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BIRDS OF A FEATHER

edited by

Atholl Anderson

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A DECEPTIVE TERRESTRIAL VERTEBRATE FOSSIL SITE
ON THE WAIPARA RIVER, NORTH CANTERBURY, NEW ZEALAND.

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Introduction

As students from the University of Canterbury, Christchurch, two of us (PG in 1972, RF in 1973) unbeknown to each other, found a few fossil bones near the Horseshoe (Fig. 2.1) in the lower Waipara Gorge, North Canterbury, New Zealand. In April 1974, the bone-producing deposit, a lens, was located. The nature of the lithology of the lens was such that, even after it had been located by use of the underwater sieving technique described by McKenna (1965), examination of the excavated surface showed no evidence of bone. Only after the matrix was sieved was bone noticeable.

Mimiomoko Pocket, the name given to the fossil deposit, was located on the south or right bank of the Waipara River near the Horseshoe (Fig. 2.1) at 43° 06' 30" S., 172° 46' 27" E., grid reference S68/137074, New Zealand Mapping Service (N.Z.M.S.) 1, Sheet S68 and S69, Amberley and Motunau, 3rd ed., 1 Oct. 1964, reprint 1970; metric grid reference N34:917887, N.Z.M.S. 260 (1975). It was about 12 metres above river level. The word "Mimiomoko", the Maori name for a nearby hill, means "Sleeping Lizard" (Hawkins, 1957). The appellation "Pocket" is appropriate, as the productive unit was a lens of limited dimensions 1.0 x 0.3 x 0.1 metres.

Mimiomoko Pocket occurs in an exposure of the Double Corner Shell-beds (Gregg, 1959) 18 metres below the contact with the overlying Greenwood Formation (Fig. 2.2). Gregg regarded the Double Corner Shell-beds as Waiuan in age in the framework of New Zealand Tertiary Stages (*ibid.*) (late middle Miocene, 10.5-14 million years before present [Berggren, 1972]). Owing to a fault, the upper Double Corner Shell-beds and lower part of the Greenwood Formation are repeated in the vicinity of Mimiomoko Pocket, the fossil site being on the downthrown block immediately east of the fault, which is clearly indicated in Gregg's fig. 2 (*ibid.*).

Two features in particular distinguish the productive lens from the surrounding rock: the presence of greywacke granules and bones of terrestrial animals. Only with difficulty could these traits be detected in the field. Both the productive lens and the surrounding rock are shell-rich calcareous quartzarenites with the venerid bivalve, Turia waiuensis Marwick, forming the bulk of the shells.

The New Zealand fossil record file numbers for collections from Mimiomoko Pocket are S68/f1258, S68/f1258A, and S68/f1258B.

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Published without Scarlett knowing where it would appear. Ed.

