

Early Eocene shorebirds (Aves: Charadriiformes) from the Tingamarra Local Fauna, Murgon, Queensland, Australia

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Abstract – The Early Eocene Tingamarra Local Fauna, from near Murgon, Boat Mountain, southeastern Queensland, has produced an array of important vertebrate fossils, including two, possibly three, taxa of non-passerine birds. The fossils described here are comparable with what have been termed the 'transitional' Charadriiformes, for which the 'form family' Graculavidae has been recognized. The post-cranial skeletal morphology of these birds is shared by early members of the Anseriformes, causing uncertainty over the correct ordinal allocation of taxa in the absence of the distinctive anseriform skull. As a conservative approach, the Murgon specimens are allocated to the Graculavidae in the Charadriiformes, pending the discovery of informative cranial elements. Because both the Graculavidae and early anseriforms are largely restricted to the period of the Late Cretaceous through Early Eocene, the occurrence of these fossils at Murgon is consistent with the date obtained from radiometric and other faunistic sources.

INTRODUCTION

The Early Eocene Tingamarra Local Fauna, from near Murgon, Boat Mountain, southeastern Queensland, has produced an array of important vertebrate fossils, most but not all of which were aquatic. In addition to teleosts, lungfish, and crocodiles, there are several taxa comprising the earliest Australian representatives of their lineages, most approaching twice the age of next oldest records. Included are remains of Australia's oldest frog *Lechriodus casca* (Tyler and Godthelp 1993), trionychid turtle (Gaffney and Bartholomai 1979), matsoiid snake (Scanlon 1993), marsupial *Thylacotinga bartholomaii* (Archer *et al.* 1993), bat *Australonycteris clarkae* (Hand *et al.* 1994), and non-volant placental mammal, the condylarth-like *Tingamarra porterorum* (Godthelp *et al.* 1992). This site has also yielded the earliest known modern, non-marine bird fauna from Australia (Boles *et al.* 1994). Included among these birds are the world's oldest known songbirds (Passeriformes), which have been reported elsewhere (Boles 1995, 1997). Remains of non-passerine birds are also represented and form the subject of this paper.

The Murgon birds are significant in the Australian fossil record because they are an indication of the occurrence of a modern, non-marine bird fauna by the Early Eocene (Boles *et al.* 1994). Older avian fossils from Australia consist of unidentified feathers (Talent *et al.* 1966; Waldman

1970), enantiornithines, including *Nanantius* (Molnar 1986; Kurochkin and Molnar 1997), and penguins (Sphenisciformes) (summarized in Vickers-Rich 1991). Natural moulds of large pedal digits from the Redbank Formation, southeastern Queensland, referred to the Dromornithidae, are of comparable age to the Murgon deposits (Vickers-Rich and Molnar 1996).

MATERIALS AND METHODS

Institutional acronyms used are AM (Australian Museum, Sydney, N.S.W.), ANSP (Academy of Natural Sciences, Philadelphia, Pa, U.S.A.), NJSM (New Jersey State Museum, Trenton, N.J., U.S.A.), QM (Queensland Museum, Brisbane, Qld), and YPM (Peabody Museum, Yale, New Haven, Conn., U.S.A.). Osteological characters are adopted primarily from Cracraft (1972) and Olson and Parris (1987), with the terminology modified to follow Baumel and Witmer (1993), except that as terms of position and direction anterior is used rather than rostral and posterior rather than caudal. These characters have been used for comparisons with the Murgon material, and have been augmented by reference to the published photographs in Olson and Parris (1987) and casts of some material. Direct comparisons between some of the specimens were made during the workshop on early Neornithes held as part of the

1996 meeting of the Society of Avian Paleontology and Evolution (SAPE). Measurements of the Murgon material follow the methods illustrated by Steadman (1980); those of specimens of Graculavidae are taken from Olson and Parris (1987) unless otherwise indicated.

