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A New Flightless Gallinule (Aves: Rallidae: *Gallinula*) from the Oligo-Miocene of Riversleigh, Northwestern Queensland, Australia

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ABSTRACT. Flightlessness in birds occurs in a taxonomically diverse array of families, but is best exemplified in the rails (Rallidae). Most flightless species of rails live on islands, where the absence of native mammalian predators may make flight superfluous. Fossil rails from Oligo-Miocene sites at Riversleigh, northwestern Queensland, Australia, are considered to represent a single species of gallinule *Gallinula*, described here as new. Compared with four Quaternary species of *Gallinula* from Australasia (two volant, two non-volant), it shows similarities with the flightless species in the development of the fore- and hindlimb elements and in other characteristics of limb bone morphology associated with flightlessness. These indicate that the Riversleigh species was non-volant. Its relationships with the Quaternary species, including the flightless *Gallinula mortierii*, now restricted to Tasmania, but known from Plio-Pleistocene deposits in eastern mainland Australia, are considered.

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Flightlessness in birds occurs in a taxonomically diverse array of families. Flightlessness per se probably conveys no adaptive value; instead, it is an consequence of morphological changes that convey other selective advantages to the bird (Livezey & Humphrey, 1986). The general consensus is that the loss of volancy results as the flight muscles and pectoral assemblage become reduced as energy-saving processes during ontogeny (Olson, 1973a). Such modifications are advantageous when they do not render the birds more susceptible to predation. The presence of flightless birds on islands is strongly correlated with the absence of predators, particularly mammalian ones. Other factors can moderate this relationship, such as the availability of sufficient cover to avoid or reduce predation, allowing birds to exist in the presence of predators, and the stability of resources, removing the need for far-ranging mobility (dispersal) (Worthy, 1988).

The developmental mechanisms involved in the loss of flight have been explored in greatest depth in the rails (Rallidae) (Olson, 1973a), the family that best exemplifies the phenomenon. About a fourth of the world's 125 or so living or recently extinct species have lost the power of flight. Most, but not all, of these are populations on islands, where the absence of native mammalian predators has reduced the benefit of the ability to fly. Those species that have become extinct usually did so at least in part from the inability to cope with the introduction of exotic predators. Prominent among the few instances of flightlessness in rails on larger landmasses are the three species of native-hens of Australia and New Zealand (*Gallinula*, subgenus *Tribonyx*) (Fig. 1). The Black-tailed Native-hen *G. ventralis*, a volant species, is widespread through mainland Australia except for the east coast and far tropical north, but does not occur in Tasmania, to where the much larger and flightless Tasmanian Native-hen *G. mortierii* is restricted. The extinct *G. hodgenorum* of New Zealand, well represented in subfossil deposits, was also flightless (Olson, 1975a). The living volant Dusky Moorhen *G. (G.) tenebrosa* is common in both Australia and New Zealand.

The remains of rails have been recovered from several Oligo-Miocene sites at Riversleigh, northwestern Queensland (Fig. 1). These are considered to represent a single species, a new gallinule of the genus *Gallinula*. Although only one skeletal element is represented by an intact specimen, there is adequate material of the wings, legs and coracoid to indicate that this form was flightless.

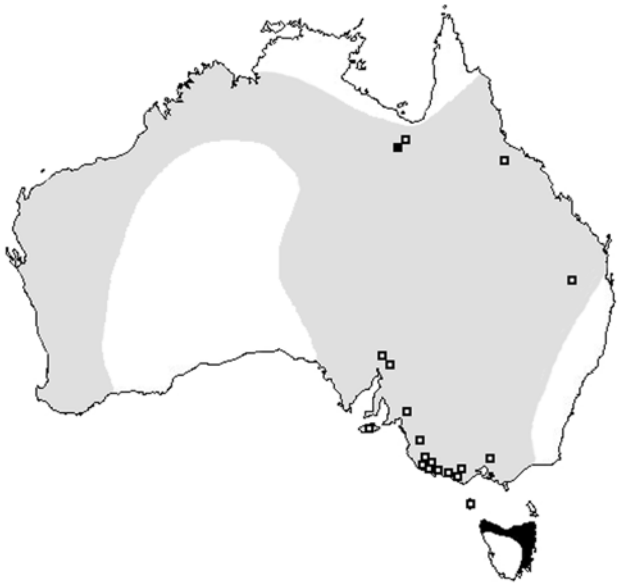

Fig. 1. Distribution of Recent and fossil Australian species of *Gallinula*. Key: black shading, current distribution of *G. mortierii*; grey shading, current distribution of *G. ventralis*; ■ Riversleigh (*G. disneyi*); □ Quaternary mainland sites producing *G. mortierii* (taken from De Vis 1888, 1892; Baird 1984, 1985, 1986, 1991b, 1992; McNamara & Baird 1991; Olson 1975b; and this work).

Materials and methods

Measurements were made with digital callipers and rounded to the nearest 0.1 mm. Length measurements of bones of *G. hodgenorum* were taken from specimens and from Olson (1975a); all other measurements were taken from specimens. Weight, wing chord and tarsus measurements of living species of *Gallinula* were taken from Marchant & Higgins (1993) and represent means for adult males. Osteological nomenclature follows Baumel & Witmer (1993), except that as terms of position and direction anterior is used rather than cranial and posterior rather than caudal. Olson (1973b) placed *Tribonyx* as a subgenus of the gallinules *Gallinula*; this was accepted by Condon (1975) and Christidis & Boles (1994), and is followed here.

Ratio-diagrams of the log differences between measurements of compared taxa were constructed following the method of Simpson (1941), wherein measurements are converted to logarithms, and one taxon is arbitrarily chosen as a standard. The difference between its converted measurements and the corresponding ones for each taxon are calculated (the logarithms of the ratios). The standard taxon thus has all ratios of 0 (zero difference in logarithms), which when plotted along a vertical axis on arithmetic graph scale, form a straight line. The logarithmic ratios for each taxon are plotted such that the points on a single horizontal line represent different values of the same variable across the taxa. Those values larger than the standard fall to the right of the standard line, the smaller ones to the left of it. The points of each taxon are connected with a line. Taxa with proportions identical to those of the standard taxon will have lines parallel to that of the standard. Variations from a parallel line are indicative of variations in the proportions from that of the standard taxon. Because only one of the fossil elements is complete, measurements of other features of the bones were used in lieu of total lengths because these should also reflect the changes in overall sizes of the elements. For the purposes of these comparisons, the values used were the means in Table 1 unless otherwise indicated.

Geology and geographical setting

The fossils described in this study were collected from the Riversleigh deposits, which are located 5 km west of the Riversleigh homestead (19°02'S 138°45'E), 200 km north of Mt Isa, northwestern Queensland, where they occur as an outcrop of Tertiary limestone overlying the Cambrian Thorntonia Limestone. There are now over 200 named Oligo-Miocene sites at Riversleigh. An informal system of grouping has been used (Systems A–C). These systems are "regionally clustered sites that appear to be superpositionally-related (differing in age but not significantly in position) and/or space-related (spatially isolated but approximately contemporaneous)" (Archer *et al.*, 1989). The principal accumulations are thought to have occurred in several episodes involving large lakes, shallow pools and cave deposits.

