Sympatric flightless rails *Gallirallus dieffenbachii* and *G. modestus* on the Chatham Islands, New Zealand; morphometrics and alternative evolutionary scenarios

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The extinct rails *Gallirallus dieffenbachii* and *G modestus* were sympatric on at least three islands of the Chatham group Morphological and genetic evidence indicates that they evolved from the same volant ancestor, putatively the banded rail, *G philippensis* Morphometric analyses were used to compare these three species and the New Zealand flightless weka, *G australis* It is evident that both the Chatham rails were flightless, and each had undergone significant changes in body shape relative to *G philippensis* *G dieffenbachii* was similar in overall form to the weka and most other flightless *Gallirallus* spp , being larger than *G philippensis* in all except the wings It is possible that *G dieffenbachii* was a generalist feeder, as is the weka *G modestus* was a considerably smaller bird with a long beak that is presumably evidence of the evolution of specialised feeding behaviour

General similarity between *G dieffenbachii*, *G australis* and most flightless members of the group results from the parallel evolution of these species in allopatry, whereby a more or less enlarged generalist feeder almost invariably results The ancestral stock of *G modestus* is hypothesised to be the more recent arrival on account of specialisation resulting from competition between the coloniser and the generalist resident, *G dieffenbachii* A general principle is proposed by which the products of later colonisations will be the more specialised through the additional selective effect of the earlier occupant

Keywords Rallidae, *Gallirallus*, *Capellirallus*, flightless rails, Chatham Islands, sympatry, morphometrics, speciation

INTRODUCTION

Island biota provide a valuable tool for the study of speciation. And, since Darwin and Wallace, studies of island birds have proven of great interest to scientists Although assemblages of flying birds on archipelagos such as Hawaii and the Galapagos permit the exploration of many aspects of speciation, secondarily flightless birds on islands may be more suitable as models of long-term evolution (Grant & Grant 1996) The presence of morphologically similar taxa on islands facilitates the study of ecological and evolutionary mechansims that lead to these similarities (Larson 1989) However, many volant and flightless birds on islands have become extinct in recent times, rendering them unavailable for behavioural and ecological study (Olson & James 1991, Steadman 1995) Where fossil or archaeological material exists, osteological evidence can tell us much about the nature of extinct species (e g Olson 1973a, Livezey 1993, Holdaway & Worthy 1996) but not the details of interactions among species The application of molecular techniques can go further in providing independent data on the phylogenetic relationships of birds in islands systems, even where these birds are recently extinct (Cooper et al 1992, 1996, Trewick 1997) Where islands are known to have been

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isolated throughout their existence, phylogenies can be used to define colonisation patterns (Thorpe & Mahotra 1996) and it is possible to make inferences about the circumstances that led to the evolution of endemic species.

In a recent paper, morphometric analyses were used to distinguish two species of large flightless rail, *Porphyrio mantelli* and *P. hochstetteri* (takahe), which are related to the volant pukeko, *P. porphyrio* (Trewick 1996). Molecular evidence supports the hypothesis based upon morphometrics that the two species of takahe, which existed on separate islands of New Zealand, were probably derived independently following colonisation by flying *Porphyrio* (Trewick 1997). If the two takahe did indeed evolve separately, it is remarkable how similar they are in general shape, despite significant differences in osteometric details. Their similarity is such that they have in the past been considered to be the same species (Greenway 1967; Ripley 1977). Further examples of similar flightless *Porphyrio* existed on more distant islands, including New Caledonia (Balouet & Olson 1989; Balouet 1991) and probably also Reunion Island (Olson 1977), although remains of these species are insufficient for detailed comparison. An equivalent coincidence of independently derived flightless forms has also been proposed for two species of extinct giant coot, *Fulica*, that existed in mainland New Zealand and in the Chatham Islands (Millener 1980; Trewick 1995).The implication of these and other examples is that where a related flightless rail is not already present (i.e. in allopatry) and where environmental conditions are similar (including absence of mammalian predators), evolution can and does follow a recurrent path and yield flightless species that are morphologically similar and ecologically equivalent. This process of parallelism has also been proposed as one explanation for the evolution of two species of dodo on separate islands (Livezey 1993).

On islands in the western Pacific Ocean there have recently existed many examples of flightless species of another rail genus *Gallirallus* (Forbes 1892; Andrews 1896a; Falla 1954; Olson 1973b, 1975; Ripley 1977; Steadman 1986, 1993; Diamond 1991). In most instances these species have a similar form, each being a larger and flightless counterpart of the only extant volant member of the genus, the buff-banded rail *G. philippensis*. It is from *G. philippensis*, which disperses throughout the southwestern Pacific (Schodde & de Naurois 1982), that these species are thought to have evolved (Andrews 1896b; Olson 1973b, 1975; Steadman 1986; Trewick 1995). Thus, in this genus too, the allopatric evolution of flightlessness is generally associated with repeatable and analogous changes in form and parallel changes in behaviour and ecology. An important feature of this process is the local extinction of the volant ancestor in the region in which a flightless species evolves. This is evinced by absence or recent re-extension of range indicated by fossils (Millener 1991) and genes (Trewick 1997). The persistance of *G. philippensis* in this context, appears to be dependent on its wide distribution, such that local extinction is balanced by recolonisation. The genetic patchwork that presumably results from this range dynamism must contribute to the likelihood of evolution of flightlessness on islands through isolation. It also means that evolution of distinct flying morphotypes is unlikely, because it is the association between islands and flightlessness that fixes genotypes, not merely wide dispersal. The absence of distinct flying species of *Gallirallus* in the western Pacific, despite the existence of closely related subspecies (Schodde & Naurois 1982), is testimony to this.

In the Chatham Islands of New Zealand, flightless rail species existed in close sympatry. The two species examined in the present study (*G. dieffenbachii* and *G. modestus*) appear to demonstrate the potential for quite different and radical form change in such circumstances. *G. dieffenbachii* and *G. modestus* were initially described from live-caught specimens, but neither species survived long after discovery. A single *G. dieffenbachii* was collected on Chatham Island by Dieffenbach in 1840 (Oliver 1930), but no other individuals were seen thereafter. *G. modestus* was discovered by Travers on the islet of Mangere in 1871, and described by Hutton (1872). More specimens of *G. modestus* were collected subsequently, but it has been extinct since the turn of the century.

