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A REVIEW OF THE EXTINCT RAILS OF THE NEW ZEALAND REGION (AVES: RALLIDAE)

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ABSTRACT

1. The subfossil rail *Rallus hodgeni,* which in the past has been referred to its own genus (*Pyramida*) and also to *Capellirallus,* is shown to be a flightless derivative of the Australian gallinules of the subgenus *Tribonyx* and becomes *Gallinula* (*Tribonyx*) *hodgeni.*

2. *Gallirallus hartreei* is considered to be a synonym of *Gallinula* (*Tribonyx*) *hodgeni.*

3. The very distinctive subfossil rail *Capellirallus karamu,* known so far only from the North Island, is further described and illustrated, and its possible relationships discussed.

4. The genus *Nesophalaris,* used for the giant extinct coots of the Chatham Islands (*chathamensis*) and New Zealand (*prisca*), is considered a synonym of *Fulica F. chathamensis* and *F. prisca* are both shown to have been flightless and of nearly the same size. A lectotype is designated for *F. prisca* and this taxon is maintained as a subspecies of *F. chathamensis,* distinguished on the basis of characters of the humerus.

5. The distribution and relationships of the Chatham Island rails *Gallirallus* ("*Nesolimnas*") *dieffenbachii, G.* ("*Cabalus*") *modestus,* and *Diaphorapteryx hawkinsi* are briefly discussed.

6. Doubt is cast upon the validity of *Gallirallus minor,* a subfossil species that has never been satisfactorily characterized.

INTRODUCTION

In the rich subfossil record of birds in the late Quaternary of New Zealand and the Chatham Islands, are found a number of interesting species of extinct rails. Recent visits to New Zealand museums have enabled me to examine specimens of these forms first-hand and to discover some previously unknown and undescribed elements. The results of these studies are presented here as part of a review of the living and fossil taxa of the family Rallidae. The taxonomy used will follow that of Olson (1973b). I have purposely excluded from the present study the fascinating genus *Aptornis,* as it is not a rail at all and will be treated in a later paper on the Aptornithidae.

THE IDENTITY OF **Rallus hodgeni** SCARLETT, 1955, AND **Gallirallus hartreei** SCARLETT, 1970

Scarlett (1955b) described a small rail from Pyramid Valley Swamp in the South Island, from pelves, leg, and wing bones, designating an incomplete pelvis (CM Av 6197) as the holotype. He determined that *hodgeni* was larger than *Capellirallus karamu* Falla, 1954, a peculiar, long-billed rail from cave deposits in the North Island, and provisionally placed *hodgeni* "in the broad genus *Rallus* until the skull is found and its generic affinities are ascertainable."

Later in the same year, Oliver (1955) studied the type material of *hodgeni* and concluded that it belonged to a gallinule "apparently . . . closely allied to *Tribonyx*." For the species he created the monotypic genus *Pyramida*. The spelling *Pyramidia* also appeared in the same work, evidently through a printer's error since in Oliver's original typescript it was *Pyramida* (MS in NMNZ). The spelling was restricted to *Pyramida* by Dawson (1957).

Scarlett (1970b) reviewed new material of *hodgeni* and of *Capellirallus karamu*, listing many new localities for both and showing that *hodgeni* occurred rather commonly in both the North and South Islands. He concluded that *hodgeni* and *karamu*, although different in size, were congeneric, and placed *hodgeni* in the genus *Capellirallus*. This treatment is followed in the official checklist of New Zealand birds (Kinsky 1970). However, until now the skull and bill of *hodgeni* have been unknown, except for two posterior portions of crania, and there were further difficulties in that some of the elements Scarlett ascribed to *hodgeni* were from other species. Furthermore, those characters of the pelvis that Oliver (1955) used to ally *hodgeni* with the gallinules are not shared with *Capellirallus karamu*—a fact that was not brought out by Scarlett (1970b).

In examining some partially sorted subfossil material from the Martinborough Caves in the North Island (see Yaldwyn 1956, 1958, for descriptions of these localities) at the National Museum of New Zealand, I found several crania, rostra, mandibles, and sterna (NMNZ S. 967-973 and unregistered material) of a small gallinule. In this same collection are limb elements (S. 974-785 and unreg. mat.) that are identical to the paratypes of *hodgeni* from Pyramid Valley. This, coupled with the fact that the pelvis of *hodgeni* shows characters typical of some of the gallinules, leaves little doubt that the crania and sterna from Martinborough are referable to *hodgeni*. These elements prove conclusively that *hodgeni* is a flightless derivative of the Australian subgenus *Tribonyx* in the genus *Gallinula*, and is not related to *Capellirallus*. Below, *hodgeni* is redescribed and compared with the forms of *Tribonyx*. The subgeneric name will be used throughout to emphasize the Australian relationships of *hodgeni*. The comparison of *hodgeni* with *Capellirallus* in the plates and tables is for economy of space and for the future convenience of those wishing to identify New Zealand fossil material and is not intended to imply an affinity between the two. Discussion of their many differences may be found in the account of *Capellirallus*.

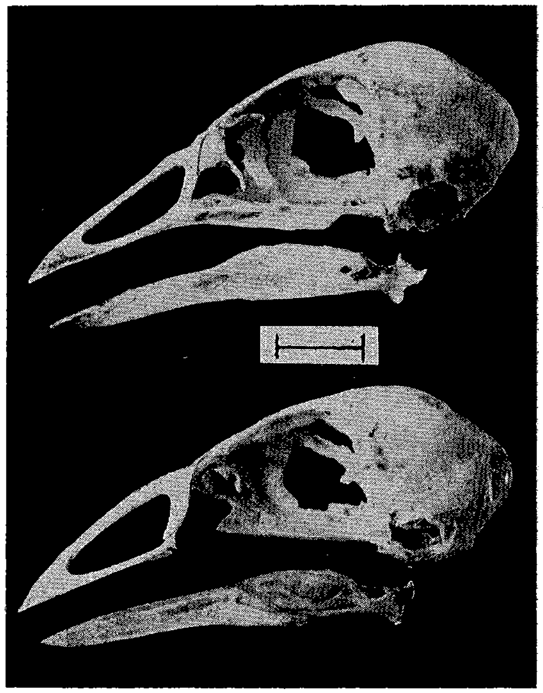

Fig. 1. Top to bottom: lateral view of skull and mandible of *Tribonyx ventralis* (MVZ 143365), *T. hodgeni* (NMNZ S 967; S 969). Scale 10 mm.

Tribonyx hodgeni is closest in size to, although somewhat smaller than, the Black-tailed Water Hen (Native Hen), *T. ventralis* (Gould), of Australia (Table 1) and is therefore much smaller than the flightless Tasmanian Water Hen, *T. mortierii* Du Bus. The extremely short, wide bill, and particularly the very short premaxilla (Figs 1 and 2) is a marked characteristic of the subgenus *Tribonyx* and demonstrates that *hodgeni* belongs with that group rather than with the typical moorhens of the subgenus *Gallinula*. Most of the skull dimensions of *T. hodgeni* are slightly smaller than those of *T. ventralis*, except for the width of

