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A preliminary analysis of the Passeriformes from Riversleigh, Northwestern Queensland, Australia, with the description of a new species of Lyrebird

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Abstract

The Passeriformes comprise more than 5000 species of Recent birds. Their Tertiary fossil record begins in Upper Oligocene deposits of France and has thus far been virtually restricted to the Northern Hemisphere. This paper is the first detailed, although still preliminary, report from Australia. It is based on 92 passerine bones from 20 sites (19 Oligo-Miocene and one Pliocene) that have been recovered from Tertiary deposits at Riversleigh, Queensland. These specimens exhibit a range of sizes and forms, and represent a number of taxa; most remain to be identified further. One carpometacarpus is referred to the Tyranni. A femur and a carpometacarpus belong to the living genera *Orthonyx* and *Menura*, respectively.

Key words: Australia; lyrebird; *Menura;* Passeriformes; Riversleigh; songbird; Tertiary; Tyranni.

Kurzfassung

Zu den rezenten Passeriformes gehören über 5000 Arten. Die bisher bekannten Fossilien dieser Ordnung reichen bis in das Ober-Oligozän Frankreichs zurück und sind auf die Nordhalbkugel beschränkt. Dieser Aufsatz ist der erste ausführliche, wenn auch immer noch vorläufige Bericht aus Australien. Er stützt sich auf 92 Sperlingsvogelknochen von 20 Fundorten (19 aus dem Oligo-Miozän, 1 aus dem Pliozän) in den tertiären Ablagerungen von Riversleigh, Queensland. Die Funde belegen einen weite Spanne von Größen und Formen und repräsentieren eine Reihe von Taxa, die größtenteils noch genauer bestimmt werden müssen. Ein Carpometacarpus wird den Tyranni zugeordnet. Die rezenten Gattungen *Orthonyx* und *Menura* werden durch ein Femur, bzw. einen Carpometacarpus belegt.

Schlagwörter: Australien; Leierschwänze; *Menura;* Passeriformes; Riversleigh; Tertiär; Tyranni.

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Introduction

The Passeriformes (songbirds) comprise about 60% of the more than 9000 Recent species of birds. Two questions about this highly successful order have attracted considerable attention: what are the intra-ordinal relationships among the families, and where did the passerines originate and radiate. It is recognized that the traditional Basel and Wetmore sequences almost certainly present quite inaccurate pictures of songbird inter-relationships. Extensive studies by SIBLEY & AHLQUIST using DNA-DNA hybridization (summarized in SIBLEY & AHLQUIST 1990) have arrived at conclusions at striking variance with the traditional classifications, with radically changed sequences and family compositions. These changes have not met with universal acceptance. Studies by other workers, however, are starting to corroborate parts of this novel arrangement, e.g., CHRISTIDIS & SCHODDE (1991).

Early theories (e.g., MAYR 1944) proposed that passerines evolved in the Northern Hemisphere, from which they invaded Australia and surrounding islands. The various morphotypes of the Australian avifauna were considered extensions of similar northern counterparts. Based on paleontological data, FEDUCCIA (1977) and OLSON & FEDUCCIA (1979) pointed out that the Passeriformes do not become prevalent in the fossil record until the Miocene. These first appear in the northern fossil record in the Late Oligocene, but do not become common until the Middle Miocene. Small land birds, dominated by Coraciiformes, are known from a number of Eocene and Oligocene sites, but other than scanty Upper Oligocene material, none are passerines. Because of this, several authors (e.g. FEDUCCIA & OLSON 1982; OLSON 1988; MACLEAN 1990) proposed that the Passeriformes originated in the Southern Hemisphere, spreading from there to the Northern Hemisphere about the Late Oligocene/Early Miocene.

SIBLEY & AHLQUIST (1985) proposed a more detailed pattern of songbird dispersion and radiation. Their data suggested that the passerines originated at least by 95 MYA. The Tyranni (sensu SIBLEY & AHLQUIST = Suboscines = Deutero-Oscines) diverged from other passerines at 90-85 MYA. The remaining passerines (Passeri = oscines) separated into two major branches at 60-58 MYA. One branch, the Passerida, originated in Africa, dispersing to Eurasia and the New World. The other branch, the Corvida, originated in Australia, radiating there in the Tertiary while the continent was isolated from other large land masses. In the Late Oligocene/Miocene, as Australian approached Asia, the ancestors of the Corvini dispersed to the Northern Hemisphere, where they radiated, before subsequently recolonizing Australia. Australian members of the Passerida are for the most part more recent colonizers. The record of the Passeriformes in Australia therefore plays an integral part in interpreting the biogeographical history of this order.

