

The early fossil record of perching birds (Passeriformes)

Albrecht Manegold

Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25,
D-60325 Frankfurt am Main, Germany

E-mail: albrecht.manegold@senckenberg.de

Present address: Iziko South African Museum, Natural History Department,
Cenozoic Palaeontology Collections, P.O. Box 61, Cape Town,
8000 South Africa

Introduction

The fossil record of the perching birds or passerines (Passeriformes) is very scarce and not well studied, but new discoveries and reinvestigations during the past few years supplement an earlier critical review by Olson (1985) and enable conclusions on the composition of Cenozoic passerine avifaunas. For a better understanding of the significance of the recent findings a short introduction of current hypotheses on the phylogeny of passerines is necessary. Passeriformes are an enormously diverse and species rich group comprising more than half of all the modern bird species described (Sibley & Ahlquist 1990; Schodde & Mason 1999). Monophyly of Passeriformes is well supported by several morphological characters (Raikow 1982), but the reconstruction of the phylogenetic relationships within this clade was only recently promoted by the application of DNA sequence analyses (Ericson *et al.* 2002a,b, 2003; Barker *et al.* 2002, 2004; Harshman *et al.* 2007). According to these studies, three major clades can be distinguished, i.e. Acanthisittidae, Oscines and Suboscines (Fig. 1).

The New Zealand wrens (Acanthisittidae) are restricted to New Zealand. Only two species of a more specious radiation survived to the present, but three additional species were described from late Pleistocene and early Holocene deposits in New Zealand (Millener 1988; Millener & Worthy 1991). Molecular-based analyses revealed that Acanthisittidae are the sister group of a clade comprising the Oscines and Suboscines (Ericson *et al.* 2002a; Barker *et al.* 2002) (Fig. 1). This particular clade was named Eupasserres by Ericson *et al.* (2003).

Suboscines have their centre of distribution in South and Central America. However, a few species of broadbills (Eurylaimidae) and pittas (Pittidae) inhabit the tropical and subtropical areas of the Old World. Surprisingly, Old World Suboscines have a representative overseas: *Sapayoa aenigma*, which occurs in the Chocó region of Panama, western Colombia and Ecuador, is not closely related to suboscine tyrant flycatchers of South America as previously thought, but turns out to be deeply nested within the broadbill clade (Fjeldså *et al.* 2003; Chesser 2004; Moyle *et al.* 2006).

The third major clade is that of the songbirds (Oscines). Several molecular based hypotheses suggest that this group originated in Australia (Barker *et al.* 2002, 2004; Ericson *et al.* 2002a), because several basal songbird groups are mainly restricted to Australia and New Guinea (Fig. 1). Although some of the Australian taxa might be

misclassified according to more recent studies (e.g. Irestedt & Ohlsen 2008), the 'out of Australia' hypothesis gains strong support (see also Sibley & Ahlquist 1990; Schodde & Mason 1999). This is even more remarkable, because the Australian passerine avifauna was traditionally supposed as being solely composed by subsequent dispersals from Asia (Mayr 1944).

Gondwanan origin for Passeriformes?

The current DNA sequence-based phylogenetic hypotheses and the distribution of the major groups are considered to support the hypothesis of a Gondwanan origin of Passeriformes (Barker *et al.* 2002, 2004; Ericson *et al.* 2002). Thus the break-up of the southern continents in the late Cretaceous is proposed to have caused the separation of the three major passerine lineages. Ericson *et al.* (2002), for example, assumed that the lineage of Acanthisittidae became separated when New Zealand was split up from rest Gondwana, 82–85 My ago. A relation between the split-up of the Gondwanan continent during the Cretaceous and the diversification of passerines was also suggested by Cracraft (1973, 2001), Sibley & Ahlquist (1990) and Hedges *et al.* (1996), but these authors based their hypotheses on different data sets and on meanwhile outdated assumptions.

However, there is as yet no fossil evidence for crown group passerines prior to the early Eocene, implying a 30 My gap in the fossil record for passeriforms. Furthermore, the few and fragmentary passerine fossils known from the Eocene cannot be assigned to any of the three major passerine lineages (see below).

