

The Late Cenozoic Passerine Avifauna from Rackham's Roost Site, Riversleigh, Australia

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ABSTRACT. The Riversleigh World Heritage Area, north-western Queensland, is one of the richest Cenozoic deposits in Australia for passerine fossils. Most of the Riversleigh passerine remains derive from the late Cenozoic Rackham's Roost Site. Here we describe 38 fossils from this site, which represent eight extant families of passerine birds. These fossils include the oldest records of Maluridae (fairywrens and allies), Acanthizidae (acanthizid warblers), Pomatostomidae (Australo-Papuan babblers), Petroicidae (Australasian robins), Estrildidae (estrildid finches), Locustellidae (songlarks and grassbirds) and Acrocephalidae (reed warblers) in Australia, and the oldest records globally of Maluridae, Acanthizidae, Pomatostomidae, Petroicidae and Estrildidae. The fossils also include the oldest known representatives of the major radiation Passerida *sensu stricto* in the Australian fossil record, indicating that the second dispersal event of this group had already occurred in this region at least by the early Pleistocene. In describing the Rackham's Roost fossils, we have identified suites of postcranial characters that we consider diagnostic for several Australian passerine families. These osteological characters can be used in future palaeontological, morphological and phylogenetic studies. The overrepresentation of small animals and the fragmentary condition of their remains suggests that the extant carnivorous Ghost Bat, *Macroderma gigas* (Megadermatidae) was the primary accumulator of the Rackham's Roost assemblage. The taxonomic composition of the Rackham's Roost passerine avifauna corroborates the palaeoenvironmental interpretation of this site as open woodland with a grassy understorey, perhaps next to a riparian forest. These passerine remains also provide a record of the avian component of the endangered Ghost Bat's diet in this part of northern Australia, an area from which it has recently disappeared.

KEYWORDS. Passeriformes; fossil bird; osteology; late Cenozoic; Riversleigh; Australia

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The Riversleigh World Heritage Area, which lies within Boodjamulla (Lawn Hill) National Park in north-western Queensland, is one of the most significant Cenozoic fossil regions in Australia. These fossil deposits are exceptional because they document regional biodiversity and faunal and environmental change over the last 25 million years, from the late Oligocene to the Holocene (Archer *et al.*, 1989, 2000). The Riversleigh deposits have yielded a spectacularly diverse fauna, including insects, ostracods, molluscs, fish, amphibians, reptiles, birds and mammals (Archer *et al.*, 2006; Arena, 2008 and references therein). Much of its rich and diverse mammalian fauna has been the focus of palaeontological, palaeoecological and phylogenetic studies (e.g., Black *et al.*, 2012). There have been considerably fewer studies on the Riversleigh avifauna, particularly the passerines (perching birds).

Numerous passerine fossils have been recovered from Riversleigh. Only a fraction of these fossils have been described so far, but they reveal a diversity of taxa. Fossil passerines from early Miocene sites in Riversleigh include: a lyrebird, *Menura tyawanoides* Boles, 1995; Australo-Papuan treecreepers, *Cormobates* sp. and *Climacteris* sp. (Nguyen, 2016); an oriolid, *Longmornis robustirostrata* Boles, 1999a; a cracticid, *Kurrartapu johnnguyeni* Nguyen, 2013; and a corvid-like passerine, *Corvitalusoides grandiculus* Boles, 2006. Middle Miocene deposits at Riversleigh have yielded a sittella, *Daphoenositta trevorworthyi* Nguyen, 2016 and indeterminate honeyeaters (Boles, 2005). Fossils of a logrunner, *Orthonyx kaldowinyeri* Boles, 1993 have been recovered from Riversleigh sites that span the late Oligocene to the late Miocene (Nguyen *et al.*, 2014).

Fossils representing three indeterminate honeyeater taxa have been reported from the late Cenozoic Rackham's Roost Site (Boles, 2005), one of the richest sites at Riversleigh for small bird bones. Most of the known Riversleigh passerine material derives from this site. The Rackham's Roost fossils, which form the basis of this paper, present an opportunity to improve our understanding of the evolutionary history and past diversity of Australia's passerine avifauna. In this study, our main aim is to describe the Rackham's Roost passerine fossils and interpret aspects of the taphonomy and palaeohabitat of this site. Our secondary aim is to identify and describe characters of postcranial bones that are informative for distinguishing selected passerine families.

Geological setting

Rackham's Roost Site once represented a long, narrow cave that was approximately 200 square metres in area and had a maximum depth of one metre (Hand, 1996; Archer *et al.*, 2000). One end of the cave opened onto a vertical cliff facing the Gregory River. More than 50 metres away from this opening was a second larger, lower entrance that opened onto an eroded karst terrain. The cave roof is now gone, but remnants of the walls and floor remain. The cave sediment is a breccia of small, mostly fragmented bones in a poorly laminated carbonate flowstone.

Rackham's Roost Site was initially interpreted to be early to middle Pliocene in age (approximately 5–3.5 Ma) based on biocorrelation of two macropodid taxa, one of which may represent *Protemnodon sneuwini* and the other a species possibly referable to *Kurrabi* (Godthelp, 1987, 1997; Archer *et al.*, 1989). Radiometric U-Pb dates were recently determined from speleothems (flowstone) at this site and returned an estimated age of early Pleistocene (2.69–1.10 Ma) (Woodhead *et al.*, 2016). This estimate is based on three dates, including one derived from a thin band of flowstone in direct contact with the bone breccia. However, all of the dated flowstone samples overlay the fossil deposit; none were obtained from within the deposit. Hence, all dates obtained represent a minimum age for the Rackham's Roost fossils (Woodhead *et al.*, 2016). Because there are no other early Pleistocene deposits known from anywhere in northern Australia, it is not yet possible to use biocorrelation to test whether the Rackham's Roost deposit is more likely to be early Pleistocene than Pliocene in age.

Materials and methods

The fossil specimens described here are registered in the palaeontology collections of the Queensland Museum, Brisbane (QM). Precise fossil locality details have been lodged with the QM. Specimens prepared and initially registered and housed in the temporary collections of the Vertebrate Palaeontology Laboratory, UNSW, Sydney, are indicated by the prefix AR.

Direct comparisons of fossil and modern material were made under a stereo microscope. Skeletal specimens of extant taxa used in this study (Appendix 1) are from the ornithology collections of the Australian Museum, Sydney (AM); Australian National Wildlife Collection, CSIRO, Canberra (ANWC); and Museum Victoria, Melbourne (NMV).

Measurements of specimens were made with a Wild MMS 235 digital length-measuring unit on a Leica Wild M3B microscope and rounded to 0.1 mm. Terminology of osteological structures follows Baumel & Witmer (1993), whereas nomenclature for ligaments and musculature follows Baumel & Raikow (1993) and Vanden Berge & Zweers (1993), respectively. Exceptions include use of the terms "proc. cranialis", introduced by Manegold (2008); "fovea lig. ventralis", following Livezey & Zusi (2006); and "proc. dentiformis", after Lambrecht (1914). Abbreviations used in the text include: *c.*, circa; *cf.*, confer; *indet.*, indeterminata; *lig.*, ligamentum; *M.*, musculus; *Ma*, millions of years ago; *proc.*, processus; *tr.*, trochlea metatarsi; and *tub.*, tuberculum. Taxonomic nomenclature follows Dickinson & Christidis (2014). Exceptions include the taxonomic treatments of *Megalurus*, which includes *Cincloramphus* and *Eremiornis*, following Alström *et al.* (2011) and Gill & Donsker (2016); and of Passerida, which excludes Eupetidae and Petroicidae, as circumscribed by Johansson *et al.* (2008).

Systematic palaeontology

Family accounts

In the following account, fossils are identified to the lowest taxonomic level using character combinations. For most of the fossils in this study, the preserved features do not allow generic determination. These fossils can only be identified to family level at present and are thus attributed as genus et species indeterminata. Within each family account, descriptions are ordered by skeletal element and comprise family characterisations and comparisons of the fossils with modern taxa. The Remarks section includes additional morphological comments and notes on foraging behaviour and habitats of modern representatives. This section also includes notes on the known fossil record of the family and on extant representatives that are currently found in the Riversleigh region.

The geographic ranges given for extant species are mainly derived from the *Handbook of Australian, New Zealand and Antarctic Birds* and the *Handbook of the Birds of the World*, unless stated otherwise. Current bird records for the Riversleigh region are derived from survey and specimen data from the Atlas of Living Australia, the Atlas of Australian Birds and Birddata (BirdLife Australia) and the Queensland Government Wildlife Online databases.

Order Passeriformes (Linnaeus, 1758)

Family Maluridae Swainson, 1831

Genus et species indet.

Fig. 1A

Material. QM F30361, distal left tibiotarsus.

Measurements (mm). Preserved length 5.2, distal width ca 1.6, depth of condylus lateralis ca 1.6, depth of condylus medialis ca 1.7.

Description and comparisons. QM F30361 (Fig. 1A) is a distal tibiotarsus with the cristae trochlea and the bony ridges for attachment of the retinaculum m. fibularis broken off. This fossil is referred to Maluridae because it possesses the following combination of features. The distal part of the shaft is craniocaudally compressed and its cranial surface is planar. The sulcus extensorius is very shallow and is displaced laterally of the medio-lateral midpoint of the shaft. The tuberositas retinaculi extensoris lateralis is situated on the proximo-lateral part of the pons supratendineus. The proximal edge of the condylus medialis is about level with the distal margin of the pons supratendineus. The condylus lateralis is greater in proximal extent than the condylus medialis. In cranial aspect, the condylus lateralis is slightly wider than its medial counterpart.

QM F30361 is smaller in size than the tibiotarsi of extant malurids studied. The fossil differs from species of *Malurus* and *Clytomyias insignis* in that the sulcus extensorius is situated further laterally, and the tuberositas retinaculi extensoris lateralis does not project beyond the proximal margin of the pons supratendineus. It differs from *Amytornis* because the length of the pons supratendineus is approximately equal to, not less than, its width and the condylus lateralis is greater in distal extent than the condylus medialis, rather than being equal in distal extent. QM F30361 is further distinguished from *Amytornis* and from *Stipiturus malachurus* (Fig. 1B) by the distal shaft being slightly narrower relative

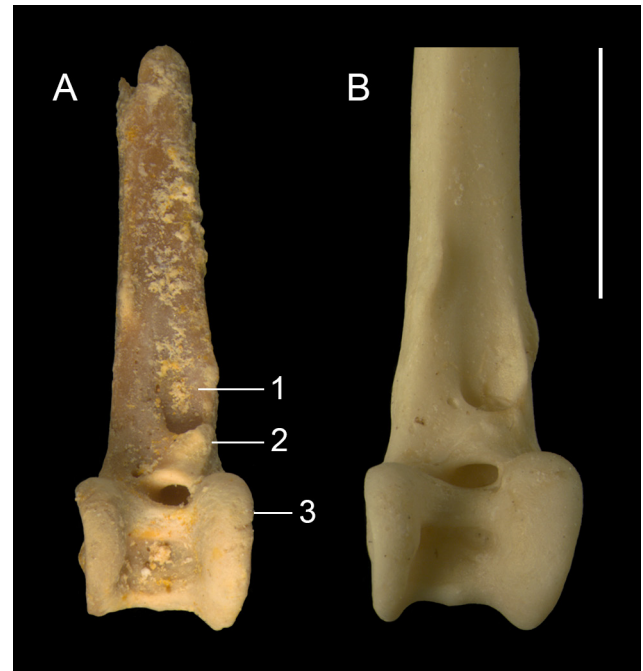


Figure 1. Distal left tibiotarsi of (A) fossil malurid gen. et sp. indet. QM F30361 and (B) *Stipiturus malachurus* AM O.68207 in cranial aspect. Some characteristic features of Maluridae shown: 1, sulcus extensorius very shallow and displaced laterally of the medio-lateral midpoint of the shaft; 2, tuberositas retinaculi extensoris lateralis situated on proximo-lateral part of pons supratendineus; 3, condylus lateralis greater in width and in proximal extent than condylus medialis. Scale bar = 2 mm.

to the width of the distal end. The fragmentary nature of the fossil precludes its referral to a lower taxonomic level, pending recovery of more complete material.

Remarks. Fairywrens, emu-wrens and grasswrens (Maluridae) are small, sprightly passerines that are primarily found in Australia but also live in New Guinea. Most species have characteristically long, cocked tails and are poor fliers, and forage on or close to the ground. They occur in sparse to dense low vegetation in a variety of habitats. In Australia, fairywrens (*Malurus*) are found in nearly every habitat, including rainforest, eucalypt woodland, grassland, coastal heath, shrubland in semi-arid and arid areas, and suburban parks and gardens. Emu-wrens (*Stipiturus*) occur in wet to dry heaths and spinifex (*Triodia*) grass in woodland. Grasswrens (*Amytornis*) inhabit spinifex-covered rocky outcrops and hillsides, desert dunes and dry flood plains in arid and semi-arid areas (Schodde, 1982; Higgins *et al.*, 2001; Rowley & Russell, 2007). Today, the Purple-crowned (*M. coronatus*), Red-backed (*M. melanocephalus*) and Variegated (*M. lamberti*) Fairywrens and the Carpentarian Grasswren *A. dorotheae* are found in the Riversleigh region.

Material referred to *Malurus* sp. has been recorded from the late Pleistocene Cloggs Cave and Holocene Mabel Cave in eastern Victoria, and the late Pleistocene Devil's Lair and Holocene Skull Cave in Western Australia (Baird, 1986, 1991a,b). Specimens identified as *Stipiturus malachurus* have been found in Cloggs Cave and the late Pleistocene Seton Rock Shelter in South Australia (Baird, 1986, 1991a). Remains of *Amytornis* were also reported from the latter site and from late Quaternary cave deposits in the Flinders Ranges and in the Nullarbor Plains region (Baird, 1986, 1990, 1991a).

Family Meliphagidae Vigors, 1825

Genus et species indet.

Figs 2–7

Material. AR21604, distal left humerus; QM F30825, distal right humerus; QM F30855, distal right ulna; AR17407, left carpometacarpus; QM F57899 (AR17401), right carpometacarpus; QM F22794, proximal left carpometacarpus; QM F30824, distal left tibiotarsus; QM F36374, proximal left tarsometatarsus; QM F57929, distal left tarsometatarsus; QM F36648, distal right tarsometatarsus.

Measurements (mm). QM F22794: preserved length 9.2, proximal width 3.9, length of os metacarpale alulare 1.9. QM F30824: preserved length 6.6, distal width ca 2.3, depth of condylus lateralis ca 2.1, depth of condylus medialis ca 2.2. QM F30825: preserved length 8.9, distal width 4.4, depth of condylus dorsalis 2.2. QM F30855: preserved length 13.2, distal width (condylus dorsalis to tub. carpale) 3.2, depth of condylus dorsalis ca 2.8. QM F36374: preserved length 12.3, proximal width 2.7, proximal depth (lateral aspect) >2.0. QM F36648: preserved length 8.8, distal width 2.2, depth of tr II ca 1.0, depth of tr III 1.5, depth of tr IV 1.3. QM F57899: preserved length 17.0, proximal width >3.9, length of os metacarpale alulare 2.0, distal width ca 3.5. QM F57929: preserved length 11.0, distal width ca 2.0, depth of tr II ca 1.0, depth of tr III ca 1.5, depth of tr IV 1.2. AR17407: preserved length 10.6, proximal width >3.1, length of os metacarpale alulare >1.5, distal width >2.2. AR21604: preserved length 9.3, distal width >4.0, depth of condylus dorsalis 2.5.

Description and comparisons. *Humerus.* QM F30825 (Fig. 2A,D) is assigned to Meliphagidae because it shares the following suite of character states with this family. (1) The distal end is (1) greatly expanded dorsally and (2) ventrally from the shaft. (3) The sulcus humerotricipitalis is deep. (4) When viewed caudally, the distal profile of the humerus between the sulcus humerotricipitalis and sulcus scapulotricipitalis is very concave. (5) The proc. flexorius is truncate. (6) The proc. supracondylaris dorsalis is bifurcated and (7) projects far dorsally. (8) The fossa m. brachialis is moderately deep.

QM F30825 is slightly smaller than the humerus of the Bell Miner, *Manorina melanophrys*. It differs from other meliphagids examined in the following features. The distal end of QM F30825 is less expanded ventrally from the shaft than in *Meliphaga*, *Anthochaera*, *Myzomela* and *Philemon*, and less expanded dorsally than in *Stomiopera* and *Melithreptus*. The fossil further differs from *Meliphaga*, *Stomiopera*, *Melithreptus* and from *Acanthorhynchus*, *Manorina* and *Nesoptilotis* in having a deeper sulcus humerotricipitalis. The fossa m. brachialis is deeper in the fossil than in *Philemon* and *Anthochaera*. In QM F30825, the ventral apex of the proc. supracondylaris dorsalis is further set off from the distal end than in *Manorina*.

AR21604 (Fig. 2C,F) is a distal humerus with breakage to the dorsal portion. It is tentatively assigned to Meliphagidae because it shares features 2–5 and 8, as described above. AR21604 is similar in size to the humerus of the Tawny-crowned Honeyeater, *Gliciphila melanops*. It differs from *Nesoptilotis*, *Melithreptus*, *Acanthorhynchus* and *Manorina* in having a deeper sulcus humerotricipitalis. The fossa m. brachialis is deeper in AR21604 than in *Stomiopera*,

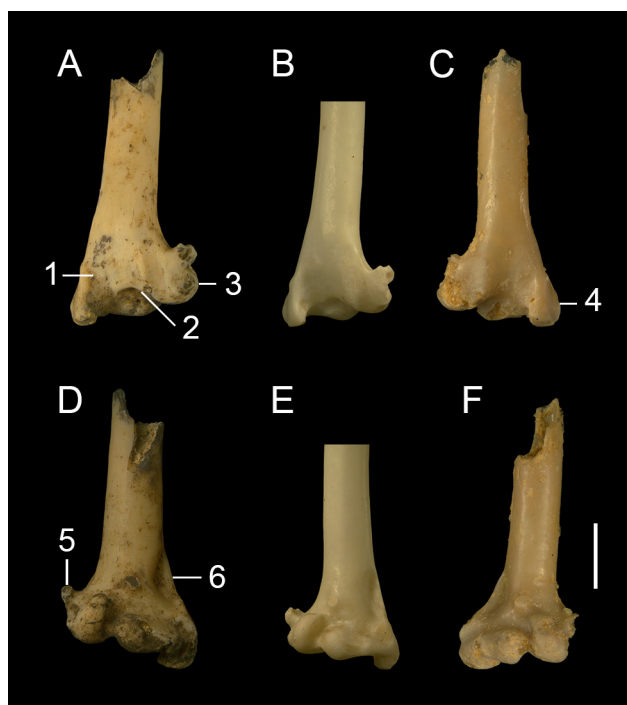


Figure 2. Humeri of (A,C,D,F) fossil Meliphagidae gen. et sp. indet., compared with the humerus of (B,E) *Conopophila albogularis* AM O.70096. (A,D) QM F30825, distal right humerus. (C,F) AR21604, distal left humerus. (A–C) caudal and (D–F) cranial aspects. Some characteristic features of Meliphagidae shown: 1, sulcus humerotricipitalis deep; 2, distal profile between sulci humerotricipitalis et scapulotricipitalis highly concave; 3, distal end greatly expanded dorsally and 4, ventrally; 5, proc. supracondylaris dorsalis bifurcated and projects well dorsally; 6, fossa m. brachialis moderately deep. Scale bar = 2 mm.