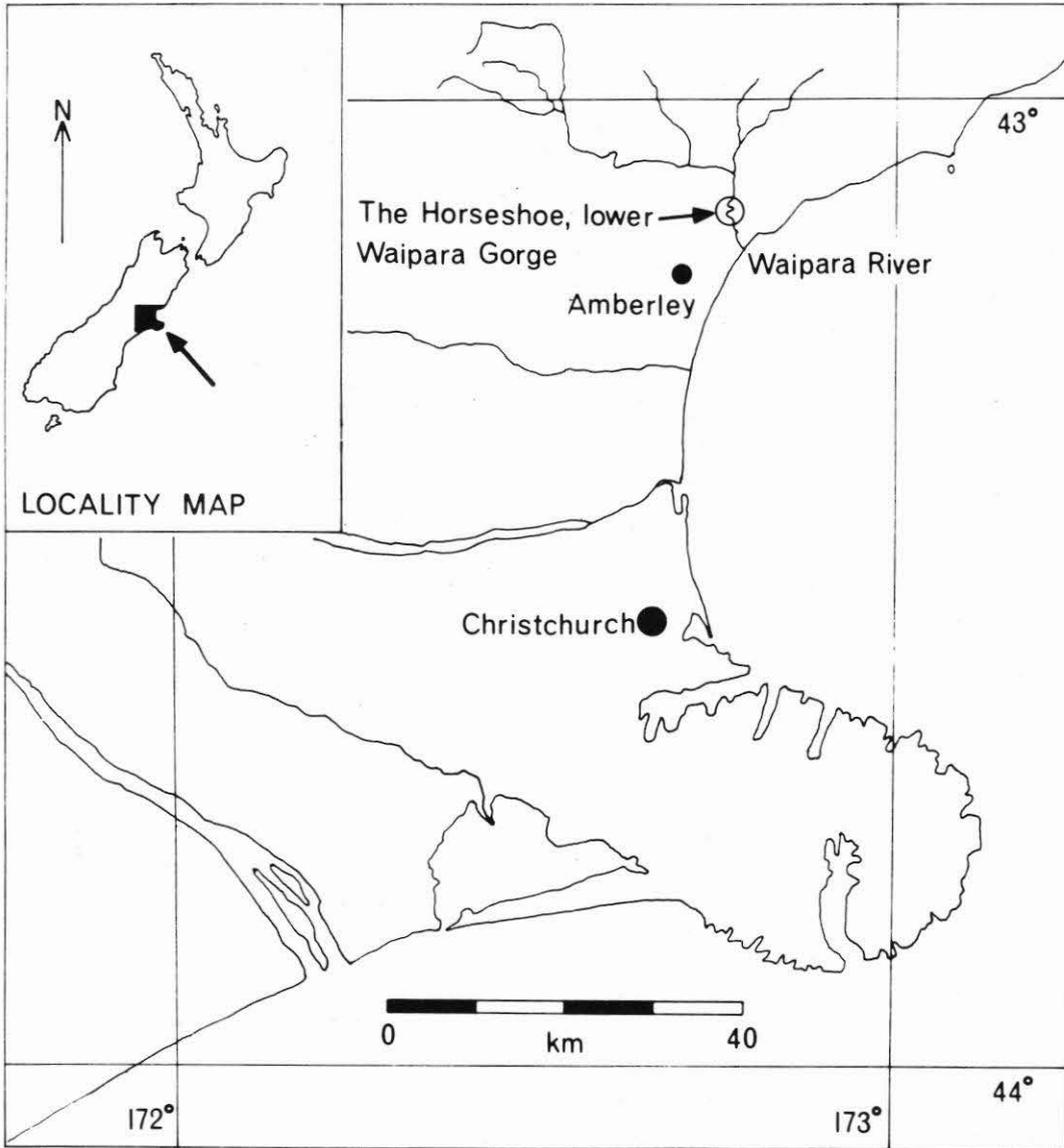


Fig. 2.1 General location of late Quaternary tetrapod site, Mimiomoko Pocket ($43^{\circ} 06' 30''$ S $172^{\circ} 46' 27''$ E).

