more developed laterally and more curved
		Tityridae											processus orbitalis much		nasal opening						processus lateralis
			Tityra semifasciata	forehead flatter	none	similar	rounded	semi-circular small rostro-ventral open area	larger	free?	well developed	both fenestrae larger	more developed rostrally; processus mandibularis more developed laterally	no	reduced, absence of gonys	yes	much thinner	less developed	slightly less developed	relatively straight edge	more developed medially and laterally
			Schiffarnis turdina	similar	none	similar	rounded	narrow oblique central bar, directed from rostro-dorsal to caudo- ventral	larger	well individualized; reaches the ectethmoid	well developed	ventral fenestra slightly reduced; dorsal fenestra larger	proc. orbitalis more ventral	no	similar; but gonys less marked and beak slightly decurved	yes: fenestra	wider and more othogonal	less pointed	slightly less developed	rounded edge	more developed latero-distally
			Tyrannus dominicensis	rather similar	none (17)	rather similar	2	over 1/3 dorsal	7	present and more or less individualized	developed	ventral fenestra much reduced ; dorsal fenestra larger	7	no	beak longer; gonys less marked	yes	developed, same shape as fossil	less developed medially	much less developed	relatively straight edge	rather similar
			Tyrannus sp.	forehead much flatter	slight crest in dorsal position	similar	donal edge flatter	over rostro-dorsal half	larger	7	slightly developed, pointed	ventral fenestra larger, separation thinner	proc. orbitalis shorter and proc. oticus wider	7	beak much longer; gonys less marked	yes	markedly less developed; point in proximal position	less developed medially	slightly less developed; hooked	relatively straight edge	developed more latero-distally
			Todirostrum sp.	similar	none	similar	rounded	over rostro-dorsal half ; very thin	more extended donally	free?	slightly developed, pointed	ventral fenestra larger, separation thinner	,	no	beak thinner and more decurved; nasal opening shorter; gonys less marked	yes	markedly less developed	less developed medially	slightly less developed	rounded edge	processus lateralis more developed laterally; more curved
		Tyrannidae	Contopus latirostris (skull)	forehead much flatter	slight crest in top-dorsal position (short in this species)	similar	rounded	(over large part)	rather similar	7	moderately developed	7	7	7	gonys less marked beak much longer, with edges parallel	7	7	7	2	?	curved ?
								donal half and 1/4				ventral fenestra more	processus mandibularis		beak slightly thinner; slightly more decurved; nasal		less developed than in the fossil; with an individualized losangic		similarly very		more developed
			Rhynchocyclus olivaceus	similar	none (17)	similar	rounded	rostral	larger	free?	more developed	reduced, dorsal fenestra larger	more shifted laterally	no	opening more reduced; gonys less marked	yes	or elliptical flat, oblique area at the extremity, ventral side.	less developed	developed; slightly hooked	relatively circular edge	e medially and laterally
			Rhynchocyclus sp.	similar	slight crest in dorsal position	similar	rounded	donal half and 1/4 rostral	larger	free?	more developed	ventral fenestra more reduced, dorsal fenestra larger	7	no	beak slightly thinner; slightly more decurved; nasal opening reduced; gonys less marked	yes	even more developed mesially than fossil; with an individualized losangic or elliptical flat, oblique area at the	less developed	slightly less developed	rounded edge	more developed medially and laterally
Passe	d	Menuridae (18)	Menura noverhallandar	7	none	7	2	none	7	present and individualized (free	developed	donal fenestra much reduced ; separation	proc. oticus reduced; processus orbitalis reduced	no	gonys less marked	yes	oblique area at the extremity, ventral side. undeveloped	7	7	2	7
(Oscii	ies)		u novembloode			<u> </u>	<u> </u>		· '	individualized (free but still in place)	venque0	reduced; separation rather wide	processus orbitalis reduced and more robust		· '	,	pea				ш.

Atrichonsithidae (18)		2	none	reduced		none	7	present, free and small	(developed)	One single large fenestra, no ossified septum	processus orbitalis reduced and more robust	Ass	7	*	very little developed	2	7	7	2
Ptilocorhynchidae (11)	Sericulus sp., Philosophyschus violoceus	7	none	large (20)	7	none		present and individualized, large	7	ventral and dorsal fenestrae reduced	proc. oticus proportionally shorter	no	7	yes	obtuse to slightly acute	7	7	7	7
Climacteridae (2)		?	none	?	*	2	7	free lacrimal absent	7	One single large fenestra, no ossified septum (2)	7	7	7	?	?	?	7	7	7
Meliphagidae	Philemon corniculatur, Meliphaga Inwini, Manarina melanacephola	?	none	large	2	none	7	free lacrimal absent	7	ventral and dorsal fenestrae reduced; a third ventral even smaller (2)	procorbitals developed more dorsally	no	,	7	very little developed	?	7	,	7
Pardalotidae	Pardalotus punctatus	?	none	large	*	none	7	7	7	One single large fenestra, no ossified septum	7	no	7	?	undeveloped	?	7	7	7
Acanthisidae	Gerygone flovolateralix	forehead flatter and longer	none	large	dorsal edge flatter	almost complete	larger	fused or absent	slightly developed	donal fenestra more developed, ventral fenestra more reduced, separation thinner	7	no	rostrum longer and thinner; mdb gonys less marked	no	less developed	much less developed	similarly very developed; much more hooked	rounded edge	more developed latero-distally
Pomatostomidae	Fornatostomus temporalis trivigatus	?	none	7	2	?	7	7	7	?	,	7	,	7	very little developed	?	7	,	7
Paradisseidae	Ptiloris paradiseus, Panadisaea minor	?	present; directed donally	large (21)	2	complete	7	present	7	One single large fenestra, no ossified septum	processus orbitalis shorter, slightly narrower, tip expanded	no	,	7	very little developed	?	7	,	7
Cether cocines								many Corvoidea: free lacrimal present; most Passerida: free lacrimal absent (2)	Corvidae: very much developed	many Corvoides: donal ferestra absent; many Passerida: donal ferestra present (2)	Corvidae: proc. oticus proportionally shorter	no	7	Corvidae: yes	absent or very little developed (in Corvidae absent)	Corvidae: developed	7	?	7
Winstochia welsal [†] (24)		?	7	more reduced (less than half of the cranium length)	?	absent	7	7	7	,	7	no	7	no	developed	not much developed	,	?	much more developed laterally