Manorina, *Philemon* and *Anthochaera*. AR21604 differs from QM F30825 in being smaller in size, and in having a more ventrally expanded distal end, a shallower sulcus humerotricipitalis and a slightly deeper fossa m. brachialis.

Within the Australian passerine avifauna, Petroicidae and Cracticidae are also characterised by a distal humerus that is considerably expanded dorsally and ventrally from the shaft. AR21604 can be excluded from Petroicidae because the distal end is deeper relative to its width, the sulcus humerotricipitalis is deep and the tub. supracondylare ventrale is more developed. This fossil can also be excluded from Cracticidae because it is considerably smaller in size, has a deep fossa m. brachialis and has a less developed ridge that ventrally bounds the sulcus scapulotricipitalis.

Ulna. QM F30855 (Fig. 3A–C) is tentatively assigned to Meliphagidae because it shares the following character states with this family. The tub. carpale is cranio-caudally compressed, short relative to the condylus ventralis, and perpendicular to the long axis of the shaft. The depressio radialis is deep. The condylus dorsalis protrudes well caudally from the shaft and its proximal extent is far greater than that of the condylus ventralis. The papillae remigales caudales are low. The sulcus intercondylaris is caudally deep and its distal profile is a moderately deep notch.

The fossil ulna is similar in size to the corresponding bone of Lewin's Honeyeater, *Meliphaga lewinii* (Fig. 3D–F). Within Meliphagidae, QM F30855 differs from the ulnae of *Gliciphila*, *Manorina*, *Lichmera*, *Nesoptilotis*, *Conopophila*

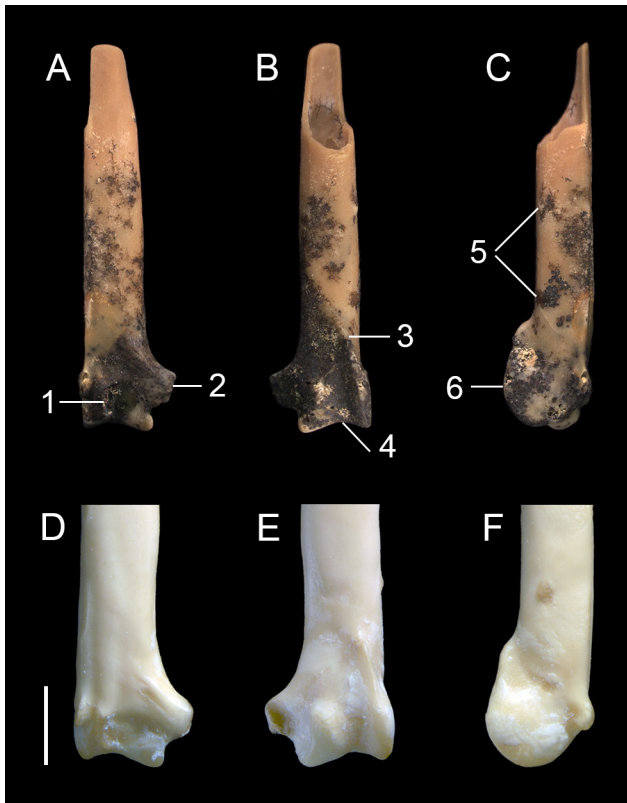


Figure 3. Distal ulnae of (A–C) fossil meliphagid gen. et sp. indet. QM F30855 and (D–F) *Meliphaga lewinii* AM O.60079 (mirrored). (A,D) cranial, (B,E) caudal and (C,F) dorsal aspects. Some characteristic features of Meliphagidae shown: 1, depressio radialis deep; 2, tub. carpale short and perpendicular to the shaft long axis; 3, condylus dorsalis far greater in proximal extent than condylus ventralis; 4, sulcus intercondylaris deep both caudally and distally; 5, papillae remigales caudales low; 6, condylus dorsalis protrudes well caudally from the shaft. Scale bar = 2 mm.

and *Philemon* in that the condylus dorsalis protrudes farther caudally of the shaft. It differs from *Philemon* in having a squarer, rather than rounded, tub. carpale. The sulcus intercondylaris is shallower in the fossil than in *Myzomela*, but deeper than in *Philemon*. QM F30855 is distinguished from *Anthochaera* by its less developed papillae remigales caudales.

QM F30855 can be distinguished from similarly medium- to small-sized birds from other Australian passerine families by the following features. The fossil ulna differs from those of Dasyornithidae, Psophodidae, Pachycephalidae, Monarchidae, Artamidae, Locustellidae and Turdidae in that the sulcus intercondylaris is deep caudally and distally. The fossil differs from Rhipiduridae in having low papillae remigales caudales and from Orthonychidae in having a cranio-caudally shallow tub. carpale. It differs from Pomatostomidae and Sturnidae because the condylus dorsalis is greater in proximal extent relative to the condylus ventralis. QM F30855 further differs from Sturnidae in having a comparatively short tub. carpale, and from Pomatostomidae in having a deeper depressio radialis.

Carpometacarpus. QM F57899 (Fig. 4A–B) is a carpometacarpus with damage to the trochlea carpalis ventralis, caudal section and distal end. This fossil specimen is referred to Meliphagidae because it exhibits the following

combination of features. (1) The carpometacarpus is straight and elongate. (2) The distal edge of the facies articularis alularis is located proximally of the large fovea lig. ventralis. (3) The fovea carpalis caudalis is deep and its distal margin is situated distally of the proc. cranialis. (4) The proc. dentiformis is low and (5) arises at about the proximo-distal midpoint of the os metacarpale majus. (6) The spatium intermetacarpale is long and narrow. (7) In dorsal aspect, a small portion of the spatium intermetacarpale is visible proximally of the proc. intermetacarpalis. (8) The distal end of the os metacarpale majus is broad and its cranial extent is greater than that of the proc. dentiformis. (9) The distal end of the sulcus tendinosus broadens into a large fossa on the distal end of the os metacarpale majus. (10) There is a distinct ventral fossa on the distal end of the os metacarpale minus.

QM F57899 is slightly smaller in size than the carpometacarpus of the Noisy Miner, *Manorina melanocephala* (Fig. 4C–D). It differs from the extant honeyeaters studied here by the following features. QM F57899 differs from all meliphagids studied except for *Xanthotis*, *Meliphaga* and *Anthochaera* in having a deeper fossa at the distal end of the sulcus tendinosus. It differs from the carpometacarpus of *Stomiopera*, *Nesoptilotis*, *Philemon*, *Anthochaera* and *Lichmera* in having a larger, more defined proc. dentiformis. It differs from *Melithreptus*, *Gliciphila*, *Ptilotula*, *Myzomela*, *Acanthorhynchus* and *Manorina* in possessing a deeper ventral fossa on the distal end of the os metacarpale minus. The fossil differs from *Stomiopera*, *Anthochaera*, *Ptilotula* and *Meliphaga* in having a larger, more convex proc. cranialis. It differs from *Acanthorhynchus*, *Meliphaga*, *Myzomela* and *Lichmera* in having a deep notch in the distal margin of the os metacarpale minus. It differs from *Conopophila*, *Xanthotis*, *Melithreptus* and *Anthochaera* in having a deeper fovea lig. ventralis. The fossil is similar in proportions and overall morphology to species of *Manorina* studied, but its fragmentary nature precludes confident identification to genus level.

QM F22794 (Fig. 4E–F) and AR17407 (Fig. 4G–H) are tentatively referred to Meliphagidae because they share the following features with this family. QM F22794 shares characters 1–3, 5 and 7 described above, whereas AR17407 exhibits characters 1, 3, 5, 7 and 10. QM F22794 is similar in size to the corresponding element of *Meliphaga lewinii*. It differs from *Ptilotula*, *Conopophila*, *Xanthotis* and *Meliphaga* in having a deeper fovea lig. ventralis. The fossil differs from *Nesoptilotis*, *Gliciphila*, *Stomiopera* and *Ptilotula* in having a larger and more convex proc. cranialis. AR17407 corresponds in size to the carpometacarpus of *Gliciphila melanops* (Fig. 4I–J). It differs from *Stomiopera*, *Anthochaera* and *Xanthotis* in having a shallower fovea carpalis caudalis. The fossil differs from *Xanthotis*, *Conopophila* and *Myzomela* in possessing a smaller proc. cranialis. It further differs from *Xanthotis* and *Conopophila* in having a deeper fovea lig. ventralis. The fossil is broken proximally of the apex of the proc. dentiformis but preserves the base of the process, where the os metacarpale majus becomes wider. This base suggests that the proc. dentiformis was more developed in AR17407 than in *Stomiopera*, *Anthochaera*, *Philemon* and *Nesoptilotis*, where it is very low. AR17407 differs from QM F22794 and QM F57899 in its considerably smaller size, and in having a shallower fovea carpalis caudalis and a smaller proc. cranialis. QM F22794 is overall similar in size and morphology to QM F57899,



Figure 4. Carpometacarpi of fossil Meliphagidae gen. et sp. indet., compared with those of extant meliphagid species in (A,C,E,G,I) ventral and (B,D,F,H,J) dorsal aspects. (A–B) QM F57899, right carpometacarpus. (C–D) *Manorina melanocephala* AM O.59876. (E–F) QM F22794, proximal left carpometacarpus. (G–H) AR17407, left carpometacarpus. (I–J) *Gliciphila melanops* AM O.65515. Some characteristic features of Meliphagidae shown: 1, distal edge of facies articularis alularis situated proximally of the level of the fovea lig. ventralis; 2, fovea lig. ventralis large; 3, distal end of os metacarpale majus broad and its cranial extent is greater than that of proc. dentiformis; 4, fossa on ventral surface of distal end of os metacarpale minus; 5, fovea carpalis caudalis deep, its distal margin located distally of the level of proc. cranialis; 6, broad fossa at distal end of sulcus tendinosus. Scale bar = 2 mm.

although the former only preserves the proximal end. The fragmentary preservation of these fossils precludes further determination of their relationships.

Apart from meliphagids, a distally situated fovea carpalis caudalis relative to the proc. cranialis is also present in campephagids, pachycephalids, corvids and monarchids. However, the tentatively assigned fossils can be excluded

from these birds (except *Colluricincla*) because they possess a proc. dentiformis. QM F22794 and AR17407 differ from species of *Colluricincla* examined in having a shorter fovea lig. ventralis and in lacking a groove cranially of the proc. pisiformis.

Tibiotarsus. QM F30824 (Fig. 5A) is provisionally assigned to Meliphagidae because it exhibits the following

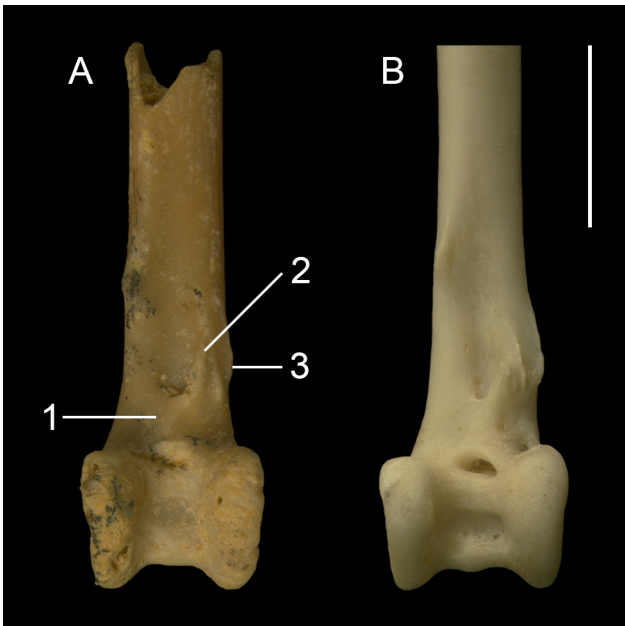


Figure 5. Distal left tibiotarsi of (A) fossil meliphagid gen. et sp. indet. QM F30824 and (B) *Ptilotula flavescens* AM O.66333 in cranial aspect. Some characteristic features of Meliphagidae shown: 1, pons supratendineus very long; 2, tuberositas retinaculi extensori lateralis low and situated on proximal edge of pons supratendineus; 3, bony ridges for attachment of retinaculum m. fibularis low. Scale bar = 2 mm.

suite of character states. The pons supratendineus is very long relative to its width. The tuberositas retinaculi extensori lateralis is low, elongate and situated on the proximal edge of the pons supratendineus. The bony ridges for attachment of the retinaculum m. fibularis are low and long. The medial bony ridge is approximately level with the tuberositas retinaculi extensori lateralis.

QM F30824 is similar in size to the corresponding bone of the Yellow-tinted Honeyeater *Ptilotula flavescens* (Fig. 5B). It differs from the extant meliphagids examined in this study in the following features. The fossil tibiotarsus differs from the corresponding bone of *Acanthorhynchus*, *Stomiopera*, *Anthochaera* and *Lichmera* in having a relatively shorter pons supratendineus. It differs from *Ptilotula* and *Melithreptus* in that the distance between the tuberositas retinaculi extensori medialis and its lateral counterpart is smaller. The tuberositas retinaculi extensori lateralis is situated further proximally relative to the pons supratendineus in the fossil than in *Myzomela* and *Conopophila*.

The tibiotarsal morphologies of meliphagids and acanthizids are very similar but can be differentiated by the following combination of features. In species of meliphagids examined, the bony ridges for the retinaculum m. fibularis are less pronounced and relatively longer than in acanthizids. The sulcus m. fibularis is shallower and the incisura intercondylaris is slightly wider. The tuberositas retinaculi extensori lateralis is less prominent and is situated further proximally on the pons supratendineus than in acanthizids studied. A long pons supratendineus is a characteristic feature of meliphagids, acanthizids and pachycephalids, but QM F30824 can be distinguished from the latter by its relatively longer pons and more cranially located epicondylus medialis. Also, the tuberositas retinaculi extensori medialis is situated further proximally of the bony ridges for the retinaculum

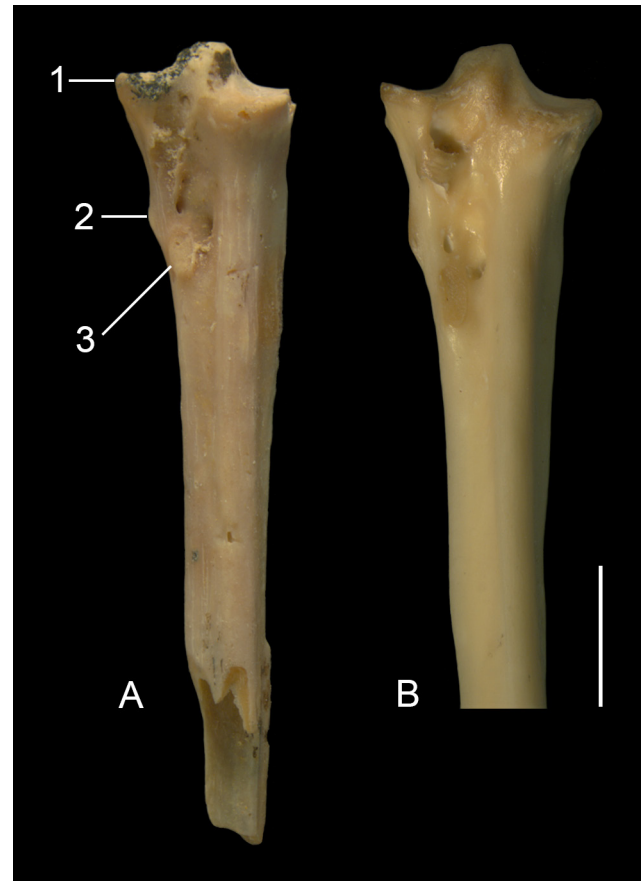


Figure 6. Proximal left tarsometatarsi of (A) fossil meliphagid gen. et sp. indet. QM F36374 and (B) *Stomiopera unicolor* AM O.70570 in dorsal aspect. Some distinguishing features for Meliphagidae shown: 1, cotyla medialis greater in proximal extent than cotyla lateralis; 2, impressio lig. collateralis medialis situated distally of arcus extensorius; 3, tuberositas m. tibialis cranialis located well distally of arcus extensorius and medially of the shaft midpoint. Scale bar = 2 mm.

m. fibularis in the fossil than in pachycephalids examined.