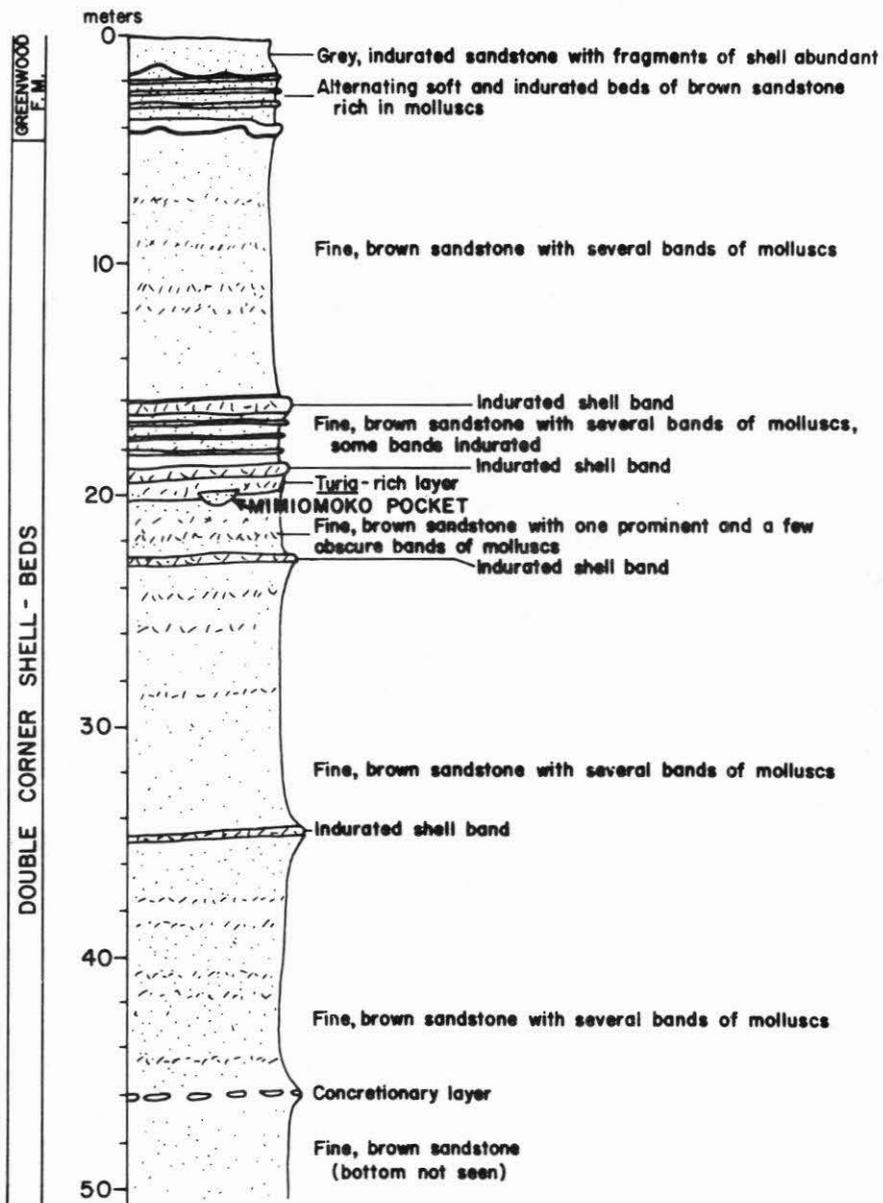


Fig. 2.2 Stratigraphic section showing position of Mimiomoko Pocket. Drawn by R. Suddarth.

Abbreviations

AV	Canterbury Museum, Christchurch, Bird Catalogue
CSIRO BS	Commonwealth Scientific and Industrial Research Organisation, Wildlife Research, Canberra
DM	National Museum of New Zealand, Wellington
NMV	Department of Ornithology, National Museum of Victoria, Melbourne
Rep	Canterbury Museum, Christchurch, Reptile Catalogue
>	greater than
‡	slightly greater than
@	approximately

Comparative Material Available

Reptilia: Osteological specimens of the following taxa were available for study. The number in parentheses after each taxon indicates the number of individuals available: Leiopelma sp. (1), Sphenodon punctatus (2), Naultinus elegans (1), Hoplodactylus duvauceli (1), and Leiopisma infrapunctatum (1).

Aves: The general avian osteological collection at the National Museum of Victoria was available, which contains at least one representative of every Australasian non-passeriform avian family except Rhynchoetidae as well as most passeriform families. More specifically, the following appropriate taxa were studied. Numbers of individuals in each taxon available are indicated in parentheses: Apterygidae: Apteryx australis (1); Procellariidae: Macronectes giganteus (3), Fulmarus glacialis (7), Thalassoica antarctica (1), Daption capense (17), Pterodroma macroptera (46), P. lessonii (30), P. brevirostris (1), P. inexpectata (2), Halobaena caerulea (32), Pachyptila vittata (2), P. salvini (26), P. desolata (51), P. belcheri (31), P. turtur (42), Procellaria cinerea (2), P. aequinoctialis (1), Puffinus carneipes (21), P. pacificus (1), P. griseus (20), P. tenuirostris (17), P. gavia (32), P. huttoni (1), P. assimilis (3), Hydrobatidae: Oceanites oceanicus (5), Pelagodroma marina (28); Pelecanoididae: Pelecanoides urinatrix (18), P. georgicus (3); Rallidae: Capellirallus karamu (2), Diaphorapteryx hawkinsi (2), Nesolimnas dieffenbachi (1), Nesophalaris chathamensis (1), Tribonyx ventralis (6), T. mortierii (4), Porphyrio porphyrio (11), Notornis mantelli (1), Rallus philippensis (18), Porzana pusilla (1), P. fluminea (1), P. tabuensis (1), Gallirallus australis (8), Fulica atra (12); Rhynchoetidae: Rhynchoetos jubatus (1).

Classification for the reptiles follows Romer (1956), while that for the New Zealand birds follows Kinsky (1970) with modifications suggested by Olson (1975).

Age of the Assemblage

The following evidence has a bearing on the age of Mimiomoko Pocket.

1. The lens appears to be conformable within the sequence. Its dip (35° west) and strike (15°) parallels that of the immediately surrounding Double Corner Shell-beds.

