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Australlus, a New Genus for *Gallinula disneyi* (Aves: Rallidae) and a Description of a New Species from Oligo-Miocene Deposits at Riversleigh, Northwestern Queensland, Australia

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ABSTRACT. *Gallinula disneyi* Boles, 2005, was based on Late Oligocene-Middle Miocene (c. 25–15 Ma) fossils from Riversleigh World Heritage Property in Boodjamulla (Lawn Hill) National Park, northwestern Queensland, Australia. If the generic assignment is correct, this species would be the earliest known crown group representative of Rallidae. We have therefore reassessed the phylogenetic relationships of this rail using both the original and newly recovered material. It is found to be a relatively basal rallid with some affinity to *Porphyrio*, and the new genus *Australlus* is erected for this taxon. A second species in the genus is described from Middle Miocene sites at Riversleigh World Heritage Property. A third rallid, smaller than either species of *Australlus*, is indicated by a mandible fragment, also from Riversleigh, but is not named. These rails are the only gruiforms known from Riversleigh and, with a single species of stork, are the only small non-passerine ground-birds known from these faunas.

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Rails (Rallidae: Gruiformes) comprise a cosmopolitan group, occurring on all continents except Antarctica. There are 140 or so living species, with another 500–1600 species hypothesized to have occurred on Pacific islands at the time of human contact (Steadman, 2006), whose extinction was mainly through anthropogenic causes. A significant number of living rails are flightless, as were the vast majority of recently extinct forms (e.g., Olson, 1977; Taylor, 1998; Steadman, 2006). Almost all non-volant species are, or were, restricted to small islands. Several Australasian taxa from larger landmasses were significant among flightless rails: the Weka *Gallirallus australis* (Sparrman, 1786) from both North and South islands of New Zealand, the takahe (*Porphyrio mantelli* (Owen, 1848) and *P. hochstetteri* (A.B. Meyer, 1883) from the North and South Islands of New Zealand, respectively) and the Tasmanian Native-hen *Gallinula (Tribonyx) mortierii* (DuBus, 1840) of Tasmania, also present on the eastern Australian continent into the Holocene (Baird, 1984; Worthy & Holdaway, 2002).

Within *Gallinula*, the extinct *G. hodgenorum* (Scarlett,

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1955) of New Zealand, well represented in late Pleistocene-Holocene fossil deposits, was also flightless (Olson, 1975). Two extant species, the Black-tailed Native-hen *G. (Tribonyx) ventralis* Gould, 1837, distributed through much of mainland Australia, and the Dusky Moorhen *G. (G.) tenebrosa* Gould, 1846, common in Australia, New Zealand and extralimitally of Australasia, are both volant. Other Recent flightless taxa of *Gallinula* are known from south Atlantic islands and Samoa (Olson, 1973a; Taylor, 1998).

The fossil form *Gallinula disneyi* Boles, 2005, is of interest because it was flightless and also occurred on the Australian mainland (Boles, 2005a). *Gallinula disneyi* was described from specimens recovered from the Riversleigh World Heritage Property in Boodjamulla (Lawn Hill) National Park, northwestern Queensland. The area has been intensively sampled for fossil vertebrates every year since 1975. Bird fossils are not uncommon in these assemblages (Boles, 1992; 1993a,b,c; 1995; 1997a,b; 2005a,b,c; 2006); however, to date the only gruiform taxon described is *G. disneyi*. Despite being a flightless form and the fact that many deposits are interpreted as pitfall traps, it is a comparatively rare species and, more surprising, other ground-dwelling gruids are entirely absent. This absence is even more notable given that ground-dwelling casuariids and dromornithids are relatively common in many sites (Boles, 1992; Archer *et al*., 2006; Nguyen *et al*., 2010). Since *G. disneyi* was described, other specimens and previously unknown elements have become available from Riversleigh faunas, which extend the skeletal representation for the species.

The generic assignment of *Gallinula disneyi* was made following comparisons of the fossil material with living taxa (Boles, 2005a) and no phylogenetic analysis was performed. Using the new fossils, together with the original material, a more detailed examination has been made here, and all available information has been incorporated into a phylogenetic analysis that allows several questions to be addressed.

Is the original generic placement of this species in *Gallinula* correct? Examination of original and new material suggests that it is not. As well as clarifying its phylogenetic position, resolving the generic placement of *Gallinula disneyi* allows reassessment of the suggestion that it might have been in the direct ancestry of the living flightless *Gallinula mortierii*.

The long temporal occurrence—Late Oligocene to Middle Miocene—of specimens originally assigned to *G. disneyi* is striking, thus inviting an assessment of whether more than one taxon is represented. That this might be so is indicated by the size variation among the original specimens, particularly the disparity between some femoral fragments. If more than one taxon is included in the hypodigm, how does this affect the temporal distributions of the respective species?

The evolutionary relationships of gruiforms have been the subject of investigation using genetic data in recent years (Houde *et al*., 1997; Fain *et al*., 2007). In the latter study, Fain *et al*. (2007) estimated the divergence times for several nodes in the phylogeny of gruiforms. In particular, they estimated the Heliornithidae–Rallidae divergence at 42.6 Ma (95% credible interval 65.5–27.1 Ma) and the base of Rallidae at 21.8 Ma (95% credible interval 35.6–12.9 Ma). The family Rallidae was represented by five taxa, with the following relationship: *(Porphyrio porphyrio + Laterallus melanophaius)* sister to *Rallus longirostris + (Porzana carolina + Fulica americana)*. Because *Gallinula* is normally considered most closely related to *Fulica* and *Porzana* (e.g., Livezey, 1998), the genus should have an origin relatively more recent than basal rallids. Thus, it is of considerable interest to note that *Gallinula disneyi* derives from Faunal Zone A and B sites at Riversleigh, which are Late Oligocene–Early Miocene in age, or about 25–23 Ma (Archer *et al*., 2006). Its presence in deposits of this age is inconsistent with a 21.8 Ma divergence for basal Rallidae (Fain *et al*., 2007). Mayr (2009) pointed out that if the assignment of *disneyi* to *Gallinula* was correct, then this species would be the earliest known crown group representative of the family, another reason that reassessment of the generic identification is desirable.

Livezey (1998) investigated gruiform relationships, sampling all genera, using a data matrix of 381 morphological characters (361 osteological, 12 of natal plumages, one of the glandula uropygialis and five of the definitive integument). His was a two level analysis, in which a first analysis resolved the relationships of all families and genera of basal rallids, but a second analysis, including an additional 189 integumental characters, was used to resolve the relationships of the large group of more derived rallids. Much of the poor resolution in the rallid phylogeny resulting from the first level revolved around taxa with missing data, flightless endemic island taxa, and many taxa of limited distributions far removed from the Australian evolutionary arena. Importantly, Livezey's (1998) preferred tree topology was concordant with the pattern of relationships found by Fain *et al*. (2007). Because Livezey's data matrix sampled all basal gruids, especially the near relatives of rallids, such as *Heliornis* and *Psophia*, and was relatively well resolved for basal rallids, it provided an independent, or objective, framework with which to assess the phylogenetic relationships of *Gallinula disneyi*.

Methods

We compared the fossil bones to gruiform specimens listed in the Comparative Material. Often, comparisons were made under magnification using a binocular microscope. Measurements (mm) were taken with Tesa dial calipers to the nearest 0.1 mm.

Anatomical nomenclature—Names for specific bone landmarks follow Baumel & Witmer (1993) and nomenclature for the hypotarsal canals follows Mayr (2004). Some common terms are abbreviated as follows: L, left; lig, ligamentum; M., musculus; proc., processus; tuber, tuberculum; Ma, million years ago; R, right. Anatomical landmarks are abbreviated in figure captions.

Taxonomic nomenclature—Nomenclature follows Christidis & Boles (2008) for Australian taxa, except that we place those species listed in *Tribonyx* at the subgeneric level in *Gallinula*, following Marchant & Higgins (1993); thus, our reference to *Gallinula* includes *Tribonyx* species. Where necessary, the latter taxa are distinguished as *Gallinula (Tribonyx)*.

Institutional abbreviations—*AM*, Australian Museum, Sydney, New South Wales, Australia; *ANWC*, Australian National Wildlife Collection, CSIRO, Canberra, Australia; *MV*, Museum Victoria, Melbourne, Victoria, Australia.

Comparative material

Rallidae: *Porphyrio porphyrio melanotus* AM A.612; *Amaurornis moluccana* AM O.59391, O.60030, O.60031, O.72349; *Gallinula (Gallinula) tenebrosa* AM O.60402, O.67057; *Gallinula (Tribonyx) ventralis* AM O.60910, O.71157, O.71392, O.72427; *Gallinula (Tribonyx) mortierii* AM O.64569; *Gallirallus philippensis* AM O.56994, O.59296, O.64202, O.70869, O.71174, O.72331, O.72342; *Gallirallus australis* AM O.53856; *Gallirallus (Tricholimnas) sylvestris* AM O.56432, O.58027, O.58028, O.64571; *Gallirallus lafresnayanus* AM B.6147; *Rallus limicola* AM O.66437; *Lewinia pectoralis* AM O.60489, O.64836; *Porzana fluminea* AM O.59879; *Porzana tabuensis* AM O.56985; *Poliolimnas cinereus* AM O.58011; *Fulica atra* AM S.558, O.57103; *Fulica americana* AM O.70191; *Coturnicops novaeboracensis* AM O.62352; Gruidae: *Anthropoides virgo* AM S.1215; Rhynochetidae: *Rhynochetus jubata* AM O.57000; Heliornithidae: *Heliornis fulica* MV B.13252.

Phylogenetic analysis

We examined the phylogenetic relationships of *Gallinula disneyi* by adding this taxon to the dataset compiled by Livezey (1998). We modified Livezey's dataset as follows. For Messelornithidae, the following character states were changed to follow Mayr (2004): character 1 to (b); 50 to (?); 176 to (a); 182 to (a), 184 to (b); 189 to (b), 201 to (a); 240 to (a); 250 to (?), 271 to (?). Character 189, the presence of a crista procoracoidei (b), *sensu* Livezey (1998) (i.e., a continuous crista linking the procoracoid to the crista medialis) is depicted by Hesse (1990: fig. 7). Also, following Mayr (2004), we altered character 240 to (a) for Rhynochetidae and character 184 to (b) for Eurypygidae. Despite these alterations, the placement of these taxa did not differ in our tree topologies compared to that obtained by Livezey.

We do not follow Mayr (2004) in considering the crista procoracoidei (char. 189) to be typically present in rallids such as *Gallirallus* and *Gallinula*, as we perceive a separation of the processus procoracoideus and crista medialis in such taxa, so they are left as (a). For character 208, we note that a distinct ventrally directed tubercle is present on the crista deltopectoralis in *Gallinula (Tribonyx) mortierii*, but not in *Gallinula (Tribonyx) ventralis*, so this character was changed to (01) in the matrix for *Tribonyx*. For *Gallinula* char 241, we recognize variation in the depth of fovea carpalis caudalis and code the genus deep to very deep (12). We coded *Gallinula disneyi* according to the definitions in Livezey (1998) and, where we found interpretation of the characters difficult, Livezey's scores for *Gallinula* and *Gallirallus* were examined and the state in *Gallinula disneyi* deduced relative to those taxa.