The taxonomic status of the two species has in its short history seen many changes. *G.*

modestus has been considered to be the juvenile of *G dieffenbachii* (Buller 1873, Forbes 1892), and also the sole representative of a monotypic genus, *Cabalus* (Hutton 1874) *G dieffenbachii* was also, at one stage, assigned to a monotypic genus (*Nesolimnas* Andrews 1896b) but has also been relegated to subspecific status as a variant of the volant species *G philippensis* (Ripley 1977) This latter situation presumably resulted from examination of the only skin specimen in existence (the holotype at BMNH, Tring), which shows that *G dieffenbachii* had very similar plumage to *G philippensis* (Diamond 1991) and does not indicate any great difference in size (pers obs) However, mitochondrial DNA sequence data does not support this conclusion, and indicates that *G dieffenbachii* and *G modestus* were about equally diverged from *G philippensis* (Trewick 1997)

Fossil bones from both species were found during the last century in limited quantities (Forbes 1893, Andrews 1896a, 1896b) This material, and that collected later, indicated that the two species had at one time been present on the same islands of the Chatham group (Forbes 1893, Falla 1960), although this interpretation was not universally accepted (Olson 1973b) Material available at the time indicated that if *G modestus* was present on Chatham Island it was much rarer than *G dieffenbachii* (Olson 1975) Collections made more recently demonstrate irrefutably that both birds existed on at least three islands of the Chatham group (Millener 1991) Material collected on Chatham Island is of sufficient quality and quantity to facilitate for the first time reliable osteometric comparison of *G modestus* and *G dieffenbachii* The close relationship of *G philippensis*, *G dieffenbachii*, *G modestus* and *G australis* indicated by both morphology-based taxonomy (Olson 1973b) and molecular evidence (Trewick 1997) provides the rationale for the comparison of species described here This paper presents osteometric data that characterises the nature and degree of differentiation between the two endemic Chatham Island rails and their putative ancestor *G philippensis* It challenges presumptions about the relationship of morphological and phylogenetic divergence with respect to these flightless rails, and explores possible ecological and evolutionary implications of these differences

METHODS

Holocene fossil material used in this study is held at the Museum of New Zealand Te Papa Tongarewa, Wellington (NMNZ) It originated from a single dry cave at Te Ana a Moe on the southern shores of Te Whanga lagoon, Chatham Island The material is abundant and of excellent quality, consisting primarily of dissarticulated skeletal elements and some tracheal rings, and represents the remains of many individuals referrable to *G dieffenbachii* and *G modestus* (Fig 1) The material includes a considerable number of skulls in near perfect condition with crania and premaxilla still joined Modern material examined consisted of associated elements from skeletonised individuals of *G philippensis affinis* collected at various sites in New Zealand (NMNZ) and in Australia *G p australis* (Australian Museum, Sydney) (Appendix 1) This material represents populations that were inseperable in a recent genetic study (Trewick 1997), and the use of both sources expanded the data set Data from a collection of thirty recently skeletonised weka (*G australis hectori*) was available for comparison (unpublished data) Osteological nomenclature follows Howard (1931) and taxonomy follows Marchant & Higgins (1993), although for convenience species are generally referred to by their specific appelation alone in the remainder of the text

Provenance of bones was confirmed by comparison with material from live-caught specimens Dimensions of *dieffenbachii* taken from the skeleton of the only individual caught live (in 1840, just before extinction of the species), and from fossil bone material at Tring (BMNH) given by Andrews (1896b), are in the upper end of the ranges found for this species in the present study Fossil material of *modestus* collected on Chatham Island and labelled "H O Forbes 1892" (NMNZ S27555) is probably that referred to in Forbes (1893), and the dimensions (tarsus 28 6, tibiotarsi 49 1, 46 9 mm) fall within the range for *modestus* determined in this study

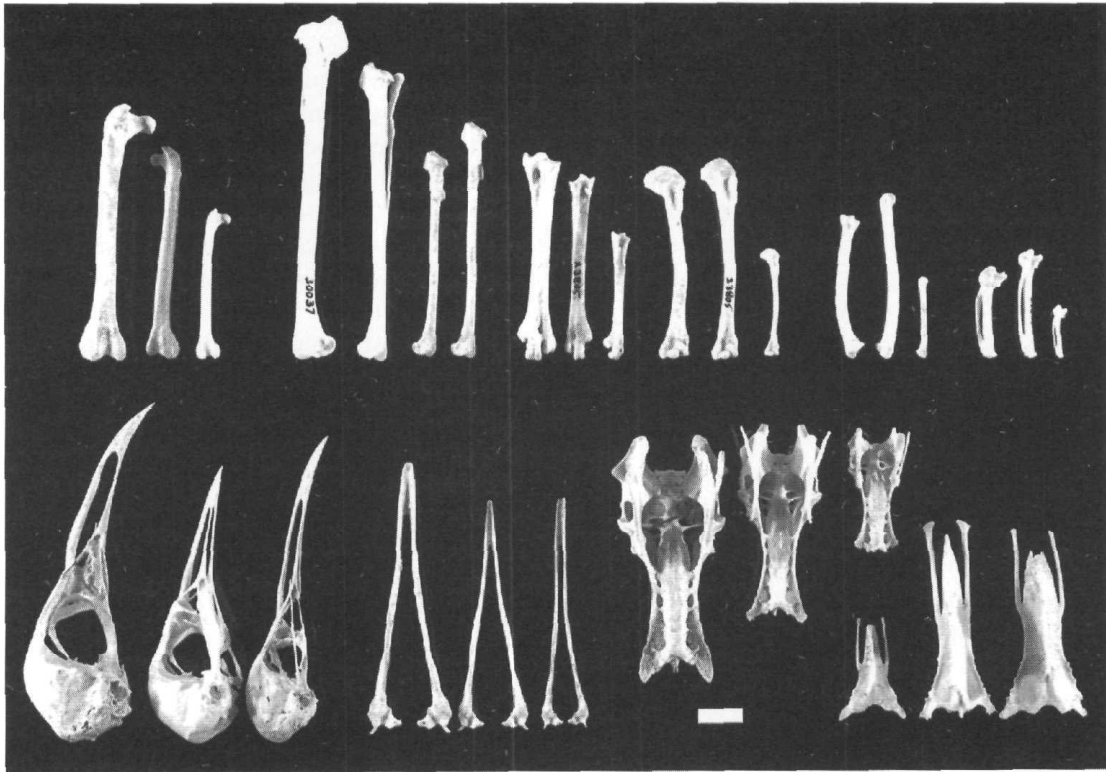Maximum linear measurements were taken from a subset (see Appendix 1) of the entire