GEOLOGY

The Tingamarra Local Fauna comes from deposits near the township of Murgon, about 160 km northwest of Brisbane, Queensland. The fossil-bearing sediments, which may form part of the Oakdale Sandstone, are authigenic green illite and smectite clays with irregular dolomitized horizons and fine sandy lenses (Hand *et al.* 1994). Potassium-argon dating of illites has given a minimum age of $54.6 \pm 0.5 \times 10^6$ years (Godthelp *et al.* 1992; Hand *et al.* 1994). The deposit is bounded above and below by basalt. The upper basalt has been dated at $29.0 \pm 0.2 \times 10^6$ years (Hand *et al.* 1994); the lower has not yet yielded samples suitable for radiometric dating.

The fossils come from fluvio-lacustrine deposits. Godthelp *et al.* (1992) considered the depositional situation to have been "a shallow, low-energy aquatic environment . . . indicated by the Tingamarra sediments, the lack of abrasive damage to the fossils and the composition of the fauna". Salisbury and Willis (1996) regarded the depositional environment as having been "a low energy freshwater lake or billabong". On the basis of the high concentration of freshwater carbonate minerals in the sediments, they inferred a situation similar to that in modern carbonate lakes in South Australia, hypothesizing "an initial perennial phase before becoming predominantly ephemeral". The period of fossil deposition was probably no more than 100–500 years (Salisbury and Willis 1996). Further details on the geology, dating and geochemistry of the Murgon site are provided by Godthelp *et al.* (1992) and Salisbury and Willis (1996).

The vegetation and climate of this area during the Early Eocene have not been determined. The early Tertiary age of this deposit is corroborated by various non-avian faunal elements.

SYSTEMATIC PALAEOLOGY

Family Graculavidae

Several bones from Murgon are similar to what Olson (1985) and Olson and Parris (1987) have termed the 'transitional' Charadriiformes. This assemblage, known mainly from the Late Cretaceous through Eocene of North America, comprises at least five and possibly more than 12 nominal genera. Most of these have provided the

basis for family-group names. Because virtually all are known only from a small number of often different fragmentary elements, their relationships and morphological innovations are difficult to interpret. To deal with this situation, Olson and Parris (1987, p. 8) adopted " . . . a version of paleobotanical convention in recognizing a 'form family' Graculavidae [based on Graculavinae Fürbringer, 1888], which implies a general similarity in morphology of the constituent taxa, although the material available is simply not sufficient for determining phylogeny or key adaptations."

The Graculavidae was recognized by Olson and Parris (1987) for a range of bones recovered from the Hornerstown Formation of New Jersey. These authors allocated about 17 bones to seven species in six genera, with the family thus encompassing the Graculavinae Fürbringer, 1888 (*Graculavus* Marsh, 1872), Palaeotringinae Wetmore, 1940 (*Palaeotringa* Marsh, 1870), Telmatornithidae Cracraft, 1972 (*Telmatornis* Marsh, 1870), and Laornithidae Cracraft, 1973 (*Laornis* Marsh, 1870). It may be necessary eventually to include four to six or more other existing family-level taxa. The background and problems of the transitional Charadriiformes have been discussed in depth by Olson (1985) and Olson and Parris (1987). Cracraft (1972), Olson (1985) and Olson and Parris (1987) drew attention to the morphological similarities between these taxa and the extant Burhinidae (stone-curlews or thick-knees).

A morphology of the post-cranial skeleton similar to that of the transitional Charadriiformes is shared by early members of the Anseriformes (Olson and Feduccia 1980a; Olson in press; P. Houde pers. comm.). This has resulted in uncertainty over the correct ordinal allocation of several taxa. Only when evidence of the distinctive anseriform skull is present, can assignment to that order be made with confidence. Recent fossil finds demonstrate that *Anatalavis* Olson and Parris, 1987, originally included in the Graculavidae, should be removed to the Anseriformes, specifically the Anseranatidae (Olson in press).

Similar to the Graculavidae is the Presbyornithidae, comprising the genera *Presbyornis* and *Telmabates*. *Presbyornis perovetus* is known from hundreds of specimens, and thus its shorebird-like post-cranial osteology and its distinctive skull, are well known (Feduccia and McGrew 1974; Olson and Feduccia 1980b; Ericson in press). P. Houde (pers. comm.) found a similar post-cranial morphology in an early anseriform with a screamer-like skull (Anhimidae), leading him to consider that charadriiform-like aspects of *Presbyornis* are characteristic, not aberrant, for Anseriformes in the early Tertiary.

