

MIOCENE SONGBIRDS AND THE COMPOSITION OF THE EUROPEAN PASSERIFORM AVIFAUNA

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ABSTRACT.—Songbirds (Passeriformes) occur in the fossil record of the Northern Hemisphere around the early Oligocene. It has recently been suggested that the major passeriform lineages diverged in Gondwana in the mid- to late Cretaceous and that the oscines, which include all extant European songbirds, originated on the Australian continental plate. Suboscines are assumed to have originated in western Gondwana. Although there is an abundant fossil record of songbirds in Europe, few attempts have been made to set those remains in a phylogenetic context. Our examination of fossil songbirds from three middle Miocene localities in Germany and France shows that many lack the derived morphology of the hypotarsus that characterizes extant Eupasserres (a taxon that comprises oscines and suboscines). We assume that these fossil taxa are outside the crown-group of Eupasserres, which indicates the presence of an ancient songbird avifauna in the Miocene of Europe, in addition to the few fossil Eupasserres already described in the literature. Received 31 October 2003, accepted 24 June 2004.

RESUMEN.—Las aves canoras (Passeriformes) aparecen en el registro fósil del Hemisferio Norte alrededor del Oligoceno temprano. Recientemente se ha sugerido que los linajes principales de Passeriformes se separaron en Gondwana durante el Cretácico medio a tardío y que los oscines, que incluyen todas las aves canoras vivientes europeas, se originaron en la plataforma continental de Australia. Se supone que los suboscines se originaron en el oeste de Gondwana. Aunque para Europa existe un registro fósil abundante, se han hecho pocos intentos de poner estos restos fósiles en un contexto filogenético. Nuestra evaluación de las aves canoras fósiles de tres localidades del Mioceno medio ubicadas en Alemania y Francia muestra que muchas de estas aves no presentan la morfología derivada del hipotarsus que caracteriza a los Eupasserres vivientes (un taxón que incluye los oscines y suboscines). Suponemos que estos taxa fósiles están fuera del grupo terminal Eupasserres, lo que indica la existencia de una avifauna de Passeriformes antigua en el Mioceno de Europa, además de los pocos fósiles de Eupasserres ya descritos en la literatura.

SONGBIRDS OR PASSERINES (Passeriformes) are the most species-rich group of birds, comprising more than half of all extant bird species (Sibley and Monroe 1990). The phylogenetic relationships between these birds have long been controversial (see Sibley and Ahlquist 1990 for a review of the history of classification), but recent molecular analyses have greatly improved our understanding of passeriform phylogeny. Those studies have shown that New Zealand wrens (Acanthisittidae) are the sister group of all other extant passerines (the Eupasserres, which are further divided into suboscines and oscines; Fig. 1; Barker et al. 2002; Ericson et al. 2002, 2003).

All extant European songbirds belong to the oscines, which are assumed to have arisen on the Australian continental plate (Barker et al. 2002). With the exception of the sister taxa broadbills (Eurylaimidae) and pittas (Pittidae) (e.g. Ericson et al. 2003), members of the suboscines are today restricted to North, Central, and South America. That pattern of distribution has led to the assumptions that (1) Passeriformes originated in the Southern Hemisphere and (2) the separation of New Zealand from Gondwana in the mid-Cretaceous (some 82–85 mya) resulted in the split into the Acanthisittidae and Eupasserres lineages (Ericson et al. 2003). The split between the oscine and suboscine lineages is assumed to have occurred in the late Cretaceous, when the South American and Indian tectonic plates became isolated (Ericson et al. 2003).

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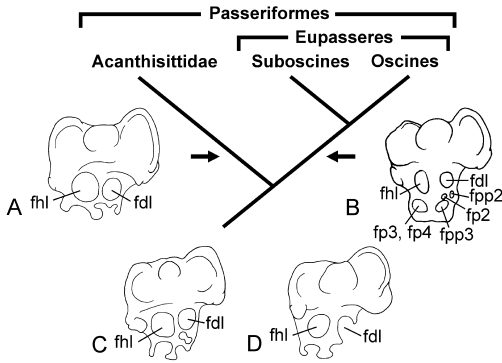


FIG. 1. Left hypotarsi of extant (A, B) and fossil (C, D) passeriform birds in comparison. (A) South Island Wren (*Xenicus gilviventris*, Acanthisittidae). (B) Garnet Pitta (*Pitta granatina*, suboscines, Eupasserres); this pattern corresponds to the derived six-canal pattern of Eupasserres. (C) Fossil species from the middle Miocene (Mlíkovský 1996) of Petersbuch 39, Germany (specimen SMF Av 496). (D) Fossil species from the middle Miocene (Cheneval 2000) of Sansan, France (specimen MNHN SA 1263c). Images are not to scale. Abbreviations of tendinal canals: fhl = *musculus flexor hallucis longus*, fdl = *musculus flexor digitorum longus*, fp = *musculus flexor perforatus*, fpp = *musculus flexor perforans et perforatus*; numerals indicate number of the toe supplied by the tendon. Phylogeny is based on recent molecular studies (Barker et al. 2002; Ericson et al. 2002, 2003).