The early fossil record of Passeriformes

There is much evidence that previous records of passerines from the early Cenozoic were based on misidentifications. *Palaeospiza bella* was initially described as a primitive songbird from the late Eocene of the Florissant Beds (Wetmore 1925), but was recently identified as a stem-lineage representative of extant mousebirds (Coliidae) (Mayr 2001: 428; Ksepka & Clarke 2009). *Neanis schucherti* from the early Eocene of the Green River Formation is not a passerine as suggested earlier (Shufeldt 1913), but a representative of Gracilarsidae. These tiny, zygodactyl and long-legged birds are probably stem-lineage representatives of woodpeckers, barbets, honeyguides and allies (Piciformes) (Mayr 2005a,b). Similarly, *Palaeogithalus cuvieri* from the late Eocene of France is now referred to another zygodactyl group of stem-lineage Piciformes, the Sylphornithidae (Mayr 1998, 2005a).

Harrison & Walker (1977) described *Primoscens minutus* from the early Eocene of the London Clay as the earliest-known passerine bird (see also Harrison 1982), but comparisons with more complete specimens support its assignment to Zygodactylidae (Mayr 2004, 2008). Despite their zygodactyl toe arrangement – i.e. fourth toe pointing backwards, which is characteristic for Piciformes, Psittaciformes (parrots) and Cuculidae (cuckoos) – Zygodactylidae are now discussed as stem-lineage representatives of Passeriformes (Mayr 2004, 2008).

For the time being, the earliest fossil record for passerines

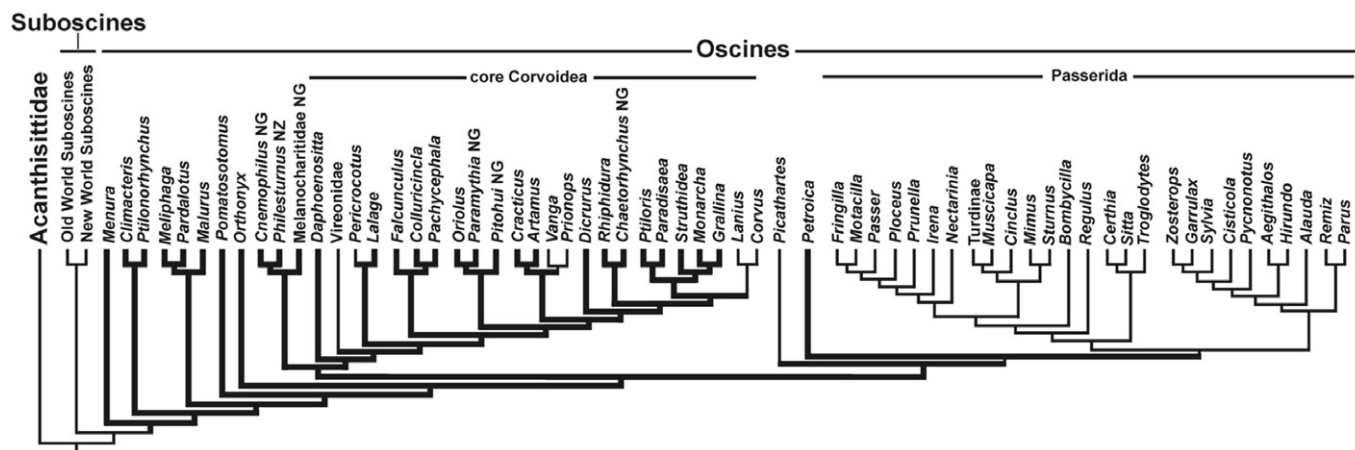


Figure 1. Phylogenetic relationships of Passeriformes based on the DNA-sequence analyses of Barker *et al.* (2004). Lineages of primarily Australian songbird taxa as well as a few taxa restricted to New Guinea (NG) and New Zealand (NZ) are highlighted in bold. Because all of the basal songbird taxa are restricted to or have their centre of distribution in the Australo-Papuan region, an Australian origin of Oscines seems evident. This hypothesis is not challenged by more recent analyses (e.g. Irestedt & Ohlsen 2008) that are in conflict with the branching pattern presented here.

dates from the early Eocene of Australia (Boles 1995a, 1997). It is based on a proximal carpometacarpus and two distal tibiotarsi discovered at Murgon, Queensland (Tingamara local fauna). The fragmentary nature of these specimens does not yet allow further phylogenetic assignments. Mayr (1998) and Louchart (in litt.) call attention to the fact that the fossils in question remain to be compared with Zygodactylidae.