No cranial material is represented among the



Figure 1 Incomplete right coracoid (QM F23649), in two fragments, from the Early Eocene Tingamarra Local Fauna, Murgon, Queensland, tentatively referred to the Graculavidae. A, shoulder extremity fragment, in medial view. B, body of the element, in ventral view. Scale bar = 10 mm.

Murgon specimens considered here. Comparisons were made with the Graculavidae, Presbyornithidae and Burhinidae.

Coracoid

Assigned to the Graculavidae is a right coracoid (QM F23649), in two fragments, the larger of which (Figure 1B) comprises the body of the element, missing the sternolateral corner, including processus lateralis, and the lateral half of facies articularis sternalis. It is broken through the shaft at the sternal base of sulcus m. supracoracoidei and processes procoracoideus. The smaller fragment of the shoulder extremity (Figure 1A) retains facies

articularis clavicularis, processus acrocoracoideus and the shoulder third of impressio lig. acrocoracohumeralis.

The fossil coracoid is larger and more robust than that of *Burhinus grallarius* but very similar to that of *Esacus magnirostris*. It is similar in shape to the latter, but the shoulder side of angulus medialis lacks the spur directed towards the shoulder (this is replaced by a low blunt process situated about half as far from angulus medialis). The broad facies articularis sternalis has a convex, rather than straight, border on the shoulder side. The lip of this facies on the ventral surface is larger and more pronounced than in *Esacus*. The foramen supracoracoideum is smaller and closer to the medial border of the element. The fragment of the shoulder extremity is triangular when viewed from the shoulder end, and is narrower than in *Esacus*. In medial view, facies articularis clavicularis is dorsoventrally deep, with a rounded border on the shoulder end, straight but angled sternal border and a flat surface. The impressio lig. acrocoracohumeralis is less pronounced than that in the burhinids.

The coracoid has not yet been reported for any species of the Graculavidae, but is known from *Telmabates antiquus* (Howard 1955), *Presbyornis pervetus* (Feduccia and McGrew 1974) and an indeterminate presbyornithid from Antarctica (Noriega and Tambussi 1995). In morphology, the Murgon fossil resembles these forms, including the development of the blunt process on the shoulder side of angulus medialis. The incompleteness of this fossil precludes most of the measurements used by Howard (1955) and Feduccia and McGrew (1974), so few direct comparisons of size can be made. The greatest width of the head (5.2 mm) is greater than that of *P. pervetus* (4.0–4.8 mm) and at the low end of the range of values for *T. antiquus* (5.1–5.9 mm). The least width of the shaft sternal to the cotyla scapularis (5.5 mm) is likewise between the measurements for *P. pervetus* (4.2–4.6 mm) and *T. antiquus* (5.7–6.0 mm).

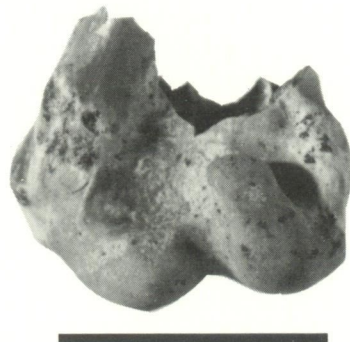


Figure 2 Distal fragment of left humerus (QM F23735) from the Early Eocene Tingamarra Local Fauna, Murgon, Queensland, tentatively referred to the Graculavidae, in anterior view. Scale bar = 10 mm.

Humerus

The humeral fragment (QM F23735; Figure 2) consists of the extreme distal end, with the break just proximal to the epicondyli dorsalis and ventralis and distal to the fossa m. brachialis (distal width 13.5 mm; depth, dorsal condyle 6.9 mm). The humerus is one of the more frequently preserved elements of nominal species within the Graculavidae and Presbyornithidae, and thus permits some limited comparisons between taxa. Distal humeral fragments are known from *Telmatornis priscus*, *Palaeotringa littoralis*?, *Presbyornis pervetus* and an indeterminate taxon of Graculavidae (Olson and Parris 1987).