Rail material has been recovered from six sites, ranging from Late Oligocene to Middle Miocene in age. Current understanding of the age of these sites is taken from Creaser (1997); other birds represented at these sites are taken from Boles (1995, 1997). White Hunter Site, Hal's Hill Sequence, D-Site Plateau, considered to be part of System A (Late Oligocene), has yielded the greatest diversity of rail specimens. The White Hunter Local Fauna also contains other birds, including the small casuariid *Emuarius gidju* (Patterson & Rich, 1987) (Boles, 1992), the dromornithid *Barawertornis tedfordi* Rich, 1979, a stork (Boles, 2005) and several passerines. LSO Site (LSO Local Fauna), from the Verdon Creek Sequence, in the northern section of the D-Site Plateau, is also regarded as System A. Another site from the D-Site Plateau, but considered part of System B (Early Miocene), is Camel Sputum Site, Godthelp Hill Sequence (Camel Sputum Local Fauna). In addition to rails, it has also provided *Emuarius, Barawertornis*, another new genus and species of dromornithid, a swift *Collocalia buday* (Boles, 2001) and several passerines. Creaser's Ramparts

Site and Dirks Towers Site are in the central and northern sections of the D-Site Plateau, respectively. Both occur at about the same level and are possibly correlated. The ages are still unclear, but may be System A or B. Other birds recovered from Dirks Towers Site are *Emuarius* and passerines. Ringtail Site forms part of the Ray's Amphitheatre Sequence on Gag Plateau. This site is included in System C, considered to be of Middle Miocene age. The Ringtail Local Fauna includes waterfowl and a number of passerines.

Systematic palaeontology

Order Gruiformes Bonaparte, 1854

Family Rallidae Rafinesque, 1815

The fossils are referred to the Rallidae and subordinate taxa on the following suites of characters (adapted in part from Baird, 1992; Gilbert *et al*., 1981; McCoy, 1963; Olsen, 1979; and Worthy, 1997).

Coracoid. The tuberculum brachiale is not undercut. The processus procoracoideus is pronounced, extending further medially than the processus acrocoracoideus. The cotyla scapularis is large and deep. The facies articularis humeralis is round, about as wide as long, and flares strongly laterally. The impressio m. sternocoracoidei is deep, extending far anteriorly.

Humerus. The incisura capitalis is deep and forms a shallow angle with the main axis of the shaft. The fossa pneumotricipitalis is shallow. The long axis of the caput humeri is roughly parallel with that of the incisura capitis. The sulcus ligamentosus transversus is shallow. The crista deltopectoralis is high, triangular and directed anteriorly. The processus supracondylaris dorsalis is small and blunt. The distal end of the element is narrow, not markedly produced laterally or medially. The processus flexorius extends further than the condylus ventralis. The fossa m. brachialis is shallow.

Carpometacarpus. The processus extensorius tends slightly proximoventrally (in anterior view). The dorsal rim of the trochlea carpalis extends far proximally and is acute at its proximalmost point. The fossa infratrochlearis is distinct, deep and circular. The os metacarpale minus is slightly curved. The facies articularis digitalis major and minor extend distally to the same extent.

Femur. The crista trochanteris is low but strongly developed proximolaterally and curves medially; there are strong ridges extending distally from its distal edge onto the anterolateral face of the shaft, where it joins the linea intermuscularis cranialis, and from near the anteriormost projection to the anterior border of the facies articularis antitrochanteris. The impressio m. iliotrochantericus caudalis is restricted to the extreme proximal end of the trochanter femoris. The collum trochanteris is distinctly narrowed both anteriorly and posteriorly. The shaft curves to meet the caput femoris in a broad, gentle curve (in anterior view). The proximal half of the shaft has a distinctive posterior inflection (in lateral view). The linea intermuscularis cranialis extends far distally from the ventral side of the crista trochanteris. The sulcus intercondylaris is moderately shallow. The fossa poplitea is shallow.

Tibiotarsus. The cristae cnemialis are strongly developed. The crista cnemialis lateralis is flattened proximodistally. The crista fibularis is well developed. The pons supratendineus is well developed. The condylus lateralis is much broader than the condylus medialis. The incisura intercondylaris is narrow and displaced medially by a broad condylus lateralis. The facies lateralis of condylus lateralis is rounded.

Tarsometatarsus. The hypotarsus is an elongated triangle (in proximal view). The crista lateralis hypotarsi is prominent, extending distally. There are two sulci hypotarsi (usually one or both enclosed), and a proximal pons tendineus on the medial side of the dorsal face. The dorsal surface of the shaft is flat, not concave. The trochlea metatarsi IV is shorter than the trochlea metatarsi III. Another useful character, which cannot be assessed on the fossil, is that the trochlea metatarsi II is much shorter than the trochlea metatarsi IV and is recessed plantarly.

Genus *Gallinula* Brisson, 1760

Gallinula Brisson, 1760, *Ornithologia sive Synopsis Methodica* vol. 1, Paris: Ad Ripam Augustinorum [50], vol. 6[2]—type species: *Gallinula* Brisson = *Fulica chloropus* Linnaeus, 1758.

Tribonyx has been distinguished from *Gallinula* by the shorter, heavier toes, longer tails, absence of white on the undertail coverts (Olson, 1973a) and short, wide bills with very short premaxilla (Olson, 1975a), all characters that cannot be assessed from the available fossil material. Osteological comparisons of a "typical" gallinule, *G. tenebrosa*, and two species of native-hens *Gallinula (Tribonyx), G. ventralis* and *G. mortierii*, found few useful characters that might permit separation of skeletal elements to subgeneric level. In the humerus of *Gallinula (Gallinula)*, the proximal end of the condylus dorsalis extends over the condylus ventralis. Brodkorb (1967) used this character to distinguish *Gallinula* (s.s.) from *Fulica*, in which the ventral extent of the condylus dorsalis is less, just reaching the dorsal border of the condylus ventralis. The species of *Gallinula (Tribonyx)* are somewhat intermediate between typical *Gallinula* and *Fulica* in this character, with a shorter, but still overlapping ventral extent of the condylus ventralis. The condylus dorsalis on the one distal humeral fossil fragment is abraded and the state of this character is equivocal. In the tarsometatarsus of *Gallinula* (s.s.), the lateral border of the shaft is about even with that of the trochlea metatarsi IV and they thus join smoothly with little lateral flaring. In contrast, species of *Gallinula (Tribonyx)* have the trochlea metatarsi IV curving outwards laterally, away from the border of the shaft. This character cannot be evaluated for the fossil material. Until skull material is recovered, it cannot be ascertained with certainty whether the Riversleigh flightless rail was indeed a native-hen.

This taxon is here diagnosed only as *Gallinula*. In the following discussion, however, extensive reference and comparisons are made to native-hens *Gallinula (Tribonyx)* because these are the only gallinules in Australia and New Zealand in which flightlessness occurs and the only ones well represented in the fossil record.

Gallinula (s.l.) can be diagnosed on the material available by the following suite of characters.

Coracoid. The processus procoracoideus extends about half way along the shaft posteriorly, joining it gradually. The impressio m. sternocoracoidei is deeply excavated mediodistally, and has a rounded border to the facies articularis sternalis.