Tarsometatarsus. QM F36374, QM F36648 and QM F57929 (Figs 6–7) are referred to Meliphagidae because they possess the following combination of characters, including those identified by Boles (2005). The cotyla medialis is greater in proximal extent than the cotyla lateralis. In proximal view, the planto-medial corner of the proximal end protrudes further medially than the rim of the cotyla. The foramina vascularia proximalia are located distally of the arcus extensorius. The tuberositas m. tibialis cranialis is low and situated well distally of the arcus extensorius. This tuberosity is located medially of the medio-lateral midpoint of the shaft. When viewed medially, the impressio lig. collateralis medialis is situated distally of the level of the arcus extensorius. The medial depth of the shaft is moderately deep at about level with the tuberositas m. tibialis cranialis. The lateral edge of the sulcus extensorius is low and the dorsal shaft surface is subsequently near perpendicular to the medial and lateral surfaces. The distal end of the tarsometatarsus is narrow, dorso-plantarly compressed and bent plantarly from the shaft. The fossa metatarsi I is large and deep. The medial shaft edge expands medially at about level with the edge of the fossa metatarsi I to form a flange that appears very shallow in medial aspect. The trochlea

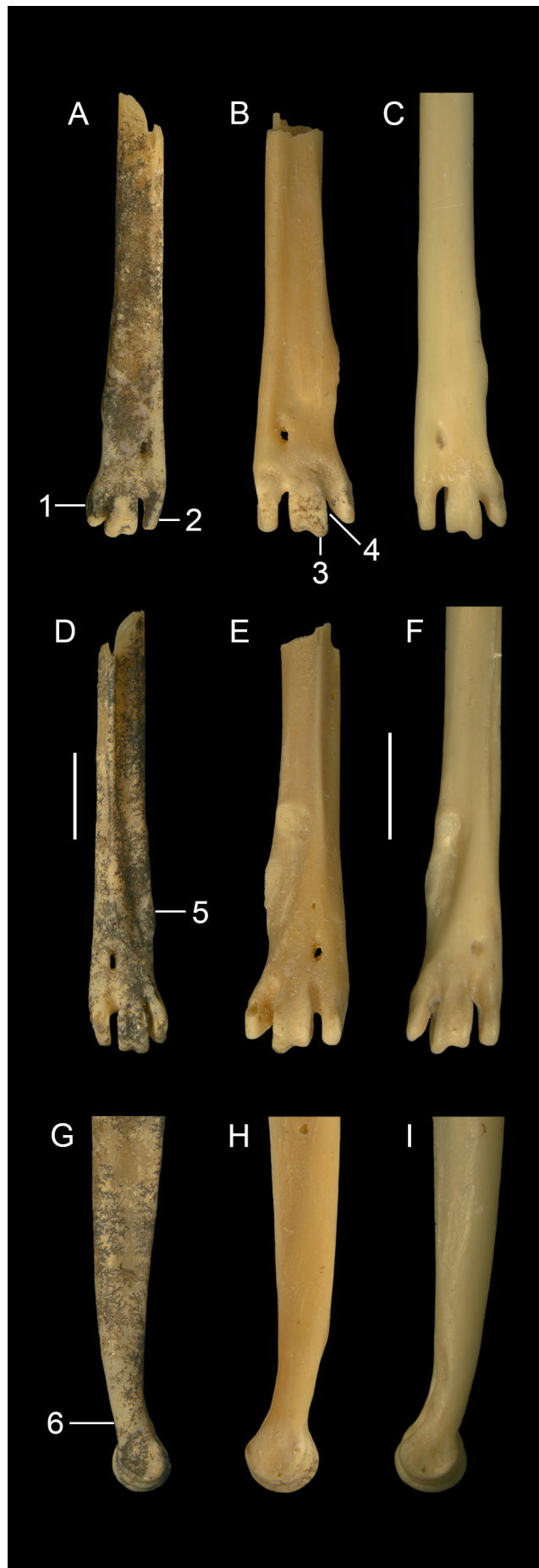
metatarsi II is short, latero-medially compressed and has a pointed distal profile. It is rotated planto-medially from the long axis of the shaft, such that the medial facies and fovea lig. collateralis medialis of the trochlea metatarsi II are visible in dorsal aspect. The incisura intertrochlearis medialis is narrower than the incisura intertrochlearis lateralis. The medial rim of the trochlea metatarsi III is greater in dorsal and distal extent than the lateral rim. The lateral edge of the trochlea metatarsi IV is located medially of that of the shaft.

QM F36374 (Fig. 6A) is similar in size to the proximal tarsometatarsus of the White-eared Honeyeater, *Nesoptilotis leucotis*. This fossil is distinguished from the extant meliphagids studied here by the following character states. It differs from *Melithreptus*, *Acanthorhynchus* and *Anthochaera* in that the proximal end is wider relative to the shaft, and further differs from *Anthochaera* in having a shallower sulcus flexorius. The fossil differs from *Melithreptus*, *Ptilotula*, *Lichmera*, *Gliciphila*, *Anthochaera* in having a more elevated impressio lig. collateralis medialis. It also differs from *Gliciphila* and *Anthochaera* in having a shallower medial depth of the shaft.

QM F36648 (Fig. 7B,E,H) corresponds in size to the Bell Miner, *Manorina melanophrys*, whereas QM F57929 (Fig. 7A,D,G) is similar in size to *N. leucotis* (Fig. 7C,F,I). The fossils differ from the extant meliphagid species studied here in the following features. They differ from *Myzomela*, *Philemon* and *Meliphaga* in having a poorly developed medial flange at about level with the fossa metatarsi I. The fossils differ from *Myzomela*, *Gliciphila*, *Conopophila* and *Anthochaera* in lacking a second medial extension of the shaft at about level with the distal edge of the fossa metatarsi I. QM F36648 and QM F57929 differ from *Nesoptilotis* and *Philemon* in that the foramen vasculare distale is situated relatively further proximally from the incisura intertrochlearis lateralis. They differ from *Lichmera*, *Acanthorhynchus* and *Manorina* in that the lateral edge of the trochlea metatarsi IV is situated further medially of that of the shaft.

QM F57929 differs from all extant meliphagids examined except for *Gliciphila* and *Conopophila* in that the trochlea metatarsi II is not as medially inflected. It differs from *Xanthotis*, *Nesoptilotis*, *Philemon*, *Melithreptus*, *Acanthorhynchus*, *Anthochaera* and *Manorina* in that the medial rim of the trochlea metatarsi III does not extend as far distally relative to the lateral rim. QM F57929 differs from QM F36648 in that the distal end is narrower relative to the shaft width, the foramen vasculare distale is situated relatively further proximally, and the medial flange at about level with the fossa metatarsi I is less developed. These differences suggest that QM F36648 and QM F57929 represent two different taxa.

Figure 7. Distal tarsometatarsi of (A–B, D–E, G–H) fossil Meliphagidae gen. et sp. indet., compared with that of (C, F, I) *Nesoptilotis leucotis* AM O.59863. (A, D, G) QM F57929, distal left tarsometatarsus. (B, E, H) QM F36648, distal right tarsometatarsus. (A–C) dorsal and (D–F) plantar aspects, and (G–I) lateral aspect of distal end. Some characteristic features of Meliphagidae shown: 1, tr II medio-laterally compressed, pointed distally and rotated planto-medially from shaft long axis; 2, lateral edge of tr IV situated medially of that of shaft; 3, medial rim of tr III greater in distal extent than lateral rim; 4, incisura intertrochlearis medialis narrow; 5, medial flange at about level with fossa metatarsi I; 6, distal end dorso-plantarly compressed and distinctly bent plantarly. Scale bar = 2 mm.



Remarks. Meliphagids (honeyeaters) are a very large and diverse radiation of passerines endemic to the south-western Pacific region, with about 178 species in 51 genera (Dickinson & Christidis, 2014). These birds are prominent elements of the Australian avifauna and act as important pollinators for many flowering plants (Longmore, 1991). As well as nectar, honeyeaters feed on fruit, lerps and psyllid larvae (Longmore, 1991; Schodde & Mason, 1999). Honeyeaters range in size from small to medium-large and utilise habitats ranging from rainforest to semi-arid woodland to subalpine shrubland (Higgins *et al.*, 2001).

Boles (2005) reported meliphagid tarsometatarsi from Riversleigh Faunal Zone C (middle Miocene) assemblages and from Rackham's Roost Site. QM F36374 is similar in size to the fossils that preserve the proximal tarsometatarsus in Boles (2005), but it is not clear that it represents the same taxon. QM F36648 likely represents a different taxon from the fossil meliphagids in Boles (2005) because it is proportionately broader, larger in size and has a more prominent medial flange at about level with the fossa metatarsi I. QM F57929 may also represent a different taxon from the previously reported Riversleigh meliphagids because it is larger in size but slightly narrower, and has a more developed medial flange and a less medially inflected trochlea metatarsi II.

Fossils of honeyeaters have been recovered from several Quaternary sites in South Australia, Victoria and Western Australia (Hope *et al.*, 1977; Baird, 1991a). These fossils include a skull of *Manorina melanocephala* from the late Pleistocene Green Waterhole Cave in South Australia (Baird, 1985), and material referred to cf. *Gavicalis* (*Lichenostomus*) *virescens* from Pleistocene cave deposits in the Nullarbor Plains region (Baird, 1990, 1991a). Holocene remains assigned to cf. *Anthochaera carunculata* and cf. *A. chrysoptera* from Amphitheatre Cave in Victoria were also reported (Baird, 1992). Today, honeyeaters are abundant in the Riversleigh region, with 19 species having been recorded.

Family Acanthizidae Bonaparte, 1854

Genus et species indet.

Fig. 8

Material. QM F57928 (AR10832), left carpometacarpus; QM F22796, distal left tibiotarsus.

Measurements (mm). QM F22796: preserved length 4.2, distal width 1.7, depth of condylus lateralis ca 1.6, depth of condylus medialis > 1.6. QM F57928: preserved length 6.8, proximal width >1.4, distal width >1.5.

Description and comparisons. *Carpometacarpus.* QM F57928 (Fig. 8A–B) is a very small carpometacarpus with damage to the proximal and distal ends, proc. intermetacarpalis and to the dorsal edge of the os metacarpale minus. This fossil is tentatively assigned to Acanthizidae because it exhibits the following suite of features. It is tiny and overall similar in proportions and shape to the carpometacarpi of acanthizids. The fovea lig. ventralis is deep and recessed cranially. The fovea carpalis caudalis is small and shallow. Although the proc. cranialis is broken off, it appears to have been approximately level with this fovea. The proc. dentiformis is well defined and located at about the proximo-distal midpoint of the os metacarpale minus. There is a moderately deep ventral fossa on the distal end of the os metacarpale minus.

QM F57928 is closest in size to the carpometacarpus of the Weebill, *Smicrornis brevirostris*. It can be distinguished from species of *Pycnoptilus*, *Calamanthus*, *Crateroscelis*, *Acanthiza* and *Sericornis* studied in that it is not as dorso-ventrally curved. The os metacarpale minus in the fossil is not bowed as in *Pycnoptilus* and *Crateroscelis*. The fossil is relatively less robust than the carpometacarpus of *Origma*, and it has a deeper ventral fossa on the distal end of the os metacarpale minus than in *Smicrornis*. In the absence of more complete fossil material, it is not possible to resolve the identification of this specimen to genus level.

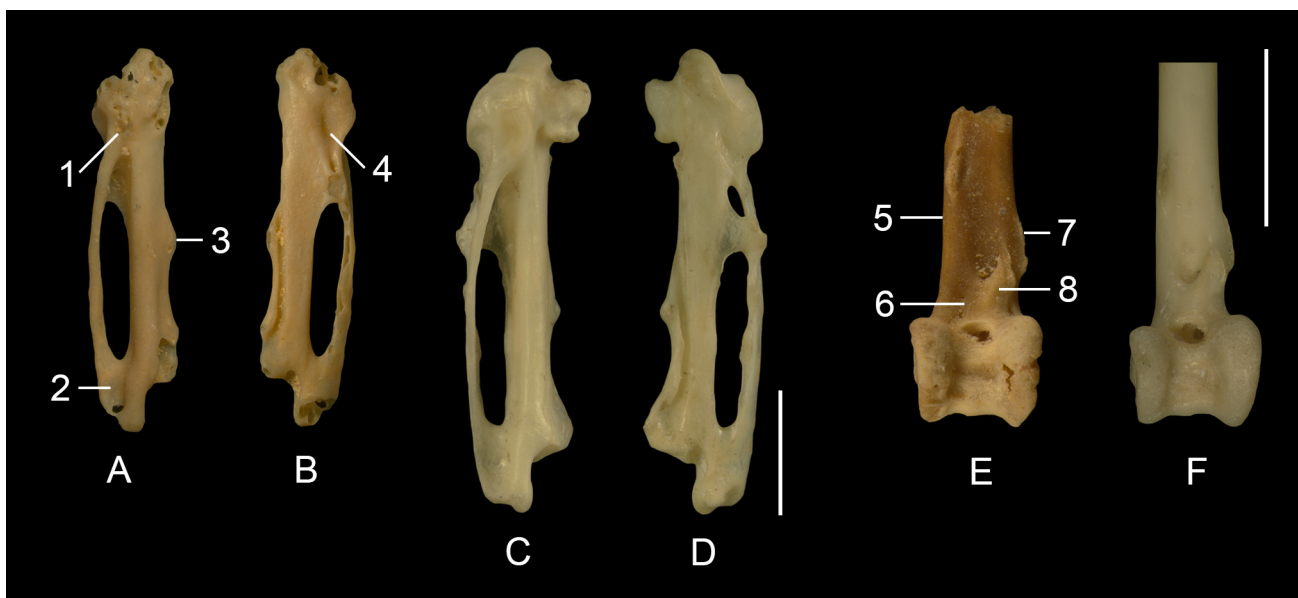


Figure 8. Comparison of fossil and extant acanthizid bones. Left carpometacarpi of (A–B) acanthizid gen. et sp. indet. QM F57928 and (C–D) *Gerygone fusca* AM O.66008 in (A,C) ventral and (B,D) dorsal aspects. Distal left tibiotarsi of (E) acanthizid gen. et sp. indet. QM F22796 and (F) *Gerygone fusca* AM O.66008 in cranial aspect. Some distinguishing features of Acanthizidae highlighted: 1, fovea lig. ventralis deep and recessed cranially; 2, ventral fossa on distal end of os metacarpale minus; 3, proc. dentiformis prominent and situated at proximo-distal midpoint of os metacarpale minus; 4, fovea carpalis caudalis small and shallow; 5, distal shaft narrow with respect to width of distal end; 6, pons supratendineus long; 7, lateral bony ridge for retinaculum m. fibularis well developed; 8, tuberositas retinaculi extensori lateralis prominent. Scale bar = 2 mm.

The fossil carpometacarpus can be excluded from other families of characteristically small passerines found in Australia, including Maluridae, small members of Meliphagidae, Pardalotidae, Rhipiduridae, Petroicidae, Estrildidae and Zosteropidae, by the following character states. QM F57928 is excluded from Maluridae because it is not bowed and the os metacarpale alulare is relatively wider. It is excluded from Meliphagidae because the depression for the *M. flexor digiti minoris* on the trochlea carpalis ventralis is deeper and the distal margin of the fovea carpalis caudalis is about level with, not distally of, the proc. cranialis. The fossil is excluded from Pardalotidae and Petroicidae because the proc. dentiformis is situated at the midpoint of the os metacarpale minus, not further distally. QM F57928 further differs from Pardalotidae because it has a ventral fossa on the distal end of the os metacarpale minus. It is excluded from Rhipiduridae because it possesses a proc. dentiformis. The fossil is excluded from Estrildidae and Zosteropidae because it has a considerably deeper ventral fossa on the distal end of the os metacarpale minus.

Tibiotarsus. QM F22796 (Fig. 8E) is a distal tibiotarsus with damage to the cristae trochleae. This fossil is provisionally referred to Acanthizidae because it possesses the following combination of features. The tibiotarsus is characteristically small and corresponds in shape and proportions to the tibiotarsi of acanthizids. The distal shaft is conspicuously narrow in comparison to the width of the distal end (except in *Pycnoptilus* and *Calamanthus*). The pons supratendineus is long with respect to its width (except in *Calamanthus*, where its length is about equal to width). The lateral bony ridge for attachment of the retinaculum m. fibularis is well developed. The tuberositas retinaculi extensoris lateralis is elongate and prominent. Although it is slightly abraded in the fossil, the tuberositas retinaculi extensoris medialis appears to have been protuberant.

QM F22796 corresponds in size to the tibiotarsus of *Sm. brevirostris*. Its overall morphology is very similar to those of the acanthizid species examined here, except that it has a relatively longer pons supratendineus than *Pycnoptilus*, *Calamanthus*, *Origma* and *Crateroscelis*. The fossil further differs from *Pycnoptilus* and *Calamanthus* in that the distal shaft is narrower with respect to the distal end.

The fossil tibiotarsus can be excluded from families of characteristically small passerines in Australia, including Maluridae, Rhipiduridae, Petroicidae, Estrildidae and Zosteropidae, because it has a long pons supratendineus. QM F22796 is morphologically similar to those of meliphagids but can be distinguished by the following combination of features. The fossil is considerably smaller in size than the tibiotarsi of meliphagids examined. The bony ridges of the retinaculum m. fibularis are relatively shorter and more prominent, and the sulcus m. fibularis is deeper. The tuberositas retinaculi extensoris lateralis is more elevated than in the meliphagids studied. This tuberosity is located on the proximo-lateral portion of the pons supratendineus, whereas in meliphagids it is situated further proximally on the pons. The incisura intercondylaris is slightly narrower in the fossil than in meliphagids.

The tibiotarsal morphologies of Acanthizidae and Pardalotidae are also very similar, but they differ in the following features. In pardalotids, the lateral shaft edge is less flared and near parallel with the shaft long axis. The condylus lateralis is greater in distal extent than its medial

counterpart, whereas in acanthizids and the fossil they are near equal. The length of the lateral bony ridge for the retinaculum m. fibularis is less than or about equal to that of the pons supratendineus in pardalotids, whereas it is greater in acanthizids as it is in QM F22796.

Remarks. Acanthizidae (thornbills, scrubwrens and allies) is a family of very small to medium-sized, wren-like passerines. It is a large, integral component of the primarily Australasian songbird infraorder Meliphagides, with about 65 species in 13 genera (Dickinson & Christidis, 2014). Acanthizids occupy a wide variety of habitats including rainforest, sclerophyll forests, mangroves, dry woodland, grasslands, heath, shrubland and saltmarsh. These birds forage in all vertical strata, from the ground to the upper canopy, and are found in tropical to arid zones (Higgins *et al.*, 2002; Gregory, 2007).

The extinct *Pycnoptilus fordii* Baird, 1993, as well as material referable to the extant Pilotbird, *P. floccosus*, were described from the late Pleistocene Pyramids Cave in Victoria (Baird, 1993). Remains of *P. floccosus* have also been identified from the late Pleistocene Cloggs Cave and Holocene Mabel Cave in Victoria (Baird, 1991b). Holocene fossils referred to *Acanthiza* sp. have been reported from Mabel Cave in Victoria and Madura Cave in Western Australia (Baird, 1986). Acanthizidae is currently represented in the Riversleigh region by *Sm. brevirostris* and the Western Gerygone *Gerygone fusca*.

Family Pomatostomidae Schodde, 1975

Genus *Pomatostomus* Cabanis, 1851

Pomatostomus sp.

Figs 9–11

Material. QM F30358, distal left humerus; QM F57939, right ulna; QM F36368, distal left tibiotarsus; QM F36670, distal right tibiotarsus; QM F30357 and QM F57900 (AR19820), proximal right tarsometatarsi.

Measurements (mm). QM F30357: preserved length 8.6, proximal width ca 2.9, proximal depth (cotyla lateralis to hypotarsus) ca 3.0. QM F30358: preserved length 5.8, distal width 4.6, depth of condylus dorsalis 2.2. QM F36368: preserved length 14.6, distal width 2.9, depth of condylus lateralis 2.7, depth of condylus medialis 3.0. QM F36670: preserved length 16.1, distal width 2.8, depth of condylus lateralis 2.8, depth of condylus medialis 3.0. QM F57900: preserved length 15.3, proximal width 3.3, proximal depth (cotyla lateralis to hypotarsus) 3.3. QM F57939: preserved length 19.7, proximal width 3.1, length of proc. cotyla dorsalis 1.3, distal width ca 2.3, depth of condylus dorsalis ca 2.0.