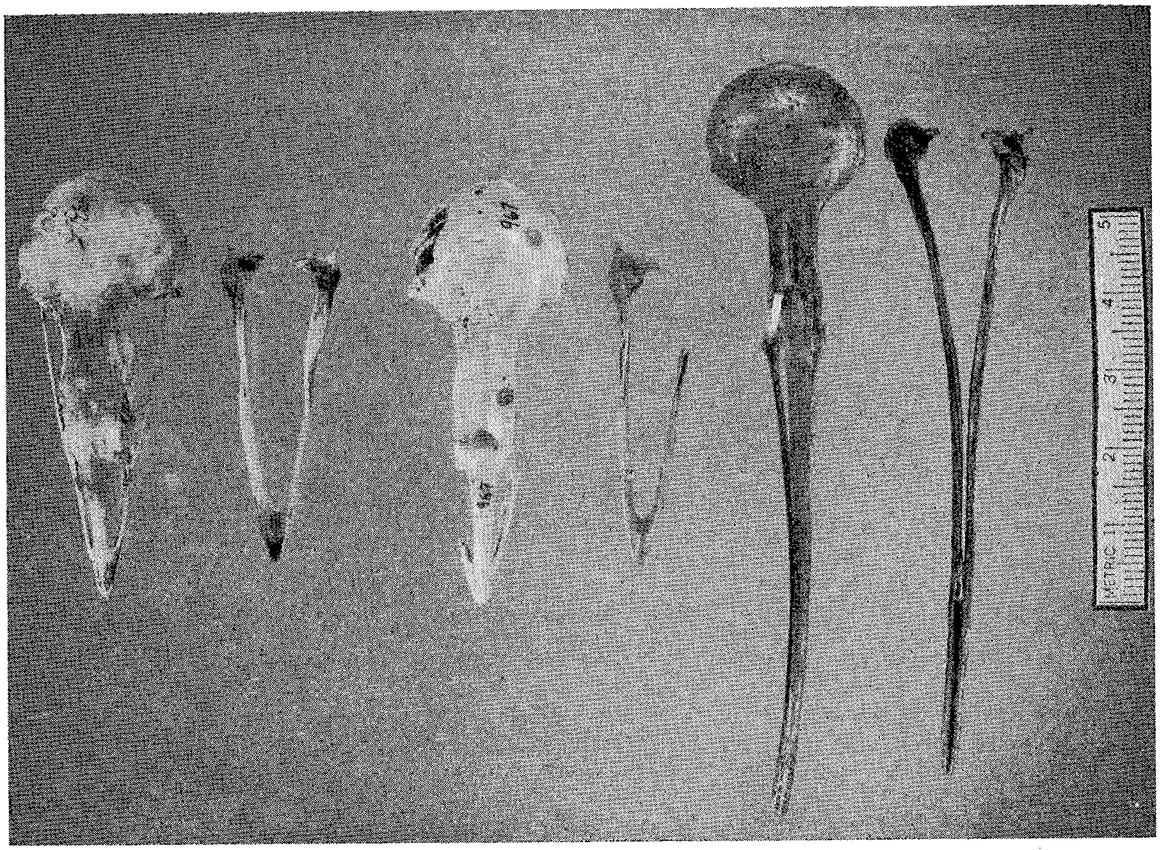

Fig. 2. Left to right: dorsal view of skull and mandible of *Tribonyx ventralis* (MVZ 143365), T. *hodgeni* (NMNZ S 967; S969), *Capellirallus karamu* (CM Av 20615).

the interorbital bridge. The narrowing of this bridge in *ventralis* appears to be correlated with better-developed supraorbital salt-excreting glands. The skull and mandible of *hodgeni* are generally similar to those of *ventralis*, but in the relatively shorter and broader bill tip and mandibular symphysis, the shorter and higher nostril, and the heavier, more arched culmen (Fig. 1), *hodgeni* more closely resembles *T. mortierii*.

Compared to those of *ventralis* the elements of the wing and pectoral girdle of *hodgeni* are greatly reduced (Figs 4 and 5; Table 1) in the manner characteristic of flightless rails. These modifications are rapidly evolved and are not of generic value (Olson 1973a). Scarlett's (1970b) description of the sternum of *hodgeni* (CM Av. 21,763I) may be disregarded as it was based on a wide sternum of *Capellirallus karamu* (see below). In the sternum of *hodgeni* (Fig. 5) the carina is even more reduced than in *T. mortierii* and although the sternal plate is shorter than in *ventralis*, it is nearly as wide as in that species. The ventral manubrial spine is virtually absent in *hodgeni* whereas it is present in flying forms (including *ventralis*) and strangely enough persists in *T. mortierii*. In dorsal aspect the sternum of *hodgeni* is remarkably concave and boatlike, much more so than in its congeners. The sterno-coracoidal processes are angled farther anteriorly and are less perpendicular to the long axis of the bone than in either *ventralis* or *mortierii*. In all respects the sternum of *hodgeni* is more divergent from *ventralis* than is that of *mortierii*, although the conformation of the sternum in flightless rails is of little taxonomic significance (Olson 1973a).

The shape of the head of the coracoid of *hodgeni* (Fig. 5) is approximately intermediate between that of *ventralis* and *mortierii*, and the procoracoid and sterno-coracoidal processes are

1

	T. ventralis				T. hodgeni				C. karamu			
	n	range	mean	s.d.	n	range	mean	s.d.	n	range	mean	s.d.
Width cranium	5	20.6- 22.2	21.2	.64	3	19.9-20.6	20.3	.29	3	19.8-20.2	20.0	.16
Length cranium from naso-frontal hinge	5	33.2- 35.3	34.1	.72	2	32.5-34.4	33.5	.99	1	---------	30.9	----
Length bill from naso-frontal hinge	4	25.4- 27.9	26.9	.98	1	---------	24.2	----	1	---------	70.5	----
Length nostril	4	13.5- 15.0	14.4	.57	3	12.1-13.3	12.7	.51	1	---------	52.1	----
Length bill tip from nostril	4	7.6- 8.4	8.1	.29	3	6.7- 7.2	6.9	.21	1	---------	18.2	----
Width interorbital bridge	5	5.5- 6.6	6.1	.43	2	6.5- 7.2	6.9	.35	1	---------	6.1	----
Length mandible	5	41.4- 47.4	43.8	2.11	1	---------	41.7	----	1	---------	83.9	----
Length mandibular symphysis	5	6.7- 9.5	8.0	.91	2	5.9- 6.5	6.2	.30	1	---------	26.2	----
Length coracoid	5	29.1- 32.0	30.7	1.22	17	17.8-21.5	19.9	.93	7	13.8-15.9	15.3	.69
Length scapula	5	50.1- 56.7	53.5	2.67	1	---------	40.2	----	1	---------	28.0	----
Width sternum across sulci	5	15.0- 17.4	16.5	.80	1	---------	16.2	----	1	---------	15.4	----
Depth carina through manubrium	5	17.5- 18.8	18.1	.61	1	---------	8.1	----	1	---------	2.4	----
Depth carina from sternal plate	5	13.6- 15.8	14.6	.94	2	4.5- 4.8	4.7	.15	1	---------	0.8	----
Length humerus	5	56.8- 63.4	59.4	2.29	30	32.4-43.2	40.4	2.52	13	21.8-28.0	25.9	1.56
Length ulna	5	48.8- 56.4	52.0	2.59	10	27.4-32.4	29.4	1.53	2	15.6-16.9	16.3	.65
Length radius	5	44.7- 52.3	48.3	2.49	1	---------	24.7	----	1	---------	15.4	----
Length carpometacarpus	5	37.0- 43.0	39.7	1.95	13	19.0-21.5	20.5	1.29	2	9.3-10.9	10.1	.80
Length femur	5	52.4- 60.5	55.3	2.91	56	52.1-63.6	57.9	2.56	21	43.0-50.0	46.5	1.63
Length tibia from cnemial crest	4	87.6-102.4	92.9	5.78	25	72.9-79.3	75.9	1.83	10	62.8-72.9	68.3	3.29
Length tibia from articular surface	4	84.6- 99.2	89.4	5.94	35	69.2-77.9	73.5	2.02	11	61.2-70.7	66.5	2.80
Length tarsometatarsus	5	56.2- 66.3	60.0	3.84	50	39.1-48.0	42.9	2.10	10	38.6-43.1	40.4	1.72
Width pelvis through antitrochanters	5	25.2- 29.3	27.5	1.43	4	24.8-25.8	25.2	.38	5	17.5-19.3	18.3	.75

Table 1. Size comparison (in mm) of *Tribonyx ventralis, T. hodgeni,* and *Capellirallus karamu.*

more reduced than in either of these species. The humerus (Fig. 4) is small and slender, agreeing with those of many flightless rails and differing from that of *ventralis* in having the head lower and flattened and the deltoid crest reduced. The ulna (Fig. 3) is short and stout, although not quite as heavy as in *T. mortierii*. The olecranon is better-developed and not squared as in *mortierii*. The carpometacarpus (Fig. 4) is not as slender and elongate as in *ventralis* and is similar in proportions to that of *mortierii*.