Humerus. The crista bicipitalis extends distally only ½–⅔ as far as the crista deltopectoralis. The border of the epicondylus ventralis is concave (in anterior view). The proximal end of the condylus dorsalis extends over the proximal end of the condylus ventralis.

Carpometacarpus. The processus alularis is broad (in proximal view). The os metacarpale minus is somewhat curved proximally, less so distally, but overall more than in *Fulica*. The distoposterior corner of the symphysis metacarpalis distalis is obliquely angular, rather than square.

Femur. The junction of the impressiones obturatoriae and trochanter femoris forms an acute angle of c. 50°. The trochanter femoris is deep, flaring from the shaft both anteriorly and posteriorly (in lateral view). There is general agreement in the size and location of the impressiones iliotrochanteria. The condylus lateralis is well produced (in lateral view). The sulcus intercondylaris is situated near the midline of the element. The condylus medialis is moderately robust (in posterior view) and well produced posteriorly (in medial view).

Tibiotarsus. The impressio lig. collateralis medialis is deep. The crista fibularis is short. There is a deep U-shaped notch on the posterolateral margin of the area interarticularis. The crista cnemialis lateralis extends to a point well proximal to the proximal end of the crista fibularis. The crista cnemialis cranialis continues as a crest along the anterior medial edge of the shaft. The fossa retropatellaris is moderately deep. The anterior surface of the proximal end is slightly convex. The condylus lateralis extends far proximally, overlapping the distal ⅓–½ of the pons supratendineus.

Tarsometatarsus. The hypotarsus extends distally, rather than being truncate (in posterior and lateral views). The shaft has roughly parallel sides throughout its length. The foramen vasculare distale is situated far distally. Other useful characters, which cannot be assessed on the fossil, are that the dorsal margin of the trochlea metatarsi II is roughly even with the plantar margin of the trochlea metatarsi III; the area proximal to the trochlea metatarsi III, medial to the foramen vasculare distale and lateral to the trochlea metatarsi II, is broad with parallel sides; and the incisura intertrochlearis lateralis is wide.

Gallinula disneyi n.sp.

Fig. 2

Holotype. Queensland Museum, QM F20906, right proximal humeral fragment, broken through the shaft, with minor damage to the tuberculum ventrale.

Fig. 2. Specimens of the fossil gallinule *Gallinula disneyi*. (*A*) coracoid, shoulder end (QM F31470; White Hunter Site); (*B*) coracoid, sternal end (QM F31477; Camel Sputum Site); (*C*) humerus, proximal end (QM F20906: holotype; White Hunter Site); (*D*) humerus, proximal end (QM F31471; White Hunter Site); (*E*) humerus, distal end (QM F31472; White Hunter Site); (*F*) carpometacarpus (QM F31478; Camel Sputum Site); (*G*) femur, proximal end (QM F36452; LSO Site); (*H*) femur, distal end (QM F31479; Ringtail Site); (*I*) tibiotarsus, proximal end (QM F31473; White Hunter Site); (*J*) tibiotarsus, distal end (QM F31475; White Hunter Site); (*K*) tibiotarsus, distal end (QM F31474; White Hunter Site); (*L*) tarsometatarsus, proximal end (QM F20799; Ringtail Site); (*M*) tarsometatarsus, distal end (QM F31476; White Hunter Site). Scale equals 10 mm.

Type locality. White Hunter Site, Hal's Hill Sequence, Riversleigh, northwestern Queensland.

Age and local fauna. Late Oligocene/Early Miocene (System A); White Hunter Local Fauna.

Paratypes. *Coracoid*. QM F30692 (Dirks Towers), right shoulder fragment broken through the processus procoracoideus on the sternal side of the cotyla scapularis; QM F31469 (White Hunter), left shoulder fragment, broken on the sternal side of the foramen n. supracoracoidei; QM F31470 (White Hunter), right shoulder fragment, broken on the sternal side of the foramen n. supracoracoidei; QM F31477 (Camel Sputum), left element, missing shoulder end beyond the sulcus m. supracoracoidei, with some damage to the medial margin. *Humerus*. QM F31471 (White Hunter), right proximal fragment, broken through the shaft, with damage to the caput humeri and the tuberculum ventrale, and abrasion to the crista deltopectoralis; QM F31472 (White Hunter), left distal fragment, broken through the shaft. *Tibiotarsus*. QM F31473 (White Hunter), right proximal fragment, broken through the shaft distal to the proximal end of the crista fibularis, with abrasion to the proximal edge of the crista cnemialis medialis; QM F31474 (White Hunter), right distal fragment, broken through the shaft, with abrasion to the rims of the condyli; QM F31475 (White Hunter), right distal fragment, broken through the shaft. QM F24130 (Camel Sputum), left proximal fragment, broken through the shaft proximal to the distal end of the crista fibularis, with damage to the crista cnemialis medialis and edges of the facies articularis medialis; QM F31480 (Dirks Towers), right distal fragment, broken through the shaft proximal to the crista fibularis, missing the crista cnemialis cranialis and much of the facies articularis medialis. *Tarsometatarsus*. QM F23723 (White Hunter), proximal right fragment, broken through shaft; QM F20799 (Ringtail), proximal left fragment, broken through shaft; QM F30720 (Creaser's Ramparts), proximal right fragment, broken through shaft.

Referred specimens. *Carpometacarpus*. QM F30908 (Dirks Towers), left element lacking the distal end and the distal half of the os metacarpale minus; QM F31478 (Camel Sputum), complete left element. *Ulna*. QM F30693 (Dirks Towers), proximal left fragment with some abrasion to the rims of the articular surfaces. The olecranon is low and the processus cotylaris dorsalis is hooked (Olsen, 1979). Its proximal width is 6.3 mm. Although this specimen agrees in configuration with ulnae of the Rallidae and of *G. ventralis* in particular, it is only tentatively assigned to this taxon. It is not considered further. *Femur*. QM F36542 (LSO), proximal left fragment, broken through the shaft about ¾ of way to the distal end; complete except for slight damage to the proximal border of the crista trochanteris; QM F 31479 (Ringtail), left distal fragment, broken through the shaft, with damage to the medial side of the condylus medialis. *Tarsometatarsus*. QM F31476 (White Hunter), distal right fragment, comprising the trochleae metatarsi III and IV.

Etymology. Named for Henry John de Suffren Disney, formerly Curator of Birds at the Australian Museum, in honour of his contributions to the study of Australian birds, particularly another flightless rail, the Lord Howe Island Woodhen *Gallirallus sylvestris*.

Diagnosis. *Gallinula disneyi* is distinguished from other species of the genus by the following suite of humeral characters. It agrees with *G. mortierii*, and differs from other species, by having the proximal end round rather than elongate proximodistally (in posterior view); it is broader than in *G. hodgenorum*. The tuberculum ventrale is situated distal to the tuberculum dorsale, and is more pronounced than in *G. mortierii*. The crista deltopectoralis is short distally; it is more produced anteriorly compared to *G. hodgenorum*. The crista bicipitalis is short distally, joining the shaft more abruptly; ventrally it is rounder than in *G. mortierii* and more produced anteriorly than in *G. hodgenorum*. The condylus lateralis is thinner, not bulbous distally, and does not extend to the lateral margin of the bone (in anterior view). The tuberculum supracondylare is narrow, not round. Compared to that of *G. hodgenorum* the condylus dorsalis does not extend as far either distally or dorsally, relative to the shaft, and the fossa olecrani is shallower with less sharply defined edges.