		Taxon		Scapula			Hume	nus.				Ulna				Carpometacarpus			Proximal wing phalanx	of major digit
										Processus	Tuberculum		Papillae							
	Sub	order to Family	Species (species seen for comparison are listed, but see *)	Outline	Fossa pneumotricipitalis	Crista deltopectoralis	Shaft shape	Depth of incisurs capitis	Processus flexorius	supracondylaris dorsalis	ligamenti collateralis ventralis	Cotyla ventralis	Papillae remigales caudales	Processus dentiformis (3)	Processus Intermetacarpalis	Distal symphysis of os metacarpale minus	Carpometacarpus outline	Processus extensorius	Blade	Processus Internus Indicis
												marked groove just distal				"suboscine type", le: short and rounded caudally, and		in dorsal aspect, the proximal border of the	"suboscine type", le:	
	Revest-des-l	Brousses fossil (early Oligo	ocene) NT-LBR-014	see illustrations	unique	see ilustrations	straight	Rather deep	Straight edge	unique, well-marked	prominent	bonder/bulge of cotyla	rather little marked	present, rather well marked	see illustrations	forming a rostrally situated	see illustrations	proximal border of the proc. extensorius forms a right angle with the rostral border of the donal edge of the trochles carpalis, without a notch in the	caudal edge convex, rounded (with the most caudal extension situated distally)	present
					Two similar fossae,							forms an angle with olecranon axis. (ventral view)				estending more distally; NB: pointed protuberance slight "suboscine type" without				-
	Aca	nthisittidae	Aconthisitta chloris (5)	much more curved distally (except Dendrosconsor)	moderate, non- pneumatic	reduced	curved (5- shaped)	shallow	7	wery little marked to absent	prominent	?	marked to very well marked	absent, or marked undulation	more proximal	pointed protuberance, to "oscine type" (le symphysis square shaped)	rather similar	variable between genera of Acanthisittidae (5)	"oscine type", le: caudal edge straight	reduced to absent
		Pittidae	Pitto sordida	wider proximally	unique, prieumatic	similar	straight	rather deep	edge deflected dono caudally	unique, well-marked	prominent	distal edge of cotyla wentr marked; no groove distal to it. Plane of cot. ventr. (in ventral view)	very well marked	present, rather well marked	similar	"suboscine type" with pointed protuberance	slightly less elongated	there is a distinct notch in the angle between the proc. ext. and the dorsal	intermediate between typical suboscine and	present
												more in continuity with olecranon axis.		very slight		Intermediate between		edge of trochlea carpalis. there is a distinct notch in	typical oscine types	
		Philepittidae	Philepitta castonea	rather similar	unique, pneumatic	similar	straight	rather deep	?	unique, well-marked	prominent	?	very well marked	undulation to absent	similar	suboscine and oscine types, nearer to suboscine type; with pointed protuberance	slightly less elongated	the angle between the proc. ext. and the donal edge of trochles carpalis.	intermediate between typical suboscine and typical oscine types	present
		Eurylaimidae	Combintonchus macrantonchas	rather similar but	unique, pneumatic	similar	straight	moderately deep	edge deflected dorso	unique. little marked		distal edge of cotyla vents marked; no groove distal to it. Plane of cot.	very well marked	present, rather well marked;	similar but less pointed	suboscine type ; pointed protuberance more	slightly more robust	there is a distinct notch in the angle between the	suboscine type, blade	present
	Eurylaimide	es corytamioae	Cymewnyntnus metranyntnus	wider	unque, prieumatic	umar	straignt	moderately deep	caudally	unique, intre manxed	prominers	ventr. (in ventral view) more in continuity with olecranon axis.	very well marked	situated more proximal	similar out less poinced	developed	signtly more robust	proc. ext. and the donal edge of trochlea carpalls.	edge slightly more rounded	present
		Calyptomenidae	Calyptomena viridis	rather similar but more curved distally	unique, prieumatic	similar	straight	rather deep	edge deflected dorso caudally	unique, little marked	prominent	distal edge of cotyla wentr marked; no groove distal to it. Plane of cot. ventr. (in ventral view)	very well marked	absent to rather well marked	similar but less pointed	rather more similar to oscine type (le square), but with a pointed	slightly more robust	there is a distinct notch in the angle between the proc. ext. and the donal	suboscine type, blade edge slightly more rounded	present
												more in continuity with olecranon axis. distal edge of cotyla				protuberance		edge of trochlea carpalis.	rounded	
		Sapayoidae	Sapayoa aenigma	similar	unique, pneumatic	similar	straight	shallow	edge deflected dono caudally	unique, well-marked	prominent	ventr marked; no groove distal to it. Plane of cot. ventr. (in ventral view) more in continuity with olecranon axis.	moderately better marked	present	more distal	suboscine type; with pointed protuberance	less elongated	there is a distinct notch in the angle between the proc. ext. and the donal edge of trochlea carpalis.	similar	present
				NB: cranial								olecranon axis.							intermediate between	
			Geositta cunicularia	extremity axially rotated	unique, pneumatic	similar	straight	shallow	straight edge	unique, very little marked	prominent	7	very little marked	absent to very slight undulation	similar	suboscine type; with pointed protuberance	similar	similar	typical suboscine and typical oscine types (closer to the latter)	present
		Furnariidae (6)	Dendrocincla fuliginosa	rather similar	unique, prieumatic	similar	straight	rather deep	7	unique, very little marked, and an even	prominent	?	lightly better marked	absent to very slight undulation	similar	suboscine type	slightly less elongated	similar	rather oscine type	almost absent
				more curved and						less marked second one			III ARG	agn cracason		rather more similar to	processus extensorius			
			Myrmotherula axillaris	more curved and more angular distally	unique, prieumatic	similar	straight	7	7	unique, very little marked	very prominent	,	similar	slight undulation	more square	oscine type (le square), but with a very slight pointed protuberance intermediate between	more the shape of an isosceles triangle	7	rather oscine type	absent
		Thamnophilidae	Sakesphorus canadensis	more curved distally	unique, pneumatic	similar	straight	7	7	unique, little marked	prominent	7	similar	absent	rather similar	suboscine and oscine types, nearer to suboscine type; with a very slight pointed	rather similar	7	intermediate between typical suboscine and typical oscine types; rather more like	absent
			Thomnophilus doliatus (skull) Thomnophilus coecus (skull)	?	?	?	7	7	?	?	?	?	?	?	?	protuberance ? ?	?	?	subascine but narrow ? ?	?
		Conopophagidae	Conopophaga ardesiaca saturata	much more curved distally	unique, pneumatic	similar	very slightly 5-shaped	,	7	unique, well marked, with a very little marked second one	prominent	7	similar	present, very well marked	slightly more developed	rather more similar to oscine type (le square), but with a pointed protuberance	(slightly more robust)	similar	intermediate between typical suboscine and typical oscine types; rather more like	absent
								rather deep; (all								protuberance			suboscine but narrow	
		Rhinocryptidae	Scytalopus unicolor	more curved distally	unique, less pneumatic	reduced	5-shaped	Rhinocryptidae: some shallower (11))	straight edge	unique, well marked	very prominent	7	very little marked	present, very well marked (11)	rather developed	suboscine type	more robust	similar	rather oscine type	almost absent
		Formicariidae	Formicarius analis	more curved distally	unique, pneumatic	similar	straight; (all Formicarlidae:	shallower; (all Formicariidae:	straight edge	unique, rather		7	moderately	very well marked in this species, but in	slightly more	subcacine type; with	similar	somehow intermediate	intermediate between typical suboscine and	very slight
		rormcanidae	Parmicarius anais	more curved distally	unque, prieumatic	umar	straight to 5-shaped (11))	some as deep as in fossil (11))	scraight edge	marked	prominers	,	better marked	majority absent in this family	developed	pointed protuberance	umar	somenow incomessuos	typical oscine types (closer to the latter)	very signt
			Ceratopipra erythrocephala	slightly more curved	unique, prieumatic	similar	straight	rather deep	straight edge	unique, well marked	prominent	similar	very little marked	absent	similar	suboscine type; with very slight pointed protuberance	similar	similar	suboscine type, very slightly narrower	present
			Neopelma sulphureiventer	,	,	7	,	,	2			similar	unmarked		less developed;	suboscine type; with slight	spatium	similar	7	
			Neopema suptureventer	,	,	,	,	,	,	,	prominent	similar	unmarked	absent	straighter	pointed protuberance	intermetacarpalis less developed distally	similar	7	,
	i i		Tyronneutes stolzmanni	slightly more curved distally	unique, prieumatic	similar	straight	moderately deep	straight edge	unique, well marked	prominent	7	very little marked	absent	similar	suboscine type; with pointed protuberance	similar	similar	suboscine type, but narrower	present
			Chloropipo holochlora viridior	rather similar	unique, pneumatic	similar	straight	shallow	straight edge	unique, well marked	prominent	7	similar	absent	rather similar	suboscine type; with pointed protuberance	rather similar	similar	identical	present
		Pigridae	Manacus manacus	distal two thirds much wider	unique, pneumatic	similar; slightly shorter (prox-distally)	straight	shallow	straight edge	unique, very well marked	prominent	2	similar	present	much more developed	suboscine type; with slight pointed protuberance	more robust	similar	similar	absent
Tyranr			Machaeropterus pyrocephalus	similar	unique, pneumatic	slightly less developed; slightly shorter (prox-distally)	straight	rather deep	straight edge	unique, well marked	prominent	?	very well marked	slight undulation	slightly more developed	suboscine type; with very slight pointed protuberance	similar	similar	suboscine type, but rarrower	present
(Subo			Chiraxiphia linearis	similar	unique, pneumatic	similar	straight	rather deep	straight edge	unique, very well marked	prominent	7	skrálar	absent	similar	suboscine type; with very slight pointed protuberance	similar	similar	suboscine type, but the most caudal extension of the blade is proximal	present
			Xenopipo atronitens	more curved distally	unique, prieumatic	similar	straight	shallow	straight edge	unique, very well marked	prominent	,	very little marked	present	similar	suboscine type; with pointed protuberance	similar	similar	similar	present
			Masius chrysopterus	rather similar	unique, pneumatic	similar	straight	shallow	straight edge	unique, very well marked	prominent	similar	very little marked	veryalight	similar	suboscine type; with very slight pointed protuberance	similar	similar	similar	present; reduced
			Antilophia galeata	similar	unique, prieumatic	similar	straight	rather deep	straight edge	marked unique, well marked	prominent	similar	similar	absent	similar	suboscine type; with very	similar	similar	suboscine type; but	neduced present
	Tyrannides															slight pointed protuberance			narrower	
			Pipreolo arcuata	7	unique, prieumatic	similar	straight	moderately deep	straight edge	unique, well marked	prominent	similar	7	undulation	more pointed	suboscine type; with slight pointed protuberance	intermetacarpalis less elongated	similar	suboscine type; but narrower	present
			Cephalopterus amatus	wider proximally	unique, prieumatic	similar	straight	shallow	edge relatively straight	unique, very little marked	prominent	similar	very well marked	absent or slight undulation	more developed	suboscine type; with pointed protuberance	simlar	similar	suboscine type ; blade even more prominent	present
																			caudally	-
			Cotinga sp	area of maximal curvature wider	unique, prieumatic	similar	straight	shallow	straight edge	unique, very little marked, and an even less marked second one	prominent	similar	moderately better marked	undulation	similar	suboscine type; with pointed protuberance	similar	somehow intermediate but closer to fossil	similar	present
		Cotingidae																		
			Procnias sp. (skull)	7	7	?	7	7	?	7	7	?	7	2	7	7	?	7	7	7
			Pipreola intermedia signata (skull)	y wider; area of	7	?	7	7	?	7	?	7	7	?	7	7	7	7	?	?
			Rupicola rupicola	wider; area of maximal curvature more proximal	7	?	7	7	?	?	7	?	7	2	?	7	?	7	7	?
			Phytotoma rara	wider and more curved distally	unique, pneumatic	similar	straight	rather deep	straight edge	unique, very little marked	prominent	similar	very little marked	very slight undulation	more pointed and narrower	suboscine type; with pointed protuberance	similar	,	very similar	present
			Oxyruncus cristatus	7	7	2	,	,	2	2	prominent	similar	skrálar	2	,	,	?	,	7	7
			and contacts		·		·		-					-		·	-		shape similar; pila cranialis slightly more	-
			Onycharhynchus coronatus	wider and more curved distally	unique, pneumatic	similar	straight	rather deep	straight edge	unique, rather marked	prominent	similar	similar	slight undulation	more developed laterally	suboscine type; with pointed protuberance	spatium intermetacarpalis more developed	similar	cranials slightly more individualized and protruding in relief ventrally, relative to the	present
		Tityridae																	blade plane shape similar; pila cranialis more	
			Tityra semifasciata	wider	unique, non-pneumatic	similar	straight	rather deep	straight edge	unique, well marked	prominent	similar	very little marked	absent	slightly more developed	suboscine type; with pointed protuberance	trochlea carpale more developed	similar; proc. ext. more developed	individualized and protruding in relief wentrally, relative to the blade plane	present
			Schiffornis turdina	more curved distally	unique, pneumatic	similar	straight	rather deep	straight edge	unique, well marked	prominent	7	(very) little marked	slight undulation	similar	suboscine type; with pointed protuberance	similar	similar	very similar	present
			Tyrannus dominicensis	similar	unique, pneumatic	similar	straight	rather deep	straight edge	unique, rather little marked	promineré	similar	moderately better marked	slight undulation	slightly less developed	suboscine type; with pointed protuberance	similar	similar	wey similar	present
			Tyrannus dominicensis Tyrannus sp.	7	7	7	2	7	7	marked ?	prominers:	7	better marked	2	2	pointed protuberance	7	7	7	present ?
			Todirostrum sp.	much wider and more curved	unique, pneumatic	similar	straight	shallow	straight edge	unique, very little marked	prominent	similar	similar	absent	similar	suboscine type; with pointed protuberance	similar	similar	very similar	present
		Tyrannidae	Contopus latirostris (skull)	7	7	7	7	,	7	7	7	,	,	7	7	7	7	7	7	?
																			shape similar; pila cranialis more individualized and	
			Rhynchocyclus alivaceus	more curved distally	unique, pneumatic	similar	straight	shallow	straight edge	unique, rather marked, wider	prominent	similar	very little marked	undulation	less pointed medially; narrower	suboscine type; with pointed protuberance	similar	similar	protruding in relief ventrally, relative to the blade plane; blade more	present
			Rhynchocyclus sp.	more curved	unique, prieumatic	similar	straight	shallow	straight edge	almost absent; and beginning of a second	prominent	similar	almost absent	slight undulation	slightly more pointed medially	suboscine type; with pointed protuberance	similar	similar	rounded. shape similar; pila cranialis more individualized and	present
					I				<u> </u>			1	l	l			I	1	individualized and protruding in relief	