Fig. 1   Bones of *G. dieffenbachii* (NMNZ 30037 #113/91), *G. philippensis* (NMNZ 23805) and *G. modestus* (NMNZ 30036 #113/91, except for carpometacarpus 29748 #120/91) arranged by element in that order (except sterna ,which are in reverse order). From left to right: (top) femora, tibiotarsi, tarsometatarsi, humeri, ulni carpometacarpi: (bottom) skulls, mandibles, pelvi, sterna. Two tibiotarsi from *G.modestus* are shown as an indication of the bimodal size range observed.

collection of crania, premaxillae, humeri, carpometacarpi, sterna (median length and carina depth), femora, tarsometatarsi and tibiotarsi (from articular surface) using Mitutoyo dial callipers (Trewick 1996). Because most of the elements examined came from disarticulated skeletons, the size relationships of the various elements could not be tested statistically, except in the complete skulls, where cranium and premaxilla were compared. Summary statistics for each element for each of the species were therefore calculated (Table 1) and graphed, using standardised mean dimensions, in two forms. First, relative dimensions of elements were calculated by division wth the equivalent element of *philippensis*, in order to show proportional differences of each element in comparison to the putative ancestral form (Fig. 2). Second, a graph in which mean dimensions of elements of each species are standardised (by division) with the femur of that species in order to represent the equivalent proportional dimensions of the various elements within each species (Fig. 3). Unpublished data from a sample of weka bones was included in this graph in order to allow comparison with an allopatric flightless relative. Using mean values for unassociated elements assumes a normal distribution of the dimensions of each element within the population and a linear relationship for the association of different elements. These assumptions appear to be valid except, perhaps, in regard to some elements of *modestus* (see text). However, the extent of the differences between mean dimensions of each of the three species is such that any intraspecific variation is unlikely to obscure inter-species comparisons.

Mean dimensions for each element were compared between species using the Tukey-HSD test with a Tukey-Kramer adjustment for unequal numbers, as implemented by Systat 5.1 (Wilkinson 1990). Scatter-plots of log-transformed data for lengths of connected crania and

premaxillae were drawn and fitted with linear regressions which were compared using ANOVA (Fig 4) A two-variable density plot of cranium length vs premaxilla length with kernel smoothing was produced (Fig 5)

RESULTS

Fossil material of the two species endemic to the Chatham Islands is readily distinguished by eye (Fig 1) Dimensions of bone elements assigned to the three species (*philippensis*, *dieffenbachii* and *modestus*) were found to be significantly different from one another ($P <$ 0 0005), and coefficients of variation (%CV) were in the range encountered for within-species variation in other rails (Trewick 1996), with few exceptions (Table 1) The use of a

Table 1   Summary statistics for lengths of osteological elements of *Gallirallus philippensis*, *G dieffenbachii*, and *G modestus* Results of comparison of means (using Tukey-HSD test with a Tukey-Kramer adjustment for unequal numbers) were significant in all cases ($P <$ 0 0005) All measurements are in millimetres Data for *Capellirallus karamu* are provided for comparison from Olson (1975)

