

Fossil honeyeaters (Meliphagidae) from the Late Tertiary of Riversleigh, north-western Queensland

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Abstract. The honeyeaters (Meliphagidae) comprise one of the most characteristic, numerous, speciose and widespread components of the Australo-Papuan avifauna. Despite their present ubiquity, these birds have a meagre fossil record restricted to the Quaternary. Described here are the first Late Tertiary records of the Meliphagidae, recovered from Pliocene and Miocene sites of Riversleigh, north-western Queensland. These records are based on the tarsometatarsus, which in honeyeaters is one of the more distinctive morphologies among the Passeriformes. The Pliocene site at Riversleigh has yielded three specimens, one of which is particularly well preserved and morphologically inseparable from the extant *Lichenostomus–Meliphaga*. Specimens from three Miocene sites exhibit differences in size and morphology that indicate that at least four taxa are involved at this age.

Introduction

The honeyeaters (Meliphagidae) comprise one of the most characteristic, numerous, speciose and widespread components of the Australo-Papuan avifauna. There are 180–185 species in 42–45 genera, concentrated in Australia (72 species/23 genera) and New Guinea (61 species/17 genera) (with 15 species/nine genera shared), with outliers west to the Moluccas and Bali, north to the Philippines, Micronesia and Hawaii, and east through New Zealand and the south-western Pacific islands to Samoa and Tahiti (Salomonsen 1967; Sibley and Monroe 1990; Dickinson 2003). Despite the present ubiquity of honeyeaters, these birds have a meagre fossil record. The only taxa published are of Quaternary age, including from Australia (Baird 1991), New Zealand (Worthy and Holdaway 2002), the south-western Pacific (e.g. Steadman 1991, 1993) and Hawaii (James and Olson 1991). Described here are the first Tertiary records of the Meliphagidae, based on tarsometatarsi from the Pliocene and Miocene of Riversleigh, north-western Queensland.

Although passerine post-cranial osteology is distinctive at the ordinal level, it has been little used for determining relationships within the order. Few post-cranial characters have been reviewed across the Passeriformes, the most thoroughly treated and best known being the fossa pneumotricipitalis (= tricripital fossa) of the humerus (e.g. Ashley 1941; Berger 1957; Bock 1962; W. E. Boles, unpublished data). Comparisons of various skeletal elements between passerine families show that there is considerable variation of potential systematic use. The tarsometatarsus is one of the more numerous passerine elements recovered from the Riversleigh deposits (Boles 1995); new specimens described

here are based on this element. Osteological nomenclature follows Baumel and Witmer (1993).

Tarsometatarsus in the Meliphagidae

Description

One of the more distinctive tarsometatarsal morphologies among the Passeriformes is that of the honeyeaters. The distinctive passerine hypotarsus is rectangular in proximal view and encloses 4–6 canales hypotarsi. In the Meliphagidae, and in other taxa with large halluces, the canalis for *M. flexor hallucis longus* is markedly enlarged, particularly relative to more plantar canales (Fig. 1a). There is a strong crista plantaris lateralis originating distal to the hypotarsus and extending distally along the lateral edge, essentially becoming a plantar extension of the lateral face. Some individuals have an ossified tendinal bridge (pons) located proximomedially on the dorsal face.

The distal end of the bone is dorsoplantarly compressed and the dorsal face is flattened, more so on the medial side, and somewhat expanded, so that it is wider than the shaft proximal to it (Fig. 1b). The lateral margin is flared only slightly, if at all. The medial margin flares outwards in a flattened flange from a point level with the proximal border of the fossa metatarsi I, which it overlies. The flange may be smooth in outline or slightly concave around the midpoint, and moderately to rather extensively produced. This flange then curves inwards to varying extents proximal to the base of the trochlea metatarsi II.

In plantar view, the fossa metatarsi I is large and deep, and expanded medially to occupy the flattened flange (Fig. 1c). Laterally it extends to, and occasionally past, the midline of

the shaft, and the most lateral point continues distally at an angle to the medial margin at the base of the trochlea metatarsi II.