Previously reported fossil passerines have originated from the Northern Hemisphere; virtually nothing has appeared on those from the South Hemisphere. Presented here is a preliminary analysis of the passerine remains recovered from the deposits at Riversleigh, the richest Tertiary source in Australia for this order.

Fossil History

While the known passerine paleofauna is by no means depauperate, few workers have devoted much effort to identifying material below ordinal level. Most nominal fossil passerine taxa presented by BRODKORB (1978) were of Pleistocene or Recent age, the majority representing neospecies. OLSON's (1985) review of the Tertiary songbird record rejected as misplaced several putative taxa, including all from the Eocene and Oligocene. He accepted as the earliest named passerines three taxa from the Early Miocene of France (MILNE-EDWARDS 1867-1871), although nothing could be said about their relationships. Other passerines of similar age have been reported, with increasing numbers being known through the Miocene, all from the Northern Hemisphere (see OLSON [1985] for references), except for that of NORIEGA & CHIAPPE (in press) from Argentina. BALLMAN's (1969) Tertiary record of the Eurylaimidae is the earliest for the Tyranni.

The most important passerine find since OLSON's (1985) review has been that of MOURER-CHAUVIRÉ et al. (1989). They reported two passerine bones from Upper Oligocene sites at Coderet (proximal tarsometatarsus) and Gannat (partial carpometacarpus), France, which they considered to be oscine. Their report constitutes the earliest unquestioned records of the Passeriformes and of the oscines. VICKERS-RICH (1991) and BAIRD (1991) reviewed Australia's Tertiary and Quaternary fossil records of passerines, respectively. Tertiary material of songbirds is known from several sites, but only from Riversleigh is there a substantial amount. BOLES (1993 a) described from Riversleigh the first Tertiary Australian passerine, a femur indistinguishable from the living logrunner genus *Orthonyx*. That and the specimens discussed herein are the only Australian Tertiary passerines that have thus far received attention. In contrast, Quaternary fossils have been extensively studied by BAIRD (1991 and papers cited therein), who found many families represented, with most diagnosable elements attributable to living species.

Taxa from Riversleigh thus far studied comprise a mixture of forms (a) indistinguishable from extant genera (*Orthonyx*, BOLES 1993 a; *Cacatua* BOLES 1993 b), (b) separate from, but obviously related to, extant genera (*Emuarius*, BOLES 1992), and (c) with no obvious relationships to other genera (accipitrid, BOLES 1993 c) or families (Dromornithidae, BOLES 1991).

Methods

For convenience of reference, the names of suprageneric taxa follow SIBLEY & AHLQUIST (1990). With only a few exceptions, this survey has been restricted to the most common elements: carpometacarpus, tibiotarsus and tarsometatarsus. Other elements are present, but little effort has been made to identify them at this time. Measurements were made with vernier calipers accurate to 0.05 mm and rounded to the nearest 0.1 mm. Terminology of bones primarily follows that of Figures 1-54 of HOWARD (1929). The Riversleigh specimens are currently held in the collection of the Vertebrate Palaeontology Laboratory, University of New South Wales (AR), but will be transfered to the Queensland Museum (QM) at the completion of this study.

Geological and Geographic Setting

The Riversleigh deposits are located 200 km north of Mt Isa, northwestern Queensland, where they occur as an outcrop of Tertiary limestone overlying the Cambrian Thorntonia Limestone (see ARCHER et al. 1989, ARCHER et al. 1991 for detailed discussion of the history of these deposits). The principal accumulation is thought to have occurred in several episodes involving large lakes, shallow pools and cave deposits. Some 150 sites are now known. The understanding of the relationships of the sites to each other is in its early stages. Three 'systems' (A, B and C) have been recognized, into which most of the Tertiary sites can be allocated. These systems are "regionally clustered sites that appear to be superpositionally-related (differing in age but not significantly in position) and/or space-related (spatially isolated but approximately contemporaneous)" (ARCHER et al. 1989).