| Element	Species	n	Range	Mean	S D	%CV
Femur	G philippensis	17	44 6–53 8	49 1	2 46	5 01
	G dieffenbachii	44	49 4–59 6	55 4	2 14	3 86
	G modestus	53	27 9–33 4	30 7	1 25	4 08
	C karamu	21	43–50	46 5	1 63	
Tibiotarsus	G philippensis	16	60 0–70 5	65 5	2 94	4 49
	G dieffenbachii	41	67 6–79 1	73 0	2 25	3 08
	G modestus	41	41 9–50 3	46 2	2 32	5 02
	C karamu	11	61 2–70 7	66 5	2 8	
Tarsometatarsus	G philippensis	15	37 8–45 5	42 2	2 24	5 31
	G dieffenbachii	41	41 3–47 8	44 6	1 78	3 99
	G modestus	55	24 6–32 4	28 8	1 83	6 35
	C karamu	10	38 6–43 1	40 4	1 72	
Humerus	G philippensis	18	40 3–50 7	45 9	2 43	5 30
	G dieffenbachii	38	41 3–46 8	43 5	1 31	3 01
	G modestus	38	22 9–27 0	24 7	1 14	4 62
	C karamu	13	21 8–28 0	25 9	1 56	
Carpometacarpus	G philippensis	15	23 5–28 3	25 5	1 55	6 07
	G dieffenbachii	29	17 0–23 0	21 0	1 26	6 01
	G modestus	37	11 4–14 2	12 7	0 71	5 60
	C karamu	2	9 3–10 9	10 1	0 8	
Sternum	G philippensis	17	35 8–44 2	39 0	2 14	5 48
	G dieffenbachii	20	29 1–43 4	35 4	3 04	8 59
	G modestus	31	12 6–17 2	15 3	1 19	7 79
Carina	G philippensis	17	10 9–14 4	12 6	1 02	8 09
	G dieffenbachii	20	6 5–9 4	8 01	0 73	9 11
	G modestus	31	1 8–3 2	2 45	0 35	14 29
Cranium	G philippensis	13	28 9–31 8	30 4	0 9	2 96
	G dieffenbachii	33	32 9–35 8	34 6	0 76	2 20
	G modestus	50	23–26 8	24 7	1 03	4 18
	C karamu	1		30 9		
Premaxilla	G philippensis	14	28 7–36 1	32 6	2 29	7 03
	G dieffenbachii	22	38 3–44 5	41 9	1 65	3 94
	G modestus	39	30 8–43 8	36 7	3 16	8 60
	C karamu	1		70 5		
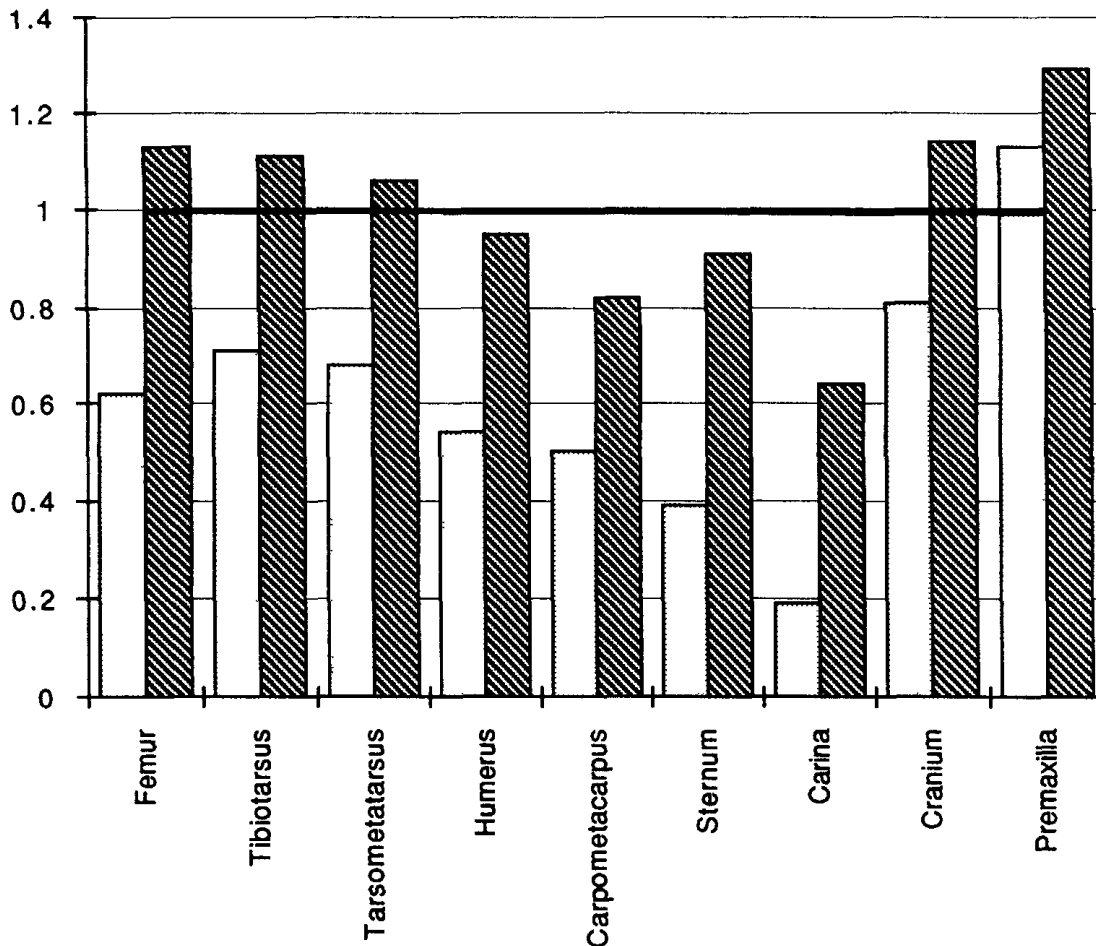
Fig. 2   Interspecific comparison of relative bone dimensions of *Gallirallus philippensis, G. dieffenbachii* and *G. modestus*. Mean values for each species have been standardised by dividing by the mean value for the appropriate variable from *G. philippensis* (Y axis), represented by a horizontal line scaled at unity. Cross-hatched bars *G. dieffenbachii*, stippled bars *G. modestus*.

small sample of *philippensis* specimens collected from a wide geographic area (Australia and New Zealand) probably contributed to relatively high %CVs for some elements of this species. The %CV for carina depth of *modestus* was also relatively high, reflecting both the variability of this structure and, possibly, a relatively higher measurement error resulting from its small size (<3.5 mm). Tarsometatarsi and tibiotarsi of *modestus* were more variable (%CV) than those of *philippensis* and *dieffenbachii* (Table 1), as a result of size-range bimodality (dimorphism) in this species (see Fig. 1).