The earliest fossil record of songbirds is from the Eocene of Australia, though the fragmentary fossils do not allow an assignment to any specific taxon within Passeriformes (Boles 1995a). From the early Miocene of Australia, crown-group oscines have been reported and even assigned to distinct extant genera (Boles 1995b, 1997), thus corroborating molecular phylogenies that indicate an origin of oscines on the Australian continental plate. There is no record of early-Tertiary Passeriformes from Africa, and only a single fragmentary passeriform humerus is known from the early Miocene of South America (Noriega and Chiappe 1993).

The earliest passeriform fossils from Europe are from the early Oligocene of Germany (Mayr and Manegold 2004) and France (Roux 2002). Songbirds have not been identified among the numerous avian remains from Eocene fossil sites in Europe and North America (Mourer-Chauviré 1995, Mayr 2000), and it is assumed that they were still restricted to the Southern Hemisphere by that time (Olson 1988, Maclean 1990, Cracraft 2001).

Passeriform birds exhibit a highly derived and very uniform osteology that facilitates their distinction from nonpasseriform birds but aggravates recognition of subgroups within the taxon. For that reason, few attempts have been made to set fossil songbirds in a phylogenetic context. However, we discovered that the hypotarsus—a bony structure at the proximal tarsometatarsus that conducts the tendons of the flexor muscles of the toes—exhibits a phylogenetically informative variation within passeriform birds.

We examined hypotarsi of representatives of all but 5 (for which no skeletons were available) of the 46 extant “families” of Passeriformes recognized by Sibley and Monroe (1990) and of fossil songbirds from three middle-Miocene localities (all from the mammalian biostratigraphic level MN 6, about 14–15 mya) in southern Germany (Petersbuch 39 and Nördlinger Ries) and France (Sansan), which yielded abundant remains of small passeriform birds. Surprisingly, many of the well-preserved fossil hypotarsi we studied differ distinctly from the pattern typical of crown-group Eupasserres.

MATERIAL AND METHODS

We examined hypotarsi of the following extant taxa in the collections of the Institut für Biologie und Zoologie, Freie Universität Berlin; the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; the Natural History Museum London; Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; the National Museum of Natural History, Washington D.C.; and the Museum für Naturkunde, Berlin (species are listed following the higher-level passerine sequence of Sibley and Monroe 1990; “Corvidae” were shown to be a paraphyletic group by Barker et al. 2002 and Ericson et al. 2002): Acanthisittidae: *Acanthisitta chloris*, *Xenicus gilviventris*. Suboscines: Pittidae: *Pitta guajana*, *P. sordida*, *P. granatina*. Eurylaimidae (including Philepittidae; see Prum 1993): *Smithornis capensis*, *Corydon sumatranus*, *Cymbirhynchus macrorhynchus*, *Psarisomus dalhousiae*, *Philepitta castanea*. Tyrannidae: *Xolmis irrupero*, *Machetornis rixosus*, *Tyrannus melancholicus*, *Megarhynchus pitangua*, *Pitangus sulphuratus*, *Phytotoma rara*, *Lipaugus subalaris*, *Xipholena punicea*, *Cephalopterus ornatus*, *Procnias nudicollis*, *Rupicola peruviana*, *Pipra erythrocephala*, *Chiroxiphia caudata*, *Manacus manacus*. Thamnophilidae: *Thamnophilus caerulescens*, *T. ruficapillus*. Furnariidae: *Furnarius rufus*, *Pseudocolaptes boissonneautii*, *Syndactyla rufosuperciliata*, *Dendrocincla cf. fuliginosa*, *Lepidocolaptes fuscus*, *Sittasomus griseicapillus*. Formicariidae: *Formicarius* sp. Rhinocryptidae: *Pteroptochos megapodius*. Oscines:

Climacteridae: *Climacteris leucophaea*. Menuridae: *Menura novaehollandiae*. Ptilonorhynchidae: *Ptilonorhynchus violaceus*. Maluridae: *Malurus splendens*. Meliphagidae: *Myzomela rubrata*, *Acanthochaera inauris*. Pardalotidae: *Pardalotus substriatus*. Petroicidae: *Eopsaltria australis*. Irenidae: *Irena puella*. Orthonychidae: *Orthonyx spaldingi*. Pomatostomidae: *Pomatostomus superciliosus*. Laniidae: *Lanius collurio*, *L. excubitor*. Vireonidae: *Vireo olivaceus*. "Corvidae": *Corcorax melanorhamphos*, *Struthidea cinerea*, *Pachycephala rufiventris*, *P. lanioides*, *Turnagra capensis*, *Pica pica*, *Corvus monedula*, *Seleucidis melanoleuca*, *Paradisaea rubra*, *Artamus pelewensis*, *Oriolus oriolus*, *Dicrurus adsimilis*, *Grallina cyanoleuca*, *Aegithina tiphia*, *Falcula palliata*. Picathartidae: *Picathartes oreas*. Bombycillidae: *Bombycilla garrulus*. Cinclidae: *Cinclus cinclus*. Muscicapidae: *Turdus merula*, *T. philomelos*, *Zoothera citrina*, *Ficedula hypoleuca*, *Erithacus rubecula*, *Luscinia megarhynchus*. Sturnidae: *Cosmopsarus regius*, *Sturnus vulgaris*, *Mino anais*, *Gracula religiosa*, *Buphagus erythrorhynchus*, *Dumetella carolinensis*, *Mimus polyglottos*. Sittidae: *Sitta europaea*. Certhiidae: *Certhia* sp., *Troglodytes troglodytes*. Paridae: *Remiz pendulinus*, *Parus caeruleus*, *P. major*. Aegithalidae: *Aegithalos caudatus*, *Ae. concinnus*. Hirundinidae: *Hirundo rustica*, *Delichon urbica*. Regulidae: *Regulus regulus*. Pycnonotidae: *Pycnonotus jocosus*, *Chlorocichla falkensteini*, *Hypsipetes madagascariensis*, *Neolestes torquatus*. Cisticolidae: *Cisticola galactotes*. Zosteropidae: *Zosterops erythropleurus*, *Z. palpebrosa*. Sylviidae: *Acrocephalus schoenobaenus*, *Phylloscopus trochilus*, *Garrulax leucolophus*, *Stachyris poliocephala*, *Turdoides squamiceps*, *Leiothrix argentauris*, *Sylvia atricapilla*, *Hippolais icterina*. Alaudidae: *Galerida cristata*, *Alauda arvensis*, *Eremophila alpestris*. Nectariniidae: *Dicaeum hirundinaceum*, *Anthreptes singalensis*, *Nectarinia asiatica*. Passeridae: *Passer domesticus*, *Motacilla alba*, *Anthus pratensis*, *Prunella*, *Quelea quelea*. Fringillidae: *Fringilla coelebs*, *F. montifringilla*, *Carduelis carduelis*, *C. spinus*, *C. chloris*, *Coccothraustes coccothraustes*, *Emberiza citrinella*, *Seiurus aurocapillus*, *Tangara nigroviridis*, *T. vassorii*, *Diglossa lafresnayii*, *Icterus dominicensis*, *Agelaius humeralis*, *Quiscalus niger*.

The fossil specimens are deposited in the following institutions: Muséum National d'Histoire Naturelle, Paris, France (MNHN); Forschungsinstitut Senckenberg, Frankfurt, Germany (SMF); and Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS). Anatomical terminology follows Baumel and Witmer (1993).

We focused on the hypotarsus because we found that element to be especially informative in regard to characterization of some major clades of passeriform birds (see below). Some of the examined specimens consist of complete bones with the highly characteristic distal end of the passeriform tarsometatarsus (e.g. trochleae of the second, third, and fourth toe arranged in a line in distal aspect; and trochleae of the second and fourth toe very narrow). A derived feature on the

proximal end that confirms passeriform affinities of the fossils is the presence of an ossified *retinaculum extensorium*; the shaft of the tarsometatarsus further shows a marked *crista plantaris lateralis*, which occurs only in songbirds and cuckoos (Cuculidae).

The pattern of hypotarsal canals in the fossils reflects the original condition of the bone and is not the result of the breakage of bony ridges (Fig. 2). The fossils are certainly from adult birds, because the tarsal cap is completely fused with the metatarsals and the proximal end of the bone does not show the blurred surface characteristic of juvenile birds. Other skeletal elements of passeriform birds in the material (carpometacarpus, humeri) cannot reliably be assigned to a given type of tarsometatarsus and thus are not considered here.