The pelvis of *hodgeni* (Fig. 5) is generally similar to that of *ventralis*, but is smaller and narrower. As Oliver (1955) noted, it agrees with *Gallinula*, *Tribonyx* and *Fulica* in having the dorsal edge of the anterior ilium nearly free of the median dorsal ridge of the sacrum, being fused for only a millimeter or two of its length. In lateral view the posterior ilium angles more ventrally than in *ventralis* or *mortierii*, the ilio-ischiatic fenestra is slightly more vertical, and ventral to it is a distinct depression in the ischium.

In the proportions of the hindlimb (Fig. 7), *hodgeni* is considerably different from either *ventralis* or *mortierii*. Compared to *ventralis* in both absolute (Table 1) and relative (Table 2) measurements, *hodgeni* has a longer femur, shorter tibiotarsus, and much shorter tarsometatarsus. A slight tendency toward these proportions is seen in *mortierii*, but that species is much nearer *ventralis* in this respect.

The femur (Fig. 7) of *hodgeni* is similar to the shorter femur of *ventralis*, although not as heavy through the head and trochanter. The tibiotarsus (Fig. 7) differs mainly in having the shaft shorter and stouter and the outer cnemial crest thicker. The short, heavy tarsometatarsus (Fig. 7) of *hodgeni* looks very different from the long, slender tarsometatarsus of *ventralis*. The ends of the bone are more expanded, the trochleae are heavier, the inner trochlea is displaced more distally and expanded farther laterally, and the distal foramen is more rounded. In most details the bone is approached by that of *mortierii*, but as mentioned above, it is proportionately shorter and also has the inner trochlea somewhat lower.

Scarlett (1970b) has implied that there may be size differences between the North and South Island populations of *T. hodgeni*, specifically that ulnae from the South Island are larger. However, ulnae identified as *hodgeni* included in the material from Pyramid Valley at the Canterbury Museum are much too heavy for that species and I believe they are referable to the dubious form known as *Gallirallus minor*, to be discussed later. Although there are few specimens from the South Island, it can be seen from Table 3 that there is very broad overlap in the size of bones from the North and South Islands. If anything, there is a tendency for smaller averages in the South Island measurements but it is impossible to differentiate between the two populations on the basis of size.

Another small rail, *Gallirallus hartreei*, was named by Scarlett (1970a) from a cave deposit about 30 miles from Napier, North Island. The holotype (CM Av. 18,475) consists of the femora, left tibiotarsus, right tarsometatarsus, and humeri of a single individual. Two additional femora and a tibiotarsus from the same locality were also referred to this species. Scarlett (1970a) repeatedly noted that *G. hartreei* was difficult to distinguish from *hodgeni*. Measurements (in mm) of the type material are as follows: femur 59.2, 53.8; tibiotarsus from cnemial crest 75.1, tarsometatarsus 41.7; humerus 41.7. Thus it is identical in size to *T. hodgeni* (Table 1). Likewise it is identical in form. Careful comparison of the type material of *G. hartreei* with the paratypes of *T. hodgeni* failed to disclose any differences between the two that may not be attributed to intraspecific variation. The holotype tibiotarsus of *hartreei* is stouter than those of many individuals of *hodgeni* but there are examples of the latter from Pyramid Valley that are even heavier. I therefore regard *Gallirallus hartreei* as synonymous with *Gallinula* (*Tribonyx*) *hodgeni*. The synonymy of *hodgeni* is then as follows:

Rallus hodgeni Scarlett, 1955b, p. 265
Pyramida [*hodgeni*]: Oliver, 1955, p. 595
Pyramidia hodgeni: Oliver, 1955, p. 596 (lapsus)
Capellirallus hodgeni: Scarlett, 1970a, p. 71; 1970b, p. 304
Capellirallus lodgeni: Scarlett, 1970b, p. 306 (lapsus)
Gallirallus hodgeni: Scarlett, 1970a, p. 71 (lapsus)
Gallirallus hartreei Scarlett, 1970a, p. 68
Pyramidula [*hodgeni*] C. A. F[leming] 1975, p. 90 (lapsus)

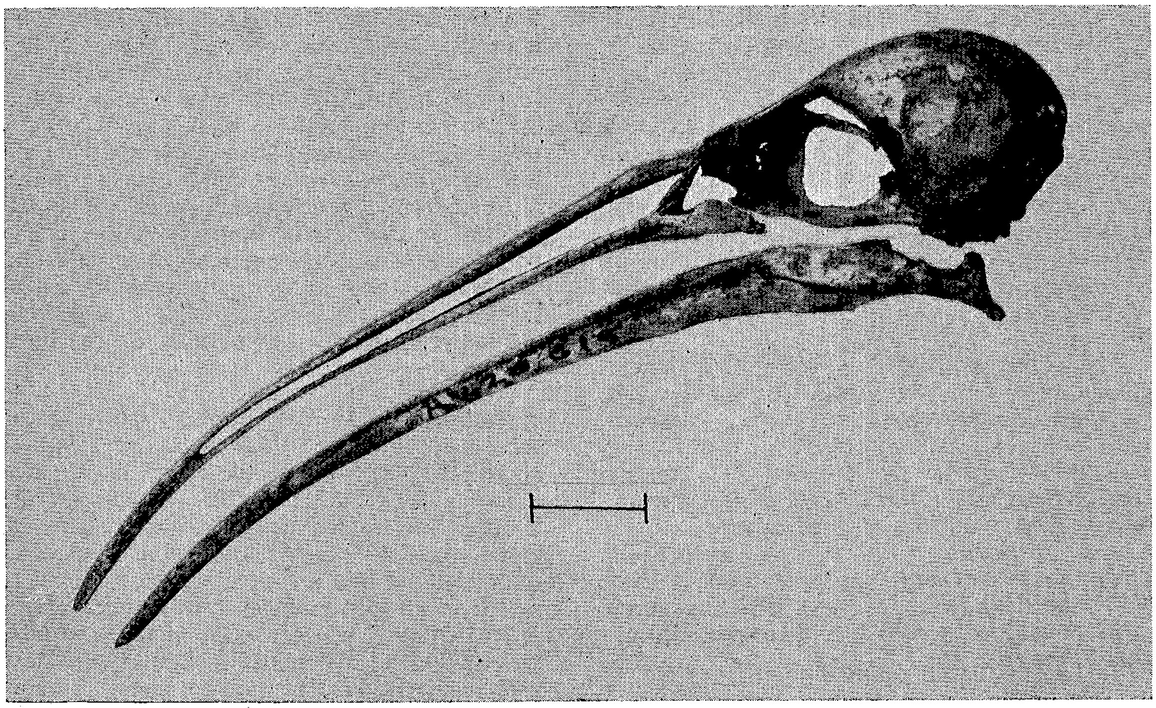

Fig. 3. Skull and mandible of *Capellirallus karamu* (CM Av 20615). Scale = 10 mm. Some of the droop in the tip of the bill is due to warping.

Gallinula (*Tribonyx*) *hodgeni:* Olson, this paper.

There is nothing in the structure of *T. hodgeni* that will allow it to be separated from *Tribonyx* at the generic level. The species undoubtedly evolved from a volant *Tribonyx* ancestor that colonized New Zealand from Australia. It is interesting to note that *T. ventralis* has reached New Zealand on more than one occasion in recent times (Kinsky 1970). Although flightless insular species of rails may have their ancestors in existing volant mainland species (Olson 1973a), there are grounds for believing that *T. ventralis* is not directly ancestral to *T. hodgeni*. It is now known that *T. mortierii* also occurred on the mainland of Australia in the Quaternary (Olson 1975) and probably evolved there. Consequently it is not a direct Tasmanian derivative of *ventralis* as it might previously have appeared to be. In the greater reduction of the pectoral apparatus and modified hindlimb proportions, *hodgeni* is even more divergent from *ventralis* than is *mortierii*. Furthermore, the skull characters of *hodgeni* are more like those of *mortierii* than *ventralis*. This suggests that *hodgeni* may have been derived from an ancestor closer to the parental stock that gave rise to both *ventralis* and *mortierii*, rather than being a direct descendent of *ventralis*.

THE NEW ZEALAND SNIPE-RAIL,

Capellirallus karamu, FALLA, 1954

Falla (1954) founded a new genus and species, *Capellirallus karamu,* for a highly distinctive, very long-billed rail from cave deposits in the North Island. His original material included no bones of the wing or pectoral girdle but he suggested that the bird was probably

Tables 2-4 (opposite)

Table 2. Hindlimb elements of three species of *Tribonyx* expressed as percent of total hindlimb length.