Measurements. See Table 1.

Description

Coracoid. The processus acrocoracoideus is flattened, more so than in the other species, and is rotated such the tip is directed ventrally, more so than in *G. ventralis*; it is not directed anteriorly but is directed more laterally than in *G. hodgenorum*. The processus procoracoideus is broader distally and more rectangular than in the other species with a blunter tip (this is pointed in *G. hodgenorum*). The facies articularis humeralis and facies articularis clavicularis are smaller. Compared with the other species, the anterior end is more gracile while the sternal end is larger and more robust, with the area encompassing impressio m. sternocoracoidei broader, particularly anteriorly, than it is in *G. ventralis*. The sulcus m. supracoracoidei is more rounded (in ventral view) than in *G. ventralis*.

Carpometacarpus. The element is rather stout; it is between those of *G. mortierii* and *G. hodgenorum* in size and robustness. The os metacarpale minus is curved posteriorly; in this it resembles *G. mortierii* and *G. hodgenorum* and differs from *G. ventralis*, in which it is straight. The symphysis metacarpalis proximalis is shortened, agreeing with *G. mortierii*. The dorsal surface is flattened, more so than in *G. hodgenorum*. Compared to *G. ventralis*, the symphysis metacarpalis distalis is broader and shorter and the spatium intermetacarpale shorter. The distal end is narrower than in *G. mortierii*.

Femur. The collum trochanteris is rather short and deep (in anterior view). The distal end of the medial branch of the linea muscularis caudalis is prominent, more so than in *G. ventralis* and *G. hodgenorum*. The trochlea fibularis is broad and robust (in posterior view), with the distolateral corner square (in posterior view) and only moderately produced laterally compared to *G. hodgenorum*. The condylus medialis is well produced posteriorly. The ridge extending proximolaterally from the condylus lateralis is slightly pronounced, less so than in *G. hodgenorum*.

Tibiotarsus. Both cristae cnemialis are proportionally deeper than in *G. hodgenorum*. The foramen interosseum

Table 1. Measurements (mm) of fossil and Recent species of Australasian *Gallinula*. Values used for *G. disneyi* are indicated in bold type. For Recent species, the mean, (standard deviation) and range are given. Means for Recent species were used for constructing log-ratio diagrams (Figs. 4–5).

	Gallinula disneyi		***Gallinula ventralis*** **n=6**	***Gallinula hodgenorum***	***Gallinula mortierii*** **n=3**	***Gallinula tenebrosa*** **n=3**
Coracoid						
anterior tip of processus	QM F30692	6.6	7.9 (0.3)	4.1	9.1 (0.4)	8.3 (0.1)
acrocoracoideus to	QM F31469	6.0	7.1–8.8		8.4–9.8	8.1–8.5
posterior border of facies	QM F31470	**6.0**				
articularis humeralis						
Humerus						
proximal width	QM F20906	**11.4**	12.2 (0.4)	7.8	14.2 (0.4)	13.3 (0.2)
	QM F31471	c.11.0	11.3–13.0		13.5–14.6	13.0–13.7
distal width	QM F31472	**9.7**	8.8 (0.2)	5.2	9.9 (0.1)	9.6 (0.2)
			8.0–9.5		9.7–10.1	9.3–9.9
Carpometacarpus						
total length	QM F31478	**28.6**	39.2 (1.0)	19.5	35.5 (0.4)	38.7 (0.5)
			35.8–42.4		35.1–36.4	37.8–39.4
proximal depth	QM F30908	8.3	8.2 (0.2)	4.9	9.1 (0.2)	8.2 (0.2)
	QM F31478	**7.3**	7.6–8.2		8.9–9.5	8.0–8.6
Femur						
proximal width	QM F36542	**10.5**	10.8 (0.3)	10.3	15.5 (1.2)	11.6 (0.2)
			10.0–11.4		13.2–16.9	11.2–11.9
proximal depth	QM F36542	**7.9**	8.5 (0.3)	8.1		9.5 (0.4)
			7.8–9.3		14.3–14.5	9.1–10.2
distal width	QM F31479	**>13**	10.2 (0.3)	9.7	16.8 (0.4)	11.2 (0.3)
			9.1–11.2		16.2–17.5	10.6–11.6
depth, condylus lateralis	QM F31479	**11.2**	8.8 (0.2)	8.1	14.7 (0.3)	9.6 (0.2)
			8.3–9.3		14.4–15.4	9.4–9.9
depth, condylus medialis	QM F31479	**>9.5**	7.9 (0.1)	7.3	13.3 (0.2)	8.9 (0.2)
			7.5–8.2		13.1–13.7	8.6–9.2
Tibiotarsus						
proximal width	QM F24130	9.7	9.0 (0.3)	7.9	15.6 (1.1)	9.8 (0.2)
	QM F31473	9.5	8.1–9.8		14.1–17.7	9.6–10.2
		9.6				
distal width	QM F31474	8.0	7.9 (0.3)	6.8	12.9 (0.1)	8.8 (0.1)
	QM F31475	8.2	7.0–8.5		12.6–13.0	8.6–8.9
		8.1				
depth, condylus lateralis	QM F31474	c.7.8	7.7 (0.2)	6.7	12.2 (0)	8.9 (0.2)
	QM F31475	8.0	7.0–8.3		12.2	8.5–9.3
		7.9				
depth, condylus medialis	QM F31474	>7.0	8.4 (0.3)	7.1	13.1 (0)	9.4 (0.1)
	QM F31475	**8.6**	7.5–8.9		13.0–13.1	9.1–9.6
Tarsometatarsus						
proximal width	QM F20799	10.4	8.5 (0.3)	7.4, 7.7	13.5 (0.1)	9.3 (0.1)
	QM F23723	9.6	7.5–9.4		13.4–13.8	9.1–9.5
	QM F30720	10.3				
		10.1				
proximal depth	QM F20799	9.5	8.3 (0.2)	7.6, 8.0	13.1 (0.1)	9.4 (0.2)
	QM F23723	9.2	7.5–9.0	13.0–13.2		9.1–9.7
	QM F30720	10.6				
		9.8				
depth, trochlea metatarsi III	QM F31476	c. **4.3**	4.6 (0.2)	4.1, 4.5	7.9 (0.2)	5.5 (0.2)
			4.2–5.1		7.6–8.1	5.3–5.8
depth, trochlea metatarsi IV	QM F31476	c. **4.4**	5.1 (0.1)	4.7, 5.1	7.7 (0.2)	6.4 (0.2)
			4.6–5.8		7.4–7.9	6.1–6.7

proximale is moderately long, extending proximally and cutting into the distal side of the facies articularis lateralis, which is consequently shortened. The impressio lig. collateralis mediale is situated more proximally than in the other species. The mediodistal portion of the shaft is not as curved medially as in the other species, while being more robust distally than in *G. ventralis*. The distal end of the sulcus extensorius is narrower and both it and the pons supratendineus are situated more medially than in the other species. The condylus lateralis is moderately flattened on the distal and anterodistal borders, and there is a greater difference between its anterior extension and that of the condylus medialis than in *G. hodgenorum*.