The trochlea metatarsi III is the largest of the trochleae. It is grooved, with the medial half projecting distally further than the lateral half. Dorsally the trochlea projects above the flattened shaft surface proximal to it. The trochlea metatarsi II has a characteristic triangular shape, with the distal margin angling from the short lateral side to the longer medial side. Compared with the trochlea metatarsi III, it does not project as far distally and, in medial view, is not as deep, overlapping the plantar two-thirds of that trochlea. The incisura intertrochlearis medialis is quite narrow. The trochlea metatarsi IV is thin and straight, and projects as far distally as the trochlea metatarsi II, but is about the same depth as the lateral side of the trochlea metatarsi III. The incisura intertrochlearis lateralis is wider than the incisura intertrochlearis medialis.

In lateral view, the dorsoplantar compression is obvious (Fig. 1*d*). From the proximal edge of this compression, the distal end is bent plantarly at an angle of $\sim 20^\circ$, an appearance accentuated by the flattening of the dorsal surface.

Riversleigh geography and geology

The Riversleigh deposits are an outcrop of Tertiary limestone located 5 km west of the Riversleigh Homestead ($19^\circ 02'S$, $138^\circ 45'E$), 200 km north of Mt Isa, north-western Queensland. For more information on the Riversleigh deposits and palaeoenvironmental interpretations, see Archer *et al.* (1989, 1994), Megirian (1992) and Creaser (1997).

Specimens herein assigned to the Meliphagidae come from four sites, three Miocene and one Pliocene. The former include Last Minute Site, considered to be a shallow water 'tufa' deposit, dominated by terrestrial fauna, and Ringtail Site, which formed in a deep water pool and is dominated by

aquatic fauna. These are considered to be from possibly Middle to early Late Miocene in age (Creaser 1997). AL'90 Site, a cave deposit, may also be of this age (Black 1997). The palaeoenvironment of Riversleigh at this time is thought to have been rainforest or gallery forest (Archer *et al.* 1989). The Pliocene deposit, Rackham's Roost Site, is the floor of a former cave, located on bluffs above the Gregory River, south of the river crossing by the main road. Small vertebrate fossils comprise mainly discarded prey remains from predatory megadermatid bats (*Macroderma*, *Megaderma*) (see Boles 1998, 1999; Hand 1995, 1996). Archer *et al.* (1989) concluded that the surrounding habitat was 'a dry sclerophyll forest or woodland with a grassy understorey, probably not too unlike the environment that dominates Riversleigh today'.

Systematic palaeontology

Pliocene site (Rackham's Roost Site)

Meliphagid tarsometatarsi are represented at this site by three specimens, one of which (QM F36443) is particularly well preserved. QM F22802 and QM F24580 are left distal fragments: QM F22802 includes about half of the shaft; QM F24580 is broken through just proximal to the flange and has some damage to the trochlea metatarsi IV. Both are about the size of the element in Brown Honeyeater (*Lichmera indistincta*), but appear not to belong to that species and represent two different taxa.

QM F36443, a complete right tarsometatarsus (length 20.7 mm), is the most informative of these specimens (Fig. 2*a*). It is morphologically inseparable from *Lichenostomus* or *Meliphaga*. The specimen is tentatively referred to cf. *Lichenostomus-Meliphaga*. No species of *Meliphaga* today occupies dry open woodland, the habitat that now prevails at Riversleigh and is considered to have been present during the Pliocene, whereas several species of *Lichenostomus* do occur there. Two of the latter species, the