Table 3. Size comparison (in mm) of North and South Island populations of *Tribonyx hodgeni.* *From cnemial crest. **From articular surface.

Table 4. Size comparison (in mm) of three forms of *Fulica.* *From cnemial crest.

2

	Femur	Tibia	Tarsus
T. ventralis	26	45	29
T. mortierii	27	44	28
T. hodgeni	33	43	24

3

	South Island				North Island			
	n	range	mean	s.d.	n	range	mean	s.d.
Humerus	2	37.1-40.5	38.8	1.70	28	32.4-43.2	40.5	2.57
Femur	11	52.1-59.3	55.8	2.21	45	54.8-63.6	58.4	2.39
Tibia*	6	73.2-79.3	75.4	2.31	19	72.9-78.8	76.0	1.66
Tibia**	10	69.2-77.9	72.3	2.39	25	70.5-76.8	74.0	1.59
Tarsus	4	39.7-42.4	41.1	1.09	46	39.1-48.0	43.0	2.10

4

	F. c. prisca				*F. c. chathamensis*				*F. atra*			
	n	range	mean	s.d.	n	range	mean	s.d.	n	range	mean	s.d.
Width pelvis	5	34.7- 38.4	35.9	1.32	21	31.7- 37.2	34.3	1.54	13	21.2- 24.7	22.6	1.11
Length femur	10	78.4- 89.8	83.2	3.57	22	77.7- 89.5	83.1	3.63	13	53.6- 60.7	56.6	2.32
Length tibia*	9	143.7-162.3	150.7	6.36	29	152.0-168.0	160.8	4.66	13	97.1-112.9	104.0	4.40
Length tarsus	7	82.1- 95.9	88.9	3.83	28	88.1-102.8	93.6	4.05	13	54.6- 63.8	59.0	2.49
Length coracoid	4	43.6- 45.2	44.6	.59	16	43.0- 48.8	45.2	1.81	13	32.8- 38.3	35.7	1.73
Depth carina	4	20.3- 21.0	20.7	.27	12	20.2- 22.1	21.0	.64	12	19.8- 23.3	21.5	1.10
Length humerus	7	87.1- 98.3	90.7	3.64	19	90.5- 99.7	94.9	3.05	13	71.0- 80.7	76.5	2.92
Length ulna	--	-----------	-----	----	16	74.3- 81.9	78.4	2.46	13	63.5- 73.0	67.9	2.76
Length carpus	--	-----------	-----	----	12	47.1- 52.3	49.5	1.72	13	39.1- 45.0	42.1	1.87
Width cranium	--	-----------	-----	----	18	25.4- 28.4	27.2	.97	12	21.2- 23.5	22.4	.93

flightless and this was later confirmed by Scarlett (1970b) who described these elements and also noted a number of new localities for the species (the femur CM Av 20,878 from Tom Bowling Bay, Northland, however, is too large and stout to be from *C. karamu* and must pertain to some other rail). In most deposits *C. karamu* is less common than *Tribonyx hodgeni* and it has not yet been found in the South Island.

In its cranial morphology, *Capellirallus* is one of the most specialized and peculiar of the Rallidae. For its size it has the longest bill of any rail (Figs 2 and 3). The bill is angled markedly downward and is flexible, with a blunt flattened tip equipped with sensory pits. The bird was evidently highly adapted for probing; Falla's allusion in the generic name to its being snipe-like is apt. The braincase is distinctly broad, flattened, and rounded posteriorly (Fig. 2), and the naso-frontal area has a strong downward slope (Fig. 3) probably correlated with the steep angle of the bill.

The specialized structure of *Capellirallus* tends to obscure its possible relationships. However, a tendency towards a long, slender, down-angled bill and sloping cranium is expressed in the extinct flightless rail *Gallirallus* (*"Cabalus"*) *modestus* (Hutton) of the Chatham Islands. While it is certain that *G. modestus* and *Capellirallus* were derived independently, it seems possible that *Capellirallus* may have evolved earlier from a *Gallirallus* (*sensu lato*) ancestor and proceeded even further along the same lines as taken later by *"Cabalus"*. The wing and pectoral elements of *Capellirallus* are too modified to permit useful comparison with other taxa, but the pelvis and hindlimb are quite similar to those of *Gallirallus;* the tarsometatarsus in particular is a near duplicate of that of the extant New Zealand Weka, *G. australis* (Sparrman), although on a smaller scale.

The following brief descriptions will augment those of Falla (1954) and Scarlett (1970b) and will aid those identifying New Zealand avian subfossils in separating *C. karamu* from *Tribonyx hodgeni.*

No one could confuse the bills of *C. karamu* and *T. hodgeni.* The cranium of *T. hodgeni* is not flattened and sloped in the peculiar manner of *C. karamu,* but is higher and narrower, the scars for the attachment of M. pseudotemporalis superficialis on the posterior wall of the orbit are smaller and extend farther dorsally on the external side, and the interorbital bridge is wider.

The wing and pectoral girdle of *Capellirallus* (Figs 4 and 5) are so much more reduced than in *T. hodgeni* that these elements of the two species may be distinguished on size alone (Table 1). There is probably no other rail with such small wing elements for its size. The humerus (Fig. 4) has a peculiar shape—wide at the proximal end and greatly reduced distally. The head is even with or lower than the internal tuberosity. The ulna and carpometacarpus (Fig. 4) are minute, the latter with its proximal end disproportionately large. The coracoid (Fig. 5) of *C. karamu* is smaller than in *T. hodgeni* and of an entirely different shape, with a large head, very slender shaft, and the sternal end not expanded, lacking the sternocoracoidal process.

The sternum in *Capellirallus* (Fig. 5) is flattened and virtually without a keel, the carina being only a slight ridge beginning at about the level of the posteriormost costal facet. It differs further from *T. hodgeni,* which has a better-developed carina, in having a broad U-shaped notch between the coracoidal sulci. There appears to be considerable individual variation in the sternum of *C. karamu.* The sternum that Scarlett (1970b) depicted as that of *T. hodgeni* is actually that of a large individual of *C. karamu* and his illustration thus gives some idea of the amount of variation to be expected within this species.

The pelvis of *C. karamu* (Fig. 6) is smaller than in *T. hodgeni* and has the anterior ilium fused along most of its dorsal margin to the dorsal median ridge of the sacrum, unlike *T. hodgeni.* The ilio-ischiatic fenestra of *C. karamu* is smaller, shaped differently, and has its long axis at a different angle from that of *T. hodgeni.*

There is virtually no overlap in the measurements of the femur and tibiotarsus between *C. karamu* and *T. hodgeni,* these elements being larger in the latter species (Table 1). The shaft of the femur in *C. karamu* is more slender and the distal end is larger relative to the shaft (Fig. 7). The tibiotarsus (Fig. 7) is somewhat