Following initial analyses with the complete taxon set, we further modified Livezey's (1998) data matrix by successively deleting taxa to seek a consensus tree with less conflict, i.e. fewer shortest trees, based on the following rationale. None of the taxa deleted resulted in any marked changes in tree topology. Because Livezey's (1998) analysis was aimed at determining the relationships of all gruiform taxa, many taxa he included were unnecessary for our purpose of determining the relationship of *Gallinula disneyi*. We deleted Phorusrhacoidea and *Heliopais*, because they are not closely related to an Australian rallid, and they were missing significant data. Further, we deleted several rallid taxa that were flightless island endemics related to *Gallirallus* (i.e., both *Aphanapteryx* species, *Nesotrochis, Diaphorapteryx, Capellirallus, Nesoclopeus, Atlantisia*). We also omitted some taxa that had much missing data and/or were very unlikely to be related closely to *Gallinula disneyi* because they were endemic to areas geographically distant from Australia (*Rougetius, Pardirallus, Cyanolimnas, Ortygonax, Rallus madagascarensis, Habropteryx, Micropygia, Coturnicops* and *Nesocrex*). We retained all species considered to have affinities with gallinules and a suite of Australasian *Gallirallus* relatives, including the flightless *Gallirallus (Tricholimnas) sylvestris, Gallirallus australis* and *Cabalus*. This ensured that we adequately examined a gallinule relationship for *Gallinula disneyi* and whether flightlessness created over-riding homoplasy. In summary, *Gallinula disneyi* was analysed with 50 remaining ingroup taxa and the seven outgroup charadriiform taxa used by Livezey (1998).

The character matrix (Appendix 2) was analysed with PAUP*4.0b10 (Swofford, 2001). Parsimony analyses used heuristic searches with tree-bisection-reconnection (TBR) branch swapping, and 1000 random addition replicates per search. Trees were rooted with outgroups forming a polytomy at the base of the tree. When calculating tree lengths, multistate taxa were treated as polymorphisms rather than ambiguity. Gaps were treated as missing data. Strict consensus trees were computed and are presented here. Bootstrapping (Felsenstein, 1985) used the same settings. Because of non resolution of parts of the Rallidae, a standard bootstrap analysis of 1000 heuristic searches each with 1000 replicates was impractical to achieve, so during the heuristic search the commands *nchuck* = 100 and *chuckscore* = 10 were used, so no more than 100 trees of score (length) greater than or equal to 10 was saved in each replicate. The analysis was aborted after 518 heuristic searches each with 1000 random addition replicates because of practical considerations of computer time (262 hrs) and the resulting values for the maximum likelihood tree used. Trees were manipulated and labelled in MrEnt (Zuccon & Zuccon, 2006).

Geology and geological setting

The Riversleigh World Heritage Propertry deposits are located 5 km west of the Riversleigh homestead (19°02'S 138°45'E), 200 km north of Mount Isa, northwestern Queensland, where they occur as an outcrop of Tertiary limestone overlying the Cambrian Thorntonia Limestone. Over 200 discrete sites are known, which have revealed more than 290 species level taxa (Archer *et al*., 2006). The sites are all within fresh water limestone. In some sites, fossils were deposited during limestone deposition behind tufa barrage dams. A majority of sites are palaeocave deposits, where fossils were deposited in caves eroded in the primary limestone. These caves have long since been completely infilled, their sediments lithified, and their sediments are now exposed on the eroding limestone surface (Travouillon, 2008). All sites have been allocated a relative age based on species assemblages and relative evolutionary grade of taxa. Sites were originally categorized as Systems A, B and C, but are now referred to as Faunal Zones A to C (Archer *et al*., 1997, 2006; Creaser, 1997; Travouillon *et al*., 2006).

Faunal Zone A correlates with faunas from the Etadunna and Namba Formations in South Australia, dated by Woodburne *et al*. (1994) as latest Oligocene (26–24 Ma). Two Faunal Zone A sites have yielded fossils of rails. The greatest diversity of specimens comes from White Hunter Site, deposited in an open aquatic situation, the sediments of which are part of Hal's Hill Sequence of the D-Site Plateau. A range of avian taxa has been found at this site. A single specimen is known from LSO Site, of the Verdon Creek Sequence, in the northern section of the D-Site Plateau.

Sites in Faunal Zone B (Early Miocene) have produced rail fossils at five sites that were mostly former caves. Camel Sputum Site, of the Godthelp Hill Sequence, also on the D-Site Plateau, has produced several avian taxa. Dirk's Towers Site and Judith Horizontalis Site are in the Verdon Creek Sequence in the northern section of D-Site Plateau. Several elements have been recovered from the former site, a single specimen from the latter. Wayne's Wok Site and Creaser's Ramparts Site are in the Hals Hill section of D-Site Plateau. A single specimen has been recovered from each.

Faunal Zone C is considered to be Middle Miocene and approximately 15 Ma old. Four sites have produced fossil rails: three specimens from the palaeocave AL90 Site; two specimens from Ringtail Site, a tufa deposit; and one each from Jim's Jaw Site and Golden Steph Site, both palaeocave deposits. The age of Ringtail Site, of the Ray's Amphitheatre Sequence, Gag Plateau, is somewhat uncertain, as discussed at the end of this paper. Golden Steph Site is tentatively assigned to this faunal zone, but there are too few taxa for confident biocorrelation. Golden Steph and Jim's Jaw Sites are both in the northern end of Gag Plateau, and AL90 is from the southern section of Gag Plateau. The rails discussed here are thus known from 11 sites across all three faunal zones, and they occur in both palaeocave and open former fluvial/lacustrine-type sites.

Results

Fossils available from the Riversleigh Oligo-Miocene deposits now provide evidence for three gruiform taxa, of which one is *Gallinula disneyi*. A second is a larger taxon, represented by both new material and some originally included in *G. disneyi*, which is described below. A third species, smaller than the previous two mentioned, is represented by a single specimen from the Ringtail Site. None of the fossils featured articulated elements. With the exception of those from the Ringtail Site, elements of only one rallid species were found in any given site, so we adopted the parsimonious position that just two larger taxa are represented (see below), and we allocated specimens to species based initially on size. Below we introduce this new material, identified as "newly referred specimen" and augment previous descriptions of known elements with consideration of features used by Livezey (1998) in his morphology-based phylogenetic analysis of rallids and other gruiforms. We especially draw comparisons with *Gallinula tenebrosa, G. ventralis*, and *G. mortierii* to examine the relationship with *Gallinula* previously proposed by Boles (2005a), and then extend our observations more widely within the family Rallidae. A number of features differentiate these rails from any known rallid taxon, so a new genus is introduced for them.

Systematic palaeontology

Order Gruiformes (Bonaparte, 1854)

Family Rallidae Rafinesque, 1815

Genus *Australlus* new genus

Type species. *Gallinula disneyi* Boles, 2005.

Etymology. From *australis*, Latin, southern, and as it relates to Australia; and *rallus*, Latin, name of rails.

Diagnosis. Differs from other genera of the Rallidae by the following unique combination of characters. Humerus with 1), crus dorsale fossae very robust; 2), tuber. ventrale relatively robust and dorsoventrally wide, with an autapomorphic arrangement of the similar sized insertion scars for the three ligaments arranged in an equilateral triangle, with that for the lig. m. coracobrachialis caudalis largest, ovate and occupying the caudal tip of the tuberculum, the scar for lig. m. subscapularis on the dorsal facies distinctly cranial to that for the lig. m. coracobrachialis caudalis and the scar for the lig. m. subcoracoideus on the ventral facies level with, but slightly cranial to, the scar for lig. m. coracobrachialis caudalis and only slightly smaller; 3), tuber. supracondylare ventrale relatively small and not extending proximally as far as condylus dorsalis; 4) and proc. flexorius projecting greatly ventrally. Coracoid, 5), with a prominent crista procoracoidei extending from the proc. procoracoideus to close to the crista medialis. Tarsometatarsus, 6), elongate, about 1.5 times the femoral length; 7), with crista medialis hypotarsi elongate, extending more than half the length of the hypotarsus; and 8), enclosing two hypotarsal canals, one for the tendon for M. flexor digitorum longus (canal 1) and the more plantar one (canal 2) that carried the two tendons, M. flexor perforatus digiti II and M. flexor perforans et perforatus digiti II.

Stratigraphy and age. All specimens of *Australlus disneyi* derive from sites of Faunal Zone A and B, except QM F20799 from Ringtail Site, which is attributed to Faunal Zone C (Travouillon *et al*., 2006), and therefore is presumed to be of Middle Miocene age. QM F20799 does not differ materially from the other specimens of *A. disneyi* and is of similar size (Boles, 2005a), so there is no reason to doubt its identity. However, its preservation is unlike the other two specimens from Ringtail and similar to specimens from White Hunter Site, so perhaps its site of origin is incorrectly recorded.

Australlus disneyi (Boles, 2005)

Gallinula disneyi Boles, 2005: 182.

Enhanced description

In the interval since Boles (2005a) described *Australlus disneyi*, more material has become available that enables a more comprehensive description of this taxon and facilitates comparison with other rallids.

Cranium (newly referred specimen QM F23806, Camel Sputum Site).

A partial cranium (Fig. 1) preserving in one fragment areas caudad of the interorbital zone with loss of the rostrum basisphenoidale and the frontoparietal areas on the left side, but relatively complete on the right side with just the loss of the tip of the proc. postorbitalis and tip of the proc. zygomaticus. Associated fragments include the right side of the nasofrontal hinge and the part of the os mesethmoidale that lies ventral to it (Fig. 1). Measurements: width at temporal fossae, 19.7 mm; cranial height, 20.4 mm; estimated squamosal width, 21.6 mm; foramen magnum width, 6.0 mm, height 5.8 mm.

This cranium is very similar to, though slightly larger than, that of *Gallinula tenebrosa*. It comes from the same locality as two of the paratypes for *Australlus disneyi*, and it is of expected size, given typical rallid proportions, for that species. The os lacrimale is unfused, and the os nasale fused with the os frontale dorsal to the lacrimal facet. The nasofrontal hinge has a flexible joint and the same structure as in *Gallinula*. The fonticuli orbitalocraniales are of a similar relatively small size located in the dorsal half of the orbits. The caudal orbital margins are drawn out farther than in *Gallinula*, with sharper, more compressed margins, which more broadly overhang the orbits. The fossa temporalis is as shallow as in *Gallinula* and the crista temporalis is minimally separated from the crista nuchalis transversus by 3 mm. While the proc. postorbitalis is mostly lost, its remaining base suggests that it was relatively small and, likewise, the proc. zygomaticus could only have been small. The crista nuchalis transversus is distinct from a point dorsal to the proc. paroccipitalis to dorsal to the foramen magnum, and there is slight inflation of the prominentia cerebellaris to form hollows either side of it. The recessus tympanicus is relatively longer than in *Gallinula*; the proc. paroccipitalis forms a prominent caudal wall strongly linked to the squamosal margin of the recess, enclosing a broad sulcus lateral to the fenestra vestibule, which forms the caudolateral buttress for the cotylae quadratica otici. This area is relatively smaller and much more fenestrated in *Gallinula* species. The basisphenoid structure does not differ significantly from the conformation seen in *Gallinula ventralis*, except that the anterior parts of the lamina parasphenoidalis are a little more inflated.

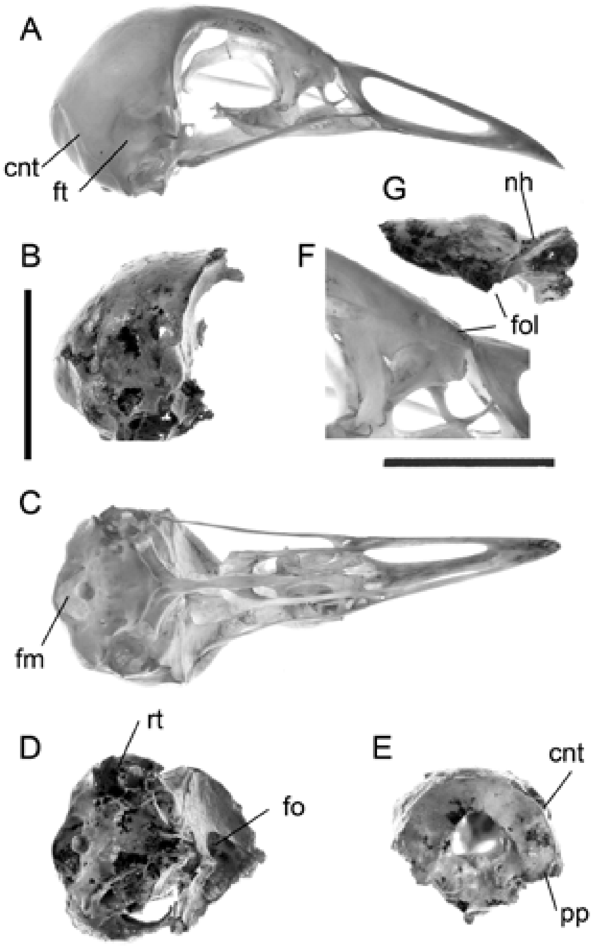

Fig. 1. Crania of *Gallinula tenebrosa* AM O.67057 *(A,C,F)* and *Australlus disneyi* QM F23806 *(B,D,E,G)* in right lateral *(A,B,F)*, ventral *(C,D)*, caudal *(E)*, and dorsolateral *(G)* views. Abbreviations: *cnt*, crista nuchalis transversus; *fo*, fonticuli orbitocranialis; *fol*, facet os lacrimale; *fm*, foramen magnum; *ft*, fossa temporalis; *nh*, nasofrontal hinge; *pp*, processus paroccipitalis; *rt*, recessus tympanicus. Scale bar for (A–E) is 20 mm and (F, G) is 5 mm.