The depression in which fossa m. brachialis is located (brachial depression of Howard 1929) is deep and extends far distally, cutting into the proximal border of the condylus ventralis humeri and extending across the proximal border of condylus dorsalis humeri almost to the dorsal edge of the bone. In anterior view, the condylus dorsalis humeri is elongate and condylus ventralis humeri oval. The tuberculum supracondylare ventrale is a prominent rounded knob located on the anterior face well in from the lateral border. Epicondyli ventralis and dorsalis are weakly developed, and processus supracondylaris dorsalis is not extended into a long process. Fossa olecrani is shallow, forming a slight shelf, which grades smoothly into the shaft. Sulcus m. scapulotricipitalis is very shallow.

The Murgon fossil is larger than *Telmatornis priscus* but similar in size to *Palaeotringa littoralis*? (NJSM 11303: distal width 12.8 mm; depth of dorsal condyle 6.9 mm) and *Burhinus grallarius* (AM collection: distal width 12.5–14.9 mm; depth of dorsal condyle 6.7–8.3 mm). It resembles *Burhinus* and the graculavids in general morphology, but differs from them in several characters described by Olson and Parris (1987), and cannot be considered to be the same taxon as any of these.

A direct comparison by the author and P.G.P. Ericson, of the Swedish Museum of Natural History, during the 1996 SAPE meeting, of the Murgon fossil with the humerus of *Presbyornis pervetus* showed that these are essentially identical in morphology, a resemblance that extends to size (distal width 12.9–14.8 mm, mean 13.8 mm; Feduccia and McGrew 1974). The Murgon specimen is smaller than *Telmabates antiquus* but of similar size to *Anatalavis rex* (distal width 13.2–13.6 mm).

Tibiotarsi

There are two distal fragments of tibiotarsi (Figure 3), apparently representing different taxa. Although the distal ends of the tibiotarsi are known for *Telmatornis priscus*, *Laornis edwardsianus*,