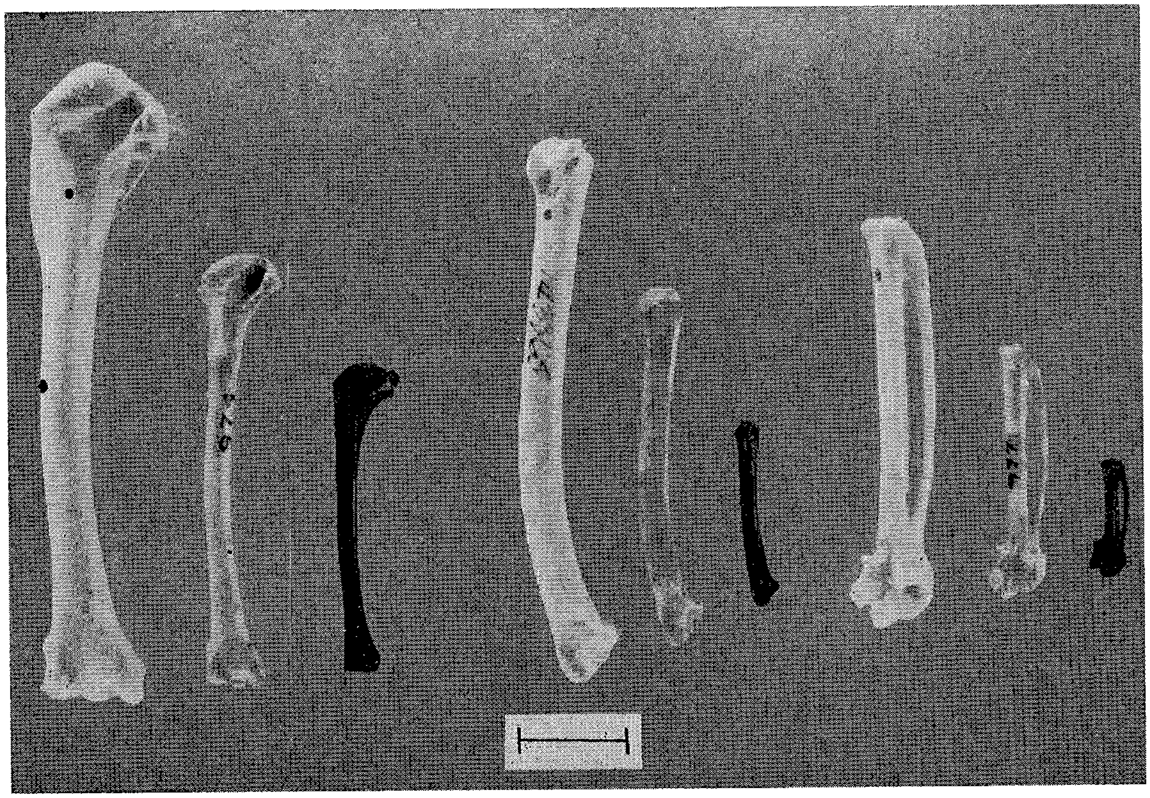

Fig. 4. Humeri, ulnae, and carpometacarpi. *Tribonyx ventralis* (MVZ 143365) is on the left in each group, *T. hodgeni* (NMNZ S 974; S 975; S 977) is in the middle, and *Capellirallus karamu* (CM Av 20615) is on the right. Scale = 10 mm.

more slender in *C. karamu* but could be difficult to separate from *T. hodgeni* if fragmentary. Generally, in proximal view the internal articular surface is more prominent and extends further anteriorly in *T. hodgeni* than in *C. karamu*.

The tarsometatarsi of the two species (Fig. 7) are difficult to distinguish because the measurements of *C. karamu* fall entirely within the lower range of *T. hodgeni* (Table 1). This apparently results from *Capellirallus* having an unusually large, heavy tarsometatarsus relative to the rest of the hindlimb. *T. hodgeni* may be distinguished from *C. karamu* by the more curved and sculptured shaft, the more prominent scar for the hallux, the more excavated internal side of the hypotarsus, and the lower, smaller, and in posterior view, more circular distal foramen. When the hypotarsus is intact, the internal canal is usually closed in *T. hodgeni* and open in *C. karamu*.

THE STATUS OF THE SUBFOSSIL COOTS OF NEW ZEALAND AND THE CHATHAM ISLANDS

Two very large subfossil coots have been named from the New Zealand region, the generic and specific status of which has remained unclear up to the present. In dune deposits on Chatham Island, H. O. Forbes (1892c) found a number of remains of coots. He originally believed that two species were represented, the smaller of which he considered identical with the extinct subfossil species *Fulica newtonii* Milne-Edwards of Mauritius, and the larger of which he named *Fulica chathamensis*. In a later report (1893b) he decided that there was only one species in the Chatham material and that it was identical to *F. newtonii*. For this far-flung "species" he created the genus *Palaeolimnas*, with *newtonii* as the type and only species. This genus, however, was based mainly on the skull characters of the Chatham birds. Milne-Edwards (1896) showed that *newtonii* was distinct from the Chatham

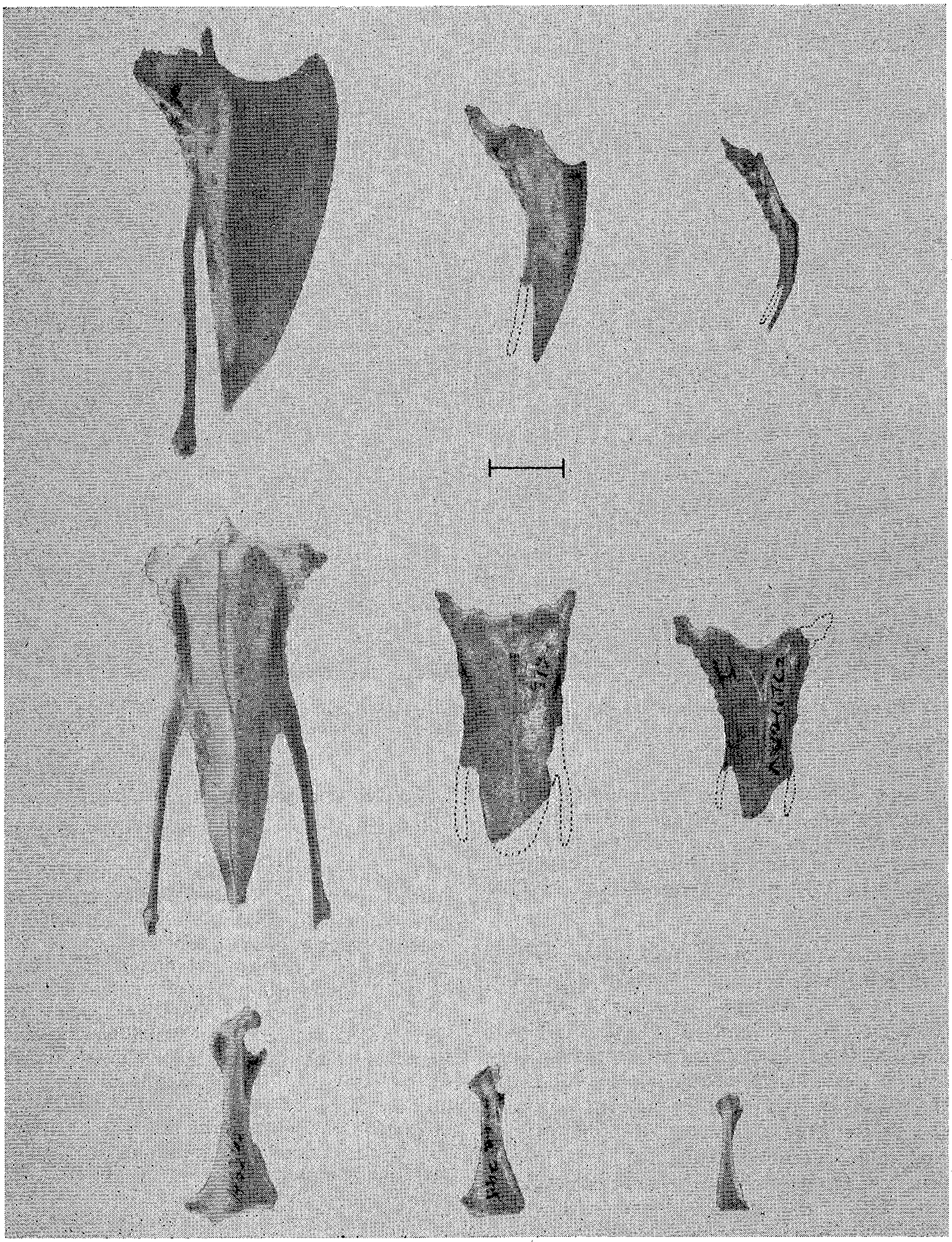

Fig. 5. Top to bottom: lateral view of sternum, ventral view of sternum, ventral view of coracoid. Left, *Tribonyx ventralis* (MVZ 143365); middle, *T. hodgeni* (NMNZ S 973; CM Av 22245); right, *Capellirallus karamu* (CM Av 21763; Av 21764). Scale = 10 mm.

birds and resurrected the name *chathamensis* for the latter, while maintaining both species in *Palaeolimnas.* Andrews (1896b) provided detailed descriptions and additional illustrations of *chathamensis.*

Meanwhile, Hamilton (1893) had discovered remains of a very large coot in cave deposits at Castle Rocks on the Oreti River in the South Island. He provisionally named it *Fulica prisca,* believing that it would "be convenient to have a name for this species" in the event it should prove separable from the Chatham and Mauritius coots. He did not compare it with either of those forms, however. Rothschild (1907) said that *prisca* differed from *chathamensis* in being volant but he did not state his evidence for this and it is not clear upon what material this opinion was based. Scarlett (1955a) reported that bones of *prisca* from Pyramid Valley were identical to *chathamensis* and relegated *prisca* to synonymy, as did Oliver (1955).