Mandible (newly referred specimen QM F54503, White Hunter Site).

Most of the paratypic material for *A. disneyi* was recovered from White Hunter Site, so it is possible that this mandible derives from one of the same individuals. This specimen is a single mandible missing its tip (Fig. 2). During preparation, the os dentale fragments were disassociated from the more posterior parts of the mandible, which are preserved in their original depositional relationship to each other by a bridge that remains from the resin used to join fragments of the specimen together when it was in limestone. Measurements (mm): greatest width across the cotyla lateralis, 22.0; width between the tip of the proc. mandibulae medialis and proc. retroarticularis, 7.6; maximum depth, left side of the mandible, 6.5.

The overall form and proportions of the mandible are similar to those of *Gallinula tenebrosa* and it has a similar ventral depression of the anterior two-thirds of the os dentale. The fenestra caudalis mandibulae is small, but it is located relatively rostrally compared to all rallids examined, such that the distance to the cotyla lateralis exceeds the length of the cotyla lateralis; in other rallids, the cotyla lateralis is longer. The proc. mandibulae medialis houses a foramen pneumaticum dorsally near the tip, and it is larger and relatively more robust toward its tip than that of *G. tenebrosa*. The cotyla medialis is larger and protrudes over the medial profile in dorsal view to make a distinct angular prominence, much more so than in species of *Gallinula*. The cotyla medialis also extends farther laterad, such that it extends past the base of the surangular and is wider than the cotyla lateralis, whereas it and the cotyla lateralis have approximately similar widths in *Gallinula* species, with the base of the surangular at their junction. The proc. retroarticularis is more robust, but shorter, unlike the thin blade-like structure in *Gallinula* species. The dorsal margin of the crista transversus fossa is nearly flat with only a very shallow notch at mid-width, whereas it is more deeply notched in all compared rallids. A further significant difference from *Gallinula* species is seen in the profile of the lateral facies ventral to the cotyla lateralis: in QM F54503,

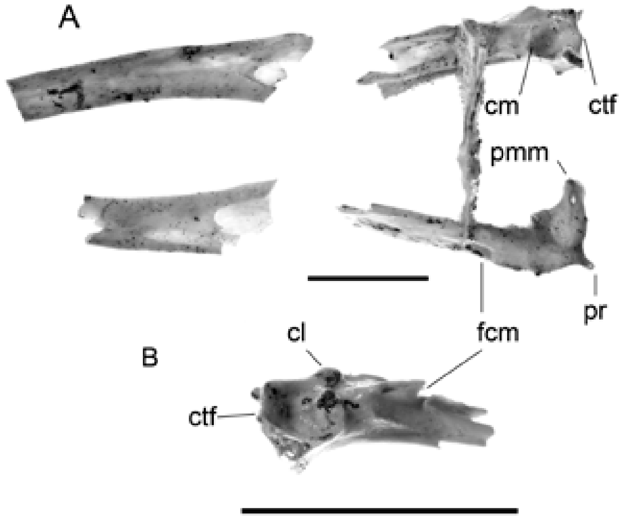

Fig. 2. Mandible fragments of *Australlus disneyi* QM F54503 *(A)* and rallid species QM F54524 *(B)*. The rami of QM F54503 are held together as fossilized by a resin bridge, but the os dentales have separated and so are shown medial facies up. Abbreviations: *cl*, cotyla lateralis; *cm*, cotyla medialis; *ctf*, crista transversus fossae; *fcm*, fenestra caudalis mandibulae; *pmm*, processus mandibulae medialis; *pr*, processus retroarticularis. Scale bars = 10 mm.

it is concave below the lip of the cotyla, whereas in species of *Gallinula*, it is convex.

Premaxilla (newly referred specimens: QM F30864, Wayne's Wok Site; QM F54505, Camel Sputum Site).

These premaxillae are both deeply vaulted ventrally between sharp tomial edges. Laterally, they have several vascular foramina; and the tips over their last 5 mm are slightly depressed relative to the more posterior tomial margin. These fossils are thus rather similar to the premaxilla of *Gallinula tenebrosa*. The referred cranium of *G. disneyi* was found in the samples from Camel Sputum Site. Measurements (mm) taken at anterior side of nasal aperture: QM F30864, length to tip, 11.3; width, 4.8; height, 4.2; QM F54505, length to tip, 11.5; width, 4.6; height, 4.7.

Vertebrae (newly referred specimens: QM F54506, cervical vertebra number 15 [where number 1 is the atlas vertebra], White Hunter Site; QM F54504, cervical vertebra number 12, White Hunter Site; QM F54507, cervical vertebrae number 11, White Hunter Site; QM F54508, cervical vertebrae number 14, White Hunter Site; QM F54515, cranialmost 4 fused vertebrae of synsacrum, White Hunter Site; QM F54509, cervical vertebra number 10, Dirk's Towers Site; QM F54510, anterior part synsacrum, Dirk's Towers Site). These vertebrae were compared with, and are very similar to, those of *Gallinula tenebrosa* (Tables 1, 2), *G. ventralis* and *Gallirallus philippensis*, and they were easily assigned to position. All came from sites where long bones of *A. disneyi* were also recovered, so they are referred to that species.

Humerus (QM F20906, proximal R, holotype, White Hunter Site, QM F31471, proximal R; QM F31472, distal L; newly referred proximal and shaft L, QM F45457 White Hunter Site).

In addition to the features described by Boles (2005a) for these specimens, we note the following:

1. The tuber. ventrale in *A. disneyi* is relatively robust and dorsoventrally wide compared to the condition in all rallids examined, in which it is typically dorsoventrally compressed and caudocranially elongated. Associated with this robust tuberculum is an autapomorphic arrangement of the insertion scars for the three ligaments inserting thereon. Typically in rallids, a large ovate scar for the insertion of M. coracobrachialis caudalis occupies the caudal tip of the tuberculum, with an elongate scar for lig. m. subscapularis positioned distinctly cranial to it on the facies bounding the incisura capitis, with a smaller ovate scar for the M. subcoracoideus adjacent to this but on the ventral facies of the tuberculum (following the terminology of Ashley, 1941). In *A. disneyi*, the holotypic specimen QM F20906 has damage to the cranial part of the tuber. ventrale and QM F31471 is more damaged, but QM F20906 reveals that the scar for the M. subcoracoideus is centred slightly farther caudocranially, but is essentially beside that for the M. coracobrachialis caudalis and is of similar size, rather than being entirely and distinctly cranial to it and smaller. This arrangement of ligament scars was not found in any Recent gruiform examined, but it is seen in the new species described below.
2. The caudal facies of the shaft distal to the crus dorsale fossae is angular.
3. The crus dorsale fossae is more robust than in species of *Gallinula* and *Amaurornis*.
4. The tuber. dorsale is relatively small, but prominent.
5. The crista bicipitalis is relatively small in *A. disneyi* with its distal junction with the shaft positioned slightly distal to the distal end of the crus dorsale fossae, resulting in its largely being occluded in caudal view.
6. The fossa pneumotricipitalis is shallow, and it is not penetrated by any pneumatic foramina.
7. The sulcus lig. transversus is much shallower in *A. disneyi* than in species of *Gallinula*, including *G. (Tribonyx) mortierii, Amaurornis* and most *Gallirallus* species, and is separated from the incisura capitis by a caudocranially thicker ridge. A similar condition is seen in *Gallirallus australis*.
8. The ventral side of the crista deltopectoralis has a distinct tubercle, which is variably present in *Gallinula*. A tubercle is present in *Gallinula (Tribonyx) mortierii* but not in *G. (Tribonyx) ventralis*. A tubercle is not present in the flightless and more modified members of the *Gallirallus* clade, such as *Gallirallus australis* and *Gallirallis sylvestris*, so its presence is not contingent on flightlessness.
9. The angulus cristata of the crista deltopectoralis is located distal to the crista bicipitalis and the part of the crista deltopectoralis distal to the angulus is less than the length proximad of the angulus. In contrast, the angulus lies proximal to the junction of the crista bicipitalis and the shaft, and the distal part of the crista deltopectoralis (i.e., that past the angulus) is longer than the proximal section in *Gallinula* and *Gallirallus*, including in the flightless taxa compared.
10. The crista deltopectoralis terminates distally on the cranial facies as opposed to on the dorsocranial margin as in most *Gallinula* and *Gallirallus* species. In flightless taxa, it is located more ventrally.

11. The crista deltopectoralis is markedly concave caudodorsally, rather than flat to convex.
12. The tuber. supracondylare ventrale is relatively small, not extending proximad so far as to be level with proximal margin of the condylus dorsalis, is wider than high, is relatively close to the condylus ventralis, and has the dorsal part of the articular facet angled dorsodistally, forming a wide angle with the ventral part of the facet. In *A. disneyi*, the fossa m. brachialis undercuts the tuberculum. In species of *Gallinula* and *Amaurornis*, the tuber. supracondylare ventrale is about as wide as long, has a similar proximal extent as the condylus dorsalis, has the dorsal part of the facet angled dorsodistally, and is distinctly separated from the condylus ventralis. In some *Gallirallus* species, such as *G. philippensis*, the tuber. supracondylare ventrale is narrower ventrodorsally, with its dorsal side directed significantly dorsally, so that it is nearly at right angles to the ventral side of the tuberculum. In the flightless *G. australis*, however, the tuberculum is wide and short and relatively small, so its reduced size in the Riversleigh fossil taxa could be related to flightlessness.
13. The proc. flexorius has relatively greater ventral projection than in *Gallinula* species, and is more robust. Viewed in cranial aspect, with both the proc. flexorius and condylus dorsalis lying on a planar surface, the dorsoventral width of the proc. flexorius exceeds half the dorsoventral width of the condylus ventralis (much thinner in *Gallinula*). The proc. flexorius extends slightly farther distad than the condylus ventralis in *A. disneyi*, as it does in *Gallinula* species.
14. The relative overlap medially of the condylus ventralis by the condylus dorsalis on its proximal side (in cranial view), used by Brodkorb (1967) to distinguish *Gallinula* from *Fulica* and discussed by Boles (2005a), was reassessed. When taxa were compared in the same orientation, where both the proc. flexorius and condylus dorsalis lay on a planar surface, we found no overlap of the condyles in *Heliornis* and *Porphyrio* species, but in all *Gallinula* species, *Amaurornis* species, *Gallirallus* species, *Rallus limicola, Fulica atra* and *F. americana*, the condyli overlapped on a plane parallel to the axis of the bone. In the material of *Australlus disneyi*, ventrodorsal overlap of the condyles is apparent.

Ulna (QM F30693, pL, Dirk's Towers).