																		ventrally, relative to the blade plane	
	Mecuridae (18)	Menura novarholiandiae	curved, more homogeneously	unique, prieumatic	reduced	straight	7	7	unique, little markeo	non- prominent: flat	2	moderately marked	present, very well marked	developed	oscine type	more robust	7	2	7
	Atrichomithidas (10)			unique, prieumatic	reduced	5-shaped	?	,	absent	non- prominent: flat	2	rather marked	slight	2	oscine type	?	7	oscine type (blade caudal edge straight)	7
	Prilonorhynchidae (III) Sericulus sp., Prilonorhynchus violocuus			unique, prieumatic	similar	straight	?	7	marked, sometimes beginning of a secon	non- prominent: almost flat	?	little marked	absent	similar	oscine type	similar	?	ascine type	absent
	Climacteridae (2)		7	unique, non-pneumatic (2)	7	7	7	?	,	,	?	?	,	,	7	?	7	7	?
	Meliphagidae	Phileman corniculatur, Meliphaga lewini, Manorina melanocephala	straighter and wider proximally	unique, pneumatic (2); (beginning of a second sometimes rather marked)	similar	straight	?	7	double, little developed	non- prominent: flat	?	?	extremely slight undulation	*	oscine type	?	?	ascine type	absent
(Osci		Pandolotus punctetus	more curved and more angular distally	unique, prieumatic	similar	straight	7	?	unique, very well marked	,	?	?	,	,	7	?	7	7	?
	Acarethiolae	Gerygane flavolaterzős	rather similar	double; dorsal fossa preumatized	similar	straight	rather deep, very narrow	straight edge	prominent (double but with very shallow division)	non- prominent: flat	distal edge of cotyla ventr. marked; no groove distal to it. Plane of cot. ventr. (in ventral view) more in continuity with olecranon axis.	moderately marked	very well marked	more proximal, less developed	ascine type	similar	similar	?	7
	Pomatostonidae	Pomatastomus temporalis trivigatus	more curved and more angular distally	unique, prieumatic	(similar)	straight	7	7	unique, little markec	non- prominent: almost flat	2	7	slight undulation	2	oscine type	?	7	oscine type	very reduced
	Paradisseldae	Ptiloris paradiseus, Porodisaeo minor	more curved and more angular distally	unique, prieumatic	similar	straight	?	7	double, rather little marked	non- prominent: flat	?	?	extremely slight undulation	similar	oscine type	similar	?	ascine type	absent
	Other decines		7	unique or double (22) (in Corvidae: unique, pneumatic)	similar	straight	?	?	Generally double (in Corvidae: double, well marked)	non- prominent: flat			absent or present (21) (in Corvidae: absent)		oscine type			ascine type	absent
	Mentiocha wellat [®] (24)			unique	?	straight	7	?	?	?	2	?	marked	more rounded	symphysis poorly developed; presents a pointed protuberance	similar	7	7	?