Overall, *dieffenbachii* was a larger and more robust bird than its putative ancestor *philippensis*, whilst *modestus* was considerably smaller (Fig. 1). However, all bones associated with flight that were measured (humerus, carpometacarpus, sternum, carina) had smaller dimensions in *dieffenbachii* and *modestus* than in *philippensis* (Fig. 2). There is therefore little doubt that both Chatham species were flightless. Also apparent in Fig. 2 is the relatively great length of the tibiotarsus and the premaxilla in *modestus*. The relative dimensions of crania and premaxillae of *philippensis* and *dieffenbachii* were similar to one another (Fig. 3). The weka (*australis*), which is a much larger bird, has proportions that are for the most part very similar to *dieffenbachii*. In the weka, the proportions of some bones (e.g. premaxilla and tarsus) are extremely close to those of *philippensis* (Fig. 3), despite differences in size and volancy.
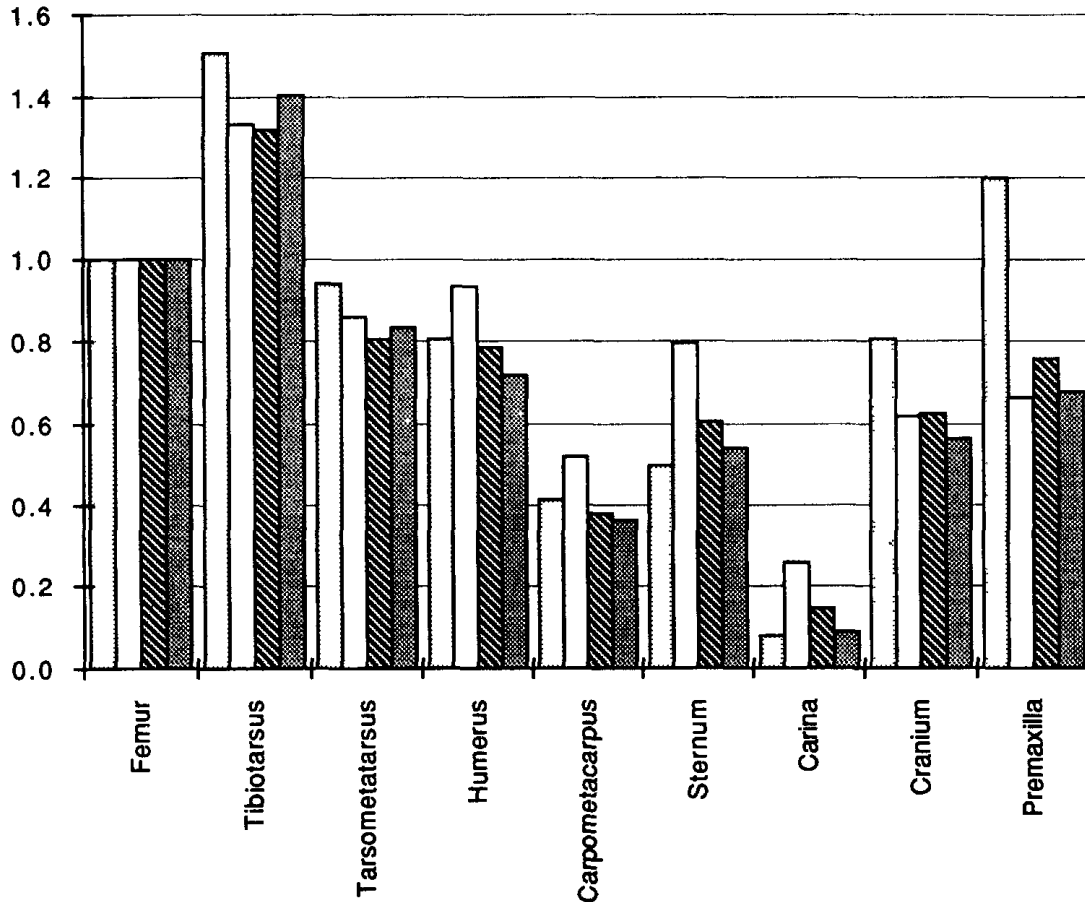
Fig. 3 Intraspecific comparison of relative bone dimensions for *Gallirallus modestus*, *G. philippensis*, *G. dieffenbachii* and *G. australis* (weka). Mean values for each variable for each species are standardised by dividing by the mean value for the femur of the appropriate species (Y axis). Thus, all femur values are scaled at unity. Pale stippled bars *G. modestus*, dark stippled bars *G. australis*, open bars *G. philippensis*, cross-hatched bars *G. dieffenbachii*.

The relationship (gradient) of log-transformed values of premaxilla length vs. cranium length were not significantly different in pairwise comparisons among the three species (Fig. 4). Pairwise comparison of the intercepts of linear regressions showed that the three species were significantly different from one another. However, the distinction between the intercepts of *philippensis* and *dieffenbachii* was marginal, and was supported at a lower probability level ($P = 0.0153$) than were differences between the intercepts of *philippensis* vs. *modestus* ($P < 0.0001$) and *dieffenbachii* vs. *modestus* ($P < 0.0001$); this is apparent in Fig. 4. Thus, relative to the size of the cranium, the premaxilla of *modestus* is much longer than that of *philippensis* and *dieffenbachii* (Fig. 4). This difference is also evident in Fig. 3.

A broad distribution of points for premaxilla and cranium dimensions of *modestus* is apparent in Fig. 4, and a bivariate size-frequency plot revealed a distinct bimodality in this distribution (Fig. 5). In *philippensis* and *dieffenbachii* the lengths of these structures appeared to be normally distributed.

DISCUSSION

Morphology and biology

Within *Gallirallus*, several independent and allopatric evolutionary events have apparently given rise to very similar flightless forms from similar (or the same) ancestral, volant species.
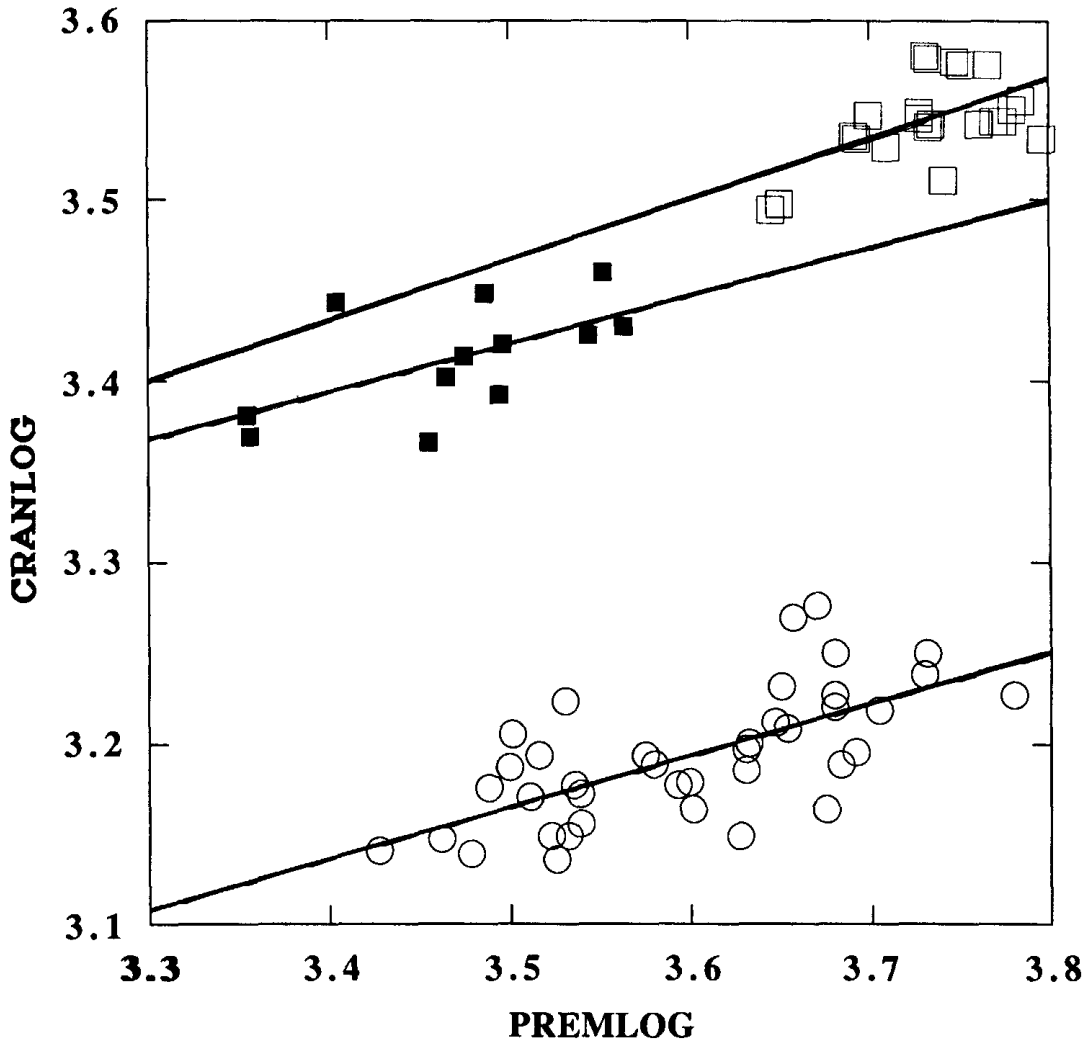
Fig. 4 Log-transformed cranium and premaxilla lengths of *Gallirllus philippensis* (filled squares),*G. dieffenbachii* (open squares), and *G. modestus* (filled circles). Linear regression equations are: *G. philippensis* LnCranium length = 2.4906 + 0.2655*LnPremaxilla length, $F_{1,10}$ = 5.4975, P < 0.05, r^2 = 0.355; *G. dieffenbachii* LnCranium length = 2.3003 + 0.333*LnPremaxilla length, $F_{1,20}$ = 8.9012, P < 0.01, r^2 = 0.308; *G. modestus* LnCranium length = 2.1726 + 0.2832*LnPremaxilla length, $F_{1,37}$ = 31.0467, P < 0.0001, r^2 = 0.456.