Description and comparisons. *Humerus*. QM F30358 (Fig. 9A–B) is identified as *Pomatostomus* because of the following combination of features. The distal humerus is very wide relative to its depth and is well expanded ventrally from the shaft edge. The sulcus humerotricipitalis is very shallow, such that it is near planar with the caudal surface of the distal humerus. The sulcus scapulotricipitalis is shallow and wide. The distal extent of the proc. flexorius is much greater than that of the condylus dorsalis. On the epicondylus ventralis, the scars for attachment of *M. pronator*

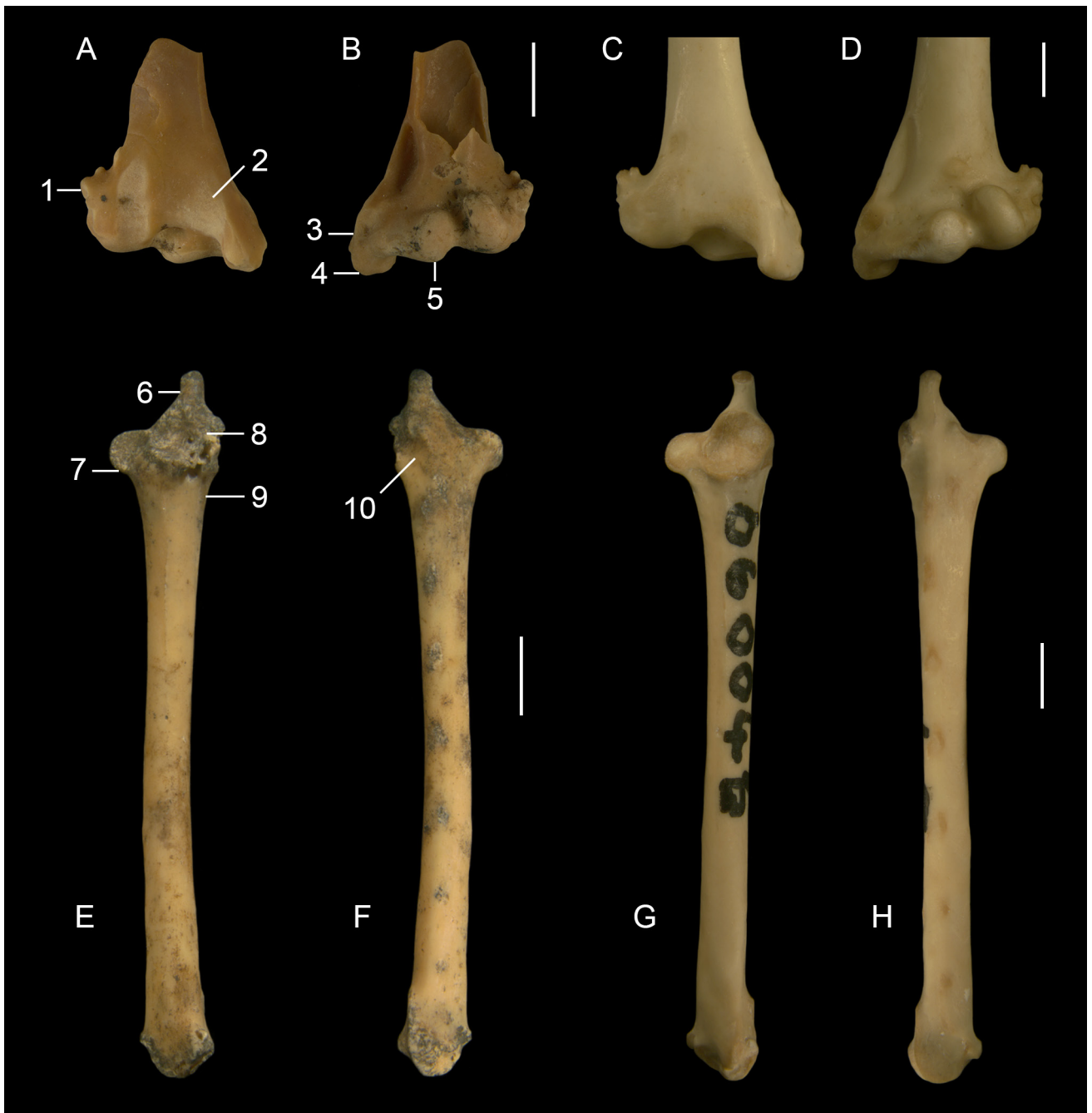


Figure 9. Comparison of fossil and extant pomatostomid wing bones. (A–B) distal left humerus of *Pomatostomus* sp. QM F30358 and (C–D) distal right humerus of *P. temporalis* AM O.65103 (mirrored). Right ulnae of (E–F) *Pomatostomus* sp. QM F57939 and (G–H) *P. ruficeps* AM O.60045. (A,C,F,H) caudal aspect; (B,D,E,G) cranial aspect. Some characteristic features of *Pomatostomus* shown: 1, proc. supracondylaris dorsalis long and bifurcated; 2, sulcus humerotricipitalis very shallow; 3, distal end of humerus well expanded ventrally; 4, distal extent of proc. flexorius much greater than that of condylus ventralis; 5, condylus ventralis long with respect to length of condylus lateralis; 6, olecranon short; 7, distal edge of proc. cotyla dorsalis about level with that of cotyla ventralis; 8, cotyla ventralis shallow; 9, impressio m. brachialis very shallow; 10, shallow depression situated distally of attachment scar for trochlea humeroulnaris. Scale bar = 2mm.

profundus and *M. flexor digiti superficialis* are marked. The proc. supracondylaris dorsalis is proximo-distally long and bifurcated. The condylus ventralis is long; its length is greater than 80% of that of the condylus dorsalis. The incisura intercondylaris is very wide and moderately deep.

The fossil humerus differs from *P. superciliosus*, *P. halli* and *P. ruficeps* in having a deeper bifurcation of the proc. supracondylaris dorsalis. The fossil further differs from *P. halli* and *P. ruficeps*, and from *P. temporalis* (Fig. 9C–D)

in that the proc. supracondylaris dorsalis protrudes slightly further dorsally. QM F30358 differs from *Garritornis isidorei* (sometimes subsumed in *Pomatostomus*, e.g., Clements *et al.*, 2015) in that the sulcus humerotricipitalis is not ventrally demarcated by a low ridge; the proc. flexorius is slightly longer; the fossa m. brachialis is deeper; and the proc. supracondylaris dorsalis protrudes slightly further dorsally.

Ulna. QM F57939 (Fig. 9E–F) is a near-complete ulna with breakage to the ventral side of the proximal end and the



Figure 10. Tibiotarsi of (A–D) fossil *Pomatostomus* sp. compared with (E–F) a left tibiotarsus of *P. temporalis* AM O. 68479. (A–B) QM F36368, distal left tibiotarsus. (C–D) QM F36670, distal right tibiotarsus. (A, C, E) cranial view, (B, D, F) caudal view. Some characteristic features are highlighted: 1, tuberositas retinaculi extensoris lateralis protuberant and at about level with the bony ridges for attachment of retinaculum m. fibularis; 2, lateral bony ridge for retinaculum m. fibularis a moderate flange, whereas medial bony ridge low; 3, trochlea cartilaginosa tibialis very wide; 4, cristae near parallel. Scale bar = 2 mm.

condyles. The fossil is referred to *Pomatostomus* because it possesses the following suite of features. The olecranon is short; its length is about half of that of the cotyla ventralis. The distal edge of the proc. cotyla dorsalis is about level with that of the cotyla ventralis. The cotyla ventralis is shallow. The impressio m. brachialis is very shallow and near planar with the shaft surface. In caudal view, there is a shallow depression distally of the attachment site of the trochlea humeroulnaris. The papillae remigales caudales are very low markings on the shaft. On the distal end, the incisura tendinosa is wide and deep.

The fossil ulna differs from *P. temporalis* in having a shallower depressio radialis and a less developed protuberance for attachment of the trochlea humeroulnaris. It differs from *P. ruficeps* (Fig. 9G–H) in having a comparatively shorter olecranon. QM F57939 differs from *Garritornis* in having a narrower, pointed olecranon and a shallower impressio m. brachialis and sulcus intercondylaris.

Tibiotarsus. QM F36368 (Fig. 10A–B) and QM F36670 (Fig. 10C–D) are referred to *Pomatostomus* because they share the following combination of character states. The distal tibiotarsus is robust. The length of the pons supratendineus is about equal to its width. The tuberositas retinaculi extensoris lateralis is prominent. This tuberosity is situated on the proximo-lateral part of the pons supratendineus and protrudes beyond the proximal edge of the pons. The lateral bony ridge for attachment of the retinaculum m. fibularis is a well-developed flange, but its medial counterpart is low. The trochlea cartilaginosa tibialis is very wide and its cristae are near parallel.

The fossil tibiotarsi differ from *P. halli* and *P. temporalis* (Fig. 10E–F) in that the tuberositas retinaculi extensoris lateralis is more elongate and the epicondylaris lateralis is less developed. The fossils differ from *P. halli* and *P. ruficeps* in that the lateral bony ridge for the retinaculum m. fibularis is longer than, not equal to, its medial counterpart. QM F36368 and QM F36670 differ from *P. ruficeps* and *P. superciliosus* in that the bony ridges for the retinaculum m. fibularis are situated at about level with the tuberositas retinaculi extensoris lateralis, not slightly further proximally. They differ from *Garritornis* in that the condylus medialis is not medially displaced from the shaft edge, and the scar for attachment of the lig. tibio metatarsale intercondylare is much shallower.

QM F36368 and QM F36670 are similar in size and in overall morphology, except that the tuberositas retinaculi extensoris medialis is less developed in the latter. QM F36670 also differs from QM F36368 in that the condylus lateralis is greater in proximal extent than the condylus medialis. This second character state was present in all specimens of *P. ruficeps* and *Garritornis* studied, but was variable among individuals of *P. halli* and *P. superciliosus* examined.

Tarsometatarsus. QM F57900 (Fig. 11A–C) and QM F30357 (Fig. 11D–F) are referred to *Pomatostomus* because they exhibit the following suite of features. The arcus extensorius is longer than its width. Although the arcus extensorius is broken off in QM F30357, the remaining bony ridges indicate that it was relatively long. The sulcus extensorius is deep. The medial shaft depth is very shallow

and the impressio lig. collateralis medialis is elongate. The tuberositas m. tibialis cranialis is low and situated close to the arcus extensorius. The tendinal bridge between the hypotarsus and crista plantaris lateralis is ossified and plantarly bounds a small foramen ('peroneal foramen' in Orenstein, 1977). In QM F30357, part of the crista plantaris lateralis is broken off, but what remains of the crista indicates that the tendinal bridge was ossified and that the foramen was small. In QM F57900, there is damage around the peroneal foramen but the ossified tendinal bridge is preserved. On the lateral surface of the tarsometatarsus there is a distinct groove for the cranial branch tendon of M. fibularis longus (Raikow, 1993), which joins to the peroneal foramen. Other features that are shared among the fossils and extant pomatostomids include a deep fossa infracotylaris dorsalis and a proximally situated cotyla medialis relative to the cotyla lateralis.

The fossil tarsometatarsi differ from those of extant species of *Pomatostomus* in that the plantar part of the hypotarsus does not project as far proximally. The fossils differ from *P. halli* and *P. ruficeps* (Fig. 11G–I) in having a more elevated impressio lig. collateralis medialis and a deeper sulcus ligamentosus. The fossils further differ from *P. ruficeps* in having a shallower groove for the cranial branch tendon of M. fibularis longus. This groove, however, is deeper in the fossils than in *P. temporalis*. QM F30357 also differs from *P. ruficeps* in having a less prominent impressio lig. collateralis lateralis (it is broken in AR19820). The fossils differ from *P. superciliosus* in having a slightly longer arcus extensorius with respect to width, whereas it is relatively shorter than in *P. temporalis*. QM F30357 and QM F57900 further differ from *P. temporalis* in possessing a shallower fossa infracotylaris dorsalis. They differ from *Garritornis* in that the impressio lig. collateralis lateralis is shorter and far less developed, and the peroneal foramen is circular rather than oval-shaped. The tuberositas m. tibialis cranialis is distally adjacent to or closely located to the arcus extensorius in the fossils, whereas in *Garritornis* the distance between the tuberosity and arcus is greater. QM F30357 differs from QM F57900 in having a shallower fossa infracotylaris dorsalis and medial shaft depth.

Remarks. Australo-Papuan babblers (Pomatostomidae) are medium-sized passerines that only superficially resemble their Eurasian, unrelated namesakes in appearance, sociability and foraging behaviour (Schodde & Mason, 1999). They typically glean and probe for insects among leaf litter, grasses and fallen trees. Some babblers, particularly the Grey-crowned Babbler *P. temporalis*, also forage in low shrubs and on trunks and branches of trees near the ground (Schodde & Mason, 1999; Higgins *et al.*, 2002). In Australia, these birds inhabit open eucalypt forests, woodlands, shrublands and semi-arid scrub (Boles, 1988; Higgins *et al.*, 2002). The Papuan Babbler *Garritornis isidorei* occurs in rainforest, tall secondary growth and lowland gallery forest (Matthew, 2007).

There are no significant morphological differences between the pomatostomid fossils and any of the extant taxa that would enable confident species determination. Nevertheless, the fossils indicate the presence of a pomatostomid smaller than the White-browed Babbler *P. superciliosus* in the Rackham's Roost Local Fauna. With a

minimum estimated age of early Pleistocene, these fossils represent the oldest known record of Pomatostomidae. Holocene fossils of *P. superciliosus* have been reported from Madura Cave in Western Australia (Baird, 1991a). Today, this family is represented in the Riversleigh region by *P. temporalis*.



Figure 11. Proximal right tarsometatarsi of (A–F) fossil *Pomatostomus* sp. compared to the corresponding bone of (G–I) *P. ruficeps* AM O.60045. (A–C) QM F57900. (D–F) QM F30357. (A,D,G) dorsal view, (B,E,H) plantar view, (C,F,I) lateral view. Some characteristic features of *Pomatostomus* labelled: 1, arcus extensorius longer than wide; 2, tuberositas m. tibialis cranialis low and located close to arcus extensorius; 3, groove for M. fibularis longus marked; 4, ossified tendinal bridge between hypotarsus and crista plantaris lateralis, enclosing a small foramen in crista. Scale bar = 2 mm.

Family Petroicidae Mathews, 1919–20

Genus et species indet.

Figs 12–13

Material. QM F57901 (AR19761), left humerus; QM F50576 (AR16065), right humerus; QM F36366, distal left humerus; QM F57931, proximal left ulna.

Measurements (mm). QM F36366: preserved length 6.9, distal width >3.8, depth of condylus dorsalis 1.6. QM F50576: preserved length ca 14.3, proximal width 4.7, length of crista deltopectoralis ca 3.6, mid shaft width 1.3, distal

width >3.5, depth of condylus dorsalis 1.6. QM F57901: preserved length 16.5, proximal width ca 4.5, length of crista deltopectoralis 2.8, mid shaft width 1.5, distal width 4.0, depth of condylus dorsalis 1.6. QM F57931: preserved length 5.0, proximal width 2.6, length of proc. cotyla dorsalis 1.3.

Description and comparisons. *Humerus.* QM F57901 (Fig. 12A,F) is a near-complete humerus with several small, shallow punctures on the cranial and caudal shaft surfaces and condyles. QM F50576 (Fig. 12D,I) is also a well-preserved humerus with breakage to the ventral parts of the proximal and distal ends and to the crista deltopectoralis. These two fossils are referred to Petroicidae because they

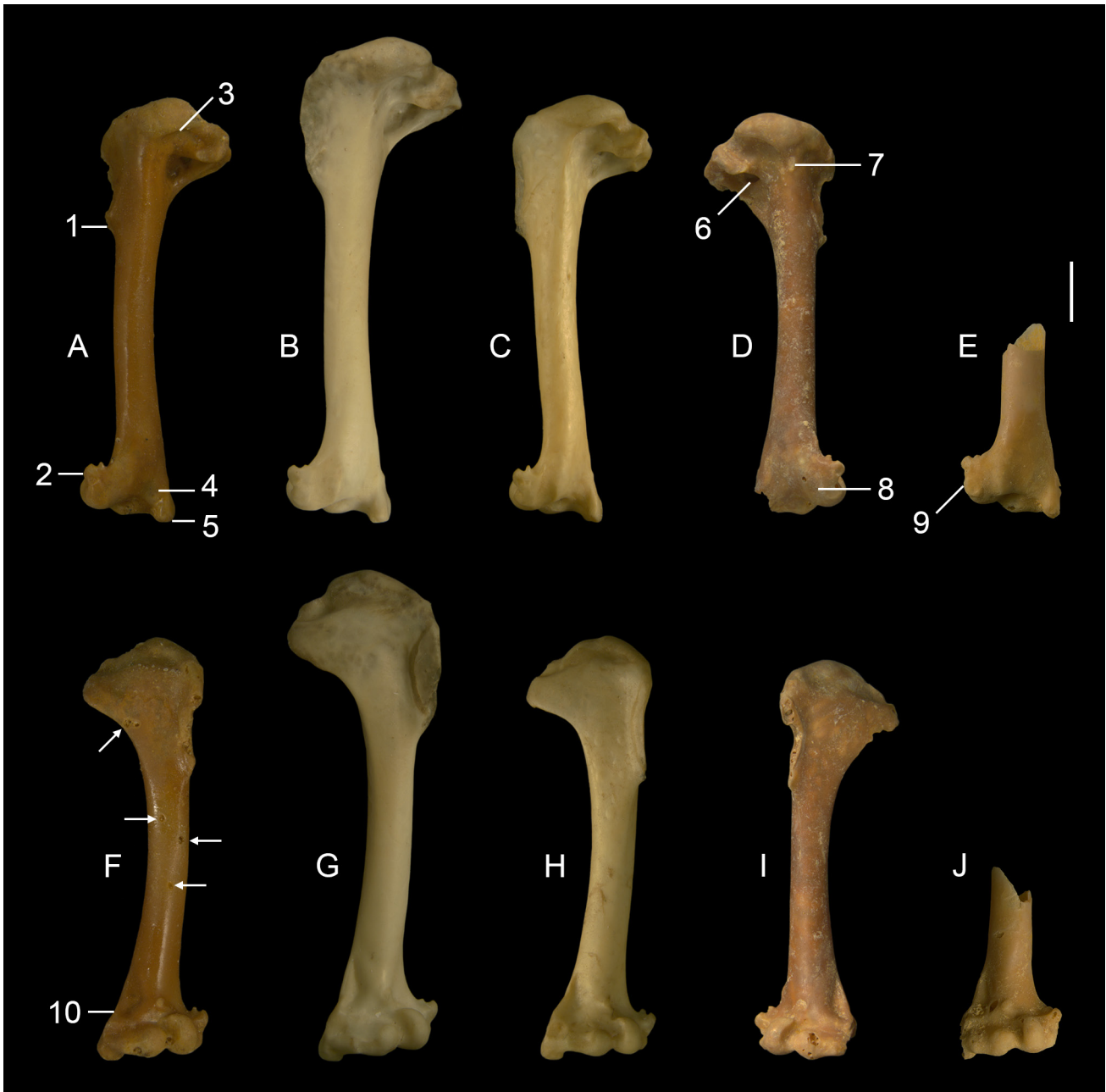


Figure 12. Humeri of (A,D–F,I–J) fossil Petroicidae gen. et sp. indet. compared with those of (B,G) *Microeca fascinans* AM O.65147 and (C,H) *Petroica phoenicea* AM O.60008. (A,F) QM F 57901 left humerus. (D,I) QM F 50576, right humerus. (E,J) QM F 36366, distal left humerus. (A–E) caudal view, (F–J) cranial view. Some distinguishing features of Petroicidae shown: 1, crista deltopectoralis terminates well distally of crista bicipitalis; 2, proc. supracondylaris dorsalis broad with two apices; 3, fossa pneumotricipitalis II shallow and separate from fossa tricipitalis I; 4, sulcus humerotricipitalis shallow; 5, proc. flexorius truncate and only slightly extends distally further than condylus dorsalis; 6, fossa pneumotricipitalis I pneumatic; 7, margo caudalis short and very low; 8, sulcus scapulo-tricipitalis wide and shallow; 9, distal end well expanded dorsally and 10, ventrally. Arrows indicate tooth punctures. Scale = 2 mm.

possess the following combination of characters. (1) The fossa pneumotricipitalis II is shallow and clearly separate from the fossa pneumotricipitalis I. This fossa is restricted to a moderately deep excavation below the caput humeri. (2) The fossa pneumotricipitalis I is pneumatic and has few large foramina. (3) The crus dorsale fossae is about perpendicular with the long axis of the shaft. (4) The margo caudalis is short and very low. (5) The crista deltopectoralis terminates well distally of the crista bicipitalis. (6) The shaft is gently curved dorso-ventrally. (7) The distal end is well expanded ventrally (in QM F57901) and (8) dorsally from the shaft. (9) The sulcus humerotricipitalis is shallow. (10) The sulcus scapulothoracicus is wide, shallow and ventrally bound by a distinct ridge. (11) In caudal aspect, the distal profile of the humerus between the sulcus humerotricipitalis and sulcus scapulothoracicus is shallowly concave. (12) The proc. flexorius is truncate and extends a relatively short distance distally of the condylus dorsalis. (13) The proc. supracondylaris dorsalis is broad and has two apices.