System A is thought to be of ?Late Oligocene-Early Miocene age. No passerine material is known from System A. Some sites are tentatively considered to be of similar age ('D-Site equivalents') although they are not contiguous with other System A deposits. Passerine remains have been recovered from one such site. System B sites are considered ?Early Miocene. Passerines are known from ten System B sites. System C is considered ?Middle Miocene to early Late Miocene in age. Passerines are known from eight sites. The only Pliocene site is a cave floor featuring a fossil accumulation by megadermatid bats. Passerines have been found at this site, but not from any Pleistocene or Recent sites.

Results

Passerines have been recorded to date from 20 sites in the Riversleigh deposits, comprising 92 bones (System A, one specimen; System B, 27; System C, 49; Pliocene, 14). About half of these are too damaged to permit assessment beyond ordinal identification. One specimen has been assigned to the Tyranni. In the following accounts, for each element are given the total number of specimens and the number of specimens/sites represented for each system (A-C, P).

Humerus (3; 1/1 B, 1/1 C, 1/1 P; Fig. 1a) - Two complete and one proximal humeri are known. The complete humeri are oscine (characters from BALLMAN 1969) and have a single pneumatic tricipital fossa (see BOCK 1962 and others), indicating that they could represent members of the Corvida. From differences in morphology two taxa are indicated. These specimens are 14.7 and 16.0 mm in length. The proximal segment has a single fossa, with perhaps a rudimentary beginning of a second, but is too damaged for further assessment.

Ulna (1; 1/1 C) - A single complete ulna is oscine (characters from BALLMAN 1969). It is 28.9 mm long.

Carpometacarpus (34; 10/3 B, 15/5 C, 8/1 P; Fig. 1b) - Many specimens are too damaged to measure; however, those which have suffered only loss of the shaft of metacarpal II or the extensor attachment can still yield a total length. Of the 16 specimens that can be measured, all but one fall within the range 7.5-16.0 mm; one measures 29.3 mm. The condition of the dentiform process (= process D of POCOCK 1969; HARRISON 1969 = carpometacarpal process) was assessed because its absence characterizes some groups of passerines. Characters given by MOURER-CHAUVIRÉ et al. (1989) for identification of Tyranni were examined.

One specimen represents a member of the suborder Tyranni (Fig. 1e). It is short (9.7 mm) and stout, with a well-formed dentiform process and pronounced curvature of metacarpal III, suggesting that the bird had reduced flight capability. It does not match any living Tyranni examined.

Two specimens are clearly oscines lacking dentiform processes. This suggests, but does not confirm, that they came from birds that belong to, or were ancestors of, the Corvoidea. These are of like size

(10.7 and 11.0 mm respectively), morphologically similar and from the same site. They come from two individuals but may represent the same taxon.

The remaining specimens are oscines with dentiform processes. The size of the process varies among the bones, from high, pointed and well defined, to low, flat and poorly defined. A cursory examination indicates that the ten complete carpometacarpi represent at least eight taxa. The largest is quite distinctive (Fig. 1d,e) and is described later in this paper.

Femur (2; 1/1 B, 1/1 C; Fig. 1f) - Only two femora have thus far been identified as passerine. One of these is of particular interest. It cannot be distinguished from the genus *Orthonyx* (logrunners; Orthonychidae: Corvoidea: Corvida), the sole component of this family of distinctive ground birds that is endemic to Australo-Papua. There are two living and two fossil (Quaternary) species. The Riversleigh form, described as *O. kaldowinyeri* by BOLES (1993 a), is somewhat smaller than the other taxa (length 19.7 mm).

The other femur, which is complete, is the only instance of association with other elements (broken tibiotarsus and tarsometatarsus). It is 19.5 mm long.

Tibiotarsus (18; 7/6 B, 8/5 C, 3/1 P; Fig. 1g) - All specimens are incomplete. No attempt has yet been made to identify these beyond the level of Passeriformes. The size range indicates that at least six taxa are represented.

Tarsometatarsus (33; 1/1 A, 7/5 B, 23/6 C, 2 P; Fig. 1h) - Only three are complete, although several others are missing only the proximal-most portion. Distal sections are by far the best represented; some of these, however, are so fragmentary that nothing more can be determined. Using characters given by BALLMAN (1969), all appear to be oscine. The complete tarsometatarsi are unrepresentative of the overall specimens by virtue of being among the largest individuals. Two are 25.7 and 20.8 mm long. The largest (QM F.20800) is significant not only for its length (40.7 mm) but for its age (Fig. 1h, top figure). It comes from White Hunter Site, a D-Site equivalent, whose age current understanding puts at ?Late Oligocene-Early Miocene. This makes the specimen the oldest passerine known from Australia and one of the oldest in the world, approaching those described by MOURER-CHAUVIRÉ et al. (1989) from the Late Oligocene of France. Its length exceeds that of all but the larger extant Australian passerines.