Note			Taxon		Femur		Tibiotarsus		1		Tarson	etatamus			Pedal p	halanges
Part							Tiny proximo-distal groove	roots does	Product formation that			Commend in section (
No. Part		Sub	conder to Family	Species (species seen for comparison	to proximal	proximalmost	retinaculi extensorius lateralis and the tuberculum retinaculi m.	ridge between the	between crists med, plantaris and	Ossified pons	Position of pons	outer (IV) trochlese tarsometatarsi (also	Trochlea	Trochlea metatarsi		Shape of claws
Note				are titled, but are y		shaft)	fibularis (see 4), lateral side of distal end, proximal to the lateral condyle, rostral aspect (Fig. 51).	condyles (dist. tbt)	crista med. hypotarsi			dorsally unless stated otherwise)			(laterally)	
		Revest-des-l	Brousses fossil (early Oligo	cene) NT-I RR-014	marked	absent	Present; (NB: seems restricted	hardy	no ; crista plantaris relatively little	present	much proximal	no	extension almost as distal	extension almost as distal as tr. mit.	no	generalist
Part		nevest-des-i	brousses rossii (earry Oligo	Cerie/ NP-EBN-014			distally owing to slight crushing)	outlined	developed	(flattened)			as tr. mitt. III	-	-	
Part		Aca	nthisittidae	Aconthisitta chloris (5)	absent	absent to present	present; short and more protruding (including laterally)	stronger	no	present	like subascines		markedly lesser distal extension	slightly lesser distal extension than II	no	more or less curved
Part			Pittidae	Pitto sordida	slighter	absent	present; less distal	slight	no; wide gap between the two crests	present	as fossil	II: only donal and slightly; IV: yes (plantar to partly donal)	as fossil	extension very slightly less distal	no	more elongated
Part			Philepittidae	Philepitta castanea	absent	slight	present; less distal	as fossil	no; crista plantaris very little developed	present	as fossil	no	as fossil	extension less distal	slightly	more elongated
Part		Eurylaimide	Eurylaimidae 25	Cymbirhynchus macrorhynchos	slighter	absent	rather similar	as fossil	no; wide gap between the two crests	present	as fossil	II: no; FV: yes (plantar only)	extension rather like fossit; tr mtt. II oriented more medially	extension less distal	,	slightly more curved
Note			Calyptomenidae	Calyptomena viridis	absent	absent	present; shorter, more in relief, more distal	as fossil	no; wide gap between the two crests	present	as fossil	II: extremely slight plantaro-dist; IV: no	like fassil; tr. mtt. II oriented	extension less distal	?	more curved
Part			Sapayoidae	Sapayoa aenigma	absent	absent	present; on a greater length	very slight	no; crista plantaris almost nonexistent	present	as fossil	It no, IV extremely slight	distal externion greater	extension slightly less distal	no	rather similar
Part			Discontinue (C)	Geositta cunicularia	marked	slight	present; less distal	slight	between the two	present		II: yes; IV: no (9)	as fossil	very narrow and reduced	no	rather tapering and curved
Part			rum <i>a</i> nose (o)	Dendrocincia fuliginosa	absent	slight	present; slightly less distal	slight	no; small gap between the two crests	present	as fossil	no	extension slightly less distal	estension slightly less distale; (NE: trochlea III very much incised by groove)	no	longer and more curved
Procedure Proc				Myrmotherula axillaris	shallow	almost absent	present; less restricted distally	slight	between the two crests	present	distal rather like in Corvidae	no	as fossil	extension less distal	no	more curved
Part			Thamnophilidae		absent	slight	present; (less restricted distally)	slight	no; rather small gap between the two crests		as fossil	no	as fossil	extension as distal as to mit. III		longer
Processor Proc			Conopophagidae	Thamnophilus coecus (skull)					no (plantar crests	?				extension slightly	2	
Provided						marked; (and			hypotansus)					ress distal		
Part			Rhinocryptidae	Scytalopus unicolor	marked	indentation proximal to the fibular crest) (11)		stronger (11)	crests	present	in Corvidae	yes (22)	signify more distal (11)	extension less distal (11)	yes	tapering and more curved
Professional Part			Formicariidae	Farmicarius analis	very shallow	absent	present; less distal	none	crests	present	rather proximal	yes (moreover the IV) (11)	as fossil	7	yes	tapering little curved
Professional Science		ni .		Ceratopipra erythrocephala	shallow	absent	present; less distal	slight	no; wide gap between the two crests	present	as fossil	only very slightly, only plantar	almost as distal as fossil	estension slightly less distal	no	as fossil
Profession Pro				Neopelma sulphureiventer	7	7	7			present	as fossil	7	7	7	?	?
Profession Pro				Tyronneutes stolzmanni	absent	absent	rather similar	wery slight		present	as fossil	no	as fossil	extension as distal as to mit. III	no	similar
Victor Core Popular				Chloropipo holochlora viridior	absent	very slight	present; less distal	very slight	crests; crista plantaris rather little developed	present	as fossil	It slightly; N: no	as fossil	extension less distal	no	narrower, longer and more curved
Michaelpha (Septiment)	Tyran		Pipridae	Manacus manacus	absent	absent	7	very slight	crests; crista plantaris rather little developed	7	7	no	as fossil	extension less distal	no	slightly narrower
Pyramides	(3000	scines		Machaeropterus pyrocephalus	absent	absent	7	very slight	crests; crista plantaris rather little developed	present	as fossil	no	as fossil	extension as distal as to mit. III	no	
Pyramides				Chiraxiphia linearis	marked	absent	present; less distal	very slight	crests; crista plantaris rather little developed	present	as fossil	It slightly, IV: no	as fossil	extension less distal	no	slightly longer, more curved and more tapering
Addition depositions and when the same of the control of the contr		Tyrannides		Xenopipo atronitens	marked	absent	rather similar	none	crests; crista plantaris very little developed	present (at least in part ossified)			as fossil	extension as distal as to mit. III	no	slightly longer and more curved
Procedura countes 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7				Masius chrysopterus	marked	absent	rather similar	as fossil		present	as fossil	It: slightly (at distal tip); IV: no	as fossil	extension less distal	no	slightly longer, more curved and more tapering
Cottograde Cottograde Cottograde Processor or (base) 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7				Antilophia galeata	absent	very slight	rather similar	as fossil	identical to fossil	present	as fossil	no	as fossil	extension less distal	no	slightly langer
Cottogidae Cottogidae Cottogidae Cottogidae Cottogidae Processor (plant) 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7				Pipreolo arcuata	7	,	7		7	7	7	7	7	7	,	2
Consignate Process on (shall) 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7				Cepholopterus ornatus	absent	absent	absent (or hardly visible)	slight / absent	no; wide gap between the two crests	present	as fossil	plantar; Il also visible	as fossil	estension slightly less distal	no	slightly more curved
Process up (shall) 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7			Cotingidae	Cotinga sp	absent	absent	present; less distal	slight	no; wide gap between the two crests	present	as fossil	I: no; IV: yes (essentially plantar)	almost as distal as fossil	extension less distal	,	slightly longer and more curved
Rupicide registed with the control of the control o				Procesias sp. (skull)	7	7	,	7	7	7	7	7	7	7	2	7
Physicians are signed and signed marked rether entire to present and based 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7				Pipreola intermedia signata (skull)	7	7	7	7	7	7	7	7	7	7	7	7
Opportunal crisiantus 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7				Rupicola rupicola	slighter	7	7	7	7	7	,	,	7	,	,	7
Only Charly frithe conditions was in figure and an extended control of the contro				Phytotoma rara	slighter	marked	rather similar		no	present	as fossil	7	7	7	no	similar
Tilgridae				Oxyruncus cristatus	,	,	,		7	,	,	7	7	,	,	7
Typested gas and the second se			Tityridae	Onycharhynchus coranatus	much slighter	marked	rather similar		no	present	as fossil	no	extension less distal	estension slightly more distal	no	more curved
Schightest furdition above wey sight sendor only only of the sendor of t				Tityra semifasciata	absent	marked	rather similar		no	7	7	It slightly, N: no	as fossil	,	no	more curved
Tyramonic disminiscration showes where the same of the				Schiffornis turdina	absent	very slight	similar	very slight	between the two crests; crista plantaris rather little	present	as fossil	It very slightly; IV: no	as fossil	extension less distal	no	longer
Tyrantidae							distal	slight	no; wide gap between the two crests	absent		both slightly plantar; II: also visible at distal tip	extension slightly less distal	distal		tapering
			Tyrannidae						no; wide gap between the two crests; crista plantaris very little	absent		It slightly, Nt no	almost as distal as fossil	extension less		
				Contopus latirostris (skull)	7	7	7			7	7	7	7	7	7	7