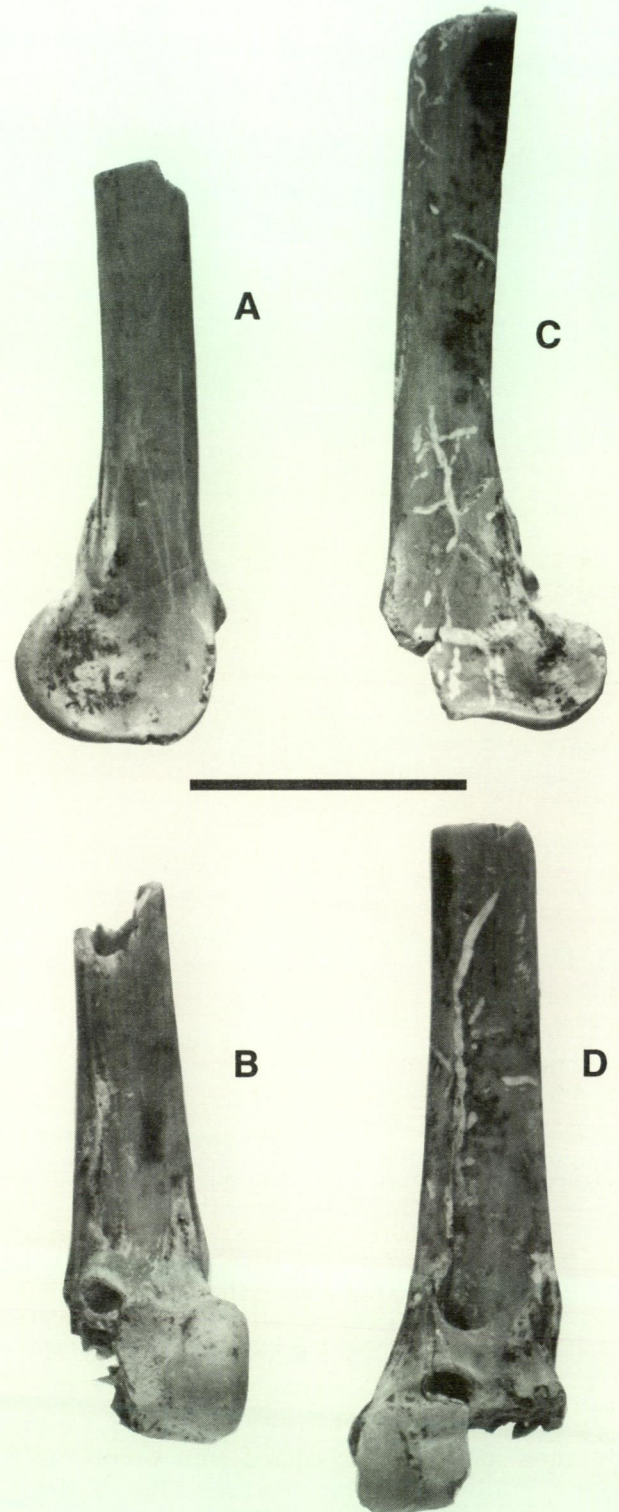


Figure 3 Two distal fragments of left tibiotarsi from the Early Eocene Tingamarra Local Fauna, Murgon, Queensland, tentatively referred to the Graculavidae. A, lateral view, and B, anterior view of QM F23736. C, medial view, and D, anterior view of QM F23737. Scale bar = 10 mm.

Palaeotringa littoralis, *P. vagans* and *Presbyornis pervetus*, most of the specimens are damaged, and Olson and Parris (1987) cited few differences other than size.

Both fragments are left elements broken through the shaft a short distance proximal to the condyli. QM F23736 (Figure 3A,B) has the condylus lateralis slightly damaged on the posterior edge; the pons supratendineus is complete; the condylus medialis has been lost. QM F23737 (Figure 3C,D) has the condylus medialis complete and the condylus lateralis absent. Although they share few common structures for useful measurements, the bones are of generally similar size (QM F23736, depth of condylus lateralis 7.6 mm; width of the shaft level with the proximal border of the pons supratendineus 6.0 mm; QM F23737, depth of the condylus medialis >8.6 mm; width of the shaft level with the proximal border of the pons supratendineus 6.7 mm).

QM F23737 has the condylus medialis flattened proximodistally with the distal border concave at the midpoint. The condylus is narrow in anterior view and roughly parallel with the shaft. The epicondylus medialis consists of a moderately strong proximodistal ridge about a third of the way from the anterior end of the condyle. The pons supratendineus is strong, roughly horizontal and situated to the medial side of the midline of the shaft, about a quarter of the shaft width from the edge. The distal opening of canalis extensorius is oval. The sulcus extensorius occupies most of the anterior surface of the shaft; the anterior face of the shaft is flat except for a ridge along the medial border; there is no ridge laterally. There is a small proximodistal ridge bordering the medial side of the sulcus M. fibularis. This sulcus is situated on the anterior surface of the lateral edge; it lacks a large nutrient foramen.

QM F23736 is generally similar in overall appearance, but differs in several key characters. The condylus lateralis is a rounded oval in lateral view and roughly parallel with the shaft. The sulcus M. fibularis is situated more on the lateral side of the edge of the shaft and has a prominent nutrient foramen. The most distinctive difference between the specimens is in the pons supratendineus. In QM F23736 it is situated much closer to the medial margin, is angled proximomedial-distolaterally and is not as robust. The distal border of the pons is curled anteriorly, forming a lip for the distal opening of canalis extensorius, which is rounder.

This suite of characters differs from most other graculavid taxa. The Murgon specimens fall within the size range of the two species of *Palaeotringa* (*P. littoralis*, YPM 830, holotype: depth, external condyle 8.2 mm; width, shaft just proximal to external condyle 7.0 mm; *P. vagans*, YPM 835, holotype: width, shaft just proximal to external condyle 5.8 mm) and are slightly smaller than *Burhinus grallarius* (depth of condylus medialis 9.6–10.9 mm; depth of condylus lateralis 8.6–9.6 mm).

Although Olson and Parris (1987) did not give characters for the tibiotarsus of *Telmatornis priscus*, QM F23737 was compared directly to ANSP 13361 (holotype of *Palaetringa vetus* Marsh, 1870, synonymized with *T. priscus* by Olson and Parris 1987). These proved a close match in morphology and size (ANSP 13361: depth of condylus medialis, c. 6.9 mm). QM F23737 resembles the tibiotarsus of *Presbyornis pervetus* but is probably not that taxon (P.G.P. Ericson, pers. comm.). Both specimens are similar in size to *P. pervetus* (depth of condylus medialis 9.9–11.1 mm; depth of condylus lateralis 9.2–10.8 mm; Feduccia and McGrew 1974).