In the northern hemisphere, fossil passerines are unknown until the Oligocene. Not a single passerine has been identified among the numerous avian remains from Eocene fossil sites in Europe and North America, such as Messel Pit, London Clay, Quercy or Green River Formation

(Mayr 2005a). Until recently, few fragmentary bones of songbirds and indeterminate passeriforms, respectively, from the late Oligocene of France rated as the earliest passerine record (Mourer-Chauviré *et al.* 1989, 2004). Meanwhile, these findings were complemented by new discoveries of fossils in France and Germany, which also indicate a more complex evolutionary history of passerines than previously thought.

An isolated cranium with lower jaw and an almost complete skeleton of a passerine were found in early Oligocene deposits of southern Germany, and described as *Wieslochia weissi* (Mayr & Manegold 2004, 2006a) (Fig. 2). These are the first associated remains of an early Cenozoic passerine

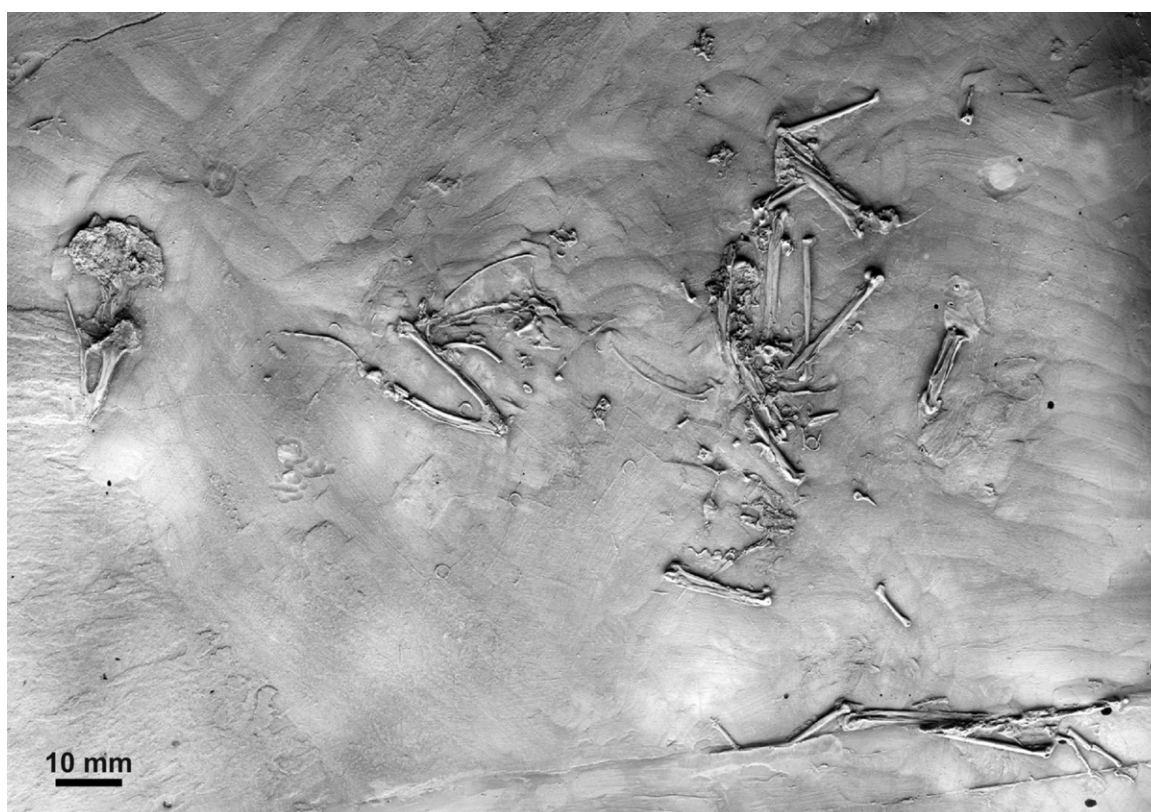


Figure 2. *Wieslochia weissi*, from the early Oligocene of Frauenweiler, Germany. It is to date the earliest record for Passeriformes in the northern hemisphere (Mayr & Manegold 2004, 2006a). Photograph by S. Tränkner.