		Rhynchacyclus alivaceus	absent	marked	rather similar		no; wide gap between the two crests; crista plantaris very little developed	present	as fossil	no	extension less distal	,	no	more curved and tapering
		Rhynchocyclus sp.	absent	marked	rather similar		no; wide gap between the two crests; crista plantaris very little developed	present	as fossil	no	as fossil	extension less distal	no	similar
	Menuridae (18)	Menura novaeholiandiae	absent	marked; and more proximal	7	marked	no; crista plantaris. little developed	present	rather proximal	yes	extension slightly more distal	estension slightly less distal	yes	2
	Atrichomithidae	1.00	absent	marked	*	little to moderately marked	no; crista plantaris little developed	present	intermediate / proximal	yes	extension slightly more distal	estension slightly less distal	yes	,
	Ptilosorhynchidae (11)	Sericulus sp., Ptilanarhynchus violaceus	absent	almost absent	hardly visible	almost absent	yes	present	7	no	extension slightly less distal	extension slightly less distal	no	7
	Climacteridae (1	7	?	7		yes (2)	7	7	7	7	7	?	2
Passei	Meliphagidae	Phileman corniculatus, Meliphaga lewini, Monorina melanocephala	absent	present, moderately marked	Ittle marked	little marked	variable: no fusion to almost fusion (apparently fusion in Philemon) (2)	present	7	no	slightly less distal	,	no	
(Oscin		Fandolotus punctotus	absent	present, moderately marked	absent (or hardly visible)	very little marked	no	?	7	no	7	*	?	,
	Acantholdse	Gerygane flavolateralis	7	present; marked	absent		yes	absent?	7	It no; IV slightly	as fossil	extension slightly less distal	7	more curved and tapering
	Pomatostomidae	Pomatostomus temponolis trivingatus	absent	7	very slight	very slight	no; small gap between the two crests	present	7	7	7	,	no	2
	Paradixaeldae	Paloris paradiseus, Porodisana minor	absent	almost absent	small	almost absent	no; wide gap between the two crests	present	7	no	oriented more medially	,	slightly	7
	Other oscines		7	absent or almost absent	Corvidae: present; less distal	absent to very slight	no (2)	generally present	Corvidae: more distal	no (or extremely slightly plantarly)	Corvidae: slightly less distal extension than III	Corvidae: very slightly less distal extension than the III	no	Corvidae: generalist
Westcho wital [†] (24)				,	7		?	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.