Tarsometatarsus. The proximal end is broader than in *G. ventralis*. The proximal end is broader relative to the shaft compared to *G. mortierii*. The hypotarsus is placed more medially than in the other species and the plantar apex is rounded. Both canales hypotarsi are enclosed. The shaft is more robust than that of *G. ventralis*. Compared to that of *G. hodgenorum*, the ridge extending distally from the hypotarsus is higher, longer and more centrally situated, thus making the plantar surface of the shaft more angular and less flattened.

Discussion

Comparison of *Gallinula disneyi* with other species

Three species of *Gallinula* live in Australia today: the typical *G. tenebrosa* and the two native-hens (*Tribonyx*), the volant *G. ventralis* and flightless *G. mortierii*. *Gallinula tenebrosa* is a heavier bird (male weight: 570 gm) than *G. ventralis* (410 gm), yet the legs are only slightly longer (male tarsus: *tenebrosa*, 63 mm; *ventralis*, 61 mm) and the wings are shorter (male wing: *tenebrosa*, 208 mm; *ventralis*, 218 mm). The wings of the much larger *G. mortierii* (males: weight, 1334 gm; tarsus, 84 mm) are both actually and proportionally small compared to those of the two volant species (wing: 202 mm).

The differences evident in external measurements are for the most part mirrored in the long bones (Fig. 2). The elements of *G. ventralis* are shorter than those of *G. tenebrosa*, except for the carpometacarpus, which is about the same length. The leg elements are more gracile in *G. ventralis* than in *G. tenebrosa*. The coracoid and hindlimb elements in *G. mortierii* are longer and more robust than both these species, whereas the ulna and carpometacarpus are shorter; the humerus is somewhat intermediate, approaching *G. tenebrosa* most closely. *Gallinula hodgenorum* is consistently smaller in all length measurements except for the femur, which is midway between the values for *G. ventralis* and *G. tenebrosa*. The carpometacarpus is the only complete element known for *G. disneyi*. It is larger than in *G. hodgenorum* but substantially smaller than in any of the living species (Table 1).

Because no direct comparisons of element lengths can be made between *G. disneyi* and the other taxa (other than for carpometacarpus), a number of measurements were taken from the fragments available for *G. disneyi*, with comparable ones from the living species. The measurements are given in Table 1 and comparisons of the elements between the taxa are shown in Fig. 4. The wing elements of *G. disneyi* are smaller than in the volant species, somewhat approaching those of *G. mortierii* and being of similar robustness. The legs of *G. mortierii* are considerably more robust. The femur of *G. disneyi* is larger and the lower leg elements are roughly intermediate between those of *G. tenebrosa* and *G. ventralis*. Its coracoid is particularly reduced, both actually and proportionally, compared to all living species. *Gallinula hodgenorum* is smaller and more gracile overall than *G. disneyi*, most markedly in the coracoid and elements of the wing (Table 1).

Using a log ratio diagram for the long bones lengths of Quaternary species of *Gallinula* (Fig. 2) shows that *G. ventralis* is similar to *G. tenebrosa*, with the major differences being the former's proportionally shorter coracoid and longer distal wing elements and tarsometatarsus. The trend in the wing is not unexpected owing to the more pronounced mobility of this highly nomadic bird. *Gallinula mortierii* and *G. hodgenorum* resemble each other (except for size), but differ from the other taxa by having the forelimb elements much shorter relative to those of the hindlimb; the femur, in particular, is proportionally long. There are slight differences between the flightless species in the relative lengths of some outer limb elements.

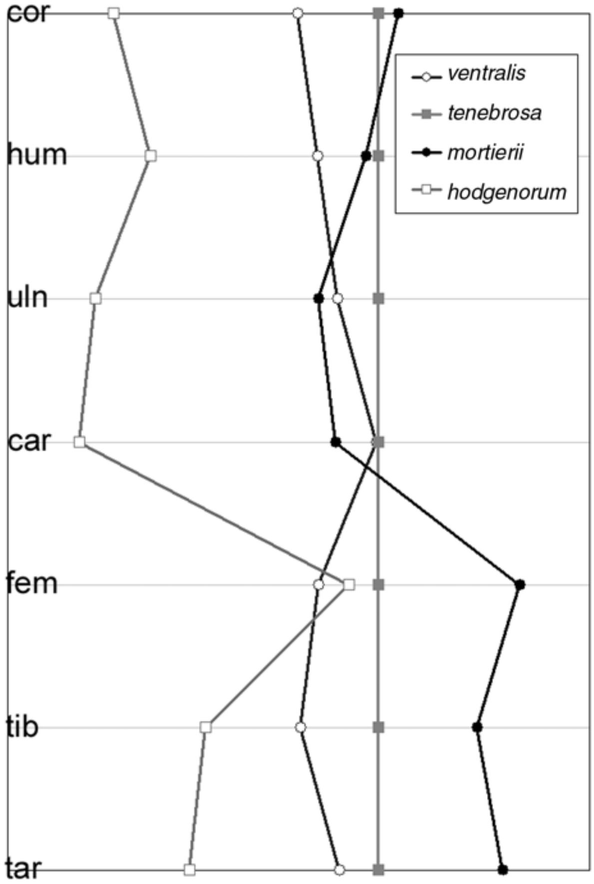

Fig. 3. Log-ratio plot of long bone lengths (coracoid, fore- and hindlimbs) of living and recently extinct Australasian species of *Gallinula*. The standard species is *Gallinula tenebrosa*. Abbreviations: *cor*, coracoid; *hum*, humerus; *uln*, ulna; *car*, carpometacarpus; *fem*, femur; *tib*, tibiotarsus; *tar*, tarsometatarsus.

Plots of the measurements from Table 1 produce overall patterns reminiscent of that in Fig. 3. Figure 5, based on the living species of *Gallinula*, is more indicative of relative robustness of elements than relative lengths, but the congruence in patterns supports the use of these measurements as indicators of major trends in the analysis. The relationship between proportions of *G. ventralis* and *G. tenebrosa* is similar to that in Fig. 3. Likewise, *G. mortierii* shows the less robust forelimbs and more robust hindlimbs.