QM F57901 and QM F50576 correspond in size to the humerus of the Lemon-bellied Robin *Microeca flavigaster*. They differ from extant petroicids studied as follows. QM F57901 is distinguished from *Kempiella* and *Devioeca* by its narrower distal end relative to the shaft width. The ventral portion of the distal end is broken in QM F50576, but it can be differentiated from *Kempiella* and *Devioeca* in being relatively smaller in dorsal extent from the shaft. The fossil humeri also differ from *Pachycephalopsis*, *Peneothello*, *Tregellasia* and *Eopsaltria* because the distal end is less expanded dorsally from the shaft. They differ from *Poecilodryas*, *Plesiodyras* and *Heteromyias* in that the distal end is less expanded ventrally. The fossils further differ from *Poecilodryas* and *Plesiodyras* in having a shallower fossa pneumotricipitalis II and from *Heteromyias* in having a relatively narrower fossa m. brachialis. QM F57901 and QM F50576 differ from *Amalocichla* in having a less curved shaft and from *Drymodes* in possessing a comparatively longer crista bicipitalis. The fossils differ from *Melanodryas* because the proc. flexorius does not project as far distally, and from *Monachella* because the crista deltopectoralis terminates further distally relative to the distal edge of the crista bicipitalis.

The fossils are similar in overall morphology to species of *Microeca* (Fig. 12B,G) and *Petroica* (Fig. 12C,H) studied, but lack significant differences to allow confident generic identification. QM F50576 differs from QM F57901 in having a slightly larger proc. supracondylaris dorsalis and a ridge on the dorsal surface of the shaft, proximally of the proc. supracondylaris dorsalis.

QM F36366 (Fig. 12E,J) is a distal humerus with breakage to the ventral portion. It is tentatively referred to Petroicidae because it shares character states 8–13 described above. This fossil humerus is similar in size to the corresponding bone of the Flame Robin *Pet. phoenicea*. It differs from *Drymodes*, *Poecilodryas* and *Petroica* in that the distal end is greater in dorsal extent from the shaft. QM F36366 differs from *Kempiella*, *Monachella*, *Peneothello* and *Tregellasia* in having a shallower fossa m. brachialis. The fossil differs from *Devioeca* in having a smaller proc. supracondylaris dorsalis, and from *Plesiodyras* in that the ventral apex of this process is blunt, not pointed. QM F36366 differs from QM F50576 and QM F57901 in that the distal end is more dorsally expanded, and it has a smaller proc. supracondylaris dorsalis that does not protrude as far dorsally.

A distal humerus that is considerably expanded dorsally (character state 8) was also observed in some species of Meliphagidae, Acanthizidae, Rhipiduridae and Monarchidae. QM F36366 can be excluded from Meliphagidae because it has a wider sulcus scapulothoracicus relative to the width of the distal end, and the proc. supracondylaris dorsalis does not protrude as far dorsally as in meliphagids. In caudal aspect the distal profile of the humerus is less concave in QM F36366 than in meliphagids. The fossil can be excluded from Acanthizidae because the sulcus humerotricipitalis is deeper, and the proc. supracondylaris dorsalis is relatively longer but does not protrude as far dorsally. QM F36366 can be excluded from Rhipiduridae because it has a relatively wider sulcus scapulothoracicus and the proc. supracondylaris dorsalis is not as set off dorsally from the distal end. It can be excluded from Monarchidae because the sulcus scapulothoracicus is relatively wider and the condylus dorsalis is shorter with respect to the condylus ventralis.

Ulna. QM F57931 (Fig. 13A–C) is referred to Petroicidae because it exhibits the following character states. The proc. cotyla dorsalis is square and its proximal edge is located well distally of that of the cotyla ventralis, by a distance greater than one-third of the length of the latter. The cotyla ventralis is shallow; the ventral portion of the cotyla is near planar. In cranial aspect, the ventral edge of the tub. lig. collateralis ventralis is near parallel with the long axis of the shaft. In ventral view, the protuberance for attachment of the trochlea humeroulnaris projects beyond the caudal edge of the olecranon. On the caudal surface of the proximal end, there is a depression located ventrally of the impressio m. scapulothoracicus. In proximal view, the protuberance for insertion of M. scapulothoracicus projects well caudally.

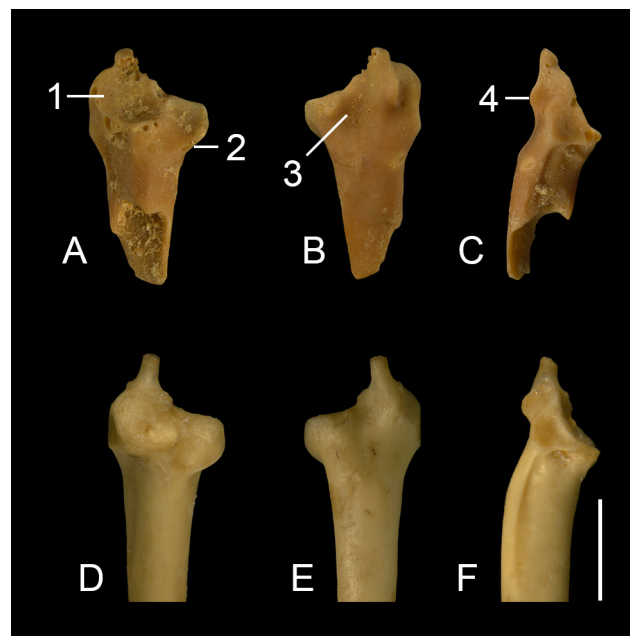


Figure 13. Proximal left ulnae of (A–C) a fossil petroicid gen. et sp. indet. and (D–F) *Petroica phoenicea* AM O.60008. (A,D) cranial view, (B,E) caudal view, (C,F) ventral view. Some characteristic features of Petroicidae highlighted: 1, cotyla ventralis shallow; 2, proc. cotyla dorsalis square and its proximal edge is located distally of that of cotyla ventralis by a distance greater than one-third the length of the latter; 3, depression situated ventrally of the impressio m. scapulothoracicus; 4, protuberance for attachment of the trochlea humeroulnaris projects beyond the caudal edge of the olecranon. Scale = 2 mm.

The fossil ulna is similar in size to the corresponding bone of *Pet. phoenicea* (Fig. 13D–F). It differs from those of extant species of petroicids studied as follows. QM F57931 differs from species of *Microeca*, *Melanodryas*, *Heteromyias*, *Monachella*, *Petroica* and *Amalocichla* examined in having a shallower cotyla ventralis. The fossil further differs from *Microeca*, *Melanodryas* and *Heteromyias* and from *Drymodes* and *Pachycephalopsis* in having a relatively shorter olecranon. It differs from *Drymodes* and *Amalocichla* in that the protuberance that bears the insertion scar for *M. scapulotriceps* projects further caudally. QM F57931 also differs from *Amalocichla* in having a depression situated ventrally of the impressio m. scapulotricepitis. This depression is deeper in the fossil than in *Eopsaltria*, *Monachella* and *Petroica*. The fossil further differs from *Eopsaltria* and *Monachella* in having a more prominent protuberance for attachment of the trochlea humeroulnaris.

Remarks. The Australasian robins (Petroicidae) are small to medium-sized, plump passerines, and comprise about 48 species in 19 genera (Dickinson & Christidis, 2014). The centre of diversity of petroicids is in Australia and New Guinea, but some species occur in Tanimbar Islands, New Zealand and the southwest Pacific islands (Schodde & Mason, 1999). Petroicids forage by pouncing on insects from an elevated perch or by catching insects on the wing (Schodde & Mason, 1999). In Australia, petroicid robins are predominantly found in wet to dry sclerophyll forests and woodlands, as well as arid scrub and mangroves. They occur in all bioclimatic zones, from rainforest to arid regions (Higgins *et al.*, 2002). The specimens described here add to the poorly known fossil record of Petroicidae in Australia, previously represented only by late Pleistocene remains of *Petroica* sp. from Cloggs Cave (Baird, 1991a). Today, three species regularly occur in the Riversleigh region: the Hooded Robin *Melanodryas cucullata*, Buff-sided Robin *Po. cerviniventris* and Jacky Winter *Microeca fascians*.

Family Estrildidae Bonaparte, 1850

Genus et species indet.

Fig. 14

Material. QM F57940, distal right humerus; QM F30821 and QM F57903 (AR19825), left carpometacarpus; QM F57933 (AR11261), right carpometacarpus.

Measurements (mm). QM F30821: preserved length 8.9, proximal width 2.8, proximal length 2.0, length of os metacarpale alulare 1.4, distal width >1.8. QM F57903: preserved length 10.1, proximal width 2.7, proximal length 2.2, length of os metacarpale alulare 1.4, distal width 2.4. QM F57933: preserved length 9.8, proximal width 3.0, proximal length 2.5, length of os metacarpale alulare 1.6, distal width 2.4. QM F57940: preserved length 4.3, distal width >3.7, depth of condylus dorsalis 2.1.

Description and comparisons. *Humerus.* QM F57940 (Fig. 14A–B) is a distal humerus with breakage to the proc. supracondylaris dorsalis and the ventral portion of the proc. flexorius. It is referred to Estrildidae because of the following combination of features. The sulcus humerotricipitalis is deep and directed proximally. It extends proximally beyond the level of the base of the proc. supracondylaris dorsalis.

The sulcus scapulotricepitis is also strongly marked. The distal profile of the condylus dorsalis is convex. The muscle attachment scar on the caudal surface of the epicondylaris ventralis is very deep. The fossa m. brachialis is elongate and very deep. The tub. supracondylare ventrale protrudes proximo-cranially. In dorsal view, the proc. supracondylaris dorsalis is proximally of the level of the condylus dorsalis.

The fossil humerus approaches the size of the corresponding bone of the Java Sparrow, *Lonchura oryzivora* (Fig. 14C–D). It is similar in overall morphology to the humeri of species of *Lonchura* examined. QM F57940 differs from extant species of estrildids studied in the following character states. It differs from all estrildids examined in having a larger fossa m. brachialis. The fossa m. brachialis is deeper in the fossil than in *Lonchura*, *Stagonopleura*, *Neochmia*, *Poephila* and *Erythrura*. The fossil further differs from *Neochmia*, *Poephila*, and *Erythrura*, and from *Heteromunia* in having a relatively shorter proc. flexorius. It differs from *Taeniopygia* in that, when viewed ventrally, the caudal edge of the proc. flexorius is angled disto-caudally and is not parallel to the long axis of the shaft.

Carpometacarpus. QM F30821, QM F57903 and QM F57933 (Fig. 14E–G, I–K) are assigned to Estrildidae because they exhibit the following suite of character states. The carpometacarpus is small and stout and has a circular-shaped trochlea carpalis ventralis. The proximal end of the os metacarpale minus is narrow and becomes wider distally. The caudal edge of the proc. intermetacarpalis is level with that of the os metacarpale minus. The spatium intermetacarpale is visible proximally of the proc. intermetacarpalis. The proc. dentiformis is located at about the proximo-distal midpoint of the os metacarpale majus. The distal end of the os metacarpale minus is square and broad. The ventral fossa on the distal end of the os metacarpale minus is very shallow. The sulcus interosseus is moderately deep.

QM F30821 (Fig. 14E,I) is most similar in size to the Blue-faced Parrotfinch, *Erythrura trichroa*, whereas QM F57903 (Fig. 14F,J) and QM F57933 (Fig. 14G,K) correspond in size to the Masked Finch *Poephila personata*. The fossil carpometacarpus differ from those of extant species of estrildids studied in the following features. QM F30821 differs from *Stagonopleura*, *Lonchura* (Fig. 14H,L) and *Taeniopygia* because it is shorter with respect to its proximal width. The fossil carpometacarpus is stouter than those of *Neochmia*, *Taeniopygia*, *Heteromunia*, *Poephila* and *Erythrura*. It further differs from *Neochmia*, *Taeniopygia* and *Heteromunia* in having a more circular trochlea carpalis ventralis. The fossil differs from *Stagonopleura*, *Lonchura*, *Poephila* and *Erythrura* in having a smaller fovea carpalis caudalis. It differs from *Heteromunia* and *Erythrura* in having a larger proc. dentiformis.

QM F57903 differs from *Neochmia*, *Taeniopygia*, *Heteromunia* and *Erythrura* in having a more circular trochlea carpalis ventralis. The fossil further differs from *Erythrura* in having a larger proc. dentiformis. It differs from *Heteromunia* and *Stagonopleura* in having a deeper ventral fossa on the distal end of the os metacarpale minus, and further differs from *Heteromunia* in being stouter. The fossil differs from *Lonchura* in that the distal end of the spatium intermetacarpale and the sulcus interosseus are narrower.

QM F57933 can be distinguished from the carpometacarpus of all estrildids examined by its relatively longer proc. dentiformis. It differs from the carpometacarpus of *Neochmia*,

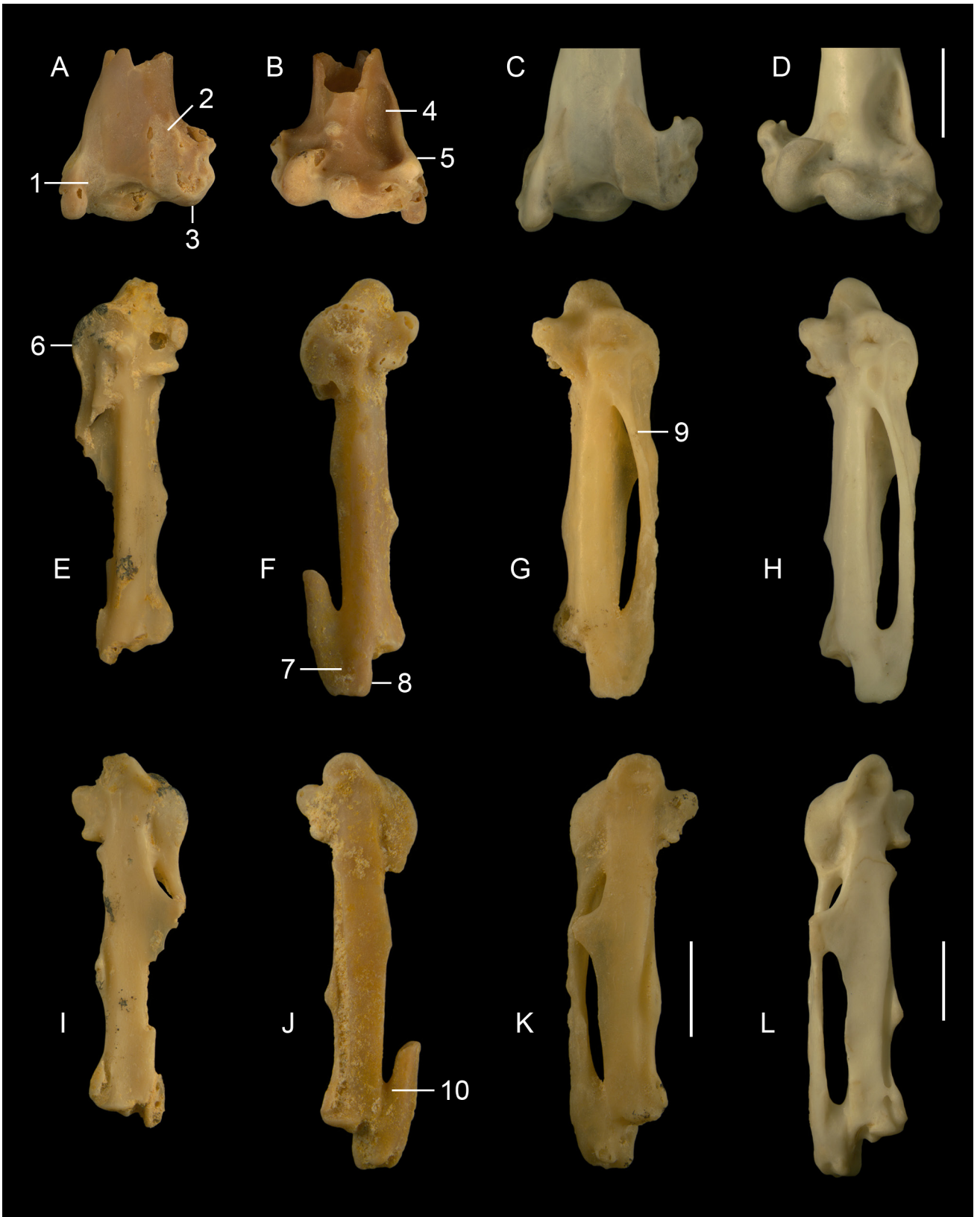


Figure 14. Wing bones of (A–B, E–G, I–K) fossil Estrildidae gen. et sp. indet. compared with those of (C–D, H, L) *Lonchura oryzivora* AM O.66319. (A–B) QM F57940, distal right humerus. (E, I) QM F30821, left carpometacarpus. (F, J) QM F57903, left carpometacarpus. (G, K) QM F57933, right carpometacarpus. (A, C) caudal view, (B, D) cranial view, (E–H) ventral view, (I–L) dorsal view. Some distinguishing features of Estrildidae shown: 1, sulcus humerotricipitalis deep and extends proximally beyond base of proc. supracondylaris dorsalis; 2, sulcus scapulothoracicus strongly marked; 3, distal profile of condylus dorsalis convex; 4, fossa m. brachialis elongate and very deep; 5, tub. supracondylare ventrale protrudes proximo-cranially; 6, trochlea carpalis ventralis circular; 7, ventral fossa on distal end of os metacarpale minus very shallow; 8, distal end of the os metacarpale minus square and broad; 9, proximal end of os metacarpale minus narrow and becomes wider distally; 10, sulcus interosseus moderately deep. Scale = 2 mm.