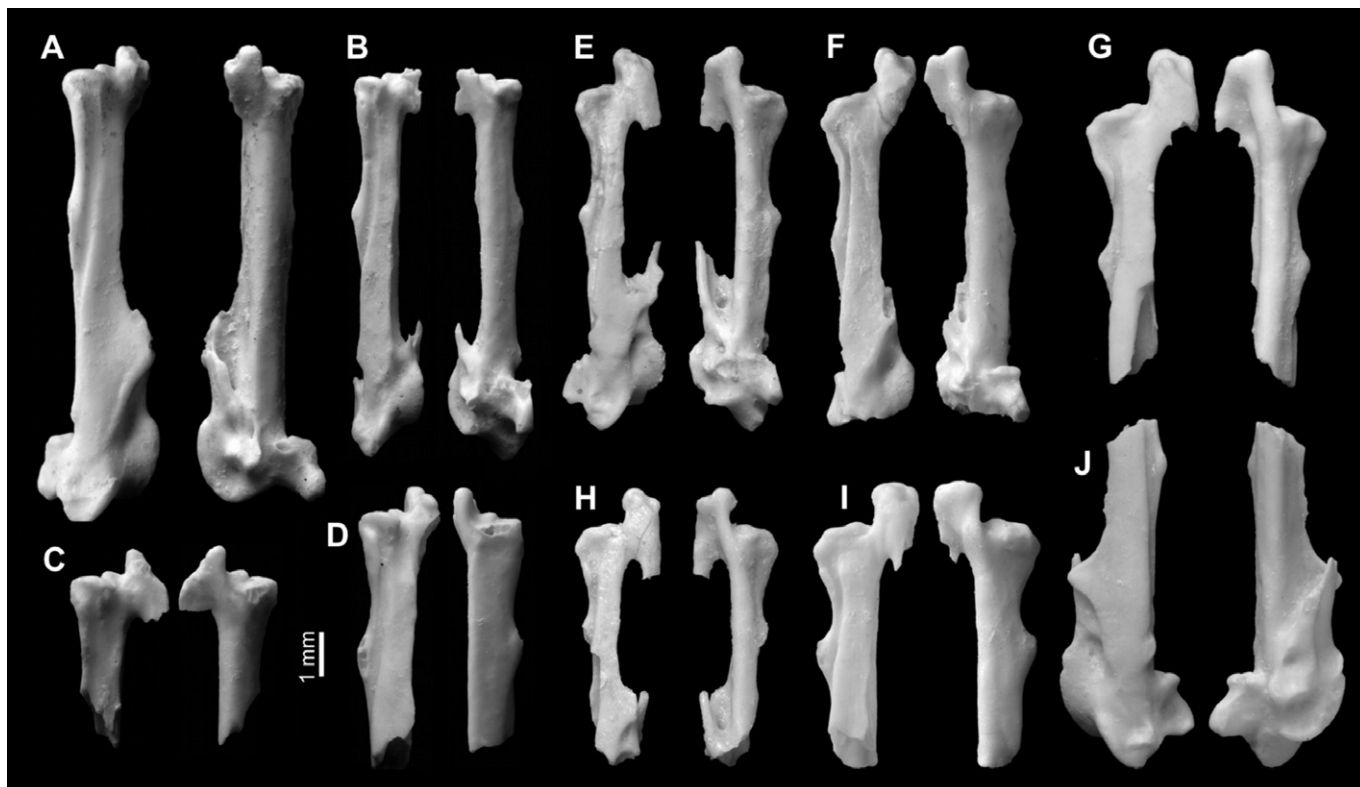


Figure 3. Isolated carpometacarpi from the late Oligocene of Herrlingen, Germany, in dorsal (left) and ventral (right) aspect. Carpometacarpi (A–D) can be assigned to Suboscines, (E–I) to Oscines. Carpometacarpus (J) might belong to another, primitive passeriform lineage (Manegold 2008a). Photograph by S. Tränkner.

described so far. *Wieslochia weissi* was a comparatively small bird, approximately of same size as a modern house sparrow (*Passer domesticus*, Passeridae). The specimens are six to ten million years older than the aforementioned fossils from France, and *Wieslochia* is clearly not a representative of crown group Oscines. Actually, a few characters indicate that this species might be outside Eupasserres (Mayr & Manegold 2006a).

Contemporaneously with *Wieslochia* was an as yet unnamed passerine from the early Oligocene of France (Mayr & Manegold 2006b). Only an isolated wing skeleton is known, but this shows derived features otherwise only known for Suboscines. Thus, it might be referable to a suboscine bird, but additional material is needed for more detailed conclusions. Another passeriform bird of the same age from the same French locality was mentioned by Roux (2002), but that specimen is still undescribed.