Pedal Phalanges

Two slender pedal phalanges (Figure 4) can probably also be allied with the preceding specimens. A phalanx 1 of digit II (ANSP 15541) was referred by Olson and Parris (1987) to *Telmatornis priscus* Marsh, 1870, and is the only pedal phalanx reported for the Graculavidae. Pedal phalanges have been reported for *Presbyornis pervetus* (Feduccia and McGrew 1974) and *Telmabates antiquus* (Howard 1955).

QM F30347, phalanx 1 of digit II (Figure 4A), is larger (length 19.2 mm, proximal width 3.3 mm)

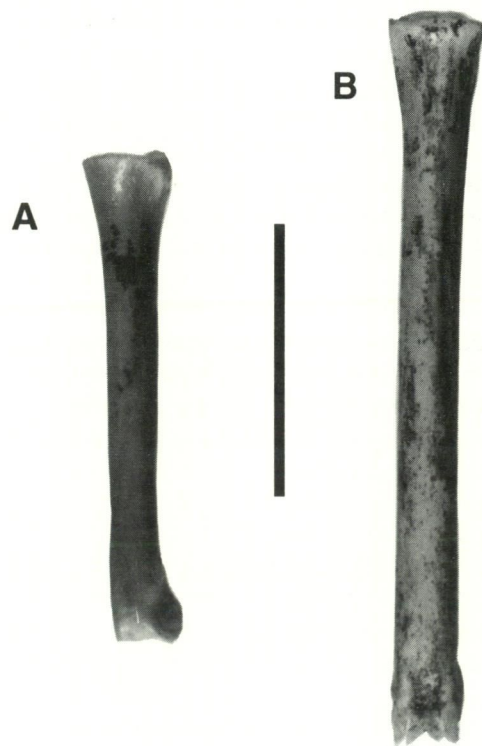


Figure 4 Two pedal phalanges from the Early Eocene Tingamarra Local Fauna, Murgon, Queensland, tentatively referred to the Graculavidae, both in dorsal view. A, phalanx I, digit II (QM F30347). B, phalanx I, digit III (QM F20872). Scale bar = 10 mm.

than the comparable element of *Telmatornis priscus* (length 14.6 mm, proximal width 3.0 mm).

QM F20872, phalanx 1 of digit III (Figure 4B), is comparable in length (length 28.2 mm, proximal width 4.8 mm) to the elongated basal phalanges of extant species of *Porphyrio* (Rallidae) and *Irediparra* (Jacanidae), but is intermediate in robustness. This specimen resembles in shape and proportions the comparable elements in the Presbyornithidae. It is smaller and more gracile than *Telmabates antiquus* (direct comparison with figure 7e of Howard 1955, published life size), and more closely approaches in size a phalanx of *Presbyornis pervetus*, falling just above the range of largest pedal phalanges (19–27 mm) reported by Feduccia and McGrew (1974).

DISCUSSION

Taxonomic Allocation

The assemblage of graculavid taxa known from the New Jersey deposits demonstrates that the group had achieved at least moderate diversity by the Paleocene. It cannot be assumed, therefore, that the Early Eocene Murgon bones referred to this family all represent the same species or even genus, and indeed it appears likely that at least two taxa are present, as indicated by the morphologically distinct tibiotarsi. In the absence of other common elements, it is not possible to say with confidence whether there are additional species. Using *Burhinus grallarius* as a comparative guide to size, there are a humerus and two tibiotarsi that are smaller and a coracoid that is larger than the respective elements in that species. Thus it is possible that there is at least one taxon at Murgon in addition to those represented by the tibiotarsi.

The proliferation of names for isolated bones in this group was instrumental in Olson and Parris (1987) introducing the concept of the form-family into palaeo-ornithology to accommodate them. Until additional specimens are recovered from Murgon, there seems little justification for adding to this present disordered situation.

It is uncertain whether the bones represent one or both of the Charadriiformes or Anseriformes, or neither. The recent identification of Anhimidae- and Anseranatidae-like birds with similar post-cranial morphologies (P. Houde pers. comm.; Olson in press) means that these families also need to be considered for the Murgon material. It is doubtful that the Graculavidae (or the Murgon fossils), are either monophyletic or all charadriiform.