There is no evidence for a second rallid in Faunal Zone A and B sites, with only Ringtail Site (Faunal Zone ?C) containing evidence of multiple species, including one fossil of a much smaller species than those described herein. There is no reason to doubt the referral of this ulna to *A. disneyi*, based on its appropriate size. The impressio brachialis in *A. disneyi* has a prominent crista brachialis (*sensu* Livezey, 1998: char 224), unlike in *Gallinula*. Otherwise, the ulna is little different from that of rallids.

Carpometacarpus (QM F30908, L, Dirk's Towers Site; QM F31478, L, Camel Sputum Site).

The labrum dorsalis (*sensu* Livezey, 1998, char 237) is relatively elongate, extending adjacent to the fovea carpalis caudalis, which is deep. In *Gallinula* species, the dorsal rim typically ends proximad of the fovea, as in *G. ventralis* and *G. tenebrosa*. The sulcus trochlearis is shallow and rounded. Otherwise, the differences between *A. disneyi* and *Gallinula* species are related to shortening of the element associated with loss of flight.

Coracoid (QM F30692, cranial part R, Dirk's Towers; QM F31469, cranial part L, White Hunter Site; QM F31470, cranial part R, White Hunter Site; QM F31477, sternal part and shaft L, Camel Sputum. Newly referred specimens: QM F39864, cranial part L, Judith's Horizontalis Site; QM F54513, cranial part and shaft L, White Hunter Site).

In addition to the features cited by Boles (2005a), we note the following in *A. disneyi*:

1 The foramen nervi supracoracoidei is large in *A. disneyi*, and it has large foramina penetrating the corpus, as in *G. (Tribonyx) mortierii*, but it is unlike that of *G. (Tribonyx) ventralis* and *G. tenebrosa*, in which the foramina opening into the corpus are very small (Fig. 3).

2 The coracoid of *A. disneyi* is characterized by a prominent, sharp crista procoracoidei (Livezey, 1998: char. 189), which extends from the proc. procoracoideus to a point close to the crista medialis, as in *Psophia* (Olson, 1973b: fig 2). The interpretation that the proc. procoracoideus extends about half way along the shaft, joining it gradually (Boles, 2005a) might have been inferred from broken specimen QM F31470. Specimen QM F31477 shows this to be incorrect. In this fragment, the proc. procoracoideus preserves its cranial margin and, although the crista is broken lateral to the foramen nervi supracoracoidei, it is clearly preserved sternal to this point. The crista procoracoidei is elongate, broad, dorsoventrally-thin, and it extends at least half the length of the impressio sternocoracoidei. Above the angulus medialis, the crista medialis is broken in QM F31477, so its connection to, or separation from, the crista procoracoidei is unknown. However, the preserved cristae are very similar to the state in *Porphyrio* and also to that seen in the coracoid attributed to the new species described below, in which the crista

Table 1. Vertebral measurements (mm) of *Gallinula tenebrosa* AM O.60402. Length is measured along midline of centrum, width is for the facies articularis caudalis. Vert # is the position in the vertebral series where the atlas is 1.

Vert #	3	4	5	6	7	8	9	10	11	12
Length	9.9	10.0	—	12.4	12.1	11.9	11.2	10.7	10.0	9.5
Width	2.0	2.2	—	3.0	3.3	3.2	3.6	3.6	3.8	4.6
Vert #	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Length	8.2	6.8	6.2	6.9	8.1	8.4	8.3	8.4	8.2	8.1
Width	5.4	5.7	5.9	4.9	4.3	4.2	4.1	4.0	4.2	4.5

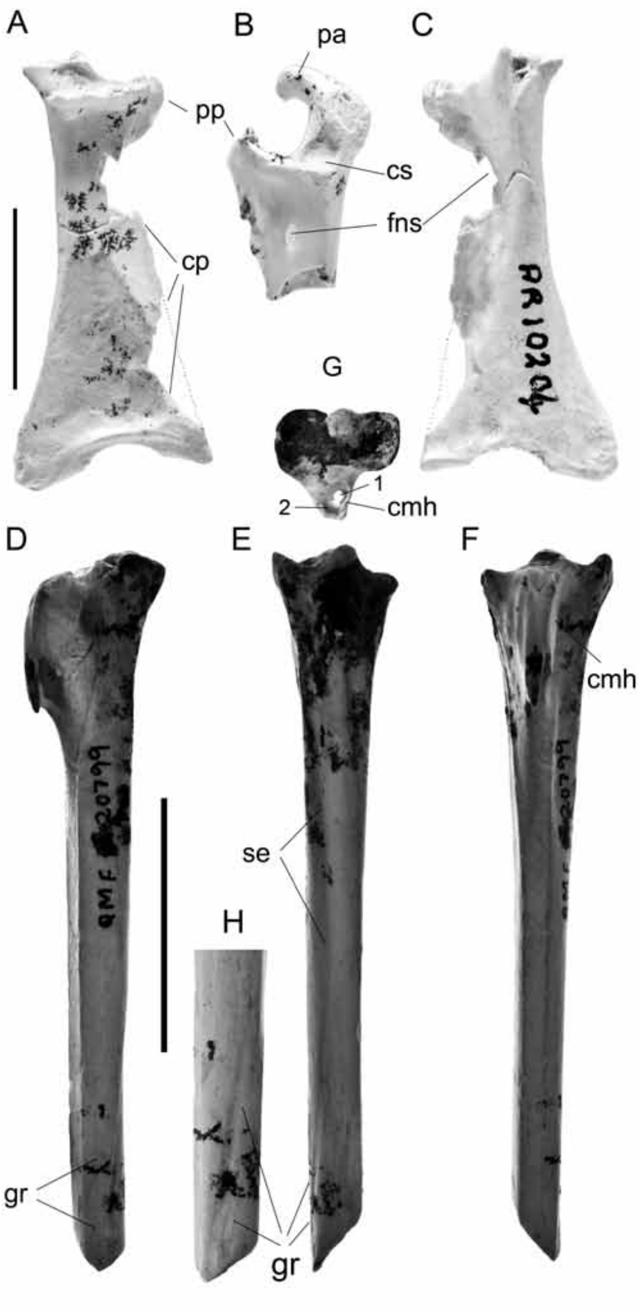

Fig. 3. Coracoids *(A–C)* of *Australlus disneyi*, left QM F31477 in dorsal *(A)* and ventral *(C)*, cranial part right QM F31470 in dorsal *(B)* views; scale bar = 10 mm. The crista medialis leading from the angulus medialis to the crista procoracoidei is broken in this specimen, as indicated by the dotted lines. Left proximal and part shaft tarsometatarsus of *Australlus disneyi* QM F20799 in medial *(D)*, anterior *(E)*, plantar *(F)*, proximal *(G)* views (scale bar = 20 mm), and medial view enlarged *(H)*. Abbreviations: *cmh*, crista medialis hypotarsi; *cp*, crista procoracoidei; *cs*, cotyla scapularis; *gr*, groove for extensor hallicus longus; *fns*, foramen nervi supracoracoidei; *pa*, processus acrocoracoideus; *pp*, processus procoracoideus; *se*, sulcus extensorius; *1*, tendinal canal 1 for M. flexor digitorum longus; *2*, tendinal canal 2 for M. flexor perforates digiti II & M. flexor perforans et perforatus digiti II.

procoracoidei extends close to, but does not connect to, the crista medialis (Fig. 3). Mayr (2004) considered the crista procoracoidei to be present in rallids, heliornithids, and messelornithids, and to support the monophyly of these taxa. We follow Livezey's definition and do not consider that the more derived rallids have a crista procoracoidei because in these birds the proc. procoracoideus merges into the shaft closer to the cranial end, and it is always separated by a broad distinct gap from the enlarged crista medialis, which extends from the angulus medialis. In *Heliornis*, there is a distinct crista connecting the proc. procoracoideus and angulus medialis, as recorded by Livezey (1998), although it is not as produced from the shaft as it is in *Psophia*.

3 The proc. acrocoracoideus overhangs the shaft ventrally somewhat more than in all *Gallinula* species, but it is more notable for the extreme rotation mediad over the sulcus m. supracoracoidei, such that its cranial margin is at a near right angle to the facies articularis humeralis.

4 The impressio lig. acrocoracohumeralis forms a shallow sulcus extending from the facies artic. humeralis to the tip of the proc. acrocoracoideus. This hollow is bisected by a laterodorsal—medioventrally aligned groove.

5 The ventral facies of the shaft is quite compressed in its cranial half (not broadly convex) making the adjacent lateral facies flattened and the resultant ridge is directed somewhat laterad, especially near the facies artic. humeralis. This causes the proc. acrocoracoideus to greatly overhang the ventromedial facies at an angle approaching 45 degrees to the sagittal plane. In all *Gallinula* species, the plane of the surface in the sulcus supracoracoideus and adjacent to the facies artic. clavicularis is essentially aligned dorsoventrally.

6 The proc. procoracoideus extends craniad beyond the cotyla scapularis.

Femur (QM F36452, pL, LSO Site).

The femur of *Australlus disneyi* is only represented by the relatively uninformative proximal fragment QM F36452. The preserved length of 39.8 mm extends just distal to the nutrient foramen, and its proximal width of 10.0 mm is similar in size and proportions to the femur of *G. ventralis* AM O.71392. Given similar total proportions, estimated total length for the fossil femur is about 54 mm. It is generally similar to those of *G. ventralis* and *G. tenebrosa*, with the most significant difference being that the insertion for the M. obturator externus is larger, causing a prominence on the caudal margin just distal to the facies articularis antitrochanterica, when viewed laterally, which is absent in extant *Gallinula* species.

Tibiotarsus (QM F31473, proximal R, White Hunter Site; QM F31474, distal R, White Hunter Site; QM F31475, distal R, White Hunter Site; QM F24130, proximal L, Camel Sputum Site; QM F31480, proximal R, Dirk's Towers Site; newly referred specimen QM F30696, distal+shaft L, Camel Sputum Site).

In addition to the points described by Boles (2005a), we note the following for *A. disneyi*. The sulcus extensorius grades into a distinct flat groove, which extends farther proximad than in *Gallinula* species. Specimen QM F30696, which we refer to *Australlus disneyi*, is instructive as it has a preserved length of 77.6 mm for a midshaft width of 4.9 mm and distal width of 9.2 mm, but the proximal and distal ends of the fibular synostosis are 70 mm and 44.5 mm from distal end, respectively. In contrast, a tibiotarsus of *G. tenebrosa* (AM O.60402) has the comparable values: midshaft width 4.9 mm, distal width 8.9 mm, and the fibular synostosis extends from 54.5 to 42.5 mm from the distal end. Both observations indicate a tibiotarsus proportionally longer than any *Gallinula* species.

QM F30696 was identified by Boles (2005a) as the tibiotarsus of a rail, but because of its more robust nature and morphological differences, it was not placed with *A. disneyi* and left unnamed. It is considered here to fall within the range of variation of that species, and it is included with it.

We take this opportunity to correct a misidentification in Boles (2005a). A distal tibiotarsal fragment (QM F24605) from the Pleistocene Floraville Local Fauna (Site 5c, Floraville Stn, Leichhardt River, North Queensland) was incorrectly regarded as *Gallinula mortierii*. It is here recognized as Anatidae, ?Dendrocygnine. As this record would have been the most northwestern one for *G. mortierii*, its reidentification considerably reduces the known mainland distribution of that species.

Tarsometatarsus (QM F20799, proximal L, Ringtail Site; QM F23723, proximal R, White Hunter Site; QM F30720, proximal R, Creaser's Ramparts Site; QM F31476, distal R fragment lacking trochlea metatarsi II., White Hunter Site)

In addition to those characters described by Boles (2005a), we note the following two significant features.