	Taxon	Skull		Hum	ierus		Ulna
Family	Species	Size of nasal opening	Lateral parts of etecthmoid	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
	est-des-Brousses fossil Oligocene) NT-LBR-014	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	Pipra erythrocephala	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	Neopelma sulphureiventer	large; more than half rostrum length	gap reduced	?	?	hollow; little developed	proximal
	Tyranneutes stolzmanni	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
4)	Chloropipo holochlora viridior	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
Pipridae	Manacus manacus	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
Pipr	Machaeropterus pyrocephalus	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	Chiroxiphia linearis	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	Xenopipo atronitens	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	Masius chrysopterus	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	Antilophia galeata	large; more than half rostrum length	gap reduced	little developed	well developed	hollow; little developed	proximal
	Pipreola arcuata	medium-sized	gap larger	well developed	well developed	flat; wide	proximal
l o	Cephalopterus ornatus	medium-sized	gap larger	well developed	well developed	flat; wide	proximal
g	Cotinga sp.	medium-sized	gap larger	well developed	well developed	flat; wide	proximal
. <u>i</u>	Procnias sp. (skull)	medium-sized	gap larger	?	?	?	?
Cotingidae	Pipreola intermedia signata (skull)	medium-sized	gap larger	?	?	?	?
0	Rupicola rupicola	medium-sized	gap larger	?	?	?	?
	Phytotoma rara	medium-sized	gap larger	well developed	well developed	flat; wide	proximal
зе	Oxyruncus cristatus	small	gap larger	?	?	flat; wide	proximal
<u>.</u>	Onychorhynchus coronatus	small	gap larger	well developed	well developed	flat; wide	proximal
Tityridae	Tityra semifasciata	small	gap larger	well developed	well developed	flat; wide	proximal
—	Schiffornis turdina	small	gap larger	well developed	well developed	flat; wide	proximal
	Tyrannus dominicensis	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal
ae .	Tyrannus sp.	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal
Tyrannidae	Todirostrum sp.	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal
/ran	Contopus latirostris	large; more than half rostrum length	gap moderate but larger than fossil	?	?	hollow; wide	distal
🖍	Rhynchocyclus olivaceus	large; more than half rostrum length	gap moderate but larger than fossil	well developed	little developed	hollow; wide	distal
	Rhynchocyclus 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

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
Caraccid	15.7	Total langth of wing homes	647	Total length of	015
Coracoid	15.7	Total length of wing bones	64.7	leg bones	84.5
Scapula	19.6				

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Supplementary Table 4 States of characters selected and coded for the radial visualisation in

6 Fig. 5. The character states are coded in order to categorize observations in Supplementary

Tables 1 and 2, as follows. State (0) corresponds to absence of the character, state (1) to

presence of the character but state different from the fossil's, and state (2) to presence of

character and state similar or identical to the fossil's. The extant species of comparison are

limited here to the Tyrannides for which all characters were assessable, and the characters are

those exhibiting heterogeneous states across the Tyrannides.

				Skull					Coracoid			Scapula		Hum	erus		Ulna			Carpometaca	irpus		Proximal wing	phalanx of major digit	Femur	Tibiotarsus		Tarsometatarsu	s	
	Cranium shape (lateral profile)	Feather crest	Relative size of orbits	nasal	Fenestra antorbitalis (proportion)	dorsal part	mandible	Processus procoracorideus	Processus acrocoracoideus		Coracoid blade shape	Outline	Crista deltopectora	Shaft alisshape	Depth of incisura capitis	Processus supracondyl dorsalis	Papillae a nis nigalis caudalis	Processus dentiformis I	Processus ^s Intermetacar	Distal symphysis of palis os metacarpale minus	carpometacarpus outline	Processus extensorius	Blade	Processus internus indicis	Hollow just distal to proximal articular surface, caudal side	Incisura intercondylaris t	Proximal arsometatarsus	Position of pons supratendineusineus	Trochlea metatarsus m II	Trochlea metatarsus IV
Fossil	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
Geositta cunicularia	2	1	1	0	1	1	1	1	1	1	1	1	2	2	1	1	1	0	1	1	1	2	1	2	2	1	1	1	2	2
Dendrocincla filignosa	1	0	1	0	1	2	1	1	1	1	1	1	2	2	1	1	1	0	1	1	1	2	1	0	0	1	1	2	1	2
Myrmotherula axillaris	2	1	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
Sakesphorus canadensis	1	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
Conopophagidae ardesiaca	1	0	1	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
Scytalopus unicolor	1	1	1	0	1	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
Formicarius analis	1	0	1	0	1	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
Pipra erythrocephala	2	1	1	1	1	1	2	1	2	1	1	1	2	2	1	2	1	0	1	2	1	2	1	2	1	1	1	2	2	2
Tyranneutes stolzmanni	2	1	2	1	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	1
Chloropipo holochlora	1	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
Manacus manacus	1	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
Machaeropterus pyrocephalus	1	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	1
Chiroxiphia linearis	1	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
Xenopipo atronitens	1	1	1	1	2	2	1	2	1	1	1	1	2	2	1	2	1	1	2	1	2	2	2	2	2	2	2	2	2	1
Masius chrysopterus	1	1	1	1	1	2	1	1	1	1	2	1	2	2	1	2	1	1	1	2	1	2	2	1	2	2	2	2	2	2
Antilophia galeata	2	2	1	1	1	1	2	2	2	2	2	2	2	2	1	2	2	0	2	2	2	2	2	2	0	2	2	2	2	2
Cephalopterus ornatus	1	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
Cotinga sp	1	1	1	1	1	2	1	1	1	2	2	1	2	2	1	1	1	0	2	1	2	1	2	2	0	1	1	2	1	2
Onychorynchus coronatus	1	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	1
Schiffornis turdina	2	1	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
Tyrannus dominicensis	2	1	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
Todirostrum sp.	2	0	1	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
Rhynchocyclus olivaceus	2	0	1	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

Supplementary Table 5 Character matrix used for the phylogenetic analyses.