Description of fossil lyrebird

This survey has not attempted to identify the Riversleigh material below subordinal level, however, several specimens are particularly distinctive. One, the *Orthonyx* femur, has been described elsewhere (BOLES 1993 a). Another, based on a carpometacarpus, is diagnosed here as representing a lyrebird *Menura* (Passeriformes: Passeri: Corvida: Menuroidea: Menuridae).

Menura comprises two of the largest living species of passerines, with the larger, *M. novaehollandiae*, reaching a mass of 850 g or more. The Riversleigh carpometacarpus, while smaller than those of *M. novaehollandiae* and *M. alberti* (36-39 mm), still exceeds in size that of most living Australasian passerines. Only some of the large corvines (e.g. *Corvus, Strepera, Gymnorhina*) are larger; in these, the dentiform process is absent, metacarpal III is straight and parallel with metacarpal II, and the bone is overall proportionally more elongate and less stout.

Menura tyawanoides n. sp. (Fig. 1c, d)

Holotype: QM F.20887 (AR 11466), complete left carpometacarpus.

Type locality and local fauna: Upper Site (System B), Riversleigh; Upper Site Local Fauna.

Age: ?Early Miocene.

Diagnosis: Differs from living species of *Menura* by its smaller size and the following suite of characters: knob distoposteriad to pollical facet much less pronounced; pisiform process rounded; internal ligamental fossa rounder, separated by ridge from depression on proximal end of metacarpal III; fossa between pisiform process and proximal ends of metacarpals II and III deeper; dentiform process narrower, more pointed; ridge on internal edge of facet for digit II lower; metacarpal III not as curved; groove on posterior surface of metacarpal III less pronounced across length.

Etymology: *tyawan*, Australian Aboriginal word meaning 'lyrebird' [*M. novaehollandiae*], from the Kumbainggiri tribe of northeastern NSW (MCCARTHY 1959); -oides, (Gr.) 'resembling'. The name indicates the resemblance of this taxon to living species of lyrebirds.

Description: Carpometacarpus: measurements, length 29.3 mm, proximal depth 8.9 mm, distal depth 6.4 mm. Stout; metacarpal I prominent and well defined, process strongly directed proximoanteriad; pisiform process situated considerably anteriad (level with anterior edge of metacarpal I); shallow foramen on wall of internal ligamental fossa posteriad to pisiform process; dentiform process well developed, slightly distal of midpoint of metacarpal II; anterior tendinal groove visible for most of length in anterior view, only slightly undercutting dentiform process on external surface; intermetacarpal tuberosity heavy and broad, fused with metacarpal III on all sides except for