The most recent assessment of the New Zealand coots is that of Brodkorb and Dawson (1962). Believing that Andrews (1896b) had "demonstrated that the Chatham coot differs from *Palaeolimnas newtoni,* and from *Fulica,* in every major element of the skeleton, even to the ribs," they proposed a new genus, *Nesophalaris,* with *chathamensis* as the type, leaving *newtonii* as the only species in the genus *Palaeolimnas.* They also considered the claim that *F. prisca* was inseparable from *chathamensis* to be undocumented and maintained *prisca* as a separate species in *Nesophalaris.*

Typical *chathamensis* is known only from Chatham Island. Forbes's type series is in the British Museum (Natural History) (Dawson 1958) and there is abundant material of the species in New Zealand museums and elsewhere. On the mainland, *prisca* has been recorded from at least 16 localities in the South Island (Brodkorb and Dawson 1962, Trotter 1965) and one in the North Island (Dawson 1962).

Hamilton's syntypes of *prisca* are in the National Museum of New Zealand. They all carry the letters CR (= Castle Rocks) and are registered as DM (now replaced by NMNZ) 379. In addition, each bone in the series has an individual Hamilton catalogue number within the sequence 350-447, written as the numerator in a fractional notation above the number 29

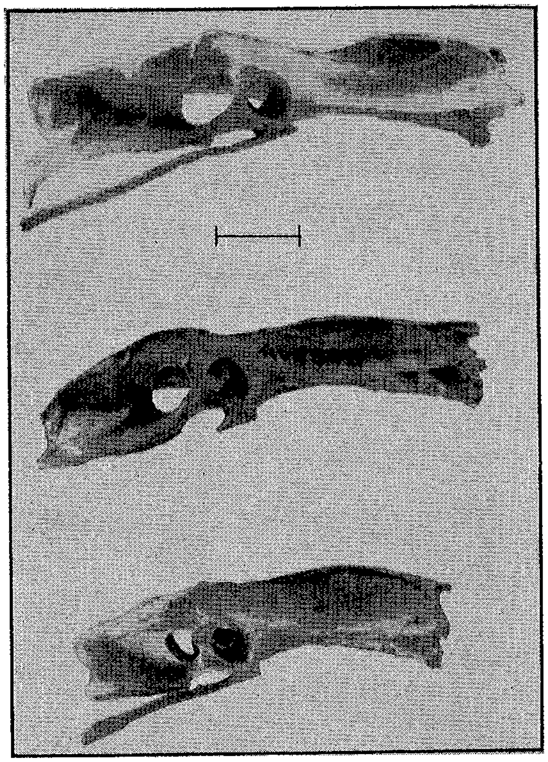

Fig. 6. Top to bottom: lateral view of pelvis of *Tribonyx ventralis* (MVZ 143365), *T. hodgeni* (CM Av 5803), and *Capellirallus karamu* (CM Av 21764). Scale = 10 mm.

as the denominator (believed to be the Hamilton locality number for the Castle Rocks site). With these syntypes is a handwritten list, apparently Hamilton's, of the specimens used in the description of *F. prisca.* If no errors were made in numbering the bones, it would seem that several bones are missing from the series—2 femora, 3 humeri, 3 coracoids, a cranium, a furcula, a pelvis, between 2 and 5 tarsometatarsi, and 2 to 5 tibiotarsi. Remaining are 8 left and 4 right femora, 10 left and 9 right tibotarsi, 9 left and 8 right tarsometatarsi, 6 left and 8 right humeri, 3 left and 2 right coracoids, 5 sterna, 5 pelves, 3 clavicles, 2 vertebrae, 4 crania, 1 rostrum, and 3 mandibles. In this series, humerus 421/29 is from the extinct duck *Euryanas finschi* and humerus 417/29 is from the Laughing Owl *Sceloglaux albifacies.* Since the type series includes more than one species and since part of this series is evidently missing, I designate the right humerus with the Hamilton number 411/29 (re-registered as NMNZ S. 990) as lectotype of *Fulica*

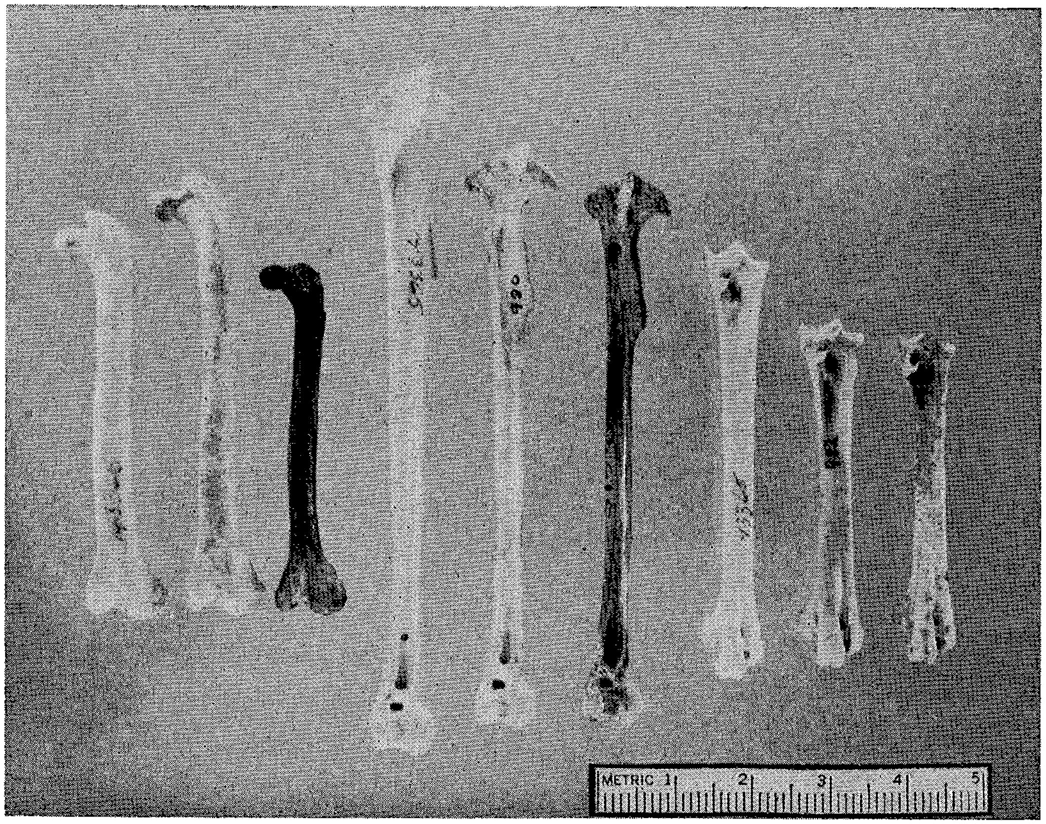

Fig. 7. Femora, tibiotarsi, tarsometatarsi. *Tribonyx ventralis* (MVZ 143365) is on the left in each group, *T. hodgeni* (NMNZ S 985; S 980; S 982) is in the middle, and *Capellirallus karamu* (CM Av 20615; Av 20615; Av 20650) is on the right.

prisca (Fig. 8). Its measurements (in mm) are: length 96.8, proximal width 20.2, shaft width 6.0, distal width 13.6.

No characters are given by Brodkorb and Dawson (1962) for the genus *Nesophalaris;* they merely cited the fact that Andrews (1896b) pointed out differences between *chathamensis* and other species of *Fulica,* including *"Palaeolimnas" newtonii.* They do not suggest which of these differences are to be considered of generic value and which of only specific value. A careful reading of Andrew's paper reveals that although differences are noted, nearly every element of *chathamensis* is described as being "very similar to" or "very like" *Fulica* or "differing only in unimportant details."