	Feather cres	Relative et of orb	esize Shap sits ori		frasal Frasal are	enestra torbitalis Or aportion)	is lacrimale	Latero-dornal part of ectethmoid	Lateral parts o etecthrooid	of Crest/ridge culmen	Fora on (foram corace) en	imen nina) of id omal pri nd	Processus ocoracoideus	Processus acrocoracoldeus	Brachial tuberosity (tuberculum brachiale)	Sulcus medialis supracoracoidei	Fossa pneumotricipitalis	Crista deltopectoralis	Crus ventra fossae	slis Crus dors fossae	alis Shaft sha	Depth of pe incluse capitis	Processus Resorius	Processus supracondylaris dorsalis	Processus supracondylari donalis	Tuberculum ligamenti is collateralis ventralis	Cotyla ventralis	Cotyla i dorsalis m	sition of the doru paimal edge of th ncisura tendinosa for me extensor tacarpi ulnaris ar densor digitonum penmunini, distal ulna	Papillae remigales id caudales	Processus dentiformis	Position of processus intermetacarpalis	Distal symphysis of os metacarpale minus	Processus extensorius	Proc Stade into inc	Hollow distal resus prosin resus articu icis surfac caudal	to Medial o mal (tiblota dar proximal ce, shaft	crest retinaculi rost and the tu fibularis, end, pro	osimo-distal groove en the tuberositas l'edensorius lateralis berculum netinaculi m lateral side of distal saimal to the lateral yle, rostral aspect	between crista med plantaris an	Ossified pons supratendineu	Position of pos supratendines	is Trochlea s metatorsi II	Trochlea metatarsi IV
Fassil	2	0		2	0	1	2	1	0	0		0	1	1	2	2	1	0	0	1	1	2	1	1	2	1	1	0	0	1	2	0	1	0		2	0		2	0	1	2	0	1
Pitta sordida Philepitta castanea	0	0		0	7	1	0	1 0	?	0	c c	0	1	1 0	9 7	9	1	0	7	?	1	1	7	1	2 2	1 1	9	?	7	3	1	0	1	1	1	1 0	0		1	0	1	2 2	0	7
Cymbirhynchus macrorhynchos	0	0		0	7	0	0	2	7	0		0	0	0	0	0	1	0	7	,	1	1	0	1	1	1	0	,	7	3	2	0	1	1	0	1	0		1	0	1	2	1	2
Calyptomena viridis	1	0		0	7	0	0	2	7	1		0	1	0	0	0	1	0	7	7	1	1	0	1	1	1	0	7	7	3	1	0	1	1	0		0		1	0	1	2	1	2
Sapayos senigms Seositta cunicularia yrmotherula axillaris	0	0		0	7 7 7	0 0	1 1	2	? ? ?	0		0 7	0 0	1 1	0	2	1	0	7 7 7	? ? ?	1 1	0 7	1 7	1 1	1 1	1 1	? ?	?	7 7 7	0 1	1 1	0	1 1	0 7	1 2	2	1 0		1 1	0	1 1	2 4 3	0 0	7
kesphorus canadensis loretoyacuensis nopophaga ardesiaca	0	0		1		0	1	0	7	0	1		0	1	0	2	1	0	7	7		,	7	1	1 2	1	,	,	7	1	3	0	1	7	1				1		1	2 2	0	1
saturata Scytalopus unicolor Formicarius analis	0	0		1	7	0	1	1	7	0	1	1	0	0	0	1	1	0	7	7	1	1	1	1	2 2	1	?	?	7	2	3 2	0	1	2	1	0	0		1	0	1	1	0	7
endrocincia fuliginosus	0	0		1	7	0	1	3	7	0		0	1	1	1	1	1	0	7	7	1	1	7	1	1	1	,	,	7	1	1	0	1	0	1		1		1	0	1	2	1	i
Pipra erythrocephala	1	0		2	0	0	2	1	0	0	c	0	1	1	,	7	1	0	0	1	1	1	1	1	2	1	1	0	0	0	0	0	1	0	0	1	0		1	0	1	2	0	1
Neopelma sulphureiventer	0	1		1	0	0	7	1	0	0		0	1	1	1	1	7	7	0	1	7	,	7	7	7	1	1	0		0	0	0	1	0	,	,	,		,	,	,	7	7	7
enneutes stolzmanni loropipo holochlora viridior	0	0		2	0	0	7	1	0	0		0	1	1	1	2	1	0	0	1	1	1 0	1	1	2 2	1	?		0	0	0		1						2		1	2 2	0	0
nacus manacus trinitatis	0	0		1	0	0	7	2	0	0	1	7	1	1	1	1	1	0	0	1	1	0	1	1	2	1	7	0	0	1	2	0	1	0	0		0		,	0	2	7	0	1
Machaeropterus pyrocephalus pyrocephalus hiroxiphia linearis	0	0		1	0	0	7 2	1	0	0	1	7	1	1	0	2	1	0	0	1	1	1	1	1	2	1	7		0	3	1 0	0	1			0			7		1	2 2		0
enopipo atronitens taskus chrysoptenus	1	0		1	0	0	2 2	3	0	0	0	0	1	0	1	2 2	1	0	0	1	1	0	1	1	2 2	1	7	0	0	0	1	0	1	0	0	2 2	0		2 2	0	1	2	0	1
intilophia galeata	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		2	0	1	2	0	7
Pipreola arcuata	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	7	7		7	7	7	7	7	7
phalopterus omatus Cotinga sp	0	0		1	1	0	2 2	1 2	2 2	0	0	0	0	1 1	2 2	0	1	0	1	1	1	0	1	1	1 1	1	1	1	0	3 2	0	0	1 1	0 2	0		0		0	0	1 1	2 2	0	1 1
Phytotoma rara	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	0	0	1	0	1	7	0	1	1		2	0	1	2	7	7
Onychorynchus coronatus	1	0		1	2	0	2	1	2	0		0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1	1		2	0	1	2	1	2
Tityra semifasciata	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		1		2	0	7	7	0	7
Schiffornis turdininus amazonus Tyrannus dominicensis	0	0					2	1	1	0	0		1	0	0	1 0	1	0	1	1 0			1	1	1	1	1	1	0	0 2	1	0	1	0	0 1				2	0	1 0	0	0	1
Todirostrum sp	0	0		1	0	0	0	0	1	0		0	0	0	1	į	1	ō	1	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0			1		2	0	0	۰	1	1
thyrichocyclus allvaceus	0	0		1	0	0	0	1	1	0		0	0	0	2	1	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1	0	1	0			1		2	0	1	2	1	7
Rhynchocyclus sp	1	0		1	0	0	0	1	1	0		0	1	0	1	1	1	0	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	0			1		2	0	1	2	1	2
Acanthisita chloris	0	1		1	7	1	0	0	7	0	1	1	0	0	7	,	0	0	7	7	0	0	7	1	0	1	,	,	7	2	0	1	1	7	2		1		1	0	1	1	1	7
Gerygone flavolateralis	0	0		0	7	0	1	0	7	0	1	1	0	0	2	1	0	0	7	7	1	1	1	0	2	0	0	7	7	2	3	1	0	0	7	,	1		0	1	0	0	1	0