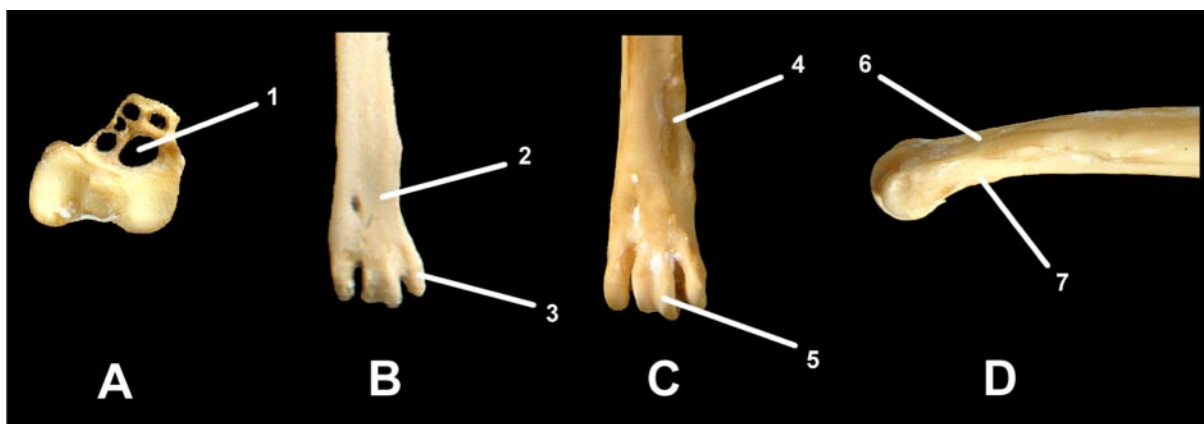


Fig. 1. Diagnostic characters of the tarsometatarsus of the Meliphagidae. (A) proximal end, proximal view; (B–D) distal end: (B) dorsal view, (C) plantar view, (D) medial view. 1, enlarged canal for *M. flexor hallucis longus*; 2, flattened, expanded medial side of dorsal face; 3, triangular-shaped trochlea metatarsi II; 4, large, deep fossa metatarsi I extending at least to midline; 5, medial side of trochlea metatarsi III projecting further than lateral side; 6, dorsoplantar compression of distal end; 7, plantar bend to distal end.

Grey-headed Honeyeater (*L. keartlandi*) and Grey-fronted Honeyeater (*L. plumulus*), have tarsometatarsi that are similar in length to the fossil but which are slightly more gracile. In the absence of more complete, associated elements it is not possible to resolve the identification of this specimen beyond *cf Lichenostomus–Meliphaga* species indeterminate.

Miocene sites

Three Miocene-aged sites have yielded three tarsometatarsal fragments of the Meliphagidae, and a fourth that is tentatively allocated to this family. Two tarsometatarsal specimens from a fifth location (Gag Site, also in the Gag Plateau Sequence) are similar to honeyeaters but are too fragmentary to allocate to this family with confidence. Of the four Miocene specimens described below, differences in size and morphology indicate that at least four taxa are involved. The size comparisons used do not imply relationships to the taxa mentioned beyond the level of family; the fossils are considered to be Meliphagidae indeterminate.

AL'90 Site. QM F24684 comprises a left distal fragment broken through about the midshaft. The morphology is similar to that of *Meliphaga–Lichenostomus*, with a moderately developed flange and fossa metatarsi I. It is roughly the size of the tarsometatarsus in Fuscous Honeyeater (*Lichenostomus fuscus*).

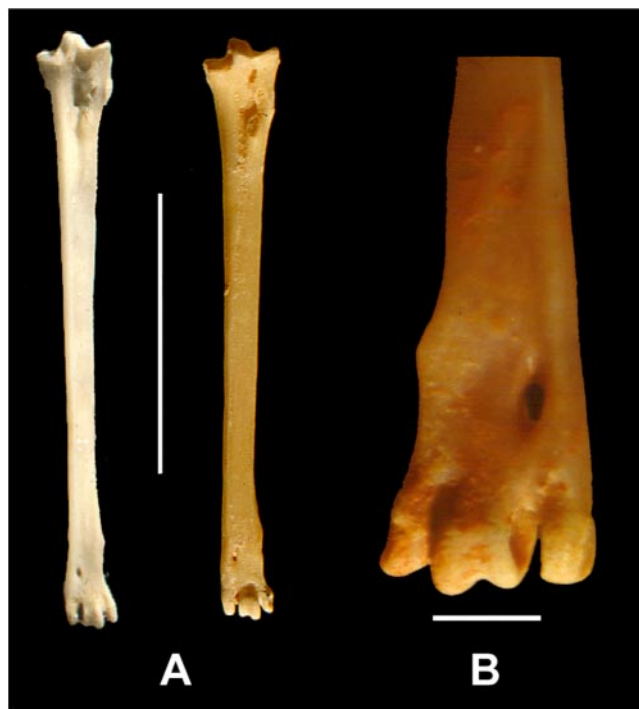


Fig. 2. Tarsometatarsi of fossil honeyeaters Meliphagidae indeterminate. (A) Complete right element, dorsal view: extant *Lichenostomus plumulus* on left, QM F36433, Rackham's Roost Site, on right (scale bar = 1 mm). (B) Distal fragment, dorsal view, QM F20622, Ringtail Site (scale bar = 10 mm).