A comparison of *G. disneyi* with the three species of *Gallinula (Tribonyx)* (Fig. 6), using *G. ventralis* as the standard taxon, exhibits roughly parallel tendencies of the three flightless species, with similar trends in the pattern of reduction of the wings and coracoid and increase in the robustness of the hindlimb elements. *Gallinula disneyi* differs from the other flightless forms in proportionally narrower proximal end of the carpometacarpus, smaller

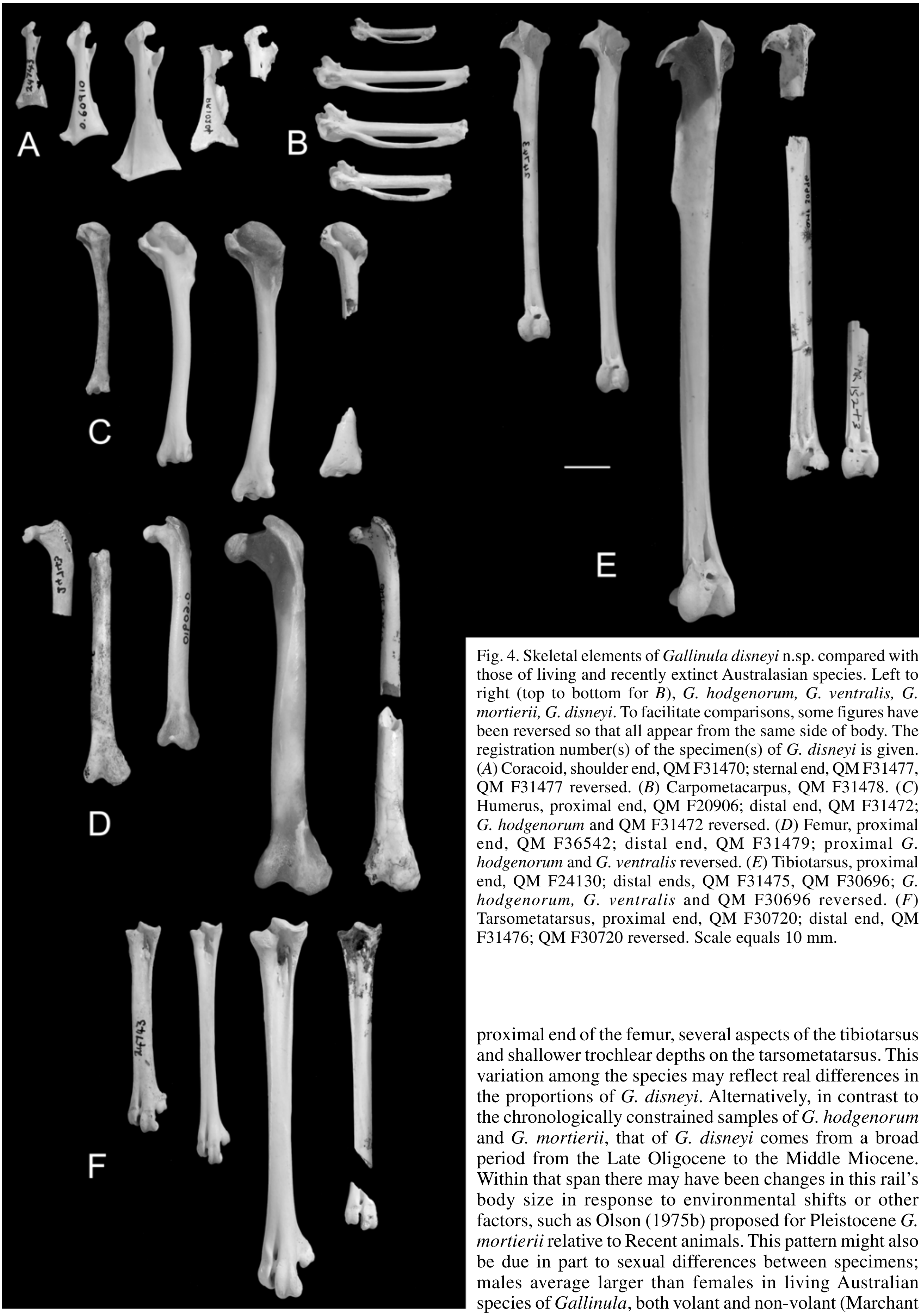

Fig. 4. Skeletal elements of *Gallinula disneyi* n.sp. compared with those of living and recently extinct Australasian species. Left to right (top to bottom for *B*), *G. hodgenorum, G. ventralis, G. mortierii, G. disneyi*. To facilitate comparisons, some figures have been reversed so that all appear from the same side of body. The registration number(s) of the specimen(s) of *G. disneyi* is given. (*A*) Coracoid, shoulder end, QM F31470; sternal end, QM F31477, QM F31477 reversed. (*B*) Carpometacarpus, QM F31478. (*C*) Humerus, proximal end, QM F20906; distal end, QM F31472; *G. hodgenorum* and QM F31472 reversed. (*D*) Femur, proximal end, QM F36542; distal end, QM F31479; proximal *G. hodgenorum* and *G. ventralis* reversed. (*E*) Tibiotarsus, proximal end, QM F24130; distal ends, QM F31475, QM F30696; *G. hodgenorum, G. ventralis* and QM F30696 reversed. (*F*) Tarsometatarsus, proximal end, QM F30720; distal end, QM F31476; QM F30720 reversed. Scale equals 10 mm.

proximal end of the femur, several aspects of the tibiotarsus and shallower trochlear depths on the tarsometatarsus. This variation among the species may reflect real differences in the proportions of *G. disneyi*. Alternatively, in contrast to the chronologically constrained samples of *G. hodgenorum* and *G. mortierii*, that of *G. disneyi* comes from a broad period from the Late Oligocene to the Middle Miocene. Within that span there may have been changes in this rail's body size in response to environmental shifts or other factors, such as Olson (1975b) proposed for Pleistocene *G. mortierii* relative to Recent animals. This pattern might also be due in part to sexual differences between specimens; males average larger than females in living Australian species of *Gallinula*, both volant and non-volant (Marchant

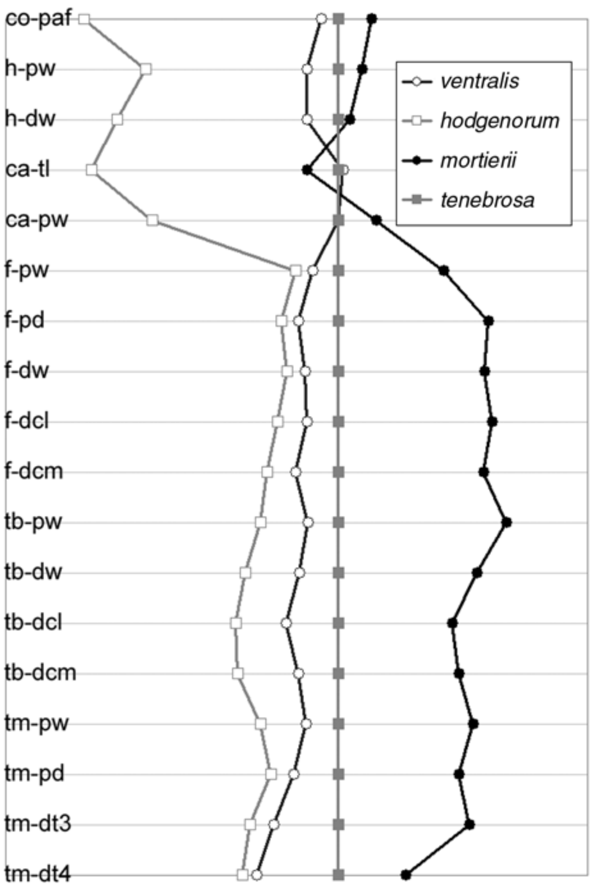

Fig. 5. Log-ratio plot of selected osteological measurements (see Table 62) of living and recently extinct Australasian species of *Gallinula*. The standard species is *Gallinula tenebrosa*. Abbreviations are *co*, coracoid; *h*, humerus; *ca*, carpometacarpus; *f*, femur; *tb*, tibiotarsus; *tm*, tarsometatarsus; *dlc*, depth of condylus lateralis; *dmc*, depth of condylus medialis; *dt3*, depth of trochlea metatarsi III; *dt4*, depth of trochlea metatarsi IV; *dw*, distal width; *paf*, processus acrocoracoideus to facies articularis humeralis; *pd*, proximal depth; *pw*, proximal width; *tl*, total length.