In my view, none of the characters of *chathamensis* or *prisca,* or of *Palaeolimnas* for that matter, will allow these forms to be separated generically from *Fulica.* They differ from the living Old World Coot *Fulica atra* Linnaeus in their much greater size (Table 4) and in modifications for flightlessness—neither of which is of generic significance. The skull characters (see below) are highly variable between individuals of the same population, and are likewise of no significance at the generic level. On the other hand, modifications such as the distinctively narrowed pelvis and the shape of the humerus are specializations typical of *Fulica* (Olson 1973b). It is obvious that *chathamensis* and *prisca* are but large flightless forms of *Fulica.* They are here returned to that genus, *Nesophalaris* being considered a synonym.

In Table 4 the dimensions of specimens of *chathamensis* in the National Museum of New Zealand (NMNZ 384, 385) and the Canterbury Museum are compared with Hamilton's type series of *prisca.* Apart from a tendency for smaller tibiae and tarsi in the small sample of *prisca,* the two forms are virtually identical in size, and overlap is nearly complete. Additional measurements of specimens of *chathamensis* in the British Museum (Natural History) are given in Cracraft (1973) and average somewhat smaller than those in Table 4, thus being even closer to *prisca.* The two forms clearly cannot be separated on the basis of size. The depth of the carina in *chathamensis* and *prisca* is identical, and since this measurement is also the same as in the volant species *Fulica atra,* which is otherwise much smaller (Table 4), it is almost certain that both of the fossil forms were flightless (*contra* Rothschild 1907).

In some skulls of *chathamensis,* the supraorbital impressions are very large, while in others they are poorly developed (Andrews 1896b). These impressions accommodate salt-excreting glands, the hypertrophy of which in some individuals of *chathamensis* is an indication that the population was adapting to the salt stress imposed on them by living in the lagoons of Chatham Island. Two of the paralectotypic crania of *prisca* (Hamilton Nos 441, 443) are peculiarly domed posteriorly (Fig. 8). One of these is of a juvenile and it may be that this abnormal shape is the result of retention of the shape of the juvenile or embryonic cranium. Some individuals of *chathamensis* also exhibit a tendency towards this domed shape, but not as pronounced. The individual variation in the skulls of *prisca* and *chathamensis* is too great to permit one to distinguish even racial differences between the two forms.

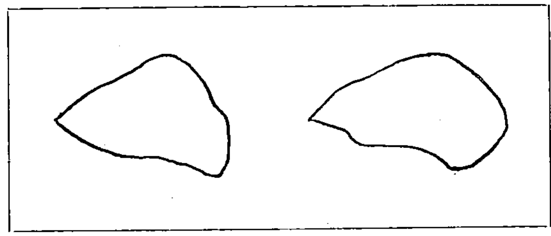

Fig. 8. Diagrammatic outlines of abnormal domed cranium (left) and normal cranium (right) of *Fulica chathamensis prisca.*

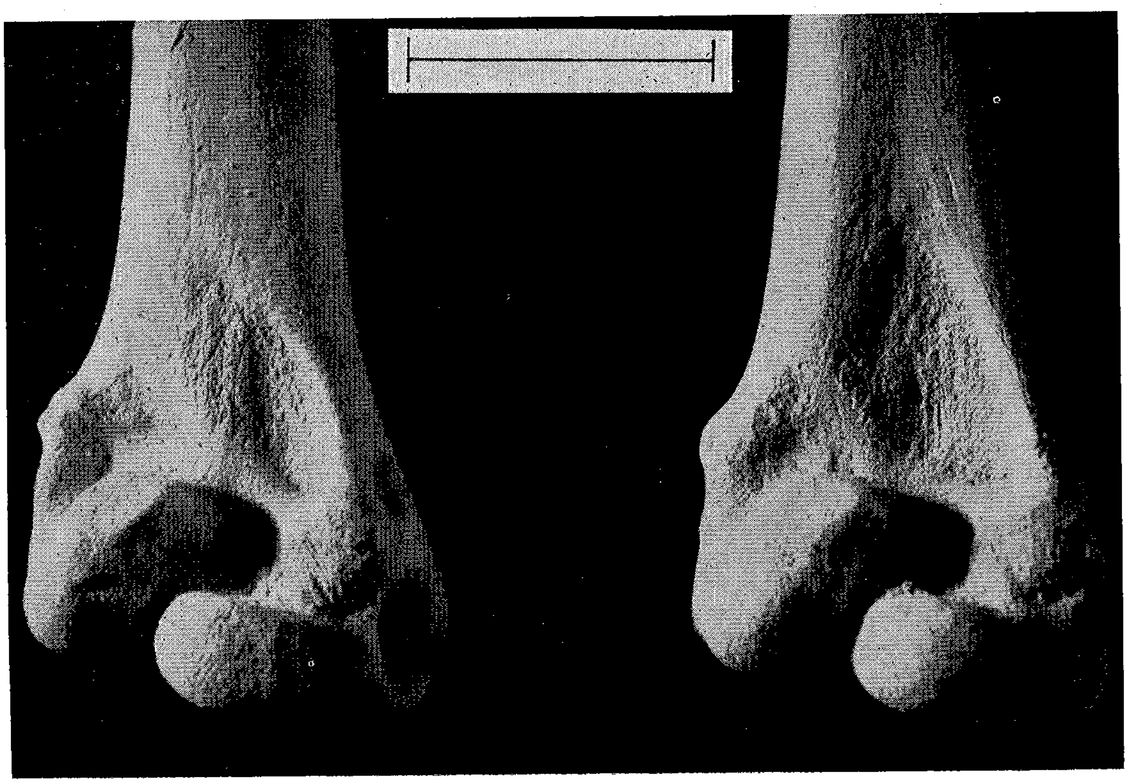

Fig. 9. Palmar view of distal end of right humerus. Left, *Fulica chathamensis prisca* (Lectotype NMNZ S. 990, Hamilton No. 411/29); right, *Fulica chathamensis chathamensis* (NMNZ 384). Scale = 10 mm.

I find one consistent difference, however, between *prisca* and *chathamensis*, and it is likely that there are others that I have overlooked. In *chathamensis* the brachial depression of the humerus is always much deeper and more extensive than in *prisca* (Fig. 9). All humeri may be separated and identified on this basis. I therefore recommend that the two forms be given subspecific status. The Chatham bird thus becomes *Fulica chathamensis chathamensis* Forbes and the New Zealand bird becomes *Fulica chathamensis prisca* Hamilton.

It is highly unlikely that *F. c. chathamensis* arrived at Chatham Island by any method other than flying. Thus it must have been derived from *prisca* stock before the latter became flightless. The two populations necessarily evolved their flightless conditions independently. Considering this, it is remarkable that they are so similar. The situation somewhat parallels that of *Gallinula nesiotis* Sclater and *G. comeri* (Allen), the two nearly identical flightless gallinules of Tristan da Cunha and Gough Island, respectively, in the Atlantic (Olson 1973a), and is a further indication of the ease and rapidity with which flightlessness evolves.

The species *F. chathamensis* probably evolved from *F. atra* stock that colonized New Zealand from Australia. It is interesting that since the extinction of *F. c. prisca,* New Zealand has been recolonized by *F. atra,* the first proven breeding occurring in 1958 (Kinsky 1970).

Remarks on the Extinct Rails of the Chatham Islands

In addition to *Fulica chathamensis,* there were at least three other species of endemic rails inhabiting the Chatham Islands. Two of these, *Gallirallus* (*"Nesolimnas"*) *dieffenbachii* (Gray) and *G.* (*"Cabalus"*) *modestus* (Hutton), although now extinct, survived until the arrival of Europeans and are known from skins as well as subfossil remains. I reviewed some of the literature and history of these two species, which I included in the genus *Gallirallus* (Olson 1973b), and concluded that no substantial evidence had been presented to document their sympatry—*dieffenbachii* being definitely known only from Chatham Island itself and *modestus* only from the islet of Mangare, but possibly from Pitt Island as well. Although this conclusion was perhaps justified on the basis of the evidence then at hand, it appears now that it was not correct. At the time, I was unaware of the great disparity in size of the two species—*dieffenbachii* being much larger. This size difference would be a factor favouring their coexistence.