1. The crista medialis hypotarsi is relatively much longer than in *Gallinula* species, extending to greater than half the length of the hypotarsus, which contributes to the strong enclosure of two hypotarsal canals, as it does in *Heliornis*. This crista is very short in most rallids (e.g., *Gallinula, Gallirallus* and *Porphyrio*), always much less than half of the hypotarsus length. The enclosure of the two canals is a feature approached in *Gallinula*, in which two canals are enclosed plantarly, but that for tendinal canal 2 (*sensu* Mayr, 2004: fig. 5) for the tendon of M. flexor perforatus digiti II (equals canal 2 of Strauch, 1978: fig. 29) is only partly or not closed. In both *Fulica atra* and *F. americana*, tendinal canal 1 (for the tendon for M. flexor digitorum longus) is fully enclosed and tendinal canal 2 is nearly closed. *Amaurornis* species variably have tendinal canal 1 closed or open, with tendinal canal 2 open. *Porzana* species have tendinal canal 1 closed, or tending so, and tendinal canal 2 open, but *Poliolimnas* species have both open.

However, closure of any tendinal canals clearly distinguishes *A. disneyi* from *Gallirallus* and its flightless relatives and *Rallus*, in which both canals are open plantarly. In *A. disneyi*, the greater extent of the crista medialis hypotarsi results in the more plantar of the two canals having carried two tendons, those for M. flexor perforatus digiti II and M. flexor perforans et perforatus digiti II (*sensu* Mayr, 2004). This arrangement is also seen in *Heliornis*. In all *Gallinula* species, the tendon for M. flexor perforans et perforatus digiti II lies in a groove that is open plantarly.

2. The tarsometatarsus is proportionally far longer than in any *Gallinula* species. The groove passing from the sulcus extensorius mediad around the shaft for the M. extensor hallicus longus (Owre, 1967) is located half way down the shaft in rallids. In the more complete QM F20799, the midpoint of this groove is 43 mm from the proximal end, suggesting a total length of about 86 mm. Such an elongate shaft is also supported by the observation that the groove traverses the medial surface at a shallower angle than in *Gallinula* and that the cristae plantares medialis et lateralis remain parallel over the entire preserved length of the fossil. The tarsometatarsus of *A. disneyi* is thus about 1.6 times as long as the femur, which was estimated above at about 54 mm (based on QM F36542). This is also in accordance with the elongate tibiotarsus mentioned above. In *Gallinula* species, the tarsometatarsus is only slightly longer than the femur.

Australlus gagensis n.sp.

Figs 4–6; Table 2

Holotype. QM F54511, complete right humerus (Fig. 4).

Diagnosis. A flightless rail having the diagnostic characters of the genus *Australlus* that differs from *A. disneyi* by its considerably larger size (humeral proximal width and distal width are 117.5% and 116.5%, respectively, of the largest values for *A. disneyi*) and by having the humeral facies bicipitalis in the area overlying the corpus depressed into a distinct depression relative to the intumescentia humeri and caput humeri; a near obsolete sulcus lig. transversus that is separated from the incisura capitis by a caudocranially thicker ridge; a less prominent proc. supracondylaris dorsalis; and proc. flexorius extending markedly further distally than the condylus ventralis.

Table 2. Measurements of fossil rail bones from Riversleigh. Vertebral position determined by comparison with AM O.60402. %L is percentage length of the comparable vertebra in AM O.60402 (Table 1).

Site	Species	Catalogue number QM F	Vertebra #	Length	Width	%L O.60402	%W O.60402
White Hunter	*disneyi*	54507	11	9.9	2.9	99.0	76.3
White Hunter	*disneyi*	54504	12	9.5	3.5	100.0	76.1
White Hunter	*disneyi*	54508	14	6.7	5.2	98.5	91.2
White Hunter	*disneyi*	54506	15	5.7	5.1	91.9	86.4
Dirks Towers	*disneyi*	54509	10	9.9	3.4	92.5	94.4
Golden Steph	*?gagensis*	36354	22	8.2	4.8	101.2	106.6
AL90	*gagensis*	54514	6	11.0	3.8	88.7	126.6

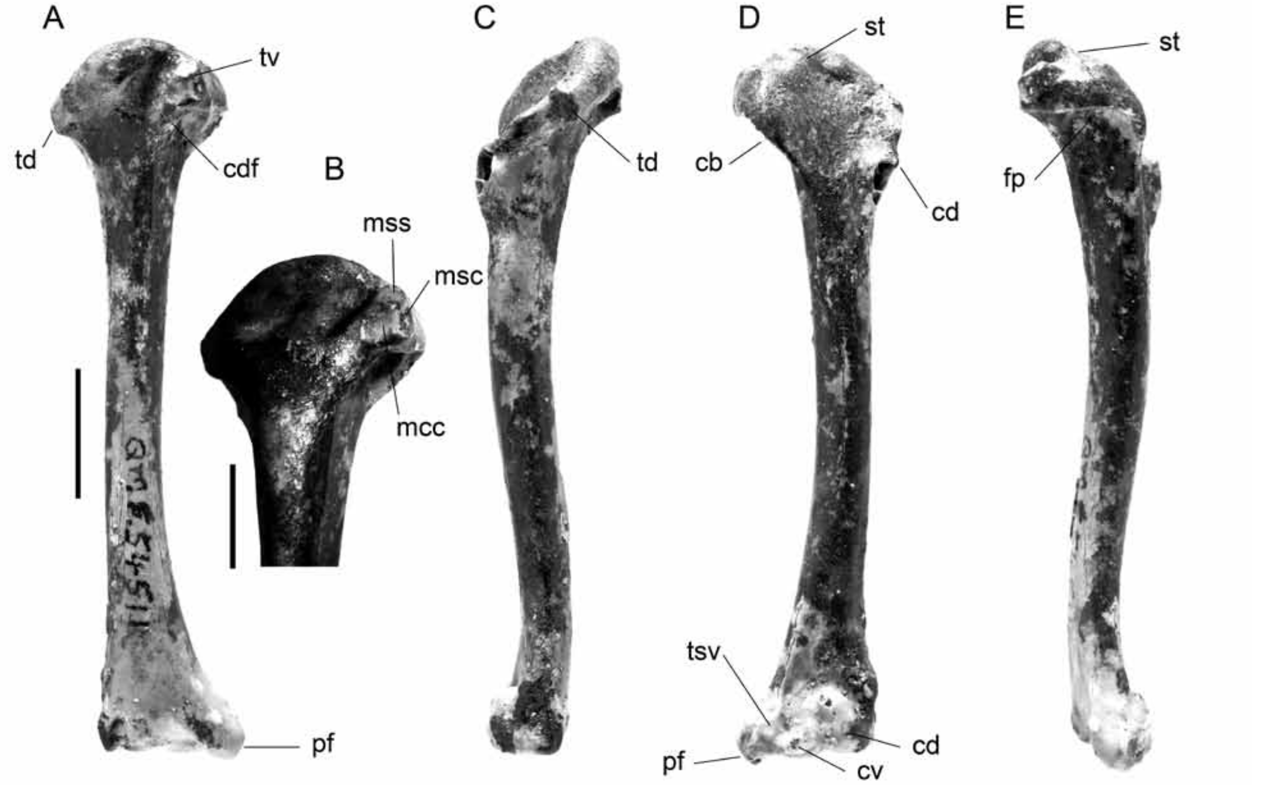

Fig. 4. Left humerus of *Australlus gagensis* (holotype) QM F54511 in caudal *(A,B)*, dorsal *(C)*, cranial *(D)*, and ventral *(E)* views. Abbreviations: *cb*, crista bicipitalis; *cd*, condylus dorsale; *cdf*, crus dorsale fossae; *cdp*, crista deltopectoralis; *cv*, condylus ventrale; *fp*, fossa pneumotricipitalis; *mcc*, M. coracobrachialis caudalis; *msc*, M. subcoracoideus; *mss*, M. subscapularis; *pf*, processus flexorius; *st*, sulcus lig. transversus; *td*, tuberculum dorsale; *tsv*, tuberculum supracondylare ventrale; *tv*, tuberculum ventrale. Scale bar left of A is 10 mm (for A, C, D, E); scale bar left of B is 5 mm.

Measurements (mm) of holotype. Length, 54.3; proximal width, 13.4; shaft width at mid-length, 4.4; maximum distal width, 11.3; depth of condylus dorsalis, 6.1.

Type locality. AL90 Site, Gag Plateau, Faunal Zone C, Riversleigh World Heritage Property, Boodjamulla (Lawn Hill) National Park, northwestern Queensland (Archer *et al*., 1989, 1994; Creaser, 1997; Travouillon *et al*., 2006). Details of the site locality are available from the University of New South Wales or Queensland Museum on request.

Stratigraphy, age, fauna and depositional environment. AL90 Site is a fossil cave pitfall deposit formed within the freshwater limestone at the Riversleigh World Heritage Property. The site is considered part of Riversleigh's Faunal Zone C deposits, which, based on stage of evolution of contained mammal taxa and faunal correlation, is Middle Miocene in age (Archer *et al*., 1997, 2006; Creaser, 1997; Travouillon *et al*., 2006).

Paratype. QM F54536, R coracoid lacking sternal end, AL90 Site (Fig. 5).

Measurements (mm) of paratype. Preserved length 25.0; length facies artic. humeralis from cotyla scapularis 5.3; maximum width proc. procoracoideus—lateral side cotyla scapularis 7.8; maximum length cotyla scapularis to proc. acrocoracoideus 7.4; width cotyla scapularis 4.5.

Referred material. QM F31479, distal L femur, Ringtail Site (previously referred to *A. disneyi*), referred to *A. gagensis* on basis of larger size than *A. disneyi* (midshaft width 5.6 mm, distal width >13 mm, depth lateral condyle 11.5 mm); QM F54512, distal L tarsometatarsus (missing trochleae metatarsi II and IV), Jim's Jaw Site. This fragment is of a significantly larger rallid tarsometatarsus than those referred to *A. disneyi*, and for this reason it is tentatively referred to the new species. QM F54514, vertebra number 6, from AL90 Site is referred to *A. gagensis*, because while it is of similar size (length) to those from, for example, White Hunter Site or *G. tenebrosa* AM O.60402 (Table 2), the centrum is proportionally wider and it is also much deeper, with the facies articularis caudalis 2.7 mm deep compared to 2.1 mm in *G. tenebrosa* AM O.60402. The single rail bone from Golden Steph Site, QM F36354, vertebra number 22, also has a stouter centrum and a larger neural canal than *G. tenebrosa* AM O.60402, though it does not differ much in length (Table 2), so is also tentatively referred to *A. gagensis*.

Etymology. The species is named after the Gag Plateau, where fossil sites containing it were located.

Description

This species differs from *A. disneyi* by its larger size and diagnostic humeral characters listed above (Fig. 4). The marked depression of the facies bicipitalis is lacking in *A. disneyi* and is likely associated with *A. gagensis* having evolved in flightless state for a longer period. Whereas in most *Gallinula* and *Gallirallus* species, there is no similar depression, in the flightless taxa that are the most divergent from the volant condition (such as Gallirallus australis and *Gallinula mortierii*), a similar depression is seen, but in both of these species the depression is shallower. Similarly, the fossa pneumotricipitalis is shallower, and the crista deltopectoralis more thickened than in *A. disneyi*. The brachial fossa is relatively shallower than in *A. disneyi* and does not undercut the tuber. supracondylare ventrale. All these features likely are associated with this taxon having been flightless longer than *A. disneyi*. As in *A. disneyi*, ventrodorsal overlap of the condyli dorsalis and ventralis is apparent.

In addition, some features are further exaggerated from the condition seen in *A. disneyi*. For example, the crus dorsale fossae is relatively stouter and the tuber. ventrale is more massive and clearly shows the generic autapomorphic triangular arrangement of the three ligamental scars that are of near equal size: that for M. coracobrachialis caudalis is positioned dorsad of that for M. subcoracoideus, which is oriented somewhat ventrally, and that for M. subscapularis is distinctly craniad of the other two scars, not on the facies lining the incisura capitis, but rather is oriented caudoproximally. We do not consider that this structure of the tuber. ventrale is related to the flightless condition: in the humerus of all *Gallirallus* and *Gallinula* species, no matter how altered by their flightless condition, the tuberculum is caudocranially elongate, with the elongate scars for lig. m. subscapularis and lig. m. subcoracoideus positioned adjacent to each other and markedly cranial to a much larger ovate scar for lig. m. coracobrachialis caudalis on the caudal tip of the tuberculum. The arrangement described for *Australlus* was not observed in any other gruiform taxon examined.