However, in the two flightless Chatham rails, *modestus* and *dieffenbachii*, it is notable that two morphologically distinct forms appear to have been derived from a similar (or the same) founder, in the same location. *G. modestus* and *dieffenbachii* each conform to one of two non-unique formats. *G. deiffenbachii* is equivalent to the skeletal morphotype of the weka (Fig. 3) and probably also to the weka's morphological counterpart (Olson 1973b), the Lord Howe woodhen *G. sylvestris*. This flightless *Gallirallus* morphotype is the most common, being repeated with some variation in overall size throughout the southwest Pacific. The weka utilises a broader range of habitats (forest, fernland, swamp) and foods (broadly omnivorous) than its volant relative *philippensis* (Ripley 1977; Beauchamp 1987), and the same can be said of other similar species, such as *sylvestris* (Lord Howe Island). *G. dieffenbachii* is likely, therefore, to have occupied a niche similar to that of *philippensis* but closer to that of the weka.
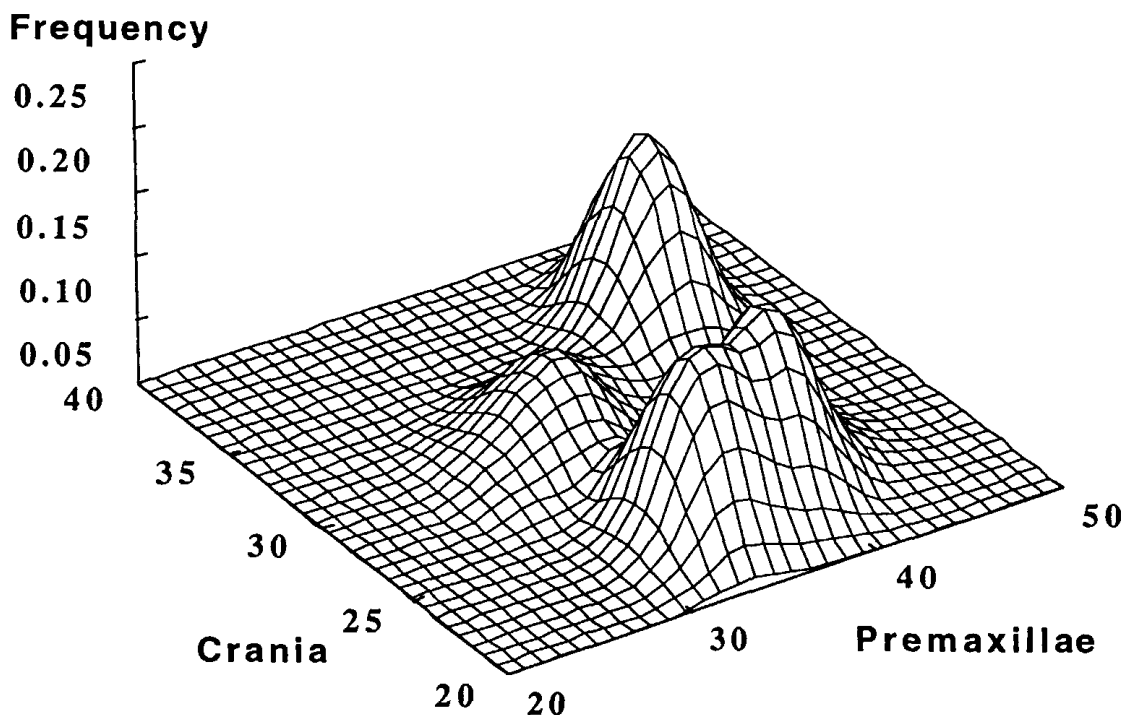
Frequency