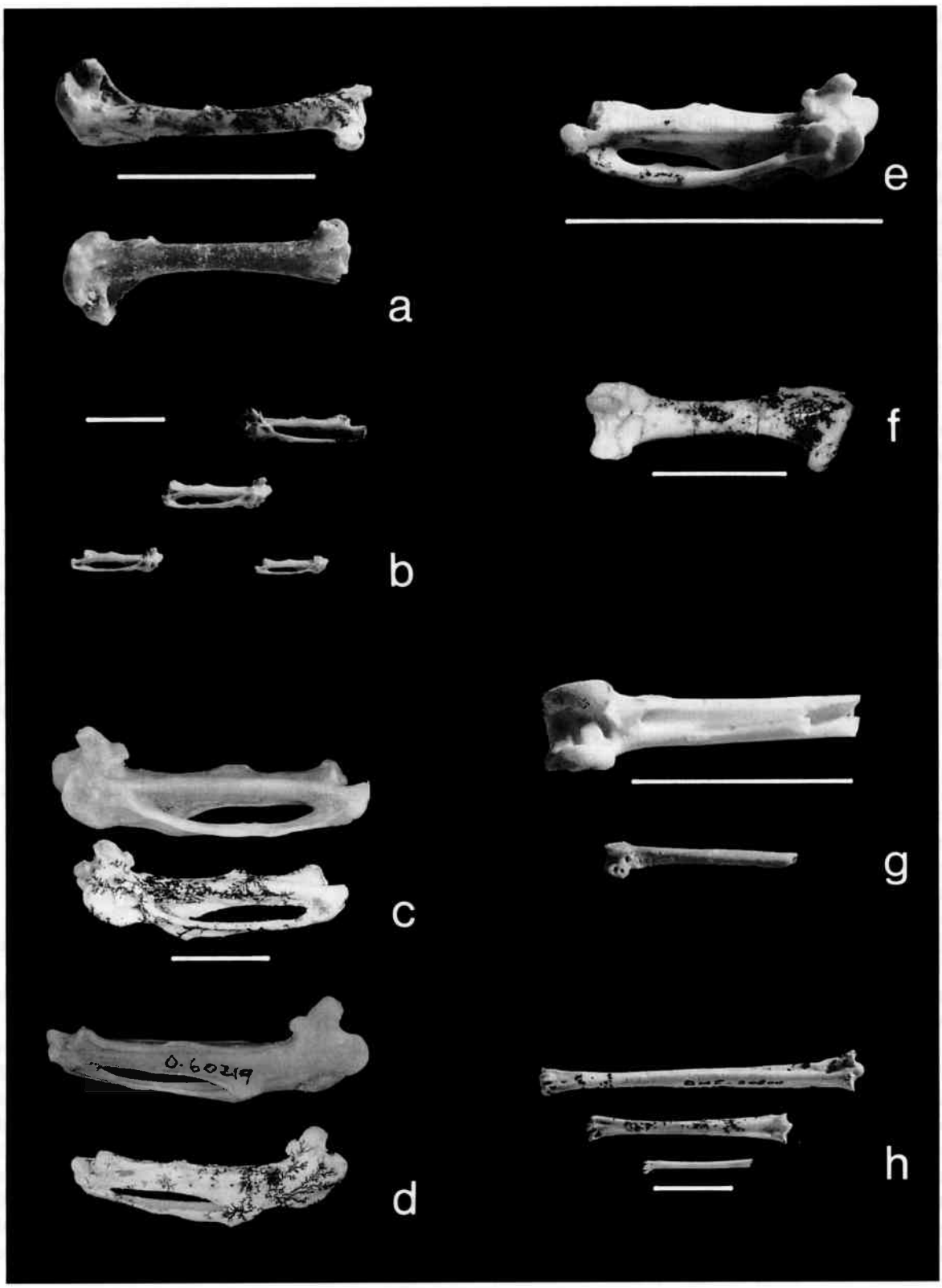

Fig. 1: Representative elements of Riversleigh passerines. a. humeri; b. carpometacarpi; c. carpometacarpi of *Menura novaehollandiae* (upper) and *M. tyawanoides* sp. nov. (lower), internal view; d. carpometacarpi of *M. novaehollandiae* (upper) and *M. tyawanoides* sp. nov. (lower), external view; e. carpometacarpus of species of Tyranni; f. femur of *Orthonyx kaldowinyeri*; g. tibiotarsi, showing size range; h. tarsometatarsi, showing size range; upper figure is from White Hunter Site, a D-Site equivalent, possibly of Late Oligocene age. The lines equal 10 mm.

foramen on proximal edge; tuberosity of metacarpal II prominent, with broad, shallow groove along base on internal face; external edge of metacarpal III posteriad to intermetacarpal tuberosity projecting posteriad; internal posterior edge of metacarpal III extending posteriad as lip; groove on posterior surface of metacarpal posteriad as lip; groove on posterior surface of metacarpal III flat, broad; metacarpal III convex, curving smoothly into posterior edge of distal metacarpal symphysis; distal metacarpal symphysis projecting distad well beyond tuberosity of metacarpal II.

Comments: The Riversleigh carpometacarpus is similar to that of the living species of *Menura*, particularly in the large size, overall stoutness and slightly curved metacarpal III. The functional correlation between degree of volancy and shape of the passerine carpometacarpus (see below) raises the possibility that this similarity is due to convergence, and the specimen represents a bird unrelated to *Menura* but roughly equivalent in size with a comparable degree of volancy. The specimen resembles living species of *Menura* closely and is quite different from any other modern passerine (see RICH et al. 1985 for osteology of *Menura*). In view of this, it seems prudent at this time to adopt a conservative approach and not introduce a new generic name. Further material will be required to test this generic allocation, and eventually a new name may be found warranted. Lyrebirds are distinctive in many skeletal elements and should be easy to recognize. For example, the tarsometatarsus in most oscines has only trochlea III grooved distally, whereas in members of the Menuroidea, with the exception of the Ptilonorhynchidae, trochleae II and IV are grooved as well.