The paratype coracoid (Fig. 5) is larger and more robust than coracoids of *A. disneyi* with a shallower cotyla

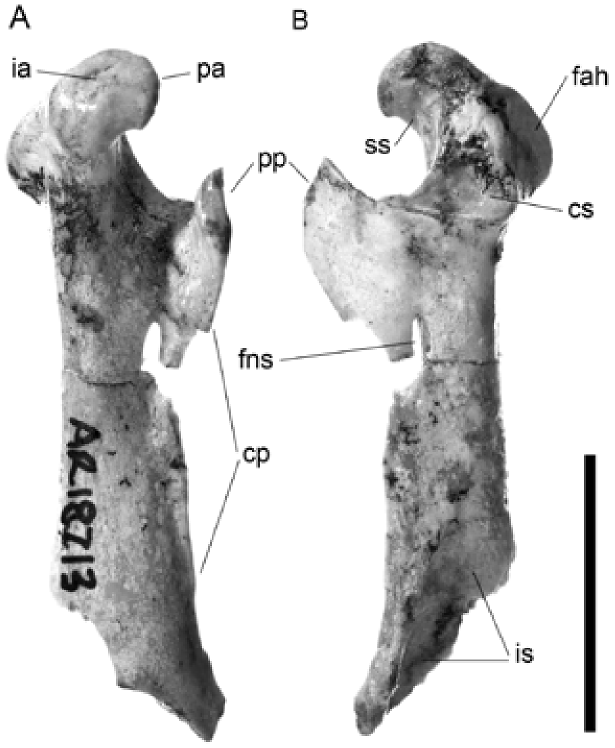

Fig. 5. Right coracoid of *Australlus gagensis* (paratype) QM F54536 in ventral view *(A)* and dorsal view *(B)*. Scale bar is 10 mm. Abbreviations: *cp*, crista procoracoidei; *cs*, cotyla scapularis; *fah*, facies artic. humeralis; *fns*, foramen nervi supracoracoidei; *ia*, impressio lig. acrocoracohumeralis; *is*, impressio m. sternocoracoidei; *pa*, processus acrocoracoideus; *pp*, processus procoracoideus; *ss*, sulcus m. supracoracoidei.

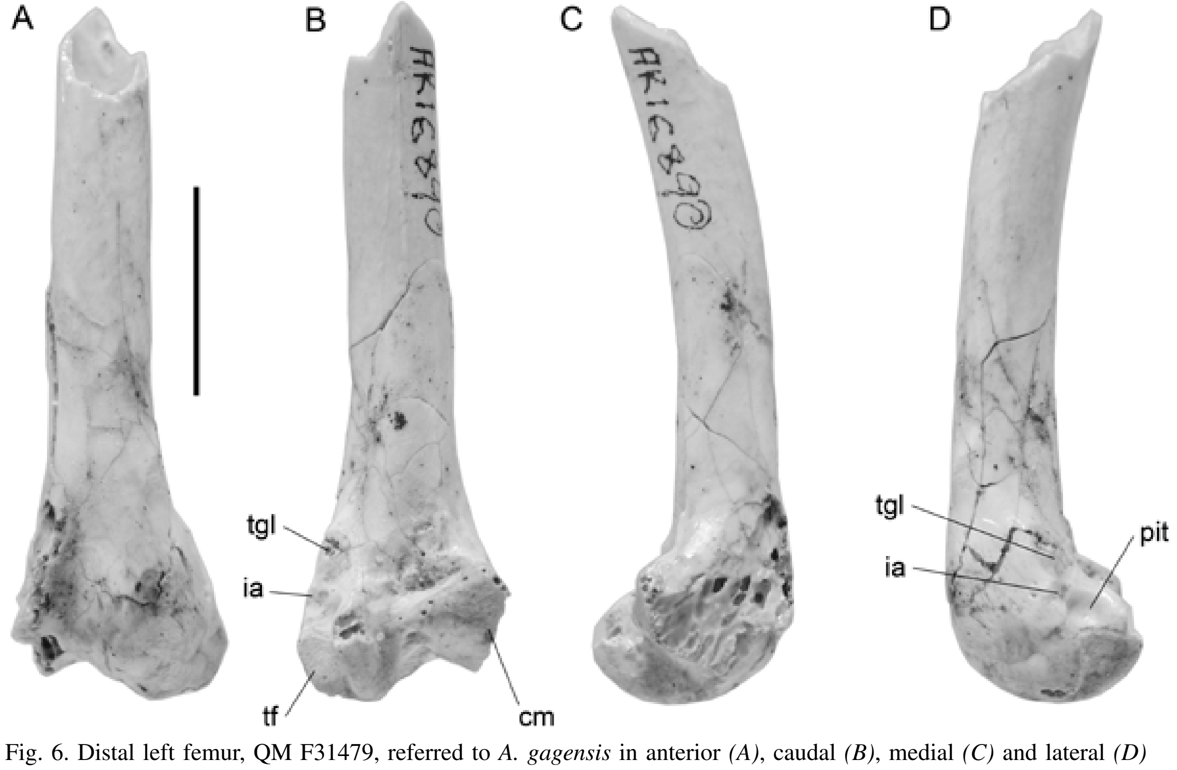

Fig. 6. Distal left femur, QM F31479, referred to *A. gagensis* in anterior *(A)*, caudal *(B)*, medial *(C)* and lateral *(D)* views. Abbreviations: *cm*, condylus medialis; *ia*, impressio M. ansa iliofibularis caudalis; *pit*, pit for the fibular stop; *tgl*, tuberculum gastrocnemialis lateralis; *tf*, trochlea fibularis. Scale bar is 10 mm.

scapularis. It has a large and elongate foramen nervi supracoracoidei with foramina penetrating the corpus. The sharp-edged crista procoracoidei extends c. 14 mm from the cotyla scapularis sternally and merges with the shaft about 1.0 mm cranially and slightly ventrally of the crista medialis: if both crista were extended, they would overlap ventrodorsally. The proc. acrocoracoideus overhangs the sulcus m. supracoracoidei and, as in *A. disneyi*, is aligned at about 45 degrees in a dorsocranial–ventrosternal plane. However, it is less protuberant over the sulcus than *A. disneyi*, extending less medially than its height cranial to the sulcus (in *A. disneyi*, medial extent is similar to cranial extent). Unlike in *A. disneyi*, the impressio lig. acrocoracohumeralis is flat, lacking both a shallow sulcus and transverse groove. Also, in contrast to *A. disneyi*, the ventral facies of the shaft is broadly convex so that the adjacent lateral facies is rounded and lacks the distinct flattened surface seen in *A. disneyi*. As in *A. disneyi*, the proc. procoracoideus extends cranially of the cotyla scapularis. The preserved part of the impressio m. sternocoracoidei is deeper than in *A. disneyi*, and it is bound medially by a strongly overhanging crest.

The new species is also represented by a distal femur QM F31479, previously referred to *A. disneyi*, from which it is distinguished by much larger size (Fig. 6). It has a distinct pit for the fibular stop and shows that the tuber. gastrocnemialis lateralis abuts the impressio m. ansa iliofibularis caudalis on the caudolateral border of the trochlea fibularis, as it does in *Gallinula ventralis*. This tuberculum is distinctly separated from the ansa impression in *G. tenebrosa, G. mortierii* and *Porphyrio porphryio*. The pit for the fibular stop is distinct and deep in *G. ventralis*, but shallow and indistinct in *G. tenebrosa* and *G. mortierii*. In species of *Amaurornis* and *Porphyrio*, it is distinct.

Rallidae, gen. et sp. indet.

Material. A single specimen, QM F54524 (= AR19964), represents a third species of rallid in Riversleigh deposits. It is the left articular of a mandible preserving the part caudal to the fenestra rostralis mandibulae, including the base of the surangular and the cotyla, but it is lacking the medial process and the tip of the processus retroarticularis (Fig. 2).

Location. Ringtail Site, considered part of Riversleigh's Faunal Zone C deposits and hence of Middle Miocene age (Archer *et al*., 1997, 2006; Creaser, 1997; Travouillon *et al*., 2006).

Description

It is considerably smaller than *A. disneyi* (preserved length 9.3 mm, length of cotyla lateralis 3.1 mm, total anterior width across cotyla 3.8 mm). It has the general form of rallids with the following notable features: 1, the dorsal margin of the crista transversus fossae linking the caudal part of the cotyla lateralis and the processus medialis is near level with only a slight concavity at mid-width, as in *A. disneyi*, but differing from all rallids examined that have a marked notch in this crista; 2, the cotyla medialis is wider than the cotyla lateralis and extends laterally to the surangular, unlike all rails examined, except *Amaurornis* and *A. disneyi* (generally rallids have the base of the surangular aligned with the junction of the two cotylae); 3, the fenestra caudalis mandibulae is small, as in *A. disneyi*, but the feature varies among rails, being similarly small in *Amaurornis, Dryolimnas pectoralis*, and *Rallina*, but relatively larger in *Gallinula ventralis, Porzana tabuensis* and *Gallirallus philippensis*; 4, the fenestra caudalis mandibulae is located relatively far anteriorly such that the distance from it to the cotyla lateralis exceeds the length of the cotyla lateralis laterally, versus this distance being equal to or shorter than the cotyla in all modern rallids examined.

Apart from being much smaller than *A. disneyi*, this specimen differs as follows: 1, the cotyla lateralis is better emarginated and raised anteriorly; 2, whereas the lateral facies forms an inflated crest on which lies the attachment of ancora ligamenti jugomandibularis externus, the facies is concave above this attachment (convex); and 3, the lateral crest extends anteriad below and anterior to the fenestra caudalis mandibulae (ends caudal to fenestra).

Results of phylogenetic analysis of *Australlus disneyi*

We were able to score 134 characters of the 381 in Livezey's (1998) dataset (Appendix 1) for *A. disneyi*. For *Australlus gagensis*, the 23 characters of the humerus and 11 of the coracoid able to be assessed do not differ from the states in *A. disneyi*. These taxa differ mainly by size and the other differences listed above are not captured by Livezey's (1998) characters, so *A. gagensis* was not included in the phylogenetic analysis. Initial analyses used all taxa in Livezey's (1998) dataset and in these the relationship of *Australlus disneyi* was recovered as sister to the clade of *Porphyrio* and relatives in a topology of a strict consensus tree otherwise very like that obtained by Livezey. However, the many taxa with considerable missing data contributed to a very large number of shortest trees and many taxa grouped in polytomies. In order to better resolve the tree, taxa were successively trimmed until all those listed in Methods were excluded. Analyses also included ordering characters as used by Livezey (1998) but, as the results did not differ significantly, we ultimately chose to present analyses of the modified database that treated all characters as unordered. In all preliminary analyses, the tree topologies we obtained were similar to, if not the same as, that presented by Livezey (1998). For our preferred analysis with 51 ingroup taxa, all characters were treated as unordered and with equal weight. A heuristic search with 1000 replicates found 1176 shortest trees, length = 805, consistency index = 0.5317, homoplasy index = 0.4683 and retention index = 0.8381.