2. None of the plant and invertebrate fossils found in the Pocket is exclusively a post-Waiauan form, and some, e.g. Turia waiauensis, are known to be no younger than Waiauan.
3. The present position of the Pocket relative to the nearby Waipara River, and the direction and extent of river erosion appear incompatible with emplacement of the Pocket by scouring, undercutting, or cave infilling by the river in recent times. If it is supposed that a shallow cave was formed during Quaternary time by action of the river when it was 12 metres higher than at present, it is necessary to infer that the bank has not receded a significant distance horizontally during the time of down cutting to the present level. Otherwise, the cave deposit would have been totally destroyed as the bank receded unless the original cave was quite deep. Today, no such deep caves are developed in the outcrop of the Double Corner Shell-beds where Mimiomoko Pocket was found.
4. Dr. R. J. Weston of the Chemistry Division, Department of Scientific and Industrial Research, Petone, New Zealand, carried out an analysis of three samples of tetrapod bones from Mimiomoko Pocket and one on a fragment of a vertebra of a marine mammal collected about sixteen metres on strike from the lens. The bones from Mimiomoko Pocket were rich in collagen indicating an age, "less than 10,000 years old and probably only about 1000 years old;" while in contrast, the marine mammal vertebral fragment contained no detectable collagen, a result consistent with a Waiauan age for that specimen (Weston, pers. comm.). Weston, Repenning, and Fleming (1973) described the technique of collagen analysis used.
5. The presence of small, subangular graywacke pebbles in Mimiomoko Pocket but not in the surrounding Double Corner Shell-beds suggests a sediment source for the lens not active when the Double Corner Shell-beds were deposited.
6. Tuatara, one of the most abundant tetrapods in the fauna, had disappeared from the mainland by two hundred years ago (Crook, 1975). This coupled with the absence of any tetrapods introduced by man supports a probable minimum age of two centuries for the site.

Evaluating the above evidence, unless some mechanism can be invoked to explain the preservation of collagen in the bones from Mimiomoko Pocket since the Miocene, the most likely interpretation is that the lens represents a late Quaternary deposit accumulated in a shallow cave. If this was the case, the cave was scoured out or excavated as a burrow site between resistant beds when well above river level, which resulted in the lens being inclined parallel to the surrounding Double Corner Shell-beds. This coupled with the cave being subsequently filled primarily by a matrix reworked from the immediate surroundings resulted in the apparent conformity between the lens and the Double Corner Shell-beds. In this reworked material were the marine invertebrates not known from rocks younger than the Waiauan Stage. During the time the cave was being filled tetrapods were present and greywacke pebbles entered the area of deposition; events that took place at least two centuries and possibly more than a thousand years ago.

This site was originally thought to be of Miocene age. It was the basis for a personal communication by one of us (TR) cited in Crook (1975) that the tuatara was known from Miocene deposits.

Flora and Non-Tetrapod Fauna

In the following list of taxa represented from the Mimiomoko Pocket, D. Mildenhall identified the plants; R. H. Hoskins, the foraminifera; and I. W. Keyes, the chondrichthyans.

Plants: Pyrrophyta (dinoflagellates), Eumycophyta (true fungi), Pteridophyta

Animals: Foraminiferida: Globigerina bulloides, G. ciperensis, G. falconensis, G. foliata, G. quinqueloba, G. woodi decoraperta, Entosolenia sp., Trifarina bradyi, Globocassidulina subglobosa, Cibicides sp., C. molestus, Notorotalia sp.

Annelida: Terebellidae? (agglutinated tubes, not determinable to genus)

Cirripedia: Balanus sp.

Echinoidea: Arachnoides sp., Cidaroides? (small, stubby spines)

Mollusca: Turia waiiauensis, Baryspira sp., Polinices sp.

Chordata: Chondrichthyes: Hypoprion sp., Deania sp., ?Dalatias sp., Pristiophorus lanceolatus, ?Trygon sp., Myliobatus sp.