- 1 References (for Supplementary Table 1)
- 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., Hugueney, M. & Jonet, P. Découverte de Passeriformes dans
- 9 l'Oligocène supérieur de France. C. R. Acad. Sci. Paris, Série II **309**, 843–849 (1989).
- 4. Boles, W. E. A new songbird (Aves: Passeriformes) from the mid-Cenozoic of Riversleigh,
- 11 northwestern Queensland. *Alcheringa* Special Issue 1, 31–37 (2006).
- 5. Millener, P. R. Contributions to New Zealand's Late Quaternary avifauna. 1: *Pachyplichas*,
- a new genus of wren (Aves: Acanthisittidae), with two new species. *Journal of the*
- 14 Royal Society of New Zealand 18, 383–406 (1988).
- 6. Millener, P. R. & Worthy, T. H. Contributions to New Zealand's Late Quaternary avifauna.
- 2: *Dendroscansor decurvirostris*, a new genus and species of wren (Aves:
- 17 Acanthisittidae). *Journal of the Royal Society of New Zealand* **21**, 179–200 (1991).
- 7. Fjeldsa, J., Irestedt, M. & Ericson, P. G. P. Molecular data reveal some major adaptational
- shifts in the early evolution of the most diverse avian family, the Furnariidae. J.
- 20 *Ornithol.* **146**, 1–13 (2005).
- 8. Tonni, E. P. & Noriega, J. I. Una especie extinta de *Pseudoseisura* Reichenbach 1853
- 22 (Passeriformes: Furnariidae) del Pleistoceno de la Argentina: comentarios
- filogeneticos. *Ornitologia Neotropical* **12**, 29–44 (2001).

- 9. Feduccia, A. & Olson, S. L. Morphological similarities between the Menurae and the
- 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*
- **65**, 91–125 (1963).
- 32 12. Olson, S. L., Parkes, K. C., Clench, M. H. & Borecky, S. R. The affinities of the New
- Zealand passerine genus *Turnagra*. *Notornis* **30**, 319–336 (1983).
- 34 13. Zuccon, D. & Ericson, P. G. P. Molecular and morphological evidences place the extinct
- New Zealand endemic *Turnagra capensis* in the Oriolidae. *Mol. Phylogen. Evol.* **62**,
- 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
- 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).

```
#NEXUS
BEGIN TAXA;
        DIMENSIONS NTAX=36;
        taxlabels
Fossil
Pitta sordida
Philepitta_castanea
Cymbirhynchus_macrorhynchos
Calyptomena_viridis
Sapayoa_aenigma
Geositta_cunicularia
Myrmotherula_axillaris
Sakesphorus_canadensis_loretoyacuensis
Conopophaga_ardesiaca_saturata
Scytalopus unicolor
Formicarius_analis
Dendrocincla_fuliginosa
Pipra_erythrocephala
Neopelma sulphureiventer
Tyranneutes_stolzmanni
Chloropipo_holochlora_viridior
Manacus_manacus_trinitatis
Machaeropterus_pyrocephalus_pyrocephalus
Chiroxiphia_linearis
Xenopipo atronitens
Masius chrysopterus
Antilophia_galeata
Pipreola arcuata
Cephalopterus_ornatus
Cotinga sp
Phytotoma rara
Onychorynchus coronatus
Tityra_semifasciata
Schiffornis_turdina_amazonum
Tyrannus_dominicensis
Todirostrum_sp
Rhynchocyclus_olivaceus
Rhynchocyclus_sp
Acanthisitta_chloris
Gerygone_flavolateralis
end;
BEGIN CHARACTERS:
        DIMENSIONS NCHAR=42;
        FORMAT SYMBOLS = "0 1 2 3 4" GAP=- MISSING = ?;
        Charlabels
Feathercrest
Sizeorbits
Formorbits
Taillenarine
```

Fenestraantorb Lacrimal LatDorsEctethmoid LatEtectmoid Crestculmen Foramencor Procoracorideus Acrocoracoideus Tubbrachiale Sulsupracoracoidei Fossapneum Cristadeltopect Crusventral Crusdorsal Curvedhum **Profcapitis** Procflexorius Procsupcondyldors Procsupcondyldors Ulna Cotylavent Cotyladors Tubconddors Papillae Procdent Positionprocintcarp **Osmetacminus** Procextens Lameborder Procindicis Fossacaud Medcrest Incintcondy Hypotarsi Ponttmt Positionponttmt Trochlint Trochlext **MATRIX**

Fossile	3	1	3	1	2	3	4
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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_sc	rdida	1	1	1	?	2	1
2	?	1	1	2	2	1	1
2	1	?	?	2	2	1	2
3	2	1	?	?	4	3	1
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Philepit	ta_casta	nea	1	1	1	?	2

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2	1	2	2	2	3		
_	ena_viri	_	2	1	1	?	1
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Sapayoa_	aenigma	1	1	1	?	2	1
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Geositta	_cunicul	aria	1	1	1	?	1
2	3	?	1	1	1	2	1
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2 Scytalon	ı us_unico		1	2	1	?	1
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1	1	1	2	1	1	1	2
1	2	1	2	2	1	2	
Neopelma	_sulphure	eiventer	1	2	2	1	
1	?	2	1	1	1	2	2
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Tyranneu	tes_stolz	zmanni	1	1	3	1	
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2	3	2	1	1	2	2	2
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Chiroxiphia_linearis	Chiroxir	nhia line	aris	1	1	2	1	1
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Antilophia_galeata 3 1 2 1 1 1 3 2 2 3 3 3 2 1 1 1 2 2 2 2	1	2	1	1	1	3	1	3
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3	Antiloph	nia dalea	ta	3	1	2	1	1
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2		_					2	
1 ?				2	1	?	2	1
Cephalopterus_ornatus		_	_	_	_	_	_	
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