As found by Livezey (1998), separation of the various gruiform families was well corroborated, but resolution within the Rallidae was poorly supported, although the strict consensus tree (Fig. 7) was relatively well resolved. The *Gallirallus*-type rails formed a clade sister to gallinules and crakes (e.g., *Porzana*), with all other rallids forming more basal branches in a tree with the same topology as found by Livezey (1998). The analysis strongly supports the inclusion of *Australlus disneyi* (and thus *A. gagensis*) in the Rallidae. Furthermore, within the Rallidae, *Australlus* is part of a clade of all rallids except *Himantornis* and *Gymnocrex*. The analysis suggests a weak affinity of *Australlus* with swamphens (*Porphyrio* and relatives), with which it formed a sister group (bootstrap support 54%), but perhaps equally likely is that *Australlus* forms an independent lineage from

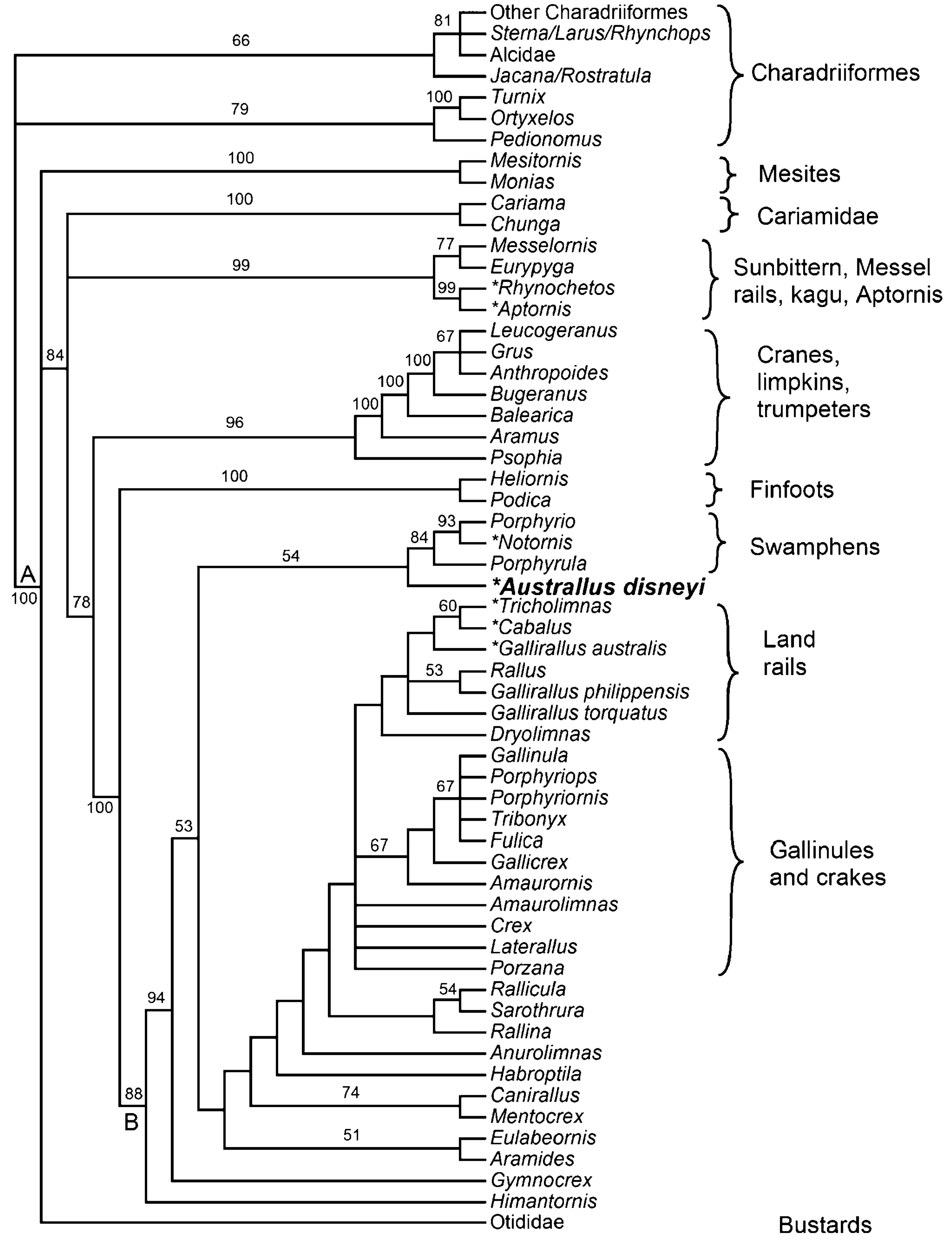

Fig. 7. A strict consensus tree obtained from Livezey's (1998) dataset, modified as described in Methods and incorporating *Australlus disneyi*. Bootstrap support >50% are shown for clades. Asterisks mark flightless taxa, although *Tribonyx* contains one flightless and one volant taxon. "A" marks the clade of Gruiformes and "B" that of the Rallidae.

the rallid stem of similar grade to *Porphyrio*. No support was found for the inclusion of *Australlus disneyi* with true gallinules, which were united in a clade with bootstrap support of 67% and deeply nested in the tree. These data suggest that *Australlus* should be considered to comprise relatively basal rallids, perhaps with some affinity to swamphens.

Discussion

We reviewed all the Oligo-Miocene gruiform fossils from the Riversleigh World Heritage Property, and found three species to be represented. All are rallids. The phylogenetic relationships of the previously described *Gallinula disneyi* were reassessed using existing and newly referred material and the species is transferred to *Australlus* gen. nov. In addition, we report a second, congeneric species that possibly co-existed with *A. disneyi*, assuming the fossils in Ringtail Site had contemporaneous deposition, which, given the aquatic nature of the depositional environment (Archer *et al*., 1994), is likely.

The specific recognition of *A. gagensis* is not dependent on size differences from *A. disneyi* alone. There is a suite of morphological characters by which these species can be separated. Australian rails show minor sexual size dimorphism, with considerable overlap in measurements between the sexes (Marchant & Higgins, 1993). The size difference between *A. disneyi* and *A. gagensis* is considerably greater than that between sexes of living taxa; thus, there is no support for the possibility that the two size classes represent different sexes of the same species. In addition, the distribution of size classes is very skewed temporally and unlikely to be that of a single, dimorphic species.

Our morphological and phylogenetic analyses demonstrate that the original allocation of *disneyi* to *Gallinula* was incorrect. An immediate ramification of this is the suggestion by Boles (2005a) that *disneyi* might have been the ancestor of *Gallinula mortierii* can be rejected. The new genus instead includes relatively basal rallids, distant from *Gallinula*, but with a weak sister-group relationship with *Porphyrio*. Although the original generic identification was incorrect, the species is still the oldest known representative of crown group Rallidae (cf. Mayr, 2009) because it lies within a clade defined by the common ancestor of *Himantornis* and *Fulica* or *Rallus* and all its descendents (Fig. 7).

The molecular study of Fain *et al*. (2007) recovered a divergence time for the base of the Rallidae of 21.8 Ma (95% credible interval 35.6–12.9 Ma). If *Australlus disneyi* did belong with the *Gallinula*-*Porzana* clade, then this would provide a strong challenge to this timing, because gallinules and crakes are regarded as among the more derived rallids. An occurrence of *Gallinula* species in Late Oligocene Faunal Zone A would require an extraordinarily rapid diversification with the Rallidae after its divergence. The finding of our analysis that *A. disneyi* belongs to a more basal genus does not overcome this problem, but it considerably reduces its magnitude. The position of *Australlus* indicates that it is part of crown-clade Rallidae and not a stem-taxon. Cranial material for *A. disneyi* reveals that this species had a conservative short, non-robust bill typical of basal taxa such as *Gymnocrex*, and most unlike the heavily built bills of swamphens, or the long, slim bills found in some specialized forms.

Both species of *Australlus* were flightless, as evidenced by the limb proportions (Boles, 2005a) or just humeral features alone that are found in flightless rallids such as *Gallirallus australis* and *Gallinula hodgenorum* (for example, a more accentuated margo caudalis adjacent to the crus dorsale fossa, relatively small crista bicipitalis and crista deltopectoralis rotated onto cranial facies rather than on dorsal margin and concave caudodistally).

The fossa pneumotricipitalis and, particularly, the sulcus lig. transversus, both of which are relatively shallow in *A. disneyi* compared to volant rallids, are much shallower in *A. gagensis* than in *A. disneyi* indicating a progression with presumed length of time since flightlessness was achieved. In addition, the development of a distinct depression in the humeral facies bicipitalis bound by the intumescentia humeri, caput humeri and crista deltopectoralis, as seen in *Gallirallus australis*, is consistent with the geologically younger species having been flightless a longer period of time. A parallel morphological transition is seen in the coracoid. That of *A. gagensis* is not only larger, but it has a more reduced proc. acrocoracoideus as expected of a bird whose lineage has been flightless longer.

Extant and recently extinct flightless rails almost always occur on islands. *Gallinula* had two exceptions that occupied larger landmasses in the Pleistocene: *G. hodgenorum* of New Zealand and extant *G. mortierii* of mainland Australia. *Australlus* provides another instance, but even more unusual in that more than one flightless species occurred on a mainland situation.

If we exclude the Ringtail Site, *Australlus disneyi* has been recovered only from Faunal Zones A and B, while *A. gagensis* is known only from Faunal Zone C. Therefore, it could be possible that they represent a temporal series. An increase in size is seen in several lineages between Faunal Zones A and B and Faunal Zone C (for example, many kangaroo and diprotodontoid lineages). The co-occurrence in Ringtail Site, usually attributed to Fauna Zone C, of both *A. disneyi* and *A. gagensis*, however, challenges this possibility. If QM F20799 is correctly attributed to the Ringtail fauna, a temporal series is still a possibility if the Ringtail Site is considered to be early Faunal Zone C and AL90 late Faunal Zone C. The large size of the tarsometatarsus QM F20799 could be interpreted to mean that it and the femur QM F31479, referred to *A. gagensis*, might represent an intermediate temporal form. Alternatively, the co-occurrence of both forms may reflect at least partial temporal overlap and sympatry of the two species. The rarity of *A. gagensis* makes it probable that the temporal range of this species is not yet established and that habitat differences, combined with biases in placement of fossil deposition sites, have combined to create an illusion of temporal separation of these taxa. Only further fossils can resolve these conflicting scenarios.

There is further reason to doubt the association of the Ringtail Site fauna with that of typical Faunal Zone C faunas. In most analyses, the Ringtail Site grouped with System C sites (Travouillon *et al*., 2006), but in some, such as cluster analyses based on sites with more than eight mammal taxa, it grouped with System B sites. Worthy (2009) tentatively identified the anseriform *Pinpanetta tedfordi* from Ringtail, which if correct, indicates an affinity with sites in the Etadunna and Namba Formations of South Australia. This would support an age for Ringtail closer to Late Oligocene or Early Miocene and hence that this site might belong to

Faunal Zone B or early Faunal Zone C. The identification of *Australlus disneyi* from Ringtail Site, if the bone is correctly attributed to site, supports the suggestion that Ringtail is older than other Faunal Zone C sites and that it most likely belongs to Faunal Zone B. Assemblages characterizing Riversleigh's Late Oligocene Faunal Zone A are most recently identified as derived from an open forest habitat, whereas the Early Miocene Faunal Zone B and Middle Miocene Faunal Zone C assemblages derive from rainforest habitats (Travouillon *et al*., 2009).

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References

Archer, M., D.A. Arena, M. Bassarova, R.M.D. Beck, K. Black, W.E. Boles, P. Brewer, B.N. Cooke, K. Crosby, A. Gillespie, H. Godthelp, S.J. Hand, B.P. Kear, J. Louys, A. Morrell, J. Muirhead, K. Roberts, J.D. Scanlon, K.J. Travouillon & S. Wroe, 2006. Current status of species-level representation in faunas from selected fossil localities in the Riversleigh World Heritage Area, northwestern Queensland. *Alcheringa, Special Issue* 1: 1–17.

Archer, M., H. Godthelp, S.J. Hand & D. Megirian, 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist* 25: 35–69.

Archer, M., S.J. Hand & H. Godthelp, 1994. *Riversleigh. The Story of Animals in Ancient Rainforests of Inland Australia*, second ed. Sydney: Reed Books.