Initial allocations can be made for some specimens using characters presented by Ericson (1998). The character states expressed in several of the fossils more closely agree with those of the Charadriiformes rather than the Anseriformes

(including the Presbyornithidae). The Murgon coracoid has the processus acrocoracoideus protruding far medially with the mediosternal part forming a posteriorly directed hook (in ventral view) while the facies articularis clavicularis is deeply undercut (character 43 of Ericson 1998); these are features of the Charadriiformes but not the Anseriformes. Striae of muscle scars on the dorsal face of the sternal end of the coracoid (character 38 of Ericson 1998), a character of the Presbyornithidae, Anseranatidae and Anatidae, are absent. Both tibiotarsal fragments have the distal opening of canalis extensorius positioned far medially, as seen in the Charadriiformes, rather than centred about equally far from either condyli, as in the Anseriformes (character 69 of Ericson 1998). Characters of the distal humerus given by Ericson (1998) do not serve to separate these groups.

Livezey (1998) remarked on "the low informativeness of post-cranial characters for the estimation of relationships" in these groups and stressed the need for skull material in making higher level taxonomic assignments. As a conservative approach the Murgon specimens are allocated to the Charadriiformes, pending the discovery of informative cranial elements. Within this order, the fossils are referred to the Graculavidae without further resolution.

Reconstruction

Presbyornis pervetus is known from many specimens, but insufficient material exists for any of the other graculavid-presbyornithid taxa to permit an accurate reconstruction. All appear to share a generalized burhinid-like post-cranial morphology, but in the absence of more characteristic elements, particularly those of the cranium, little more can be inferred. The phalanges of these taxa, where known, are unlike those of the Burhinidae. In contrast to the short toes of those almost exclusively non-aquatic forms, the bones are long and thin; few large charadriiforms living today have such long phalanges. The known graculavid-presbyornithids comprised a wide size range.

The proportions of the phalanges suggest that the graculavid-presbyornithids were birds of the shore or water. Previous authors have considered the depositional environments to be aquatic, whether shallow lakes, both freshwater (Howard 1955) and saline (Feduccia and McGrew 1974), or marine (Olson and Parris 1987; Olson 1994). The first of these is concordant with the palaeoenvironmental reconstructions by Godthelp *et al.* (1992) and Salisbury and Willis (1996).

Biogeography and Age

Published records of the transitional Charadriiformes, and those taxa considered

possibly closely related, are mostly restricted to North America, with some recent but undetailed finds announced from Asia. The Hornerstown Formation of New Jersey has been thought to be Late Cretaceous (Maastrichtian) (e.g. Olson and Parris 1987; Kennedy and Cobban 1996) or Palaeocene (e.g. Olson 1994). Hope (in press) reported a new species of *Graculavus* from the Cretaceous of Wyoming. Kurochkin (1995) mentioned several new graculavids from the Late Cretaceous of Mongolia, and a possible representative of this group was reported by Nesson (1992) from the lower Paleogene of Kazakhstan, an identification that has been questioned by S. Hope (pers. comm.). Other taxa that Olson and Parris (1987) suggested may be related to the Graculavidae (Apatornithidae Fürbringer, 1888; Cimolopterygidae Brodkorb, 1963; Torotigidae Brodkorb, 1963; Lonchodytidae Brodkorb, 1963; Dakotornithidae Erickson, 1975; Scaniornithidae Lambrecht, 1933) are from Late Cretaceous or early Tertiary deposits in North America, except for the last, which is European. In contrast, fossils referred to the Presbyornithidae have been reported from North America (Late Cretaceous - Early Eocene - Wetmore 1926; Feduccia and McGrew 1974; Olson 1985, 1994; Benson in press; S. Hope pers. comm.), Argentina (Early Eocene - Howard 1955), Mongolia (Paleocene - Olson 1985; Late Cretaceous - Kurochkin 1988 [cited in Kurochkin 1995]), France (Paleocene - Mourer-Chauviré 1994), and Antarctica (Late Cretaceous - Noriega and Tambussi 1995). Some of these reports are based on postcranial material that may be too fragmentary to support the identifications (Livezey 1998).