There is still a big gap of several million years in the fossil record of passeriforms, but from the late Oligocene onwards, passerines are very abundant in corresponding deposits in the northern hemisphere. Fissure fillings in southern Germany dating from the late Oligocene provided the earliest evidence for the coexistence of Oscines and Suboscines as well as a surprisingly high diversity of perching birds (Manegold 2008a). Remains of at least two suboscine and about ten oscine species could be identified, but there were possibly representatives of another, now completely extinct passerine lineage at the same locality too (Manegold 2008a) (Fig. 3). Enigmatic passerines are also known from the mid Miocene of Germany and France (Manegold *et al.* 2004). They lack a derived character on the tarsometatarsus apomorphic for

Eupasserres which might indicate that the fossils are not part of this clade.

There are no records of early Cenozoic songbirds from Africa and Asia, and the oldest New World songbirds are of early Miocene age (Olson 1985; Noriega & Chiappe 1993). A partial skeleton from the Early to Middle Miocene of Japan is the oldest record for passerines in Asia (Takegawa & Hirao 2003). The authors abstain from a more detailed classification of the conspicuously small specimen, but the lack of a processus dentiformis on the well-preserved carpometacarpus indicate that the fossil belongs to the core Corvoidea *sensu* Barker *et al.* (2004), a group comprising bush-shrikes, cuckoo-shrikes, shrikes, orioles, monarchs, crows, ravens and others (Fig. 1).

As far as the pre-Pliocene record is concerned, only few passerine fossils could be assigned to extant subordinated clades within Oscines and Suboscines, respectively (Olson 1985). For northern Africa, remains of a proximal humerus and an almost complete carpometacarpus from the middle Miocene of Morocco were tentatively referred to the modern common nightingale (*Luscinia* cf. *megarrhynchos*, Oscines) (Brunet 1961), but this identification was justifiably questioned by Olson (1985). Passeriform remains from the early Miocene of Africa south of the Sahara are listed by Pickford (1986) for two fossil sites in Koru/Songhor/Muhoroni Area, western Kenya, but no further information or illustrations are available.

Fossil broadbills (Eurylaimidae, Suboscines) are known from the early Miocene of Bavaria, Germany (Ballmann 1969). *Certhiops rummeli*, the earliest fossil representative of a clade comprising extant nuthatches and treecreepers (Certhioidea, Oscines) showing adaptations for climbing

was discovered in a contemporaneous and close by fossil locality (Manegold 2008b).

In the southern hemisphere, evidence for fossil representatives of lyrebirds (*Menura*) and logrunners (*Orthonyx*) dates from the early Miocene of Australia (Boles 1993, 1995b). Remains of several species of honeyeaters (Meliphagidae) were described from the middle to early late Miocene of Australia (Boles 2005) and suggest an already high diversity of passerine birds at that time. A fragmentary scapula from the early to middle Miocene of New Zealand was tentatively assigned to the butcherbirds (Cracticidae) by Worthy *et al.* (2007). Cracticidae are no longer part of New Zealand's avifauna, but today restricted to Australia and New Guinea. So far, only a single passerine is described from the early Miocene of South America. A fragmentary humerus shows suboscine features, but could not be further identified (Noriega & Chiappe 1993).

Discussion

The fossil record of passerines does not contradict the DNA sequence based hypotheses that this clade originated and diversified in the southern hemisphere. However, the proposed late Cretaceous age for the three major passerine lineages seems to be less convincing from a palaeontologist's perspective, although several molecular clock estimates received similar assumptions (Cooper & Penny 1997; Van Tuinen & Hedges 2001). Interestingly, more recent molecular clock estimates considering latest insights into the fossil record of birds for calibrating splits found no solid molecular evidence for an extensive pre-Cenozoic radiation of Neoaves (Ericson *et al.* 2006), though assuming that the split between Oscines and Suboscines occurred during the Paleocene. Unfortunately, Acanthisittidae were not included in that particular analysis. A Cretaceous age for the major passerine lineages is not in concordance with the fossil record of birds in general and with that of passerines in particular. Bird fossils from the late Cretaceous and the Paleogene were identified as stem-lineage representatives of modern taxa, but no crown-group representatives of any modern family-level taxa are known from pre-Oligocene deposits (Mayr 2005a). The only known stem-lineage representatives of Passeriformes, the Zygodactylidae, appear for the first time in the early Eocene of Europe and North America (Mayr 2008). Enigmatic fossils like *Wieslochia* also indicate that additional and now extinct passerine lineages dwelled in the northern hemisphere, probably before the dispersal of suboscine and oscine birds.