Archer, M., S.J. Hand, H. Godthelp & P. Creaser, 1997. Correlation of the Cainozoic sediments of the Riversleigh World Heritage Fossil Property, Queensland, Australia. In *Actes du Congrès BiochroM '97*, ed. J.-P. Aguilar, S. Legendre & J. Michaux. *Mémoires et Travaux de l'Institut de Montpellier de l'Ecole Pratique des Hautes Etudes* 21: 131–152.

Ashley, J.F., 1941. A study of the structure of the humerus in the Corvidae. *Condor* 43: 184–195.
doi:10.2307/1364331

Baird, R.F., 1984. The Pleistocene distribution of the Tasmanian Native-hen *Gallinula mortierii mortierii*. *Emu* 84: 119–123.
doi:10.1071/MU9840119

Baumel, J.J., & L.M. Witmer, 1993. Osteologia. In *Handbook of Avian Anatomy: Nomina Anatomica Avium*, ed. J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans & J.C. Vanden Berge. *Publications of the Nuttall Ornithological Club* 23: 45–132.

Boles, W.E., 1992. Revision of *Dromaius gidju* Patterson and Rich, 1987, with a reassessment of its generic position. In Papers in Avian Paleontology Honouring Pierce Brodkorb, ed. K.E. Campbell, Jr. *Natural History Museum of Los Angeles County, Science Series* 36: 195–208.

Boles, W.E., 1993a. A new cockatoo (Psittaciformes: Cacatuidae) from the Tertiary of Riversleigh, northwestern Queensland, and an evaluation of rostral characters in the systematics of parrots. *Ibis* 135: 8–18.
doi:10.1111/j.1474-919X.1993.tb02804.x

Boles, W.E., 1993b. A logrunner *Orthonyx* (Passeriformes: Orthonychidae) from the Miocene of Riversleigh, northwestern Queensland. *Emu* 93: 44–49.
doi:10.1071/MU9930044

Boles, W.E., 1993c. *Pengana robertbolesi*, a peculiar bird of prey from the Tertiary of Riversleigh, northwestern Queensland, Australia. *Alcheringa* 17: 19–25.
doi:10.1080/03115519308619485

Boles, W.E., 1995. A preliminary analysis of the Passeriformes from Riversleigh, Northern Queensland, Australia, with the description of a new species of lyrebird. *Courier Forschungsinstitut Senckenberg* 181: 163–170.

Boles, W.E., 1997a. A kingfisher (Halcyonidae) from the Miocene of Riversleigh, Northwestern Queensland, with comments on the evolution of kingfishers in Australo-Papua. *Memoirs of the Queensland Museum* 41: 229–234.

Boles, W.E., 1997b. Riversleigh birds as palaeoenvironmental indicators. *Memoirs of the Queensland Museum* 41: 241–246.

Boles, W.E., 2005a. A new flightless gallinule (Aves: Rallidae: *Gallinula*) from the Oligo-Miocene of Riversleigh, northwestern Queensland, Australia. *Records of the Australian Museum* 57(2): 179–190.
doi:10.3853/j.0067-1975.57.2005.1441

Boles, W.E., 2005b. A review of the Australian fossil storks of the genus *Ciconia* (Aves: Ciconiidae), with a description of a new species. *Records of the Australian Museum* 57(2): 165–178.
doi:10.3853/j.0067-1975.57.2005.1440

Boles, W.E., 2005c. Fossil honeyeaters (Meliphagidae) from the Late Tertiary of Riversleigh, northwestern Queensland. *Emu* 105: 21–26.
doi:10.1071/MU03024

Boles, W.E., 2006. The avian fossil record of Australia: an overview. In *Evolution and Biogeography of Australasian Vertebrates*, ed. J.R. Merrick, M. Archer, G.M. Hickey, and M.S.Y. Lee, pp. 387–411. Oatlands, NSW: Auscipub Pty Ltd.

Bonaparte, C.L., 1854. Conspectus Systematis Ornithologae. *Annales des Sciences Naturelles (Paris)* (ser. 4) 1: 105–152.

Christidis, L., & W.E. Boles, 2008. *Systematics and Taxonomy of Australian Birds*. Collingwood, Australia: CSIRO Publishing, x + 277 pp.

Creaser, P., 1997. Oligo-Miocene sediments of Riversleigh: the potential significance of topography. *Memoirs of the Queensland Museum* 41: 303–314.

Fain, M.G., C. Krajewski, & P. Houde, 2007. Phylogeny of "core Gruiformes" (Aves: Grues) and resolution of the Limpkin–Sungrebe problem. *Molecular Phylogenetics and Evolution* 43: 515–529.
doi:10.1016/j.ympev.2007.02.015

Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
doi:10.2307/2408678

Hesse, A., 1990. Die Beschreibung der Messelornithidae (Aves: Gruiformes: Rhynocheti) aus dem Alttertiär Europas und Nordamerikas. *Courier Forschungsinstitut Senckenberg* 128: 1–176.

Houde, P., A. Cooper, E. Leslie, A.E. Strand & G.A. Montaño, 1997. Phylogeny and evolution of 12S rDNA in Gruiformes (Aves). In *Avian Molecular Evolution and Systematics*, ed. D.P. Mindell, pp. 121–158. San Diego: Academic Press.
doi:10.1016/B978-012498315-1/50009-1

Livezey, B.C., 1998. A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). *Philosphical Transactions of the Royal Society of London. B* 353: 2077–2151.

Livezey, B.C., & R.L. Zusi, 2006. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. I. Methods and Characters. *Bulletin of the Carnegie Museum of Natural History* 37: 1–544.
doi:10.2992/0145-9058(2006)37[1:PON]2.0.CO;2

Marchant, S., & P.J. Higgins (co-ordinators), 1990. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 1. Ratites to Ducks*. Melbourne: Oxford University Press.

Marchant, S., & P.J. Higgins (eds), 1993. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 2. Raptors to Lapwings*. Melbourne: Oxford University Press.

Mayr, G., 2004. Phylogenetic relationships of the early Tertiary Messel rails (Aves, Messelornithidae). *Senckenbergiana Lethaea* 84: 317–322.
doi:10.1007/BF03043474

Mayr, G., 2005. The Paleogene fossil record of birds in Europe. *Biological Review* 80: 515–542.
doi:10.1017/S1464793105006779

Mayr, G., 2009. *Paleogene Fossil Birds*. Springer, Heidelberg.
doi:10.1007/978-3-540-89628-9

Nguyen, J.M.T., 2010. New material of *Barawertornis tedfordi*, a dromornithid bird from the Oligo-Miocene of Australia, and its phylogenetic implications. *Records of the Australian Museum* 62(1): 45–60.
doi:10.3853/j.0067-1975.62.2010.1539

Olson, S.L., 1973a. Evolution of the rails of the South Atlantic islands (Aves: Rallidae). *Smithsonian Contributions to Zoology* 152: 1–53.
doi:10.5479/si.00810282.152

Olson, S.L., 1973b. A classification of the Rallidae. *The Wilson Bulletin* 85(4): 381–416.

Olson, S.L., 1975. A review of the extinct rails of the New Zealand region (Aves: Rallidae). *National Museum of New Zealand Records* 1(3): 63–79.

Olson, S.L., 1977. A synopsis of the fossil Rallidae. pp. 339–373 *In*: Ripley, S.D. *Rails of the World: A Monograph of the Family Rallidae*. David R. Godine, Boston.

Owre, O., 1967. Adaptations for locomotion and feeding in the Anhinga and the Double-crested Cormorant. *Ornithological Monographs* 6: 138–276.

Rafinesque, C.S., 1815. *Analyse de la Nature, ou Tableau de l'Univers et des Corps Organisés*. Palermo, Italy: published by the author.

Steadman, D.W., 2006. *Extinction and Biogeography of Tropical Pacific Birds*. Chicago: University of Chicago Press.

Strauch, J.G., 1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. *Transactions of the Zoological Society of London* 34: 263–345.
doi:10.1111/j.1096-3642.1978.tb00375.x

Swofford, D.L., 2001. *PAUP*: Phylogenetic Analysis Using Parsimony (* and other methods)*. Version 4.0b10. Computer program and documentation. Sinauer Associates, Sunderland, Massachusetts. Documentation has 128 pages.

Taylor, B., 1998. *Rails. A Guide to the Rails, Crakes, Gallinules and Coots of the World*. Sussex: Pica Press.

Travouillon, K.J., 2008. *Palaeoecological and Biochronological Studies of Riversleigh, World Heritage Property, Oligo-Miocene Fossil Localities, North-Western Queensland, Australia*. PhD Thesis, University of New South Wales, Sydney. 301 pp.

Travouillon, K., M. Archer, S.J. Hand & H. Godthelp, 2006. Multivariate analyses of Cenozoic mammalian faunas from Riversleigh, northwestern Queensland. *Alcheringa Special Issue* 1: 323–349.

Travouillon, K.J., S. Legendre, M. Archer & S.J. Hand, 2009. Palaeoecological analyses of Riversleigh's Oligo-Miocene sites: Implications for Oligo-Miocene climate change in Australia *Palaeogeography, Palaeoclimatology, Palaeoecology* 276: 24–37.
doi:10.1016/j.palaeo.2009.02.025

Woodburne, M.O., B.J. MacFadden, J.A. Case, M.S. Springer, N.S. Pledge, J.D. Power, J.M. Woodburne & K.B. Springer, 1994. Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (Late Oligocene) of South Australia. *Journal of Vertebrate Paleontology* 13: 483–515.
doi:10.1080/02724634.1994.10011527

Worthy, T.H., 2009. Descriptions and phylogenetic relationships of two new genera and four new species of Oligo-Miocene waterfowl (Aves: Anatidae) from Australia. *Zoological Journal of the Linnean Society* 156: 411–454.
doi:10.1111/j.1096-3642.2008.00483.x

Worthy, T.H., & R.N. Holdaway, 2002. *The Lost World of the Moa: Prehistoric Life of New Zealand*. Indiana University Press, Indiana. Xxxiii + 718 pp.

Zuccon, A., & D. Zuccon, 2006. *MrEnt: a drawing tool for phylogenetic trees*. Version 1.2. Department of Vertebrate Zoology and Molecular Systematics Laboratory, Swedish Museum of Natural History, Stockholm, Sweden. Documentation has 24 pp.

Appendix 1. Scoring of 381 characters for analysis in Livezey's (1998) matrix; * score for character 244 is (02).

Gallinula disneyi

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Appendix 2. A list of all rallid specimens from Riversleigh by Faunal Zone.

Faunal Zone A

Australlus disneyi. White Hunter Site: mandible (QM F54503), vertebrae (QM F54506, QM F54504, QM F54507, QM F54508, QM F54515), humerus (QM F20906, QM F31471, QM F31472, QM F45457), coracoids (QM F31469, QM F31470, QM F54513), tibiotarsus (QM F31473, QM F31474, QM F31475), tarsometatarsus (QM F23723, QM F31476); LSO Site: femur (QM F36452).

Faunal Zone B

Australlus disneyi. Camel Sputum Site: cranium (QM F23806), premaxilla (QM F54505), carpometacarpus (QM F31478, QM F31477), tibiotarsus (QM F24130, QM F30696); Dirk's Towers Site: vertebrae (QM F54509, QM F54510), ulna (QM F30693), carpometacarpus (QM F30908), coracoid (QM F30692), tibiotarsus (QM F31480); Judith's Horizontalis Site: coracoid (QM F39864); Wayne's Wok Site: premaxilla (QM F30864); Creaser's Ramparts Site: tarsometatarsus (QM F30720).

Faunal Zone C

Australlus disneyi. ?Ringtail Site: Tarsometatarsus (QM F20799),
Australlus gagensis. AL90 Site: humerus (QM F54511), vertebra (QM F54514), coracoid (QM F54536); Ringtail Site: femur (QM F31479).
?Australlus gagensis. Golden Steph Site: vertebra (QM F36354); Jim's Jaw Site: tarsometatarsus (QM F54512),
Rail species 3 Ringtail Site: mandible (QM F54524).