Taeniopygia, *Erythrura*, *Poephila* and *Heteromunia* in being stouter. It further differs from *Erythrura*, *Poephila* and *Heteromunia* in that the proc. intermetacarpalis does not protrude beyond the caudal edge of the os metacarpale minus. The fossil differs from *Erythrura* in having a shallower ventral fossa on the distal end of the os metacarpale minus, and from *Poephila* in having a shallower sulcus interosseus. It differs from *Heteromunia* in having a more circular trochlea carpalis ventralis. The fossil carpometacarpus is relatively shorter than the corresponding bone of *Stagonopleura*. QM F57933 differs from *Lonchura* in that the distal end of the spatium intermetacarpale and the sulcus interosseus are narrower. The fovea carpalis caudalis is shallower than in *Neochmia*, *Lonchura*, *Erythrura* and *Heteromunia*.

QM F30821 differs from QM F57903 and QM F57933 in being stouter. QM F57903 is distinguished from the other two fossil carpometacarpi by its shorter and more pointed proc. dentiformis. QM F57933 differs from the other two fossils in having a deeper fossa for the M. flexor digiti minoris. The fossil carpometacarpi indicate at least two taxa; one of which is represented by the stouter QM F30821, and the second taxon by QM F57903 and QM F57933. Additional fossil material and comparisons with a wider range of extant taxa will help to clarify the relationships of these specimens.

Remarks. Grassfinches and waxbills (Estrildidae) are small, often brightly coloured songbirds and comprise about 134 species in 32 genera (Dickinson & Christidis, 2014). Their range encompasses Australasia, the Pacific islands, South and Southeast Asia, Eurasia and Africa (Payne, 2010). Within Australia most estrildid finches are found in grassy areas, often close to water. Their habitats include open sclerophyll woodland with a grassy understorey, grassland, grassy shrubland and swamp vegetation (Higgins *et al.*, 2006). Estrildid finches are typically gregarious and primarily feed on grass seeds on the ground and from low grass heads, but can also seek nectar, fruit, foliage, insects and other invertebrates (Schodde & Mason, 1999; Higgins *et al.*, 2006; Payne, 2010). Late Pleistocene remains of indeterminate estrildids have been recorded from cave deposits in Victoria and Western Australia (Van Tets, 1974; Baird, 1991a). This family is currently represented in the Riversleigh region by 9 species.

Family Locustellidae Bonaparte, 1854

Genus *Megalurus* Horsfield, 1821

(including *Cincloramphus* Gould, 1838 and *Eremiornis* North, 1900)

Megalurus sp.

Figs 15–16

Material. QM F30820, QM F30852, right carpometacarpi; QM F57934 (AR19823), left tarsometatarsus; QM F30360, proximal right tarsometatarsus; QM F57935 (AR21602), QM F57936, QM F57937, distal left tarsometatarsi.

Measurements (mm). QM F30360: preserved length 11.5, proximal width ca 3.2, proximal depth (lateral aspect) >2.1. QM F30820: preserved length 13.9, proximal width 3.4, length of os metacarpale alulare 1.9, distal width 2.7. QM F30852: preserved length 11.5, proximal width 3.1, length

of os metacarpale alulare 1.5, distal width 2.4. QM F57934: preserved length 24.8, proximal width 2.8, proximal depth (cotyla lateralis to hypotarsus) 2.4, distal width ca 2.3, depth of tr II 0.9, depth of tr III 1.2, depth of tr IV 0.9. QM F57935: preserved length 7.8, distal width 2.3, depth of tr II 1.0, depth of tr III 1.2, depth of tr IV 1.0. QM F57936: preserved length 11.7, distal width 2.2, depth of tr II 0.9, depth of tr III 1.1, depth of tr IV 0.9. QM F57937: preserved length 3.4, distal width 2.5, depth of tr II 1.0, depth of tr III 1.4, depth of tr IV >0.8.

Description and comparisons. *Carpometacarpus*. QM F30820 (Fig. 15A,D) has damage to the trochlea carpalis and the distal end, and most of the os metacarpale minus is broken off. QM F30852 (Fig. 15B,E) is near complete with minor damage to the proc. alularis and the distal end of the os metacarpale majus. These fossil carpometacarpi are referred to *Megalurus sensu lato* (Alström *et al.*, 2011; Gill & Donsker, 2016) because they exhibit the following suite of features. The cranial extent of the proc. extensorius is far greater than that of the proc. alularis. The trochlea carpalis ventralis only slightly extends caudally beyond the os metacarpale minus. The proc. cranialis is long. The depression for the origin of M. flexor digiti minoris terminates distally of the proximal edge of the proc. pisiformis. The proc. intermetacarpalis does not protrude or only slightly protrudes beyond the caudal edge of the os metacarpalis minus. In dorsal view, the spatium intermetacarpale proximally of the proc. intermetacarpalis is visible and moderately wide. The proc. dentiformis is situated distally of the proximo-distal midpoint of the os metacarpale majus. In caudal aspect, the dorsal edge of the os metacarpale minus is slightly undulated. The sulcus interosseus is shallow.

QM F30820 falls within the size range observed for the carpometacarpi of *M. cruralis* and *M. mathewsi* (Fig. 15C,F), whereas QM F30852 is slightly larger than the corresponding bone of *M. timoriensis*. These fossils differ from *M. carteri* in being larger in size and proportionately longer. They further differ from *M. carteri* in that the os metacarpale minus is straight, not slightly curved cranio-caudally, and the fovea carpalis caudalis is deeper. In the fossils, the proc. dentiformis is more pointed and situated further distally on the os metacarpale minus than in *M. carteri*. QM F30820 differs from *M. timoriensis* in that the fossa for the M. flexor digiti minoris and the ventral fossa on the distal end of the os metacarpale minus are deeper. Both fossils differ from *M. gramineus* in that the distal end is squarer and less pointed. The fossil carpometacarpi differ from *M. mathewsi* and *M. cruralis* in that the trochlea carpalis dorsalis does not extend as far proximally. QM F30852 further differs from *M. mathewsi* and *M. cruralis* in having a shallower ventral fossa on the distal end of the os metacarpale minus. It differs from *M. cruralis* in having a shallower fovea carpalis caudalis. QM F30852 differs from QM F30820 in having a slightly more prominent proc. dentiformis, a notched distal end and a shallower ventral fossa on the distal end of the os metacarpale minus.

Tarsometatarsus. QM F57934 (Fig. 16B) is a near-complete tarsometatarsus, with the hypotarsus and proximal part of the crista plantaris lateralis broken off and the trochleae metatarsorum II and IV abraded. QM F30360 (Fig. 16C) preserves the proximal tarsometatarsus, whereas QM F57935 (Fig. 16G), QM F57936 (Fig. 16D) and QM F57937 (Fig. 16E) preserve the distal end. QM F57936 in particular bears shallow punctures, a deep scratch and some breakage



Figure 15. Comparison of (A–B, D–E, G) fossil bones of *Megalurus* sp. with those of (C, F, H) extant *M. mathewsi* AM O.59292. (A, D) QM F30820, right carpometacarpus. (B, E) QM F30852, right carpometacarpus. (G) QM F57941 distal left tibiotarsus. Some distinguishing features of *Megalurus* labelled: 1, cranial extent of proc. extensorius far greater than that of proc. alularis; 2, depression for attachment of *M. flexor digiti minoris* terminates distally of proximal edge of proc. pisiformis; 3, proc. dentiformis situated distally of midpoint of os metacarpale majus; 4, proc. cranialis long; 5, sulcus interosseus shallow; 6, distal edge of tuberositas retinaculi extensoris medialis at about level with bony ridges for retinaculum m. fibularis; 7, bony ridges for attachment of the retinaculum m. fibularis long and prominent flanges; 8, tuberositas retinaculi extensori lateralis occupies most of lateral half of pons supratendineus and does not protrude beyond its proximal edge; 9, condylus lateralis wider than condylus medialis; 10, incisura intercondylaris wide and its distal profile asymmetrical. Scale = 2 mm.

of the shaft, as well as damage to the trochleae metatarsorum. These fossil tarsometatarsi are assigned to *Megalurus sensu lato* (Alström *et al.*, 2011; Gill & Donsker, 2016) because they possess the following combination of character states. On the proximal end, the tuberositas m. tibialis cranialis is distally adjacent to the arcus extensorius and located medially of the shaft midpoint. The lateral foramen vasculare proximale is large. The crista plantaris lateralis is deep. In medial aspect, the shaft is very shallow and forms a sharp crest. The impressio lig. collateralis medialis is oval-shaped and at about level with or proximally overlaps with the arcus extensorius. The sulcus flexorius on the proximal half of the tarsometatarsus is very shallow.

On the distal tarsometatarsus, the foramen vasculare distale is small and situated far proximally of the incisura intertrochlearis lateralis by a distance about equal to or greater than twice the length of the trochlea metatarsi IV. The trochlea metatarsi II is about similar in width to the trochlea metatarsi III. There is a moderately deep furrow circumscribed along the entire trochlea metatarsi II that becomes deeper plantarly. The distal profile of the trochlea metatarsi II is notched, and the medial rim of this trochlea extends far distally of its lateral counterpart. The medial portion of the trochlea metatarsi II is greater in dorsal extent than the lateral portion. The incisura intertrochlearis medialis is narrow and relatively shorter than the lateral incisura. In dorsal aspect, the lateral margin of the trochlea metatarsi IV is situated medially of that of the shaft. The distal edge of the trochlea metatarsi IV is at a disto-lateral angle to the long axis of the shaft.

The fossil tarsometatarsi are similar in size to the corresponding bone of the Tawny Grassbird *M. timoriensis* (Fig. 16A). They also fall within the size range observed for songlarks *M. mathewsi* and *M. cruralis* (Fig. 16H), both of which exhibit sexual size dimorphism (Higgins *et al.*, 2006). In QM F57935 and QM F57937 the medial edge of the trochlea metatarsi II is a pronounced bulge that abruptly protrudes from the shaft margin (Fig. 16E, G), which is characteristic of *M. mathewsi* and *M. cruralis*. In QM F57934 and QM F57936, however, the trochlea metatarsi II does not protrude as far medially (Fig. 16B, D). The medial edge of this trochlea gradually merges with that of the shaft, as in *M. gramineus*, *M. timoriensis* and *M. carteri*.

Apart from the medial projection of the trochlea metatarsi II, the tarsometatarsal morphology is very similar among the species of *Megalurus* examined. The fossils differ from the extant species in a few features. They differ from *M. carteri* in that they are larger in size and proportionately more elongate. The fossils that preserve the proximal tarsometatarsus (QM F30360 and QM F57934) differ from *M. carteri* in that the impressio lig. collateralis medialis is more developed. The fossils differ from *M. carteri* and *M. gramineus* because the crista plantaris lateralis terminates at

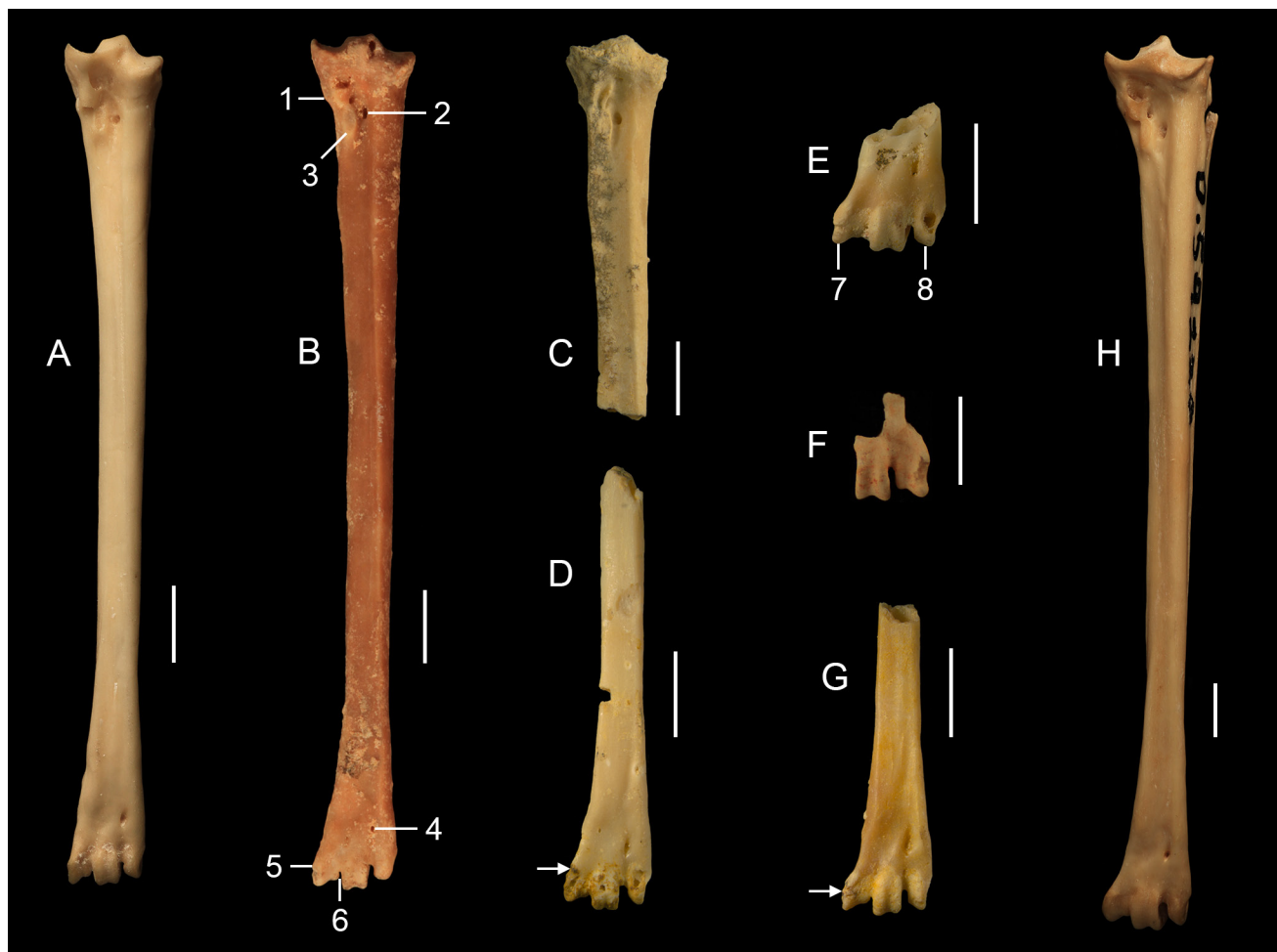


Figure 16. Tarsometatarsi of (B–G) fossil *Megalurus* sp. compared with the corresponding bones of (A) *M. timoriensis* AM O.65209 and (H) *M. cruralis* AM O.59220 in dorsal view. (B) QM F57934, left tarsometatarsus; (C) QM F30360, proximal left; (D) QM F57936, distal left; (E) QM F57937, distal left; (F) QM F30375, distal right; (G) QM F57935, distal left. Some distinguishing features labelled as follows: 1, impressio lig. collateralis medialis at about level with arcus extensorius; 2, lateral foramen vasculare proximale large; 3, tuberositas m. tibialis cranialis located distally adjacent of arcus extensorius and medially of shaft midpoint; 4, foramen vasculare distale situated proximally of incisura intertrochlearis lateralis by distance of $\geq 2 \times$ length of tr IV; 5, tr II similar width to tr III; 6, incisura intertrochlearis medialis narrow; 7, medial rim of tr II greater in distal and dorsal extents than lateral rim; 8, distal edge of tr IV at disto-lateral angle to shaft long axis. Arrows indicate different extent of medial protrusion of trochlea metatarsi II. Scale = 2 mm.

about level with the fossa metatarsi I, not proximally of the fossa. They further differ from *M. carteri* and *M. gramineus*, and from *M. timoriensis*, in that the medial rim of the trochlea metatarsi II extends slightly further distally relative to the lateral rim. QM F30360 and QM F57934 differ from *M. timoriensis* in having a slightly more elevated tuberositas m. tibialis cranialis. The fossil distal tarsometatarsi (except for QM F57937) differ from *M. mathewsi* in that the foramen vasculare distale is situated proximally of the incisura intertrochlearis lateralis by a distance of about twice the length of the trochlea metatarsi IV. In QM F57937 and *M. mathewsi*, however, this distance is greater. The fossils differ from *M. cruralis* in having a slightly shallower sulcus extensorius on the distal tarsometatarsus.

QM F57934 and QM F57936 differ from QM F57935 in having a more prominent crista plantaris lateralis on the distal shaft. QM F30360 differs from QM F57934 in having a deeper sulcus extensorius. Owing to the condition of the fossils and the overall similarity in tarsometatarsal morphology across species of *Megalurus*, the fossils cannot be confidently determined to species level.

Genus et species indet.

Figs 15G, 16F

Material. QM F57941, distal left tibiotarsus; QM F30375, distal right tarsometatarsus.

Measurements (mm). QM F30375: preserved length 2.0, distal width >1.7 , depth of tr II 0.9, depth of tr III ca 1.2. QM F57941: preserved length 9.4, distal width 2.9, depth of condylus lateralis 2.6, depth of condylus medialis 2.9.

Description and comparisons. *Tibiotarsus.* QM F57941 (Fig. 15G) is tentatively referred to Locustellidae because of the following suite of features. In cranial view, the condylus lateralis is wider than the condylus medialis. The condylus medialis is moderately displaced medially relative to the shaft edge. The incisura intercondylaris is wide and its distal profile is asymmetrical, with the medial portion being more proximally excavated than the lateral portion. The tuberositas retinaculi extensorii lateralis occupies most of the lateral half of the pons supratendineus and does not protrude beyond the proximal edge of the pons. The bony ridges for attachment of

the retinaculum m. fibularis are long and prominent flanges. The tuberositas retinaculi extensori medialis is mostly broken off in the fossil but part of its base is preserved. The base of this tuberosity indicates that its distal edge is at about the level of the bony ridges for the retinaculum m. fibularis, as in extant locustellids studied. The trochlea cartilaginosa tibialis is moderately wide.