& Higgins, 1993). The most likely cause(s) cannot be identified until more material of common skeletal elements is available from the same sites.

Worthy (1997) pointed out exceptions to the assertion that "in all flightless birds, flightlessness is associated with increased body size" (Livezey & Humphrey, 1986). This contradiction is also demonstrated by the gallinules. While *G. mortierii* is consistent with this statement relative to other members of the genus, the flightless *G. hodgenorum* is the smallest member of *Gallinula (Tribonyx).*

Flightlessness in *Gallinula disneyi*

The major morphological consequence of flightlessness is a reduction of the pectoral assemblage and forelimb. Concurrent with this is an increase in the size of the pelvic limb. The most obvious morphological change in the legs is an increase in the robustness of the elements. In the wing there are several structures that undergo obvious and characteristic modifications with the loss of flight.

Olson (1975a) and Rich *et al*. (1985) presented a range of features that characterize the humerus of non-volant birds. These are evident in a comparison between the Riversleigh fossils and the similar-sized humerus of *Gallinula ventralis*. In the fossils, the incisura capitis is directed more proximodistally, bringing it more in line with the shaft; this is caused by the entire proximal end of the humerus being tilted laterally relative to the rest of the element. By virtue of this tilting, the tuberculum ventrale becomes on the same proximal level as the caput humeri. The caput itself is considerably flattened and elongate. The crista deltopectoralis is thickened, reduced and rotated proximomedially in respect to the shaft. The crista bicipitalis is reduced. The shaft is curved and stout; however, this has not been preserved in the fossils. Other changes are seen in the fossil carpometacarpus. Compared to this element in the volant species, it is reduced, becoming shorter as well as stouter, os metacarpale majus is bowed in anterior view, and os metacarpale minus is more curved. Changes in the coracoid related to flightlessness include a more robust processus acrocoracoideus and a broader and more medially directed processus procoracoideus lacking the ventrally directed twist of the tip.

The proportional reduction in length is not uniform across the wing elements. There is a gradient in this proportion, with increased reduction from the proximal to the distal elements (Livezey, 1995). This is characteristic of flightless birds, not just rails (see, for example, Gadow, 1902; Livezey, 1989, 1990, 1992; Livezey & Humphrey, 1986; Worthy, 1988). Direct comparison of the fossils with comparable elements of the volant *Gallinula ventralis* demonstrates that the fossil rails also exhibit this trend (Fig. 6). The proximal end of the fossil humerus is slightly smaller than that of *G. ventralis*, primarily through the reduction of the caput humeri and cristae deltopectoralis and bicipitalis, while the distal end is larger. The carpometacarpus of the fossil is substantially shorter (78% of length) and more robust. In contrast, all fragments of the fossil's hindlimb elements are considerably larger than the comparable sections of the bones of *G. ventralis*. Its larger legs and smaller wings compared to *G. ventralis* are a good indication that it was unable to fly.

Although *Gallinula hodgenorum* had greater reduction of the wings and pectoral apparatus, and more pronounced morphological differences from *G. ventralis* than had *G. mortierii* (Olson, 1975b), it showed trends in the hindlimb that are also evident in the Riversleigh bird. The shafts of both the tibiotarsus and tarsometatarsus are heavier those of *G. ventralis*. The crista cnemialis lateralis of the tibiotarsus is thicker. The proximal end of the tarsometatarsus is more expanded, as are the trochleae, which are also heavier. It is difficult to compare these usefully with the trochleae of *G. disneyi* because abrasion to the latter gives an underestimate of their size (see Fig. 6).

Distribution of *Gallinula disneyi*

Gallinula disneyi, like *G. mortierii*, is unusual because of its continental distribution. *Gallinula mortierii*, now restricted to Tasmania, once extended well into eastern mainland Australia, where it has been recorded from Pleistocene and possible Pliocene deposits (Fig. 1), with the youngest record at 4670±90B.P. (Baird, 1991a). It is extensively represented in deposits in southeastern Australia in the Murray-Darling River system, with a northernmost record from Wyandotte Creek, northeastern Queensland

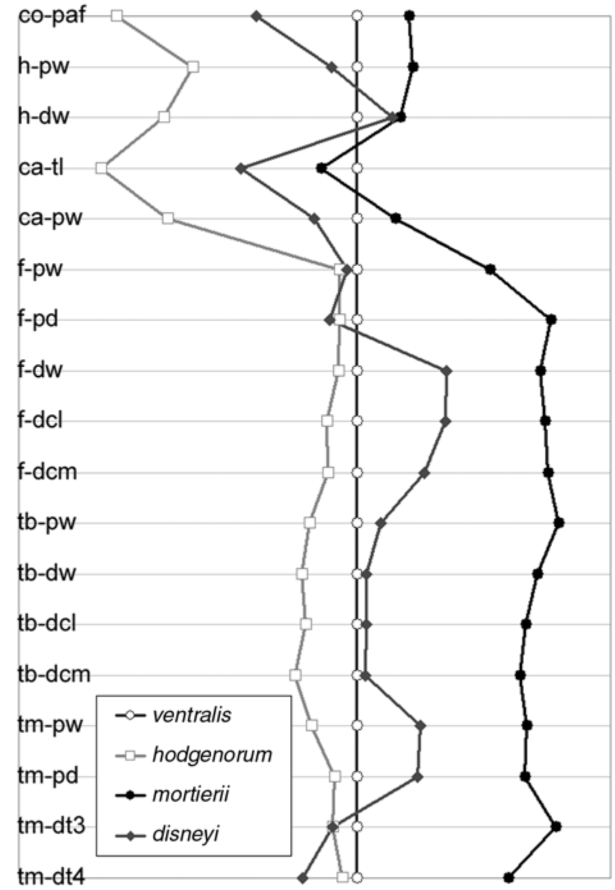

Fig. 6. Log-ratio plot of selected osteological measurements (see Table 62) of *Gallinula disneyi* and living and recently extinct species of native-hens *Tribonyx*. The standard species is *Gallinula ventralis*. Abbreviations are *co*, coracoid; *h*, humerus; *ca*, carpometacarpus; *f*, femur; *tb*, tibiotarsus; *tm*, tarsometatarsus; *dlc*, depth of condylus lateralis; *dmc*, depth of condylus medialis; *dt3*, depth of trochlea metatarsi III; *dt4*, depth of trochlea metatarsi IV; *dw*, distal width; *paf*, processus acrocoracoideus to facies articularis humeralis; *pd*, proximal depth; *pw*, proximal width; *tl*, total length.