RESULTS

The hypotarsus of the Acanthisittidae, sister taxon of the Eupasseres, bears only two ossified canals for the deep flexor tendons of the toes (fhl and fdl in Fig. 1B); whereas the superficial flexor tendons (fp2-4 and fpp2-3 in Fig. 1B) run through bony grooves on its plantar surface

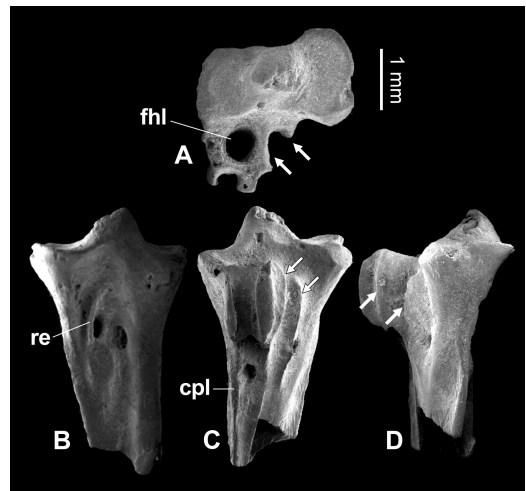


FIG. 2. Scanning electron microscope photographs of the proximal end of a left tarsometatarsus from the middle Miocene of Sansan, France (specimen MNHH SA 1263c). (A) Proximal view on hypotarsus. (B) Dorsal view. (C) Plantar view. (D) Medial view. Abbreviations: cpl = *crista plantaris lateralis*, fhl = ossified canal for tendon of *musculus flexor hallucis longus*, re = ossified *retinaculum extensorium* (broken). Arrows indicate the bony ridges that border the canal for the tendon of *musculus flexor digitorum longus* (note that these do not show any sign of breakage).

(Fig. 1A). In crown-group Eupasserres, in contrast, the flexor tendons typically run through six ossified canals arranged in a unique complex pattern found in no other living or fossil avian taxon (Figs. 1B and 3). In most Eupasserres, the canals for the superficial tendons are completely ossified (some canals may be fused, as in some Turdidae and Zosteropidae; see Figs. 3L, J); very rarely, the canal for fp3–4 is plantarly open (e.g. in all Eurylaimidae investigated; Fig. 3K).

Among the numerous passeriform taxa we examined, only in the South American *Pteroptochos megapodius* (suboscines, Rhinocryptidae) and *Xipholena punicea* (suboscines, Tyrannidae), the African *Picathartes oreas* (oscines, Picathartidae), and the Palaearctic *Cinclus cinclus* (oscines, Cinclidae) are the canals plantarly open for both the superficial tendons fp3–4 and fpp3 (Figs. 1B and 3M–O). That condition was also mentioned by Feduccia and Olson (1982) for the rhinocryptid genera *Scelorchilus* and *Myornis* and illustrated by Rich et al. (1985) for the two species of Australian *Atrichornis* (oscines, Menuridae).

We found the derived “six-canal pattern” of crown-group Eupasserres to be present in

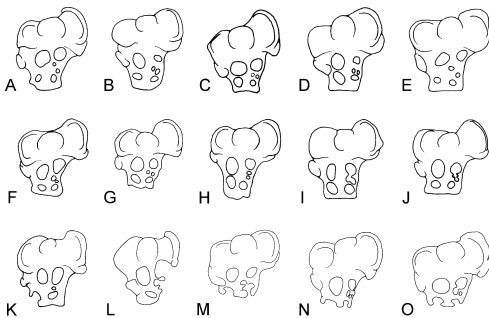


FIG. 3. Selected hypotarsi of extant suboscines (A–D, K–M) and oscines (E–J, N–O). Note that the exceptions from the Eupasserres type are over-represented in the figure. (A) *Tyrannus melancholicus* (Tyrannidae). (B) *Phytotoma rara* (Tyrannidae). (C) *Thamnophilus caerulescens* (Thamnophilidae). (D) *Furnarius rufus* (Furnariidae). (E) *Dicrurus adsimilis* (Dicruridae). (F) *Paradisaea rubra* (Paradisaeidae). (G) *Falcula palliata* (Vangidae). (H) *Hirundo rustica* (Hirundinidae). (I) *Turdus merula* (Turdidae). (J) *Zosterops erythropleurus* (Zosteropidae). (K) *Cymbirhynchus macrorhynchus* (Eurylaimidae). (L) *Lepidocolaptes fuscus* (Furnariidae). (M) *Pteroptochos megapodius* (Rhinocryptidae). (N) *Picathartes oreas* (Picathartidae). (O) *Cinclus cinclus* (Cinclidae). Images are not to scale.