The fossil tibiotarsus corresponds in size to that of *M. mathewsi* (Fig. 15H). A tuberositas retinaculi extensori lateralis that occupies the lateral half of the pons supratendineus was also observed in members of Dasyornithidae, Orthonychidae, Cinclosomatidae, Corvidae, Corcoracidae and Turdidae. QM F57941 can be excluded from Corvidae and Turdidae because the condylus medialis is narrower than the condylus lateralis, not equal in cranio-caudal width. The fossil is excluded from Orthonychidae and Cinclosomatidae because the shaft is narrow compared to the width of the distal end, not considerably broad. QM F57941 is excluded from Corcoracidae because the bony ridges for the retinaculum m. fibularis are well developed, not low. It is excluded from Dasyornithidae because the shaft is narrower with respect to the distal end and the lateral bony ridge for the retinaculum m. fibularis is a prominent flange.

Tarsometatarsus. QM F30375 (Fig. 16F) preserves only the trochleae metatarsorum II and III. This fossil specimen, however, is distinctive enough to allow its assignment to Locustellidae because it possesses the following features. The widths of the trochleae metatarsorum II et III are near equal. There is a deep furrow on the trochlea metatarsi II, resulting in a notched distal profile. The medial rim of the trochlea metatarsi II is greater in distal extent than the lateral rim. Although it is damaged, the preserved medial rim of this trochlea is dorsally elevated from the lateral rim.

The tarsometatarsi of locustellids are similar to that of *Acrocephalus australis* in that they share a distinctly deep furrow on the trochlea metatarsi II. However, QM F30375 can be excluded from *Acrocephalus* because it has a trochlea metatarsi II that is about equal in width to the trochlea metatarsi III, not narrower. In the fossil the medial and lateral rims of the trochlea metatarsi III are of equal distal extent, whereas in *Acrocephalus* the medial rim is greater in distal extent. It further differs from *Acrocephalus* because the notch in the distal profile of the trochlea metatarsi II is deeper. In dorsal aspect, the incisura intertrochlearis medialis is narrow but the trochleae metatarsorum II et III are clearly separated. In *Acrocephalus*, however, this incisura is much narrower and the trochleae metatarsorum II et III are in contact.

Remarks. Locustellidae is a family of small insectivorous passerines that are represented in Africa, Eurasia and Australasia (Alström *et al.*, 2011). In Australia, this family is represented by five species in the genus *Megalurus* (as recognised by Gill & Donsker, 2016) which were formerly assigned to Megaluridae (Christidis & Boles, 2008). Songlarks, *M. cruralis* and *M. mathewsi* (sometimes placed in *Cincloramphus*), are endemic to Australia and are commonly found in open eucalypt woodlands and forests with scattered trees, grasslands, shrublands and savanna. Grassbirds, *M. timoriensis* and *M. gramineus*, occur in reedbeds, grasslands, swamps, marshlands and wet coastal heathlands in Australo-Papua and Southeast Asia. The Spinifexbird, *M. carteri* (previously in *Eremiornis*), is endemic to Australia and inhabits spinifex (*Triodia*) grass near ranges and along watercourses (Pringle, 1982; Bairlein

et al., 2006; Higgins *et al.*, 2006). All of these species forage for small invertebrates and occasionally seeds on or near the ground. The Rufous Songlark, *M. mathewsi*, Brown Songlark, *M. cruralis* and *M. timoriensis*, occur in the Riversleigh region today.

In Victoria, late Quaternary fossils of *M. timoriensis* and *M. cruralis* have been recorded from Mabel Cave; those of *M. mathewsi* were reported from Harman's Cave; and remains of *M. cruralis*, *M. mathewsi* and *Megalurus* (*Cincloramphus*) sp. were identified from Cloggs Cave (Baird, 1986, 1991a). Late Pleistocene material referred to *M. cruralis* and cf. *Megalurus* (*Cincloramphus*) were found in Koonalda Cave in the Nullarbor region, Western Australia (Baird, 1991a). The specimens described here, which are at least early Pleistocene in age, represent the geologically oldest fossils of Locustellidae found in Australia. Fossils of *Locustella* spp. were reported from late Miocene and Pliocene deposits in Hungary (Kessler, 2013).

The fossil tarsometatarsi QM F57935 and QM F57937 share with songlarks a characteristically protuberant trochlea metatarsi II. In QM F57934 and QM F57936, however, the trochlea metatarsi II is not protuberant but gradually merges with the medial shaft edge, as in grassbirds and spinifexbirds. The differences in morphological features among these specimens indicate that at least two locustellid species were present in the Rackham's Roost avifauna.

Family Acrocephalidae Salvin, 1882

Genus *Acrocephalus*

Naumann & Naumann, 1811

Acrocephalus sp.

Fig. 17

Material. QM F30356, right carpometacarpus; QM F57902 (AR 10838), left carpometacarpus.

Measurements (mm). QM F30356: preserved length ca 11.75, proximal width >2.26, distal width >2.23. QM F57902: preserved length 11.93, proximal width ca 2.49, proximal length >1.91, length of os metacarpale alulare >1.27, distal width 2.42.

Description and comparisons. QM F57902 (Fig. 17A–B) and QM F30356 (Fig. 17C–D) are referred to *Acrocephalus* because they possess the following combination of features. The carpometacarpus is straight and elongate. The trochlea carpalis ventralis moderately protrudes caudally from the edge of the os metacarpale minus (damaged in QM F30356). The depression for the origin of *M. flexor digiti minoris* is deep and terminates distally of the proximal edge of the proc. pisiformis. In dorsal view, the spatium intermetacarpale proximally of the proc. intermetacarpalis is visible. The proc. intermetacarpalis is moderately short and does not protrude beyond the caudal edge of the os metacarpale minus. The fovea carpalis caudalis is small and deep. In QM F30356 and *A. australis* (Fig. 17E–F), the proc. dentiformis is long, low and situated well distally of the proximo-distal midpoint of the os metacarpale minus. Although the tip of the proc. dentiformis is broken in QM F57902, its base indicates that it was located well distally of this midpoint. The distal end of the os metacarpale minus is square and bears on its ventral surface a large, deep fossa.

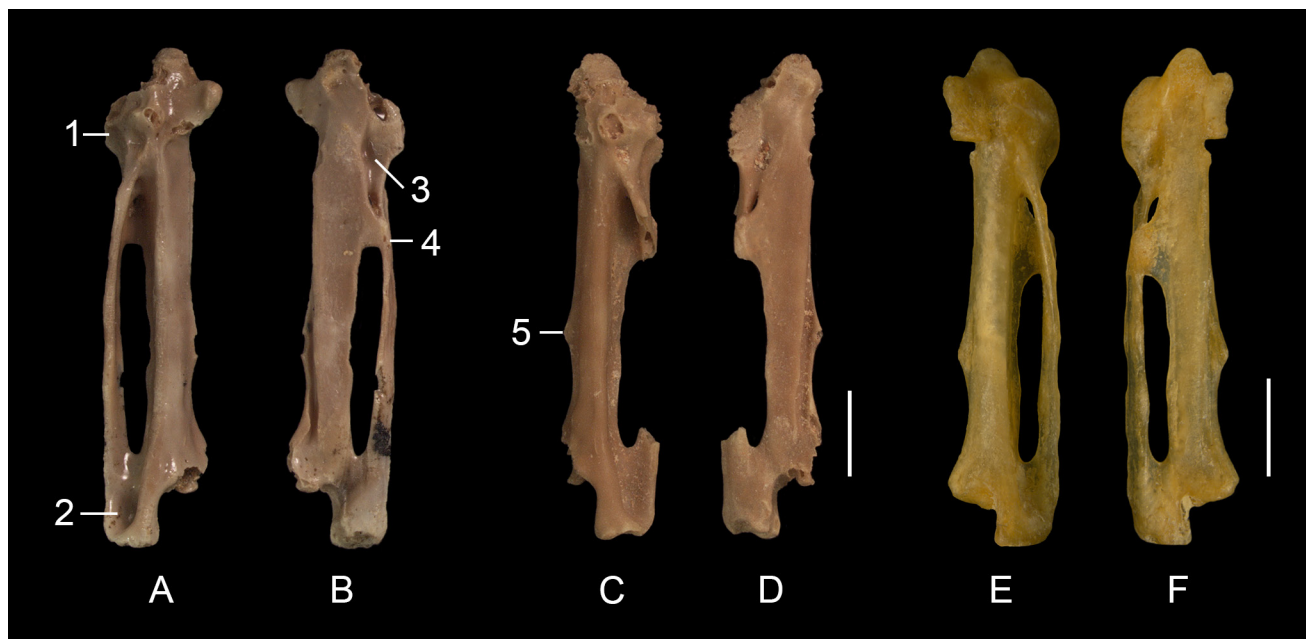


Figure 17. Carpometa-carpals of (A–D) fossil *Acrocephalus* sp. compared with the corresponding element of (E–F) *A. australis* AM O.58015. (A–B) QM F57902, left carpometa-carpus. (C–D) QM F30356, right carpometa-carpus. Some characteristic features of *Acrocephalus* shown: 1, depression for origin of *M. flexor digiti minoris* deep, terminates distally of proc. pisiformis; 2, ventral fossa on distal end of os metacarpale minus large and deep; 3, fovea carpalis caudalis small and deep; 4, proc. intermetacarpalis moderately short and does not protrude beyond caudal edge of os metacarpale minus; 5, proc. dentiformis long, low and situated well distally of midpoint of os metacarpale minus. Scale = 2 mm.

The fossil carpometa-carpals differ from that of *Acrocephalus australis* in only a few features. In the fossils, less of the spatium intermetacarpale is visible proximally of the proc. intermetacarpalis. The ventral fossa on the distal end of the os metacarpale minus is larger and deeper in the fossils, especially in QM F57902, than in *A. australis*. QM F57902 differs from QM F30356 and *A. australis* in having a slightly shorter proc. intermetacarpalis.

QM F30356 and QM F57902 are morphologically similar and are likely to represent one species. These fossils resemble *A. australis* in size and overall morphology but they cannot be confidently assigned to this species, owing to their fragmentary nature and unavailability of comparative material for other species of *Acrocephalus*.

Remarks. Reed warblers (*Acrocephalus* spp.) are small passerines that are currently distributed in the Old World: in Africa, Eurasia, Australasia and the west Pacific islands (Bairlein *et al.*, 2006). They inhabit aquatic or riparian areas with a dense cover of reeds, rushes, sedges, grasses and other rank vegetation (Pringle, 1982; Higgins *et al.*, 2006). These areas include reed beds, swamps, marshes and occasionally mangroves (Courtney-Haines, 1991; Higgins *et al.*, 2006). As well as these habitats, reed warblers have been recorded foraging in shrublands and woodlands close to wetland nesting sites (Gynther, 1994). These birds forage through dense growth for mainly insects and spiders (Courtney-Haines, 1991; Higgins *et al.*, 2006).

The Rackham's Roost material described here represents the only known fossil record of Acrocephalidae in Australia. Fossil species of *Acrocephalus* and *Hippolais* have been described from pre-Pleistocene sites in Hungary (Jánossy, 1991; Kessler, 2013). Acrocephalidae is currently represented in Australia by the Oriental Reed Warbler *A. orientalis* and the Australian Reed Warbler *A. australis*, the latter of which occurs in the Riversleigh region.

Family, genus et species indet.

Material. *Passeriformes indet.*: AR21856, distal right humerus; AR21857, distal left ulna; QM F30853, left carpometa-carpus; QM F29628, right carpometa-carpus; QM F36371, QM F36646, QM F39851, proximal right carpometa-carpals; AR21603, distal left carpometa-carpus; AR21858, AR21859, proximal left femora; AR21860, distal left femur; QM F30362, proximal right tibiotarsus; AR21861, distal left tibiotarsus; AR21862, proximal right tarsometatarsus; AR17405, AR21863, AR21864, AR21865, distal left tarsometatarsi; QM F30822, QM F36370, AR21866, AR21867, distal right tarsometatarsi. *Passeri indet.*: QM F30369, proximal left humerus; AR19822, right ulna; AR21868, AR21869, proximal left ulnae; AR21870, proximal right ulna; AR16067, AR19824, right carpometa-carpals; AR10837, AR21871, distal left carpometa-carpus; AR21872, AR21873, AR21874, distal right carpometa-carpals. *Corvides indet.*: QM F36672, left carpometa-carpus.

Remarks. Thirty-five Rackham's Roost postcranial fossils are identifiable as passerines but, owing to their fragmentary condition, they cannot be assigned to a family. Differences in morphology and size of these fossils suggest that they represent a minimum of 5 taxa. Of these fossils, QM F36646 represents the largest bird and is comparable in size to the carpometa-carpus of *Meliphaga lewinii*. AR21863 represents the smallest individual and is similar in size to the corresponding bone of a White-browed Scrubwren, *Sericornis frontalis*. Five of the indeterminate passerine fossils (AR16067, AR19824, QM F30822, QM F36672, AR21862) represent immature birds because the bone surfaces have a pitted appearance and the articular facets are incompletely ossified (Campbell, 1979). Four of the fossils (QM F30369, QM F30822, AR21858, AR21860) bear tooth punctures.

Among the indeterminate passerine fossils, 14 can be assigned to the suborder Passeri (oscines or songbirds). A proximal humerus, QM F30369, is identified as Passeri because it has a deep fossa pneumotricipitalis II that merges with the fossa pneumotricipitalis I and a crus dorsale fossae that is reduced to a small ridge. Together, these features are present in Pardalotidae and are characteristic of several families within Passerida *sensu stricto* (Johansson *et al.*, 2008) (Bock, 1962; Jánossy, 1983), a major songbird radiation that is primarily distributed in the Northern Hemisphere. Its fragmentary condition precludes the fossil from being excluded from Pardalotidae and referred to Passerida *sensu stricto*. Four ulnae are identified as Passeri because they have a reduced tub. lig. collateralis ventralis, which is characteristic of oscine passerines (Ballmann, 1969). Eight carpometacarpi are identified as Passeri because the disto-caudal portion of the os metacarpale majus is planar, and because they lack a distally protruding process on the disto-cranial edge of the os metacarpale minus. In Suboscines and Acanthisittidae, the disto-caudal portion of the os metacarpale majus protrudes dorsally (Manegold, 2008). Suboscines are further differentiated from other passerines by a distinct process on the distal end of the os metacarpale minus (Mourer-Chauviré *et al.*, 1989; Mayr & Manegold, 2006; Manegold, 2008), which is absent in all of the fossil carpometacarpi in this study.

One fossil is further identified as a member of the infra-order Corvides (formerly “core Corvoidea”), which includes the “crow-like” songbirds and kin. The carpometacarpus QM F36672 is referred to Corvides because it lacks a proc. dentiformis. This process is present in Acanthisittidae and suboscines but is absent in several oscine taxa within Corvides, including Campephagidae, Oriolidae, Artamidae, Rhipiduridae, Laniidae, Corvidae and Corcoracidae (Pocock, 1966; Harrison, 1969; JMTN, pers obs.). The proc. dentiformis is also absent in some ptilonorhynchids (in other species it is extremely reduced, JMTN, pers obs.). However, QM F36672 can be excluded from Ptilonorhynchidae because it is considerably smaller in size and the trochlea carpalis dorsalis is relatively shorter. In the fossil, the distal edge of the trochlea carpalis ventralis smoothly merges with the caudal edge of the os metacarpale minus, whereas in ptilonorhynchids it is angular and abruptly joins the os metacarpale minus.

Discussion

Significance

The Rackham’s Roost fossils described here fill a substantial gap in the global passerine record and provide new insights into Australia’s avifaunal history. The material, which is at least early Pleistocene in age, represents eight families and considerably increases the diversity of birds known from Rackham’s Roost Site (Table 1) and the Riversleigh deposits overall. All of the Rackham’s Roost specimens described here can be attributed to extant families. Most represent the first records of these groups from the Riversleigh World Heritage fossil deposits. These newly reported families include Maluridae (fairywrens and allies), Acanthizidae (acanthizid warblers), Pomatostomidae (Australo-Papuan babblers), Petroicidae (Australasian robins), Estrildidae (estrildid finches), Locustellidae (songlarks and grassbirds)

and Acrocephalidae (reed warblers). The fossils that represent these families form the oldest described records of these groups in Australia. The fossils referred to Maluridae, Acanthizidae, Pomatostomidae, Petroicidae and Estrildidae in this study also represent the oldest known occurrences of these families globally.

Remains of Estrildidae, Locustellidae and Acrocephalidae from Rackham’s Roost are significant because they provide the earliest known evidence of the major oscine radiation Passerida *sensu stricto* (Johansson *et al.*, 2008) in Australia. It is thought that Passerida originated from an ancestral species that dispersed from the Australasian region, and diversified and expanded globally (Johansson *et al.*, 2008; Barker, 2011). This dispersal from Australasia has been estimated to have occurred in the Eocene around 53–34 Ma (Barker *et al.*, 2004; Ericson *et al.*, 2014; but see Mayr, 2013) to even as late as the Oligo-Miocene (Prum *et al.*, 2015; Selvatti *et al.*, 2015), although there is debate about whether this ancestral passeridan lineage dispersed from Australasia to Asia (Barker *et al.*, 2002, 2004; Ericson *et al.* 2002) or to Africa (Fuchs *et al.*, 2006; Jönsson & Fjeldså, 2006; Jönsson *et al.*, 2007). Phylogenetic studies of Passerida have suggested that several families of the radiation, including Locustellidae and Acrocephalidae, re-entered Australia later but the timing of this second dispersal event is still uncertain (Schodde, 2006; Roshier & Joseph, 2014). The Rackham’s Roost fossils thus provide a minimum early Pleistocene age for this second dispersal event (see Geological Setting).

Despite their enormous abundance and diversity, passerines do not exhibit the same degree of morphological variation as non-passerine birds. Apart from their bills and overall proportions, passerines have traditionally been thought to be morphologically relatively uniform (e.g., Wetmore, 1960; Bock, 1962; Olson, 1985). This uniformity makes it easy to distinguish them from non-passerines, but difficult to separate them below the subordinal level. Identification and detailed study of fossil passerines has long been hindered by this traditional view, as well as the lack of phylogenetically informative characters identified for these birds, despite numerous studies of their morphology (Olson, 1985). Recent studies of fossil passerines have shown that there are phylogenetically informative osteological features that can be used to distinguish among passerine subclades (e.g., Manegold *et al.*, 2004; Manegold, 2008; Zelenkov & Kurochkin, 2012). However, there are few studies that have identified such characters for Australian passerines (e.g., Baird, 1992, 1993; Boles, 2005; Nguyen *et al.*, 2013). In identifying the Rackham’s Roost fossils, we have identified suites of characters that we consider diagnostic for a range of passerine groups that occur in Australia, including endemics and more widespread taxa. These character descriptions can be used in future palaeontological, morphological and phylogenetic studies of passerines.