Fig. 5 Size frequency distribution of cranium and premaxilla length (mm) with kernel smoothing Vertical axis = frequency Peaks are *Gallirallus philippensis* (lowest, left), *G dieffenbachii* (single high peak at back), and *G modestus* (twin peaks, front) Height of peaks is a reflection of sample size alone
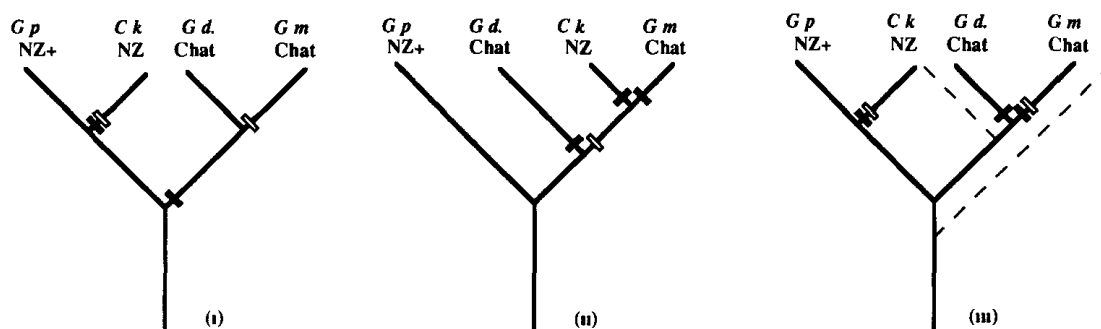

Fig. 6 Alternative phylogenetic hypotheses for the speciation of *G modestus* (G m), *G dieffenbachii* (G d) and *Capellirallus karamu* (C k) G p refers to *G philippensis*, the only volant species NZ and Chat refer to New Zealand and Chatham Islands respectively (i) Sympatric speciation of *G modestus* and *G dieffenbachii*, (ii) common flying ancestor of *G modestus* and *C karamu*, (iii) speciation from separate colonisations by the 'same' volant ancestor Loss of flying ability is indicated by a black bar across branch, and development of long bill by open bar Broken lines (iii) indicate equally consistent alternative positions for branch to *C karamu*

G modestus, however, was morphologically quite different from the above species, having a small body and a long bill The only similar probable *Gallirallus* derivative is the extinct *Capellirallus karamu*, which existed on the North Island of New Zealand (Falla 1954, Olson 1975) Both species appear to have become specialist rather than generalist feeders In fact, in its plumage and its long bill and legs, as well as its nocturnal habit (Travers & Travers

1873), *modestus* is superficially reminiscent of an extremely small kiwi. As such, it would appear that *modestus* had joined the guild of probing specialists, and presumably fed on ground invertebrates. Atkinson & Millener (1991) noted that on the New Zealand mainland a number of different taxa, including snipe, kiwi, *C. karamu* and even an acanthisittid wren may have been members of a ground-probing insectivore guild. In the Chatham Islands, probable members of this guild were a snipe and the rail *Diaphorapteryx hawkinsi*, both of which were considerably larger than *modestus*. There may therefore have been ecological space which a small, specialised flightless rail could occupy whilst remaining in sympatry with a generalist congener (*dieffenbachii*). As any specialisation is also a constraint, it seems unlikely that the long bill of the tiny *modestus* would have served effectively for collecting other foods such as fruit, nor that the bird's digestive system would have efficiently processed such markedly different food. Although Atkinson & Millener (1991) proposed that *modestus* ate both invertebrates and fruit, the diet of most small rails does not generally include plant material (Ripley 1977; Baker & Vestjens 1994), and the only recorded observations of the diet of *modestus* before its extinction state that "they live on insects, principally the sand-hoppers [Crustacea, Amphipoda], which travel in to the bush here a long way" (Forbes 1893). *G. philippensis* is almost exclusively insectivorous, and only rarely known to take plant matter, including fruit (Marr 1993; Baker & Vestjens 1994).

As further evidence of the specialised nature of *modestus*, it is apparent that this species was dimorphic. This is most strongly indicated by examination of the relative proportions of crania and premaxillae (Fig. 4, 5), but also by the high CVs of most of its bones (Table 1). This dimorphism, which can most simply be attributed to sexual differentiation, may have been an adaptive specialisation favouring food partitioning, or resulted from male/male intrasexual competition and sexual selection favouring large males, or might even have resulted from the retention, in this species, of a relatively large egg, favouring larger females (as with the kiwi). Dimensions of the eggs of the larger *philippensis* range from 32 × 24 mm to 37 × 29 mm (Oliver 1930; Ripley 1977), and the single record of an egg from the tiny *modestus* is at the upper end of this range, being 37 × 28 mm (Forbes 1893; Oliver 1930).

Evolutionary history

The greater disparity in external characters between *modestus* and *philippensis* than is apparent between the latter species and *dieffenbachii* has led to the proposal that *modestus* evolved from an earlier invasion of a *philippensis*-like ancestor than that giving rise to *dieffenbachii* (Andrews 1896b; Olson 1975; Ripley 1977). In the words of Andrews (1896b) "the most highly modified forms being the outcome of earlier, the less altered of later colonisation." With respect to similarities between *modestus* and *karamu* Olson (1975) suggests the latter may have "evolved earlier from a *Gallirallus* (sensu lato) ancestor and proceeded even further along the same lines taken later by "Cabalus" [=*G. modestus*]." This hypothesis is presumably based on the dubious assumption that morphological divergence is simply correlated with the passage of time. *C. karamu* did indeed bear some similarity to *modestus* suggesting that the two evolved in response to similar selective pressures, but the extent of morphological divergence from the ancestral type probably tells us more about the nature of selection and competition than the passage of time. Simply because it is the less derived form (i.e. most similar to the proposed founding species), *dieffenbachii* cannot be presumed to be of more recent origin than *modestus*. Nearly all of the related and independently derived species of flightless rail on other islands are morphologically similar to *dieffenbachii* and behaviourally similar to one another (Beauchamp 1987). This generalisation includes the weka, even though it is indicated by molecular data to be much older than any of the other species discussed here (Trewick 1997). Therefore, instead of being "obviously the more recent arrival" (Olson 1975), *dieffenbachii* might equally be considered to be older than *modestus* as it conforms to the generalised morphotype—this form apparently being the one most readily evolved.