Miocorvus larteti from the middle Miocene of Sansan (specimens MNHN SA 1267, MNHN SA 1289, MNHN SA 1491). Surprisingly, the canals for the superficial tendons fp3–4 and fpp3 are plantarly open in all of the 13 well-preserved fossil hypotarsi from the German localities Petersbuch (specimens SMF Av 487–496) and Nördlinger Ries (specimens SMNS 86822, SMNS 86825, SMNS 86826) (Fig. 1C). The canals for those tendons are also plantarly open in 8 of the 26 well-preserved specimens from Sansan (specimens MNHN SA 1259–1262, MNHN SA 1263a, b, c, d) (Figs. 1D and 2), in which only the lateral canal for the deep flexor tendons (fhl) is completely ossified, a condition we found in the South American Lesser Woodcreeper (*Lepidocolaptes fuscus*, Furnariidae, Suboscines; Fig. 3L) but not in the closely related *Dendrocincla* cf. *fuliginosa* and *Sittasomus griseicapillus* (see Irestedt et al. 2002).

DISCUSSION

Outgroup comparisons with any extant non-passeriform avian taxon show the unique six-canal pattern to be derived within passeriform birds. A six-canal pattern is present in almost all members of suboscines and oscines, including basal taxa (e.g. Barker et al. 2002), and thus almost certainly was also present in the last common ancestor of crown-group Eupasserres. It is the first morphological apomorphy of crown-group Eupasserres identified so far and supports the molecular results concerning the sister-group relationship between Acanthisittidae and Eupasserres.

Judging from current phylogenies, the presence of plantarly open canals for the superficial tendons fp3–4 and fpp3 in a few extant Eupasserres is most likely a reversal to the primitive condition in those unrelated taxa nested deeply within crown-group Eupasserres (e.g. Barker et al. 2002). Apart from the suboscines *Xipholena punicea* and *Lepidocolaptes fuscus*, all the birds in question are ground-dwelling, non-perching birds. Although it thus appears as if there was a functional correlation between that way of living and ossification of the hypotarsus, other ground-dwelling songbirds, such as pittas (Pittidae; Fig. 1B) and lyrebirds (Menuridae), exhibit the Eupasserres’ typical six-canal pattern.

The considerable variation in the hypotarsi of the fossil taxa (Fig. 1C, D) indicates a high

taxonomic diversity and a radiation of at least one extinct passeriform taxon (there is no evidence that the fossil birds in question are members of a monophyletic group). If the absence of the derived Eupasserer pattern in the fossil specimens was also a secondary reversal to the primitive condition, it raises the question of why taxa without the six-canal pattern are the exception among extant passerines, whereas they appear to be abundant and diverse in the middle Miocene. Because of the geological age of the specimens, we consider it likely that absence of the six-canal pattern in the fossil hypotarsi is indeed primitive and indicates that the taxa are outside the crown-group Eupasserer.

The as-yet-unnamed early-Oligocene songbird from Germany described by Mayr and Manegold (2004) is too poorly preserved for detailed comparisons. However, a plesiomorphic morphology of the coracoid also suggests that it is outside the crown-group Eupasserer. The hypotarsus morphology of that specimen is unknown. The early-Oligocene songbird from France mentioned by Roux (2002) has not yet been described.

Few late Oligocene or early to middle Miocene songbirds have been described from Europe so far, and all were considered to be within the Eupasserer—representatives either of the suboscines (Ballmann 1969, Mourer-Chauviré 1995, Cheneval 2000) or of the oscines (Mourer-Chauviré et al. 1989, Cheneval 2000). Although the hypotarsus of most fossil specimens is either unknown or too poorly preserved to allow recognition of the canal pattern, some identifications of Eupasserer in the Miocene of Europe are certainly correct—for example, *Miocorvus larteti* (see above) or the as-yet-unnamed taxon of Eurylaimidae reported by Ballmann (1969) from the early Miocene of Germany. We thus do not question the existence of Eupasserer in the Miocene of Europe (see also Steadman [1981] concerning the presence of Eupasserer in the Miocene of North America). However, our study indicates for the first time that fossil songbirds outside the crown-group Eupasserer (i.e. taxa other than suboscines and oscines) may have been present in the Miocene of Europe. Our study focuses on fossils from one period, the middle Miocene (MN 6). Further studies of older (Oligocene or early-Miocene) songbird remains are needed for learning more

about the temporal distribution of these taxa. With accumulation of more fossil material, it may also be possible to assign other skeletal elements to the tarsometatarsi, which may provide additional clues on the phylogenetic position of these fossil songbirds.

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