The evidence for Suboscines in the northern hemisphere already inspired new hypotheses on the biogeography of the extant *Sapayoa*, the Old World suboscine in the New World (Fjeldså *et al.* 2003; Moyle *et al.* 2006), but the relationships of the Miocene broadbills of the different suboscine species from the late Oligocene are still obscure. The dramatic increase in diversity and abundance of songbirds in the northern hemisphere during the Oligocene might be correlated with the contemporaneous approach of the Australian continental plate to Eurasia (Hall 1998; Smith *et al.* 1994) facilitating the dispersal of

many songbird lineages (Ericson *et al.* 2002a,b). Sustained northward moving of Australia permitted further faunal exchanges between Australia and Eurasia by the formation of the Indo-Australian Archipelago during the Miocene (Olson 1988; Briggs 1995), but detailed reconstructions of the biogeography of selected groups within the songbirds is still in the beginning, and the study of fossil passerines might be crucial in such attempts.

I thank Sven Tränkner (Forschungsinstitut Senckenberg) for taking the photographs. I also thank Antoine Louchart and an anonymous reviewer for improving the manuscript with their helpful comments. Referred studies by the author got support by the German Research Foundation (DFG) grants MA 2328/3-1 and MA 2328/3-2. Participation at the 15th Biennial PSSA Conference and ongoing studies at the Iziko South African Museum are supported by the German Academy of Sciences Leopoldina grant BMBF-LPD 9901/8-183.

REFERENCES

- BALLMANN, P. 1969. Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. *Zitteliana* **1**, 5–60.
- BARKER, F.K., BARROWCLOUGH, G.F. & GROTH, J.G. 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proceedings of the Royal Society London B* **269**, 295–308.
- BARKER, F.K., CIBOIS, A., SCHIKLER, P., FEINSTEIN, J. & CRACRAFT, J. 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Science USA* **101**, 11040–11045.
- BOLES, W.E. 1993. A Logrunner *Orthonyx* (Passeriformes: Orthonychidae) from the Miocene of Riversleigh, North-western Queensland. *Emu* **93**, 44–49.
- BOLES, W.E. 1995a. The world's oldest songbird. *Nature* **374**: 21–22.
- BOLES, W.E. 1995b. A preliminary analysis of the Passeriformes from Riversleigh, northwestern Queensland, Australia, with the description of a new species of lyrebird. *Courier Forschungsinstitut Senckenberg* **181**, 163–170.
- BOLES, W.E. 1997. Fossil songbirds (Passeriformes) from the early Eocene of Australia. *Emu* **97**, 43–50.
- BOLES, W.E. 2005. Fossil honeyeaters (Meliphagidae) from the Late Tertiary of Riversleigh, north-western Queensland. *Emu* **105**, 21–26.
- BRIGGS, J.C. 1995. *Global Biogeography*. Developments in Palaeontology and Stratigraphy **14**. Amsterdam, Lausanne, New York, Oxford, Shannon, Tokyo, Elsevier.
- BRUNET, J. 1961. Oiseaux. *Notes et Mémoires du Service Géologique (Maroc)* **155**, 105–108.
- CHESSER, R.T. 2004. Molecular systematics of New World suboscine birds. *Molecular Phylogenetics and Evolution* **32**, 11–24.
- COOPER, A. & PENNY, D. 1997. Mass survival of birds across the Cretaceous/Tertiary: molecular evidence. *Science* **275**, 1109–1113.
- CRACRAFT, J. 1973. Continental drift, palaeoclimatology, and the evolution and biogeography of birds. *Journal of Zoology* **169**, 455–545.
- CRACRAFT, J. 2001. Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proceedings of the Royal Society London B* **268**, 459–469.
- ERICSON, P.G.P., CHRISTIDIS, L., COOPER, A., IRESTEDT, M., JACKSON, J., JOHANSSON, U.S. & NORMAN, J.A. 2002a. A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proceedings of the Royal Society London B* **269**, 235–241.
- ERICSON, P.G.P., CHRISTIDIS, L., IRESTEDT, M. & NORMAN, J.A. 2002b. Systematic affinities of the lyrebirds (Passeriformes: *Menura*), with a novel classification of the major groups of passerine birds. *Molecular Phylogenetics and Evolution* **25**, 53–62.
- ERICSON, P.G.P., IRESTEDT, M. & JOHANSSON, U.S. 2003. Evolution, biogeography, and patterns of diversification in passerine birds. *Journal of Avian Biology* **34**, 3–15.
- ERICSON, P.G.P., ANDERSON, C.L., BRITTON, T., ELZANOWSKI, A., JOHANSSON, U.S., KÄLLERSJÖ, M., OHLSON, J.I. PARSONS, T.J., ZUCCON, D. & MAYR, G. 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. *Biology Letters* **2**, 543–547.
- FJELDSÅ, J., ZUCCON, D., IRESTEDT, M., JOHANSSON, U. & ERICSON, P.G.P. 2003. *Sapayoa aenigma*: a New World representative of 'Old World suboscines'. *Proceedings of the Royal Society of London B (Suppl.)* **270**, S238–S241.
- HALL, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: Hall, R. & Holloway, J.D. (eds.), *Biogeography and Geological Evolution of SE Asia*, 99–124. Leiden, Backhuys Publishers.