(Olson, 1975b; Baird, 1984, 1986; McNamara & Baird, 1991). A new record from the Plio-Pleistocene Floraville Local Fauna (west of Leichhardt River, south of Floraville Homestead, northwestern Queensland; 18°17'S 139°52'E), represented by a tarsometatarsus (QM F24605), extends the western edge of the known distribution (unpublished data). During the Plio-Pleistocene, *G. mortierii* persisted despite the presence of native marsupial carnivores, even as it does today in Tasmania in the company of the Tasmanian Devil *Sarcophilus harrisii* and, previously, the Thylacine *Thylacinus cynocephalus*. Baird (1984, 1986, 1991a,b) hypothesized that its extinction on the mainland was probably due to a combination of changing environmental conditions and the introduction of the Dingo *Canis familiaris dingo* (earliest known occurrence 3450±95B.P.; Milham & Thomson, 1976). Ridpath (1972) noted that the native marsupial species were/are nocturnal, and the diurnally active *G. mortierii* has evolved several methods of avoiding ground predators. The Dingo, in contrast, forages extensively during the day when the native-hens would receive no benefit from darkness. *Gallinula disneyi* also co-existed with numerous native marsupial carnivores (large Dasyuridae, Thylacinidae, Thylacoleonidae), and it is doubtful that any of these could have caused its eventual extinction (see Baird, 1991a). As discussed below, it is possible that rather than becoming extinct, *G. disneyi* may have evolved into the living *G. mortierii*.

Species relationships in *Gallinula (Tribonyx)*

The pattern and sequence of speciation in the native-hens *Gallinula (Tribonyx)* are unclear. The progenitor of *G. hodgenorum* would have colonized New Zealand from Australia (Olson, 1975a,b). Olson (1975b) considered that *G. hodgenorum* "probably arose from an ancestor closer to the common ancestor of both *mortierii* and *ventralis* than to *ventralis* itself". In bill structure it more closely resembled *G. mortierii* than *G. ventralis*, and was more divergent from *G. ventralis* than *G. mortierii* in morphology of the fore- and hindlimbs (Olson, 1975a). *Gallinula disneyi* obviously could not have been ancestral to either *G. ventralis* or *G. hodgenorum*, but it is possible that this species was in the direct lineage of *G. mortierii* (see below).

It is known that *G. mortierii* is not an insular derivative of *G. ventralis*; these species have been separated for a long time (Olson, 1975b). Olson (1975b) considered that *G. mortierii* was not a Tasmanian autochthon, instead probably having colonized Tasmania from the mainland during a period of low sea level. Tasmania has been alternately connected and separated from mainland Australia by changes in sea levels during the Tertiary. Although oscillations during the Quaternary are well documented, there have been other periods in the Tertiary during which lower sea levels would have exposed the intervening land. Thus the loss of flight in this lineage could have occurred in Tasmania before the Quaternary. Both *G. disneyi* and *G. mortierii* may have evolved in insular Tasmania while that island was isolated and then subsequently invaded the mainland when the connection to the mainland was re-established. The fossil record of Tasmania is thus far inadequate to determine whether a species of flightless *Gallinula* occurred there in the Tertiary.

Another possibility is that there was but a single event of this kind, which gave rise to *G. disneyi*. This species, in turn, was the direct ancestor of *G. mortierii*. Retreat and restriction of the latter to Tasmania was a Quaternary event. This scenario has other possible ramifications. Representatives of many lineages, across a variety of vertebrate groups, exhibited marked increases in body size through the latter half of the Pliocene, peaking during the Pleistocene. These were usually the largest members of their respective lineages (megafauna). Subsequently, the megafauna elements either died out about 40–50,000 years ago or became smaller (dwarfing), continuing as the modern representatives. It is possible that the transition of *G. disneyi* to the much larger *G. mortierii* was part of this phenomenon. Any Late Quaternary dwarfing of *G. mortierii* was minimal, however, leaving this species a large-bodied animal.

Olson (1975b) recognized a chronosubspecies (*G. m. reperta*) for specimens from Chinchilla, Queensland, on the basis of their overall smaller size than modern birds. Baird (1984) found considerable overlap in measurements between modern and Late Pleistocene specimens of *G.*

mortierii, and consequently synonymized the Chinchilla material with the living form. A more refined temporal division of specimens may yet demonstrate that size differences do exist between Pliocene and Late Pleistocene/ Holocene specimens. The Chinchilla deposit is now considered to be of Early to Middle Pliocene age (Woodburne *et al.*, 1985), earlier than previously thought. If *G. mortierii* evolved directly from *G. disneyi*, then such smaller *mortierii*-type birds would not be unexpected.

If *G. disneyi* gave rise to *G. mortierii*, the rate of such a change would have been very marked between the Late Miocene and the Pliocene. *Gallinula disneyi* is known from a time span of about 15 million years. The sample size is too incomplete to track major morphological changes across this period; however, there is no indication of any noticeable increase in size. The tarsometatarsus shows no shift towards *mortierii*-like size or robustness between the System A White Hunter Site and System C Ringtail Site. Between these widely separated times, sufficient anagenetic change in this lineage might be expected such that samples would exhibit recognisable morphological differences. In *G. disneyi-mortierii*, sudden changes in size might have been related to the onset of the aridification of Australia, starting in the Late Miocene. A possible argument against a *G. disneyi-G. mortierii* ancestor-descendant relationship is that there is no evidence of an ongoing decrease in the coracoid and forelimb, as might be expected in a flightless lineage of such long duration.

Other Riversleigh rails

Two additional specimens of rails have been recovered at Riversleigh. One shows differences from the comparable elements of *G. disneyi* and may belong to a different species. The other is tentatively referred to this family and represents a considerably smaller animal. Both are considered Rallidae indeterminate at this time.

A tibiotarsus (QM F30696) of a rail from Camel Sputum Site, from where material referred to *G. disneyi* has been recovered, consists of a left distal fragment retaining much of shaft (length as preserved 77.5 mm). It has damage to its posterodistal face and most of the condylus medialis. The shaft is of comparable in width to that of *G. disneyi* as retained on a proximal fragment (QM F24130). Compared with the two distal tibiotarsal fragments of *G. disneyi* (QM F31474, QM F31475) the distal end of this specimen is more robust, with a greater width, both actually and proportionally relative to the shaft; the condylus lateralis is deeper. Morphological differences between this specimen and the other tibiotarsi include the position of the condyli; rather than being more or less parallel and in line with the margins of the shaft, the condyli of the Camel Sputum specimen are placed further laterally and medially, respectively. This makes the distal end flare outwards from the shaft much more. The condylus lateralis is inclined more proximomedially-distolaterally. Distal width > 9.3 mm; depth of condylus lateralis 8.6 mm. In view of these differences in size and morphology, this tibiotarsus is not placed with *G. disneyi*. It may be that these features fall within the variation of that species, although it is not evident from the other specimens, nor is there an indication of such a range of differences in modern species.

A small, damaged left carpometacarpus (QM F40203), still attached to the rocky matrix, from Dunsinane Site (System A; Arena, 1997), appears to be that of a rail. Because sections of the proximal end are missing, a definite identification is precluded. This specimen is substantially smaller than the carpometacarpus of *G. disneyi*, and is comparable in size to the living *Rallus pectoralis*; there is no indication that it represents a juvenile It is tentatively assigned to the Rallidae.

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