In the Canterbury Museum there is an anterior end of a mandible (Av. 27,507) from dune deposits on Chatham Island that appears to be of *modestus,* as it is rather small and slender. If *modestus* occurred on Chatham it was certainly much less numerous than *dieffenbachii,* as the latter is very abundant in the extensive collections of subfossil material from that island.

Falla (1960) reported on a small collection of bird bones in the National Museum from Pitt Island, of which Mangare, the known home of *modestus,* is but a small satellite. One rail with a maxilla length of 38 mm and a tibia length of 79 mm was identified as *Gallirallus minor,* a highly unlikely occurence. Bones of a second rail (not now available) were said to be "much smaller" than the first species "but the same shape," and their size "fell within the range accorded to *R. dieffenbachii.*" However, the dimensions of the larger specimens exactly match those of some subfossil specimens of *dieffenbachii* from Chatham Island. Furthermore, in the NMNZ I examined a small lot of unregistered bird remains from Pitt Island containing six bones that are inseparable from those of *dieffenbachii* (S. 1005-1010). No bones in this lot appear to be referable to *modestus.* Whether the smaller bones from Pitt reported by Falla are also from *dieffenbachii,* which the abundant Chatham remains indicate was quite variable in size, or from *modestus,* has yet to be determined, but it seems unlikely that *modestus* would have been absent from Pitt.

While the evidence for the actual sympatry of *dieffenbachii* and *modestus* is still rather tenuous, it is now clear that the former was present on Pitt Island as well as Chatham Island. It might be suggested that *dieffenbachii,* which was the least modified of the two species and obviously the more recent arrival on the Chatham Islands, may have been in competition with the smaller and more specialized *modestus* and had all but replaced it except on the islet of Mangare.

The most distinctive rail of the Chatham Islands was *Diaphorapteryx hawkinsi* (Forbes), a very large, heavy, flightless species first described from deposits on Chatham Island by H. O. Forbes (1892a), who placed it in the Mascarene genus *Aphanapteryx*. For his new species he shortly thereafter created the genus *Diaphorapteryx* (1892d), which he just as quickly rejected to return to *Aphanapteryx* (1893a). The flurry of closely spaced communications from Forbes tends to obscure the original citations for both the species and the genus, neither appearing correctly in Brodkorb (1967). The original description of *Aphanapteryx hawkinsi* is a one sentence telegram published in *Nature* (Forbes 1892a) and is not either of two subsequent notes (Forbes 1892b, 1892c). Brodkorb (1967) erroneously lists a skeleton as the type, but the original description was based on a skull only. Although not mentioned by Dawson (1958), there is a series of skulls of *Diaphorapteryx* in the Forbes collection at the British Museum (Natural History) (Dawson, pers. comm.). Presumably this series contains the type, although it may not now be identifiable as such. Forbes's original description of the genus *Diaphorapteryx* is that in the *Bulletin of the British Ornithologists' Club* (1892d) and not the verbatim reprint in *Ibis* (1893 Ser. 6, 5:253-254).

Diaphorapteryx resembles *Aphanapteryx* mainly in the superficial similarity of the pointed decurved bill. There are a number of striking differences between the two genera, the most noticeable of which is in the tarsometatarsus, which in *Diaphorapteryx* is very short and stout, while in *Aphanapteryx* it is long and slender. Other differences were detailed by Andrews (1896a), who concluded that the two genera had evolved quite independently of each other. Concerning the origin and relationships of *Diaphorapteryx* it is appropriate to turn to the same author's remarks (Andrews 1896a:84), which, particularly considering the period when they were written, can hardly be improved upon: "In the case of *Diaphorapteryx* this ancestor was most likely some widespread form such as [*Gallirallus philippensis*] is at the present day, individuals of which from time to time reach New Zealand, Lord Howe Island, and the Chatham Islands . . . The modified descendants of these birds are now referred to the genera *Diaphorapteryx, Cabalus,* and *Ocydromus,* the most highly modified forms being the outcome of earlier, the less altered of later colonizations." In this regard it may be noted that an approach to the bill shape and deep temporal fossae of *Diaphorapteryx* is seen in the much smaller living species *Gallirallus sylvestris* (Sclater) of Lord Howe Island.

It appears that in the New Zealand region there has been a diverse radiation of rails of a *Gallirallus* stock that has given rise to *Gallirallus australis, G.* (*"Nesolimnas"*) *dieffenbachii, G.* (*"Sylvestrornis"*) *sylvestris, G.* (*"Cabalus"*) *modestus* and such divergent forms as *Capellirallus* and *Diaphorapteryx*. There is as much diversity in skull morphology in this group as may be observed throughout the rest of the family Rallidae. A comparative study of the skulls of these forms would probably provide as instructive an example of morphological adaptive radiation from a common stock as can be found in any group of non-passerine birds.

ON Gallirallus minor

Our knowledge of the rail known as *Gallirallus minor* is very imperfect and will not be much improved upon here. The species was named in a provisional manner by Hamilton (1893:103) thus: "I had in the first draft of this paper proposed the name of *O.* [*cydromus*] *minor;* but I can hardly venture to inflict a fresh name without a larger series of measurements for comparison." With Hamilton's characterization of a series of bones from Castle Rocks, South Island, as being smaller and more slender than the living *Gallirallus australis,* his use of *minor* nevertheless constitutes a valid description. Hamilton's own reservations notwithstanding, the name has been perpetuated, and even though the "species" has never properly been defined or illustrated, it has still been listed from a number of fossil localities in various parts of New Zealand.

The syntypical series of *minor* as listed by Hamilton (1893) consisted of 2 pelves, 7 femora, 6 tibiotarsi, 5 tarsometatarsi, and the anterior portion of a sternum. The two pelves (NMNZ S. 987, S. 988) and the sternum (S. 989) are in the National Museum of New Zealand, together with a note to the effect that

5	n	range	mean	s.d.
Castle Rocks	56	49.3-70.8	61.1	5.61
G. a. scotti	14	50.7-60.5	56.4	3.26
G. a. australis	32	54.4-72.5	63.4	4.95
G. a. greyi	14	57.0-70.5	62.4	4.29

Table 5. Tarsal measurements (in mm) of bones of South Island subfossil *Gallirallus* compared with measurements obtained from skins of modern *G. australis*.

they are part of Hamilton's type material and that the remainder of the series is missing.

In handling subfossil material of flightless *Gallirallus* from New Zealand, one does find specimens that are smaller and more delicate than in any available modern skeletons of *G. australis*. This may in part be due to a lack of adequate series of recent skeletons. There is considerable individual, sexual, and geographic variation in the size of *G. australis*. Birds from Stewart Island (*G. a. scotti*), for instance, are smaller than those from the mainland. Hamilton (1893) gives a tarsus length of 53 mm for *minor*, which is within the range of variation of *G. a. scotti* and very nearly within the lower limits of *G. a. australis* and *G. a. greyi* (Table 5). In the NMNZ there is an unregistered series of 56 subfossil tarsometatarsi of *Gallirallus* from various localities in the South Island. Some of these specimens are smaller than modern *G. australis*. Four are even smaller than the "syntype" tarsus measurement of *G. minor* given by Hamilton (1893). Yet together, this series averages the same size as modern *G. australis* (Table 5). When plotted, the measurements appear to fall into two groups, but this is probably due to sexual dimorphism because the dividing line between them is well within the size range of modern *australis* and there is no point where the smaller individuals of the size of "*minor*" can be separated from the larger ones.

It is possible that the former populations of *Gallirallus australis* may have included a greater range of size variation and more smaller individuals than do the modern populations. Introduced predators might then have selected against the smaller individuals, thus eliminating the lower ranges of size variation within the species and leaving the larger forms known today as *Gallirallus australis*. I find it difficult to believe that at one time there were two nearly identical species of *Gallirallus* in New Zealand that differed so little in size. It will be necessary to undertake a detailed study of individual and geographic variation in the subfossil forms before the actual status of *G. minor* can be determined. Until this is done, the validity of *minor* can be neither justified nor completely denied, but I am highly sceptical that it will prove to be an entity entirely distinct from *G. australis*.

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