Osteichthyes: Teleostei

Systematics of Tetrapods

Class Reptilia

Subclass Lepidosauria

Order Rhynchocephalia

Family Sphenodontidae

Sphenodon

Sphenodon punctatus

Material: Two right (Rep. 401-402) and two left (Rep. 403-404) humeri, nearly complete but lacking epiphyses. Proximal half of left humerus lacking epiphysis, Rep. 405. Right femur, nearly complete but lacking epiphysis, Rep. 406. Left tibia, nearly complete but lacking epiphysis, Rep. 407. Distal half of right fibula, lacking only epiphysis, Rep. 408. Partial left scapula and coracoid, Rep. 409. Partial right coracoid, Rep. 410. Partial left scapula, Rep. 411. Two teeth on bone fragment, Rep. 412. Centrum of anterior cervical vertebra, Rep. 413. Two centra of caudal vertebrae, Rep. 414, 415. Proximal one-third of left rib, Rep. 416. First phalanges, Rep. 417, 418. Second through fourth phalanges, Rep. 419-430. Terminal phalanx, Rep. 431.

Measurements (in millimetres):

	Length of Diaphysis or Midshaft	Minimum Diameter of Diaphysis or Midshaft		
<u>Humerii</u>				
Rep. 401	21.5	2.0		
Rep. 402	>21.9	2.8		
Rep. 403	>20.7	2.3		
Rep. 404	21.8	2.3		
Rep. 405	-	1.7		
<u>Femur</u>				
Rep. 406	35.9	2.7		
<u>Tibia</u>				
Rep. 407	23.8	2.3		
<u>Fibula</u>				
Rep. 408	-	1.3		
	Centrum Length		Dorsoventral Diameter of Centrum, Anterior End	
<u>Anterior Cervical Vertebra</u>				
Rep. 413	5.0		5.0	
<u>Caudal Vertebrae</u>				
Rep. 414	-		1.5	
Rep. 415	-		1.3	
Second to Fourth Phalanges	Length	First Phalanges	Length	
Rep. 419	4.2	Rep. 417	>7.3	
Rep. 420	>2.9	Rep. 418	>5.7	
Rep. 421	>3.1			
Rep. 422	5.0	Terminal phalanx		
Rep. 423	>4.5	Rep. 431	3.4	
Rep. 424	4.1			
Rep. 425	5.1			
Rep. 426	4.6			
Rep. 427	>4.3			
Rep. 428	>3.8			
Rep. 429	>3.5			
Rep. 430	4.6			

Diagnosis (Same as for genus, only known species): Larger than any other member of the Sphenodontidae except the genera Monjurosuchus and Anisodontosaurus (Broili, 1925; Endo, 1940; Gilmore, 1909; Hoffstetter, 1955; Welles, 1947). Distinguished from Monjurosuchus by having amphicoelous rather than opisthocelous dorsal vertebrae and broad based rather than acutely conical teeth (Endo, 1940). Distinguished from Anisodontosaurus by posterior mandibular

teeth that are asymmetrical in lateral view, the anterior side of the teeth being nearly vertical and the posterior sloping at about 45° rather than both sides sloping at about the same degree and the inclination of the sides increasing progressively anteriorly from 45° to vertical by the middle of the tooth row (Welles, 1947). Distinguished from all Cenozoic reptiles except Gekkonidae and some dorsals of Chelonia by amphicoelous vertebra perforated for passage of notochord in adult (Romer, 1956). Distinguished from amphicoelous dorsals of Chelonia by width of centrum greater than, rather than less than one-half the length. Distinguished from amphicoelous Gekkonidae by absence of paired foramina subcentralia (Hoffstetter and Gasc, 1969). Distinguished from all other Cenozoic reptiles and rhynchosauroids by the presence of an entepicondylar foramen on the humerus (Romer, 1956).

Discussion: Sphenodon punctatus is the sole surviving rhynchocephalian and structurally, one of the most primitive living reptiles. Many of the osteological features of this species are duplicated nowhere else among living reptiles but are common to entire orders of extinct ones.

No single bone of Sphenodon punctatus can be distinguished from the same element in every other reptile. Only by examining different bones known to be parts of one individual can a specimen be unequivocally diagnosed as belonging to this species. However, it is possible to distinguish isolated vertebrae and humeri of S. punctatus from all other known Cenozoic reptiles. In light of the fact that Mimiomoko Pocket is probably late Quaternary in age and certainly no older than Miocene, a more limited diagnosis from Cenozoic reptiles is useful, for it is unlikely that this material represents a late Cenozoic example of some taxon previously thought restricted to the Mesozoic or Paleozoic.

Order Squamata
Suborder Lacertilia
Infraorder Indet.