Harrison and Walker (1976, 1978, 1979) referred two taxa to the Presbyornithidae, but these actions have been questioned. *Agnopterus* (?) *hantoniensis* Lydekker, 1891 (Upper Eocene, Great Britain), originally associated with the flamingos, was assigned to the Telmabatidae (= Presbyornithidae) by Harrison and Walker (1976), who created for it the genus *Headonornis*. Later (Harrison and Walker 1979), they referred further material, which extended the age range of this taxon into the Lower Oligocene. Olson and Feduccia (1980b) criticized this action and commented that "until a proper comparative study is made, the significance of these specimens to the evolution of either the flamingos or the Presbyornithidae cannot be determined". The putative heron *Proherodius oweni* Lydekker 1891 (Lower Eocene, Britain) was transferred to the Presbyornithidae by Harrison and Walker (1978); however, Olson (1985) considered "their reasons for placing it with the Presbyornithidae . . . not at all convincing".

The Anseranatidae, represented by *Anatalavis*,

has been reported from the Hornerstown Formation (Olson and Parris 1987) and London Clay (Lower Eocene) (Olson in press).

Other than the record of the putative graculavid *Headonornis hantoniensis* from the Lower Oligocene (Harrison and Walker 1976), the Graculavidae, Presbyornithidae and possible relatives are largely restricted to the period of the Late Cretaceous through Early Eocene. The presence of graculavid material at Murgon is thus of particular relevance in understanding the dating of this deposit. Woodburne and Case (1996) have challenged the Early Eocene age, arguing that the illites from which the radiometric dates were obtained are probably of comparable age to those of other mineralogically similar sites in Australia. They also questioned the higher level taxonomic allocations of the mammals *Tingamarra porterorum* and *Thylacotinga bartholomaii*, but gave no consideration to the bats and other, non-mammalian fauna that have been recovered from Murgon. The circumscribed time period from which graculavid-presbyornithids are known provides a reasonably reliable, albeit broad, basis for faunal correlation between sites. The occurrence of these birds at Murgon is consistent with the date obtained from radiometric and other faunistic sources.

Evolutionary Significance

The transitional shorebirds are one of the few groups of modern birds (Neornithes) that are known from the Cretaceous; the others include the Gaviiformes, Pelecaniformes, Anseriformes, Galliformes and possibly Procellariiformes (Olson and Parris 1987; Olson 1992; Kurochkin 1995; Chiappe 1996; Chatterjee 1997; S. Hope pers. comm.). Regardless of whether the New Jersey graculavids are now considered to be Late Cretaceous or Paleocene in age, they play an important role in recent theories on the early radiations of modern birds. Feduccia (1995, 1996) considered these shorebirds to be "prime candidates for the wellsprings of most of the modern avian radiation". He envisaged "an extraordinarily explosive evolution, one that may have produced all of the living orders of birds within a time frame of some 5 to 10 million years" following the end of the Cretaceous and extinction of the Enantiornithes and other non-neornithine birds. A similar idea was previously presented by Wilson (1988). Other workers, notably Chiappe (1995) and Cooper and Penny (1997), have rejected this model, and consider that the radiation of modern orders took place in the Cretaceous and the apparently sudden appearance of these birds in the early Tertiary is an artefact of the scantiness of the fossil record. The growing number of living neornithine orders now being recognized from the Late Cretaceous undermines the basis of Feduccia's

theory. That the graculavid-like post-cranial morphology is possibly primitive and widespread in different groups of Late Cretaceous and Early Tertiary birds generates uncertainty about the correct taxonomic allocation of currently known forms, and thus compromises any conclusions based upon them.

The post-cranial morphology exhibited by graculavids and presbyornithids appears to have been a generalized one characteristic of several groups of early neornithine birds. Previously, all reports of fossils with this morphology have come from the Northern Hemisphere, with the exception of the Antarctic presbyornithid announced by Noriega and Tambussi (1995). The Murgon specimens provide further evidence that this morphology was also present in the Southern Hemisphere during the early Tertiary. An understanding of the extent of these birds in Australia must await the discovery of other sites of suitable age.

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