- HARRISON, C.J.O. 1982. Cuculiform, piciform and passeriform birds from the Lower Eocene of England. *Tertiary Research* **4**, 71–81.
- HARRISON, C.J.O. & WALKER, C.A. 1977. Birds of the British Lower Eocene. *Tertiary Research Special Paper* **3**, 1–52.
- HARSHMAN, J. 2007. Classification and phylogeny of birds. In: Jamieson, B.G.M. (ed.), *Reproductive Biology and Phylogeny of Birds – Part A*, 1–35. Enfield, N.H., Science Publishers.
- HEDGES, S.B., PARKER, P.H., SIBLEY, C.G. & KUMAR, S. 1996. Continental breakup and the ordinal diversification of birds and mammals. *Nature* **381**, 226–229.
- IRESTEDT, M. & OHLSEN, J.I. 2008. The division of the major songbird radiation into Passerida and ‘core Corvoidea’ (Aves: Passeriformes) – the species tree vs. gene trees. *Zoologica Scripta* **37**, 305–313.
- KAKEGAWA, Y. & HIRAO, K. 2003. A Miocene passeriform bird from the Iwami Formation, Tottori Group, Tottori, Japan. *Bulletin of the National Science Museum, Series C* **29**, 33–37.
- KSEPKA, D.T. & CLARKE, J.A. 2009. The affinities of *Palaeospiza bella* and a phylogeny of mousebirds (Aves, Coliiformes). *Auk* **126**, 245–259.
- MANEGOLD, A. 2008a. Passerine diversity in the late Oligocene of Germany: earliest evidence for the sympatric coexistence of Suboscines and Oscines. *Ibis* **150**, 377–387.
- MANEGOLD, A. 2008b. Earliest fossil record of the Certhioidea (treecreepers and allies) from the early Miocene of Germany. *Journal of Ornithology* **149**, 223–228.
- MANEGOLD, A., MAYR, G. & MOURER-CHAUVIRÉ, C. 2004. Miocene songbirds and the composition of the European passeriform avifauna. *Auk* **121**, 1155–1160.
- MAYR, E. 1944. Timor and the colonization of Australia by birds. *Emu* **44**, 113–130.
- MAYR, G. 1998. ‘Coraciiforme’ und ‘piciforme’ Kleinvögel aus dem Mittel-Miozän der Grube Messel (Hessen, Deutschland). *Courier Forschungsinstitut Senckenberg* **205**, 1–102.
- MAYR, G. 2001. New specimens of the Middle Eocene fossil mousebird *Selmes absurdipes* Peters 1999. *Ibis* **145**, 427–434.
- MAYR, G. 2004. The phylogenetic relationships of the early Tertiary Primoscenidae and Sylphornithidae and the sister taxon of crown group piciform birds. *Journal of Ornithology* **145**, 188–198.
- MAYR, G. 2005a. The Paleogene fossil record of birds in Europe. *Biological Reviews* **80**, 515–542.
- MAYR, G. 2005b. Phylogenetic affinities and composition of the early Eocene Gracilitarsidae (Aves, ?Piciformes). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **2005**, 1–16.
- MAYR, G. 2008. Phylogenetic affinities of the enigmatic avian taxon *Zygodactylus* based on new material from the early Oligocene of France. *Journal of Systematic Palaeontology* **6**, 333–344.
- MAYR, G. & MANEGOLD, A. 2004. The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften* **91**, 173–177.
- MAYR, G. & MANEGOLD, A. 2006a. New specimens of the earliest European passeriform bird. *Acta Palaeontologica Polonica* **51**, 315–323.
- MAYR, G. & MANEGOLD, A. 2006b. A small suboscine-like passeriform bird from the early Oligocene of France. *Condor* **108**, 717–720.