Ringtail Site. QM F20621 consists of a left distal fragment, including a section of shaft, about the size of the element in Dusky Honeyeater (*Myzomela obscura*); the sulcus intertrochlearis medialis is somewhat wider than in *Meliphaga*. QM F20622 is a left distal fragment similar in size to QM F20621, but differing in several morphological aspects (Fig. 2b). It represents a different taxon of honeyeater.

Last Minute Site. QM F36444 is a left proximal fragment broken through about the midshaft. In size it approximates White-plumed Honeyeater (*Lichenostomus penicillatus*), with which it displays excellent agreement in morphology. The proximal end of the tarsometatarsus is less diagnostic than the distal end, and this specimen is only tentatively referred to the Meliphagidae.

Discussion

Similar taxa

Identification of tarsometatarsi as meliphagid is dependent on a suite of characters. Several taxa exhibit one or more of these characters, but provided a specimen is sufficiently complete, proper family allocation can be made. Aspects of this morphology are shared by other passerine taxa with large halluces, in particular, the Australo-Papuan babbler (Pomatostomidae), butcherbirds, currawongs and magpies (Artamidae, including Cracticidae), and ravens and crows (Corvidae). The tarsometatarsi of these forms resemble those of honeyeaters to varying degrees.

The Australo-Papuan babbler, in particular, can present some difficulties in separation as they are similar in size to large honeyeaters and exhibit the distal flattening, medial flange, plantar bend, strong crista plantaris lateralis and proximal pons tendineus on the dorsal surface, also found in the Meliphagidae (W. E. Boles, unpublished data). The babbler tarsometatarsus can be distinguished from that of similar-sized honeyeaters by the following suite of characters: (proximal end) the rim of cotyla medialis projects further dorsally and the cotyla lateralis is somewhat smaller relative to the cotyla medialis; the canalis for *M. flexor hallucis longus* is smaller; (distal end) the trochlea metatarsi IV is much smaller (in lateral view) and markedly shorter (dorsal view) relative to the trochlea metatarsi III and its lateral border is not contiguous with that of the shaft (i.e. it is situated more medially); the trochlea metatarsi II is also relatively shorter relative to the trochlea metatarsi III, although not to the same extent; and the fossa metatarsi I is less extensive proximally and less excavated (shallower) distally.

Most of the other taxa with large halluces differ from the honeyeaters in the relative sizes of the trochleae and incisurae intertrochlearis, the absence of the plantar bend of the distal end, the less distally and laterally extensive fossae metatarsi I, and crista plantaris lateralis that are not as confined to the lateral margins. They often have the canales for *M. flexor digitorum longus* substantially enlarged as well.

Systematic use

The description of the tarsometatarsus presented above is that of the 'typical' honeyeater condition, exemplified by the morphology of species of *Meliphaga* and *Lichenostomus*. This is found in the majority of taxa, with most of the variation being in relative lengths of the trochleae and of relative lengths of the lateral and medial portions of trochlea III, shape and medial extent of the flange lateral, distal extents of fossa metatarsi I, and the extent of the plantar bending. Baird (1991) remarked that because of 'the morphological uniformity [of the skeletal elements] within the group, generic separation is not currently considered possible except where unique characters provide additional information'. Some features of the meliphagid tarsometatarsus show variation across the family, but without disguising the characteristic honeyeater morphology. With further examination these may prove useful in the diagnosis of some genera.

Two examples of intra-familial variation were noted during comparisons with the fossils. In the only specimen examined of Tawny-crowned Honeyeater (*Phylidonyris melanops*), the trochlea metatarsi II is fused dorsally with the trochlea metatarsi III for most of its length, becoming separate only when its lateral margin angles medially away from trochlea metatarsi III. In species of *Melithreptus*, the trochleae are short and, most strikingly, the lateral side of the trochlea metatarsi III has a short distal extension and the medial side a markedly longer one.

Unassociated fragments of bone, such as the fossils described above, provide only a small subset of the systematically important osteological characters found in the entire skeleton of a bird. In contrast, with living taxa there is the benefit of other skeletal elements, allowing identifications and systematic conclusions to be based on a greater range of characters. While examination of the tarsometatarsal morphology alone should not be the basis for taxonomic decisions about modern taxa, structural features of this element might lend corroborative support for proposals established on other characters. There are several examples of this in relation to recent studies.