Taphonomy

The Rackham’s Roost assemblage is dominated by rodents, with several thousand specimens representing at least twelve taxa (Godthelp, 2001), including *Zyomys rackhami* Godthelp, 1997 and *Leggadina gregoriensis* Klinkhamer & Godthelp, 2015. There are many specimens representing at least ten species of bats (Hand, 1996), including *Macroderma gigas* (see Hand, 1996), *Megaderma richardsi* Hand, 1995 and *Hipposideros winsburyorum* Hand & Godthelp, 1999.

Table 1. Summary of passerine birds from the Rackham's Roost Local Fauna studied to date. *Indet.* = indeterminate; *N* = number of specimens; *MNI* = minimum number of individuals (determined by counting the most abundant element from a particular side of the body).

Taxon		N	MNI
Maluridae	Gen. et sp. indet.	1	1
Meliphagidae	Gen. indet. sp. indet. 1 (Boles, 2005)*	1	1
	Gen. indet. sp. indet. 2 (Boles, 2005)	1	1
	Gen. indet. sp. indet. 3 (Boles, 2005)	1	1
	Gen. indet. sp. indet. 4	3	1
	Gen. indet. sp. indet. 5	1	1
	Gen. indet. sp. indet. 6	1	1
?Meliphagidae	Gen. indet. sp. 1	2	1
	Gen. indet. sp. 2	2	1
	Gen. indet. sp. 3	1	1
Acanthizidae	Gen. et sp. indet.	2	1
Pomatostomidae	<i>Pomatostomus</i> sp.	6	2
Petroicidae	Gen. et sp. indet.	3	1
?Petroicidae	Gen. et sp. indet.	1	1
Estrildidae	Gen. indet. sp. indet. 1	2	1
	Gen. indet. sp. indet. 2	1	1
	Gen. indet. sp. indet. 3	1	1
Locustellidae	<i>Megalurus</i> sp. indet. 1	4	2
	<i>Megalurus</i> sp. indet. 2	3	2
	Gen. et sp. indet.	2	1
Acrocephalidae	<i>Acrocephalus</i> sp.	2	1
Passeriformes	Passeriformes indet.	22	6
	Passeri indet.	12	3
	Corvides indet.	1	1
		76	34

* Boles (2005) tentatively referred a tarsometatarsus (QM F36443) to cf. *Lichenostomus-Meliphaga*, but Gardner *et al.* (2010) and Nyári & Joseph (2011) found that *Lichenostomus* is paraphyletic. The 20 species that were formerly united in *Lichenostomus* have been split into seven genera (Nyári & Joseph, 2011; Dickinson & Christidis, 2014). Therefore, the taxon represented by QM F36443 is identified here as meliphagid genus et species indet.

In addition to honeyeaters (Boles, 2005), other bird fossils previously reported at this site include those of the extant Budgerigar, *Melopsittacus undulatus* (see Boles, 1998). Also recorded from Rackham's Roost Site are fragmentary remains of frogs, lizards, snakes, dasyurids (*Planigale*, *Sminthopsis*), bandicoots, possums (*Petroseudes dahli*) and macropodoids (e.g., *Bettongia*, *Protemnodon*, *Macropus*) (Hand, 1996; Archer *et al.*, 2000, 2006).

Dense bone accumulations of microfauna typically result from carnivore latrines or predatory bird roosts (Andrews, 1990). In the main, the accumulation of bones at Rackham's Roost Site suggests it was an accumulation site for remains of the prey of an early population of the still-surviving carnivorous Ghost Bat, *Macroderma gigas* (Megadermatidae) (Hand, 1995, 1996; Boles 1999b). This is suggested by the overrepresentation of small nocturnal animals at the site, the highly fragmented nature of their remains and the occasional indication of penetration by small but powerful canines (Figs 12F, 16D). Snakes and other bat species probably co-habited the cave, while the macropodoids may have used it for shelter.

Ghost Bats capture vertebrate and invertebrate prey by gleaning, landing on top of them or capturing them in the air. Prey are eaten at the point of capture or carried back to roosting caves. Small mammals are ingested whole whereas parts of birds and larger mammals, such as skulls, feathers, legs and tails, are dropped to the ground. Discarded remains

accumulate, providing an indication of the prey species of the Ghost Bat (Douglas, 1967, Guppy & Coles, 1983; Tidemann *et al.*, 1985; Boles, 1999b). Small dentary fragments and isolated teeth are often the only diagnostic elements remaining for mammalian prey (Hand, 1996). Boles (1999b), however, showed that while the pectoral regions of birds sustain severe damage by Ghost Bats, the distal elements of the wings and hind limbs often remain undamaged. This pattern is evident in the small passerine bones recovered from Rackham's Roost, which mostly consist of distal elements including carpometacarpi, tibiotarsi and tarsometatarsi. Most of the breaks in these bones appear to have resulted from predepositional damage by these volant predators.

The size range of avian prey taken by Ghost Bats is 6–60 g, but there is a bias towards smaller prey weighing 35 g or less (Schultz, 1986; Boles, 1999b). The passerine fossils from Rackham's Roost represent small birds that are within this latter range. Some of these birds (malurids, pomatostomids and locustellids) have living relatives that forage on the ground, but Ghost Bats opportunistically select their prey and capture them in a wide range of situations. Boles (1999b), however, found an overrepresentation of avian prey species of Ghost Bats that aggregate when roosting. The Rackham's Roost fossils include representatives of estrildid finches, which roost in close association (Higgins *et al.*, 2006) and may have thus been more easily located by Ghost Bats. Extant pomatostomids also roost in close aggregations but

in enclosed roosting nests (Boles, 1999b; Matthew, 2007).

This presumed entrapment mechanism for the Rackham's Roost passerines differs from those in other Australian fossil bird deposits. In contrast to the Riversleigh fossils, the main taphonomic accumulator of passerines in several Quaternary cave deposits in Victoria, South Australia and Western Australia were tytonid owls (Tytonidae) (Baird, 1989, 1991a; Baird and Rowley, 1990). Bones accumulated by tytonid owls are characterised by relatively good preservation and representation of all skeletal elements. Owl pellets contain undamaged whole bones as well as bones corroded from stomach acid (Andrews, 1990; Worthy & Holdaway, 1994). Owl prey are largely terrestrial species and gregarious volant birds, similar to those accumulated by Ghost Bats, but their prey size is much greater, with a body-size distribution up to 100 g (Baird & Rowley, 1990). Boles (2000) did not find evidence of owl predation in any of the Riversleigh bird assemblages, and no predatory bird remains have yet been recovered at Rackham's Roost (Boles, 1997). Prey bones from the pellets of diurnal raptors are heavily fragmented and few remains are recognisable (Bocheński, 2002; Worthy & Holdaway, 2004).

Although it is possible that some of the predation that contributed to the Rackham's Roost deposit was the result of marsupial carnivores (dasyurids and/or bandicoots), these non-volant, 'handed' predators do not as a rule leave the distal elements of their prey intact in the manner normal for megadermatids. With manual dexterity and because they feed on the ground, dasyurids normally consume all parts of their smaller prey. Bone fragments recovered in marsupial carnivore lair deposits have as a result ordinarily been commuted into small pieces by the teeth before being passed through the digestive tract. As a result, they commonly exhibit signs of acid dissolution. Larger reptiles have been similarly shown to leave distinctive tooth marks on bone (Bassarova, 2004; Nguyen *et al.*, 2010) but there is no evidence that predatory reptiles made any significant contribution to this assemblage. Further, the stomach acid of at least snakes completely dissolves the bones that these reptiles consume.

Bird bones from late Oligocene to middle Miocene Riversleigh fossil sites also show evidence of predation by older megadermatids. Seven Riversleigh megadermatids have been described from late Oligocene to Recent deposits (Hand, 2006), most being related or referable to the endemic Australian genus *Macroderma*. Megadermatids are commonly found throughout the Riversleigh deposits, with often two species co-occurring in single sites. They range in size from one-half to two-thirds that of the living *M. gigas* to approximately the same size as *M. gigas* or larger. Given the apparent scarcity of carnivorous birds in the Miocene deposits of Riversleigh (Boles, 2000), megadermatids appear to have been the most significant aerial predators of small vertebrates in Riversleigh's mid to late Cenozoic forests (e.g., Hand, 1990).

Our study of the Rackham's Roost birds also provides a record of the avian diet of Australia's endangered *Macroderma gigas* in the Gulf Region of northwestern Queensland, before it became locally extinct. The disappearance of the Ghost Bat from the Riversleigh-Lawn Hill area during the last decade is thought to be at least in part due to the recent inclusion in its diet of the toxic

invasive Cane Toad *Bufo marinus* (White, 2014). Seven of the eight of families represented by the Rackham's Roost fossils (Maluridae, Meliphagidae, Acanthizidae, Pomatostomidae, Petroicidae, Estrildidae, Locustellidae) have been recorded in modern *M. gigas* prey accumulations in the Pilbara region, Western Australia (Douglas, 1967); Pine Creek area, Northern Territory (Pettigrew *et al.*, 1985; Schulz, 1986; Boles, 1999b); and Fitzroy Caves National Park and Mt Etna, Queensland (Toop, 1985).

Palaeoenvironmental interpretation

In the later Cenozoic, global climate fluctuated markedly with the expansion and contraction of the Arctic and Antarctic ice sheets, but with an overall decline in temperature and rainfall (Zachos *et al.*, 2001). During the Pliocene much of Australia remained forested, the vegetation being mainly sclerophyll/woodland but with vegetation gradients across the continent with wetter forests closer to the continental margins and arid shrublands and grasslands emerging in central Australia in the later Pliocene (Martin, 2006). In the Pleistocene, glaciation was limited to parts of south-eastern Australia, with glacial periods generally characterised by dry, cold conditions and interglacial periods by warmer, wetter climates (McGowran *et al.*, 2000), resulting in expansion of forests and woodlands during interglacials and spread of open shrublands and grasslands during glacials (Martin, 2006).

The palaeoenvironment of Rackham's Roost Site has been interpreted to represent open woodland with a grassy understorey, possibly adjacent to riparian forest, similar to that of the Riversleigh region today (Archer *et al.*, 1989). This environmental interpretation is based on the site's fossil mammalian fauna, which comprises taxa characteristic of open habitats rather than rainforest (Archer *et al.*, 2000). Mammal groups that were dominant in the Oligo-Miocene rainforest communities at Riversleigh went extinct, migrated or adapted when the environmental conditions changed during this time (Archer *et al.*, 2000). This palaeoenvironmental interpretation is supported by current understanding of mid to late Cenozoic environmental change in Australia (McGowran *et al.*, 2000; Martin, 2006; Woodhead *et al.*, 2016).

The habitat of the Rackham's Roost passerines can be inferred if we assume that they have ecological characteristics similar to their living relatives (Boles, 1997). The majority of these fossil passerines have modern counterparts that occupy a wide range of terrestrial habitats. Extant malurids, meliphagids, acanthizids, pomatostomids and petroicids occur in closed to open forests and woodlands in tropical to arid bioclimatic zones. Acrocephaline warblers, however, are strongly associated with dense vegetation near water, such as lake edges and swamps. Estrildid finches predominantly feed on grass seeds and are often found in grassy habitats close to water. Living species of *Megalurus* are found in open environments, including grassy open woodland, grassland and shrubland, as well as marshy habitats. Together, the presence of these passerines at Rackham's Roost does not contradict the palaeoenvironmental interpretation of this site as open woodlands with a grassy understorey in the immediate area, probably with adjacent areas of denser riparian forest bordering the Gregory River.

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Appendix 1. Comparative material examined in this study.

- Maluridae.** *Clytomyias insignis* Sharpe, 1879 NMV B20773. *Malurus elegans* Gould, 1837 AM O.70782. *Malurus lamberti* Vigors & Horsfield, 1827 AM O.56650; AM O.56651; AM O.56652. *Malurus cyaneus* (Ellis, 1782) AM O.64810; AM O.66037; AM O.66344. *Malurus splendens* (Quoy & Gaimard, 1832) AM O.70220. *Malurus melanocephalus* (Latham, 1801) AM O.68203; AM O.68204. *Stiptiturus malachurus* (Shaw, 1798) AM O.66310; AM O.68207; AM O.68274. *Amytornis woodwardi* Hartert, 1905 ANWC PASS-389. *Amytornis purnelli* (Mathews, 1914) NMV B8975.
- Meliphagidae.** *Acanthorhynchus tenuirostris* (Latham, 1801) AM O.59216; AM O.65136. *Meliphaga lewinii* (Swainson, 1837) AM O.58069; AM O.60079. *Ptilotula flavescens* (Gould, 1840) AM O.66333; AM O.70452. *Stomiopera unicolor* (Gould, 1843) AM O.70570. *Manorina melanophrys* (Latham, 1801) AM O.59295; AM O.60071. *Manorina melanocephala* (Latham, 1801) AM O.59896; AM O.66137. *Anthochaera carunculata* (Shaw, 1790) AM O.56971; AM O.60082; AM O.71379. *Conopophila albogularis* (Gould, 1843) AM O.70096. *Conopophila rufogularis* (Gould, 1843) AM O.70563. *Myzomela obscura* Gould, 1843 AM O.64726; AM O.65082. *Gliciphila melanops* (Latham, 1801) AM O.65515. *Lichmera indistincta* (Vigors & Horsfield, 1827) AM O.65514; AM O.73853. *Nesoptilotis leucotis* (Latham, 1801) AM O.59863; AM O.60943. *Melithreptus lunatus* (Vieillot, 1802) AM O.59865; AM O.60051. *Philemon citreogularis* (Gould, 1837) AM O.60084; AM O.60938. *Xanthotis flaviventer* (Lesson, 1828) AM O.60487; AM O.62425.
- Pardalotidae.** *Pardalotus punctatus* (Shaw, 1792) AM O.60927; AM O.72294. *Pardalotus striatus* (Gmelin, 1789) AM O.58065; AM O.64706; AM O.66120.
- Acanthizidae.** *Gerygone fusca* (Gould, 1838) AM O.65081; AM O.66088. *Smicrornis brevirostris* (Gould, 1838) AM O.60946; AM O.71367. *Pycnophilus floccosus* Gould, 1851 AM O.58083; NMV B.14071; NMV B.20710. *Pyrrholaemus sagittatus* (Latham, 1801) AM O.64948; AM O.65127. *Calamanthus pyrrhopygius* (Vigors & Horsfield, 1827) AM O.59226; AM O.70212. *Origma solitaria* (Lewin, 1808) AM O.58928; AM O.66315. *Crateroscelis robusta* (De Vis, 1898) ANWC PASS-1052. *Sericornis frontalis* (Vigors & Horsfield, 1827) AM O.68202. *Acanthornis magna* (Gould, 1855) ANWC 24392. *Aphelocephala leucopsis* (Gould, 1841) AM O.66346; AM O.68276; AM O.73293. *Acanthiza pusilla* (Shaw, 1790) AM O.65114; AM O.65846.
- Pomatostomidae.** *Garritornis isidorei* (Lesson, 1827) NMV B19239; NMV B19279. *Pomatostomus temporalis* (Vigors & Horsfield, 1827) AM O.65103; AM O.65522; AM O.68150; AM O.68479. *Pomatostomus halli* Cowles, 1964 AM O.67636; AM O.68250; AM O.73294. *Pomatostomus superciliosus* (Vigors & Horsfield, 1827) AM O.60416; AM O.60904; AM O.67641. *Pomatostomus ruficeps* (Hartlaub, 1852) AM O.60045; AM O.67045.
- Petroicidae.** *Amalocichla incerta* (Salvadori, 1876) ANWC 24513. *Pachycephalopsis poliosoma* Sharpe, 1882 ANC 24511; ANWC 24512. *Petroica phoenicea* Gould, 1837 AM O.60008. *Petroica goodenovii* (Vigors & Horsfield, 1827) AM O.59862; AM O.65851. *Kempiella flavovirescens* (G.R. Gray, 1858) ANWC 24468; ANWC 24469. *Devioeca papuana* (A.B. Meyer, 1875) ANWC 24472. *Monachella muelleriana* (Schlegel, 1871) ANWC 26732. *Microeca flavigaster* Gould, 1843 ANWC 24470; ANWC 24471. *Microeca fascians* (Latham, 1801) AM O.60400; AM O.65147. *Drymodes superciliaris* Gould, 1850 AM O.60089. *Drymodes brunneopygia* Gould, 1841 ANWC 48484. *Plesiodyras albonotata* (Salvadori, 1875) ANWC 24503; ANWC 27385. *Poecilodyras cerviniventris* (Gould, 1858) ANWC 28435; ANWC 28436. *Heteromyias albispecularis* (Salvadori, 1876) ANWC 39640. *Heteromyias cinereifrons* (EP Ramsay, 1876) AM O.70453; AM O.71332. *Eopsaltria australis* (Shaw, 1790) AM O.60955; AM O.65085. *Eopsaltria griseogularis* Gould, 1838. AM O.58906; ANWC 24499. *Tregellasia leucops* (Salvadori, 1875) AM O.57716; AM O.60951. *Tregellasia capito* (Gould, 1854) AM O.59874; AM O.60010. *Melanodyras cucullata* (Latham, 1801) AM O.62422; AM O.64764. *Melanodyras vittata* (Quoy & Gaimard, 1830) ANWC 20581. *Peneothello sigillata* (De Vis, 1890) ANWC 24510. *Peneothello cyanus* (Salvadori, 1874) ANWC 24504.
- Estrildidae.** *Lonchura castaneothorax* (Gould, 1837) AM O.73354; AM S.817. *Lonchura oryzivora* (Linnaeus, 1758) AM O.66319. *Heteromunia pectoralis* (Gould, 1841) AM O.64839. *Stagonopleura bella* (Latham, 1801) AM O.64561. *Stagonopleura guttata* (Shaw, 1796) AM O.64967. *Neochmia phaeton* (Hombron & Jacquinot, 1841) AM O.60073; AM O.72296. *Neochmia ruficauda* (Gould, 1837) AM O.60050. *Poephila personata* Gould, 1842 AM O.64756; AM O.64843. *Poephila acuticauda* (Gould, 1840) AM O.60445; AM O.70095. *Taeniopygia guttata* (Vieillot, 1817) AM O.64559; AM O.66347. *Taeniopygia bichenovii* (Vigors & Horsfield, 1827) AM O.70208; AM O.71329. *Erythrura trichroa* (von Kittlitz, 1833) AM O.59218.
- Locustellidae.** *Megalurus mathewsi* (Iredale, 1911) AM O.59225; AM O.59292; AM O.66320. *Megalurus cruralis* Vigors & Horsfield, 1827 AM O.59220; AM O.70458; AM O.72289. *Megalurus gramineus* (Gould, 1845) NMV B8604; NMV B20313. *Megalurus carteri* (North, 1900) AM O.64767; AM O.68253. *Megalurus timoriensis* Wallace, 1864 AM O.60401; AM O.65209; AM O.71682.
- Acrocephalidae.** *Acrocephalus australis* (Gould, 1838) AM O.58015; NMV B31488.