The shape of the carpometacarpus suggests that it came from a bird that had lost some of its flying ability. In passerines, this bone exhibits several changes with the reduction of volancy. It becomes "short and stout with broad intermetacarpal tubercle and exceptionally large carpometacarpal process [= dentiform process]" (RICH et al. 1985, Table 2). Metacarpal III, which is straight in volant forms, becomes broadened and curved (posteriorly convex). Among passerines, this stoutness and curvature are indications of reduced flying ability. Within modern Australasian passerines, it is found across the taxonomic and size range, including, but not limited to, *Menura* (Menuridae; RICH et al. 1985), *Atrichornis* (Atrichornithidae; RICH et al. 1985), *Psophodes, Ptilorrhoa* (Corvidae: Cinclosomatinae; pers. obs.), and *Eremiornis* (Sylviidae; pers. obs.). All are characterized by living primarily on or near the ground, usually in dense vegetation. Their wings are rounded and proportionally short for the sizes of the birds, whereas the legs are usually strongly developed. None of these birds is entirely flightless, but at best they are reluctant though competent fliers. When pursued, they prefer to make use of the vegetation cover, through which they pass with ease, or escape on foot.

The Upper Site Local Fauna is particularly rich and diverse. Less than two cubic meters have yielded a range of invertebrate and vertebrates, including 64 species of mammals. The habitat in which this deposit accumulated is thought to have been lowland tropical rainforest, a vegetation type characterized by a dense understorey. This is consistent with the idea that *M. tyawanoides* was similar to living species of *Menura* in aspects of its form and lifestyle: a large, mainly terrestrial passerine with proportionally short wings and possibly reduced flight ability, living in dense vegetation. Nothing can be inferred about the likelihood of a similarly developed plumage or display behavior.

Like *Orthonyx*, *Menura* is an example of one of Australo-Papua's most distinctive genera appearing in modern form by the Miocene. Both genera are considered elements of the Tumbunan fauna, the earliest of Australo-Papua's biogeographic units. This fauna is believed to have originated in the subtropical and temperate rainforests that were dominant over much of Australian landmass in the early Tertiary (SCHODDE & FAITH 1992, and references therein). Living species of both genera are largely centred on rainforests, and the presence of fossil representatives in the presumed rainforests of Riversleigh adds support to this view.

Discussion

A number of Tertiary sites yielding bird remains are known from Australia. Most are dominated by waterbirds and/or large terrestrial forms. Riversleigh is important because it combines these with an array of smaller landbirds, passerines being prominent among these (BOLES 1991). At least ten taxa can be readily distinguished, which, because it is the minimum based on a single element, is certainly a considerable underestimate of the material presently available. Although the songbirds have yet to be studied in detail, they already represent the richest accumulation of this age on the continent, and promise to provide valuable insight into the history of the order. Like the Northern Hemisphere, the songbird fauna of Riversleigh is diverse by the Middle Miocene; however, in contrast, it has also a substantial number of passerines from the Early Miocene. One specimen approaches, or possibly equals, in age the oldest Northern Hemisphere record. Any more useful statements about the early history of

songbirds in Australia must await finer taxonomic resolution of the Riversleigh material.

There are a limited number of taxonomically useful osteological characters that have been identified for the Passeriformes, and those that have been recognized have been surveyed in only general terms (e.g., tricipital fossa, dentiform process). These surveys were carried out before the realization that many groups of Australian passerines were only convergent with, not related to, Northern Hemisphere forms. Consequently, the surveys assumed that the Australian taxa conformed to their supposed northern relatives. Examination by the author of some of these characters for Australian taxa shows that these early assumptions were often invalid. The surveys also did not look in depth at the significance and range of more subtle variations of a character. For example, the dentiform process may be present in a range of taxa, but there are differences in its prominence and position along metacarpal II, which may prove to be taxonomically valuable.

Although apparent anomalies remain, it is worth noting the higher correlation between the distribution of the character states and higher taxonomic groups in the SIBLEY and AHLQUIST classification than in the Basel or Wetmore sequences. This will surely benefit attempts to correctly place songbird fossils within the scheme of higher passeriform classification and, subsequently, evolutionary biogeography.

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