The existence on the New Zealand mainland of *Capellirallus karamu*, a species with some

similarity to *modestus* (i.e. a relatively long bill), raises the possibility of an even more complex history for these birds. If their similarities were the result of common ancestory rather than convergence, then evolution of *modestus* on the Chatham Islands could have involved little change other than flightlessness. In fact, there were few similarities between *karamu* and *modestus*. Certainly both had unusually longs bills for their body size, but in absolute terms the bill of *karamu* was much longer than that of *modestus* (Table 1). The downward curvature of the bill cited as a feature common to the two (Olson 1975) is also present in *dieffenbachii* (Fig. 1), as noted by Marchant & Higgins (1993), and in *Diaphorapteryx*. *C. karamu* was altogether much larger than *modestus*, being almost identical in leg length and head size to the volant species *philippensis* and closer to *dieffenbachii* than *modestus*. It shared with *modestus* only similar relative size of wings, which carries no phylogenetic significance, being obviously convergent.

Three alternative scenarios can be proposed for the origin of the sympatric Chatham rails (Fig. 6). None of these hypotheses are in themselves inconsistent with evidence from DNA (Trewick 1997).

(i) They evolved in sympatry after a single colonisation by the volant ancestor (Fig. 6i). Given the evidence of DNA data and the location of the species concerned, this is the most parsimonious explanation of the evolution of *modestus* and *dieffenbachii*. However, without evidence for a specific ecological mechanism to explain the initial divergence of the species it would be hard to favour this hypothesis in its most rigid form (but see 6iii). Obviously, if *modestus* and *dieffenbachii* evolved in sympatry in a single speciation event then *karamu*, being on a separate landmass, must have speciated independently. Thus, any similarities between *karamu* and *modestus* would have to be convergent, as are similarities between other flightless rails.

(ii) They evolved independently from separate colonisations by separate and distinct ancestors, one of which also gave rise to *karamu* (Fig. 6ii). This would have required the contemporaneous existence of two closely related volant species in the New Zealand region. There is no evidence of a second species, fossil or otherwise, nor is it obvious why, if such a species were once ecologically viable, it subsequently ceased to be. The proposal of morphologically distinct volant ancestors for flightless rails generally appears redundant, despite morphological distinctiveness of some species. This is because a single volant ancestor is sufficient where the range of this species extends over many oceanic islands on which flight loss can occur after colonisation. Distance and flight loss being sufficient to fix new species and allow for subsequent reinvasion. The existence on the Chatham Islands of a further endemic rail of probable *Gallirallus* origin, *Diaphorapteryx hawkinsi*, and the weka on the New Zealand mainland support this. Given these points, and the observations above that *karamu* and *modestus* do not share similarities beyond those that can easily be attributed to convergence, the simplest explanation of the available distributional, genetic, morphological and fossil evidence suggests that a single volant species is likely to have given rise to each of the flightless species discussed (Fig. 6).

(iii) They evolved from separate colonisations by the same volant ancestor, in allopatry/ partial sympatry (Fig. 6iii). In this scenario, *modestus* would be implicated as the more recent arrival, becoming more specialised as an evolutionary response to selection pressure exerted by the presence of the generalist *dieffenbachii*. The existence of *karamu* on the North Island of New Zealand could be viewed as a parallel of this, as a *Gallirallus* generalist (weka) also existed there. It is notable that none of the many flightless *Gallirallus* found singly on islands (Diamond 1991) are of a specialised form. Morphotypic congruence among independently evolved flightless birds on separate islands is common (Trewick 1995), with examples in *Porphyrio* (Olson 1977; Balouet & Olson 1989; Trewick 1996, 1997), *Fulica* (Olson 1977; Trewick 1995) and dodo (Livezey 1993). In each instance a single species is known from each island, and as each is distinct from the putative ancestor it seems plausible that a second invasion of the

ancestor could, even after a small period of separation found a second species. Thus, two 'populations' would have the potential to remain distinct and indeed speciate fully, not necessarily as a result of the evolution of mate recognition systems, as has generally been argued in such cases (Grant & Grant 1996 and references therein), but through partitioning in space and perhaps time of resources and habitat (Bush 1994). This scenario of temporal displacement of evolutionary origins simply provides the initial impetus for speciation in sympatry. Similar phenomena appear to have occured with other 'flightless' taxa on islands including *Cerion* snails (Woodruff & Gould 1980), *Anolis* lizards (Roughgarden & Pacala 1989), skinks (Bruna et al. 1996) and *Partula* snails (Clarke et al. 1996).

Either way, the earlier hypothesis that *dieffenbachii* evolved more recently and "may have been in competition" (Olson 1975) with *modestus*, and eventually replaced it (Olson 1975; Ripley 1977), is unsupported. It is not consistent with the presence of abundant remains of both species at the same site, and the extensive morphological divergence between them, nor with the existence of allopatric species similar to *dieffenbachii* on other islands. The rarer evolution of specialised body form, and presumably behaviour, suggests that sympatry may provide the source of selection pressure favouring the development of a more distinctive form. Unfortunately, in the present instance the nature, extent and direction of this competition cannot be determined.

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APPENDIX

Bone material examined for this study.

G. dieffenbachii and *G. modestus* bones measured are indicated as such in the NMNZ collection.
National Museum of New Zealand Te Papa Tongarewa (NMNZ)

Gallirallus philippensis
NMNZ 24058, 23800, 23804, 22107, 24642a, 23801, 23996, 23821, 23805, 23803, 23802. DM 15138, 12318

Gallirallus modestus
NMNZ S27188 (#132–5), S27182 (#132–4), S27169 (#132–2), S30036 (#113/91), S29748 (#120/91), S30051 (#18A/91)

Gallirallus dieffenbachii
NMNZ S27502 (#42), S27422 (#43), S27502 (#42), S27422 (#43), S29494 (#93/91), S30037 (#113/91), S31706 (#127/92), S32161 (#152/92), S32168 (#152/92), S32169 (#152/92), S32166 (#152/92), S31778 (#132/92), S32092 (##152/92), S32195 (#153/92), S32198 (#153/92), S29494 (#93/91), S32171 (#152/92)

Australian Museum, Sydney, Australia
Gallirallus philippensis
59296, 56701, 64704, 56994, 64702