- MILLENER, P.R. 1988. Contributions to New Zealand’s late Quaternary avifauna 1. *Pachyplichas*, a new genus of wren (Aves, Acanthisittidae), with two new species. *Journal of the Royal Society of New Zealand* **18**, 383–406.
- MILLENER, P.R. & WORTHY, T.H. 1991. Contributions to New Zealand’s late Quaternary avifauna. 2. *Dendroscansor decurvirostris*, a new genus and species of wren (Aves, Acanthisittidae). *Journal of the Royal Society of New Zealand* **21**, 179–200.
- MOURER-CHAUVIRÉ, C., BERTHET, D. & HUGUENEY, M. 2004. The late Oligocene birds of Cr  chy quarry (Allier, France), with a description of two new genera (Aves: Pelecaniformes: Phalacrocoracidae, and Anseriformes: Anseranatidae). *Senckenbergiana lethaea* **84**, 303–315.
- MOURER-CHAUVIR  , C., HUGUENEY, M. & JONET, P. 1989. D  couverte de Passeriformes dans l’Oligoc  ne sup  rieur de France. *Compte Rendu de l’Acad  mie des Sciences II* **309**, 843–849.
- MOYLE, R.G., CHESSER, R.T., PRUM, R.O., SCHIKLER, P. & CRACRAFT, J. 2006. Phylogeny and evolutionary history of Old World suboscine birds (Aves: Eurylaimides). *American Museum Novitates* **3544**, 22 pp.
- NORIEGA, J. & CHIAPPE, L. 1993. An early Miocene passeriform from Argentina. *Auk* **110**, 936–938.
- OLSON, S.L. 1985. The fossil record of birds. In: Farner, D.S., King, J.R. & Parkes, K.C. (eds.), *Avian Biology – Volume 8*, 79–238. New York, Academic Press.
- OLSON, S.L. 1988. Aspects of global avifaunal dynamics during the Cenozoic. In: Ouellet, H. (ed.), *Acta XIX Congressus Internationalis Ornithologici, Ottawa, 1986*, 2023–2029. Ottawa, National Museum of Natural Sciences.
- PICKFORD, M. 1986. Cainozoic paleontological sites of Western Kenya. *M  nchner Geowissenschaftliche Abhandlungen (A)* **8**, 1–151.
- RAIKOW, R.J. 1982. Monophyly of Passeriformes: test of a phylogenetic hypothesis. *Auk* **99**, 431–445.
- ROUX, T. 2002. Deux fossiles d’oiseaux de l’Oligoc  ne inf  rieur du Luberon. *Courrier scientifique du Parc naturel r  gional du Luberon* **6**, 38–57.
- SCHODDE, R. & MASON, J.J. 1999. *The Dictionary of Australian birds – Passerines*. Canberra, CSIRO Publishing.
- SHUFELDT, R.W. 1913. Fossil feathers and some heretofore undescribed fossil birds. *Journal of Geology* **21**, 628–652.
- SIBLEY, C.G. & AHLQUIST, J.E. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. New Haven, CT, Yale University Press.
- SMITH, A.G., SMITH, D.G. & FUNNELL, B.M. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge, Cambridge University Press.
- WETMORE, A. 1925. The systematic position of *Palaeospiza bella* Allen, with observation on other fossil birds. *Bulletin of the Museum of Comparative Zoology* **67**, 184–193.
- WORTHY, T.H., TENNYSON, A.J.D., JONES, C., McNAMARA, J.A. & Douglas, B.J. 2007. Miocene waterfowl and other birds from Central Otago, New Zealand. *Journal of Systematic Palaeontology* **5**, 1–39.
- VAN TUINEN, M. & HEDGES, S.B. 2001. Calibration of avian molecular clocks. *Molecular Biology and Evolution* **18**, 206–213.