DNA–DNA hybridisation (Sibley and Ahlquist 1990), protein allozyme (Christidis and Schodde 1991; Christidis *et al.* 1993) and microcomplement fixation (Baverstock *et al.* 1991) have confirmed that the ephthianurine chats are closest to the honeyeaters, and Driskell and Christidis (2004), using DNA sequences, found that they were embedded in this family. Sibley *et al.* (1988), Sibley and Monroe (1990) and Christidis and Boles (1994) subsequently included the chats as a subfamily of the Meliphagidae. *Ephthianura* shares the meliphagid morphology of the tarsometatarsus. Compared with the 'typical' morphology of *Meliphaga*, the distal end is slender, with the flange only little produced medially, and the trochleae are rather short. Otherwise, the fossa metatarsi I, plantar bend and other

characteristics of the honeyeater foot are present. *Ashbyia* is similar, but the trochleae are slightly shorter and are more flared (distally divergent).

The aberrant genus *Timeliopsis* was confirmed as being a honeyeater by Christidis *et al.* (1993). This placement is also supported by the morphology of the tarsometatarsus.

In contrast, *Toxorhamphus* and *Oedistoma*, long kept in the honeyeaters, have been shown to have affinities elsewhere (Sibley and Ahlquist 1990; Christidis *et al.* 1993; Barker *et al.* 2002). These genera are now placed in the Melanocharitidae (Sibley and Monroe 1990; Barker *et al.* 2002). The tarsometatarsus of *Toxorhamphus* and *Oedistoma* superficially resembles that of the Meliphagidae: the flange is long and little produced medially; the distal extent of the fossa metatarsi I stops well proximal to the trochlea metatarsi II; the medial border of the bone is deeply incised between the flange and the trochlea; the trochlea metatarsi II is long (as long or longer than the trochlea metatarsi III) and raised dorsally on its medial margin; and the trochlea metatarsi IV is short and raised dorsally on its lateral margin, although to a lesser extent. A plantar bend, present in *Toxorhamphus poliopterus*, is absent in *Oedistoma iliophus*.

More detailed study of its variation within the family is needed before tarsometatarsal morphology can make a significant contribution to intergeneric comparisons.

Evolutionary history

The records of the Meliphagidae presented here are the earliest for the honeyeaters. This family is considered an old, near-endemic Australasian group, whose presence in the Miocene would be expected. It no doubt originated much earlier, and clues to its early history must await specimens from older deposits.

Schodde (1975) considered that, among living taxa, the large-bodied honeyeaters 'as a rule retain more ancestral characters than the smaller', with the most generalised taxa centred in the cool rainforests of highland New Guinea, a conclusion not supported by recent molecular investigations (Driskell and Christidis 2004). The Riversleigh habitat during the Miocene was considered by Archer *et al.* (1989) to be 'dense, species-rich gallery rainforests probably similar to those that persist today in mid-montane New Guinea'. If Schodde's view is correct, it implies that the honeyeaters at Riversleigh during the Miocene would, at least in part, comprise larger-bodied animals. In light of this, it is interesting that only small forms thus far have been found. Because some of the specimens were accumulated by megadermatid bats, these may represent the size range of prey species of these predators, rather than the absence of large honeyeaters. Most species of honeyeaters recorded as prey of the living Ghost Bat (*Macroderma gigas*), the largest known species of megadermatid, are in a size range comparable to those recovered from Riversleigh (Boles 1999); although the largest honeyeater was a Silver-crowned Friarbird (*Philemon*

argenteiceps), birds of this size are infrequent as prey, with the bats showing a marked preference for those with body masses below 35 g. The absence of large honeyeaters at Riversleigh does not argue against Schodde's (1975) ideas on evolution of the Meliphagidae.

If, as seems reasonable, the earliest honeyeaters evolved in rainforest, then the mesic-centred relatives of genera now found only in drier, more open habitats might be found in the Miocene record from Riversleigh. By the Pliocene, a different palaeoenvironment characterised the Riversleigh area. It is thought to have resembled the habitat that prevails today, with an avian community that also exhibited a high level of similarity. Parrot material described previously from Rackham's Roost Site is indistinguishable from the modern Budgerigar *Melopsittacus undulatus* (Boles 1998), and it would not be surprising if the honeyeater material were also referable to living species.

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