Material: Proximal ends of two right humeri, Rep. 432, 433. Distal ends of two humeri, right and left respectively, Rep. 434, 435. Tooth in right maxilla fragment, Rep. 436. Teeth in bone fragments, Rep. 437, 442. Right mandible fragment with bases of the most anterior seven teeth preserved, Rep. 438.

Discussion: The presence of epiphyses on the humeri fragments supports the assignment of these specimens to the lizards. Other than lizards, only in Sphenodon punctatus and crocodiles, plus some other rare cases, are epiphyses developed among reptiles (Romer, 1956). These specimens are much too small to be referable to either adult S. punctatus or crocodiles (see Fig. 2.3).

Infraorder Nyctisauria (Gekkota)
Family Gekkonidae
Genus et species indet.

Material: Two dorsal vertebrae, Rep. 439, 440. Caudal vertebrae, Rep. 441.

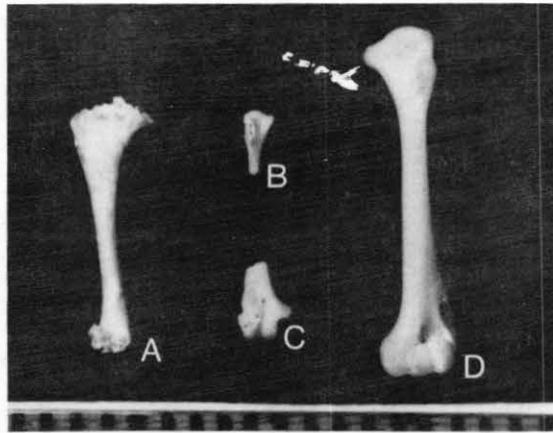


Fig. 2.3 A. Midshaft of right humerus of Hoplodactylus duvauceli, modern specimen.
 B. Proximal end of right humerus of small lizard, Mimiomoko Pocket, Rep. 432.
 C. Distal end of right humerus of small lizard, Mimiomoko Pocket, Rep. 434.
 D. Left humerus of Leiolopisma infrapunctatum, modern specimen. Scale, each division equals 1 mm.

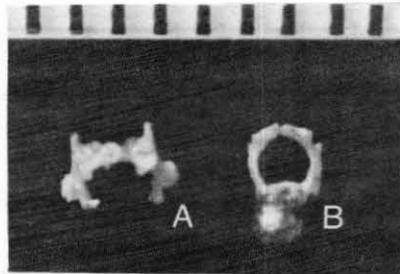


Fig. 2.4 A. Neural arch of modern specimen of Hoplodactylus duvauceli, posterior view. B. Posterior view of Gecko vertebra from Mimiomoko Pocket, Rep. 439. Neural arch of H. duvauceli figured here is from the same individual as the humerus midshaft illustrated in fig. 3A. Closeness of the neural canals in size indicates the similarity in size of the H. duvauceli specimen and the Mimiomoko Gecko figured, whereas the two limb fragments from Mimiomoko are from a much smaller adult animal than this specimen of H. duvauceli. Scale, each division equals 1 mm.

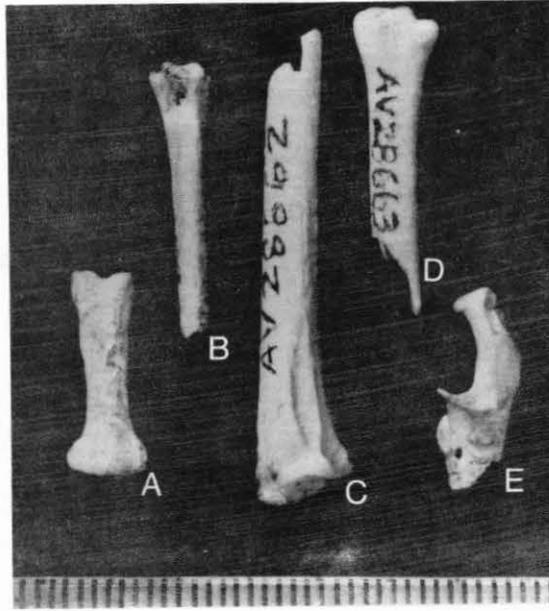


Fig. 2.5 A, cf. Apterygidae, phalanx, AV28667; Procellariidae: B, tarsometatarsus, AV28665; C, ulna (proximal) AV28662; D, ulna (distal), AV28663; and E, coracoid, AV28671. Scale, each division equals 1 mm.

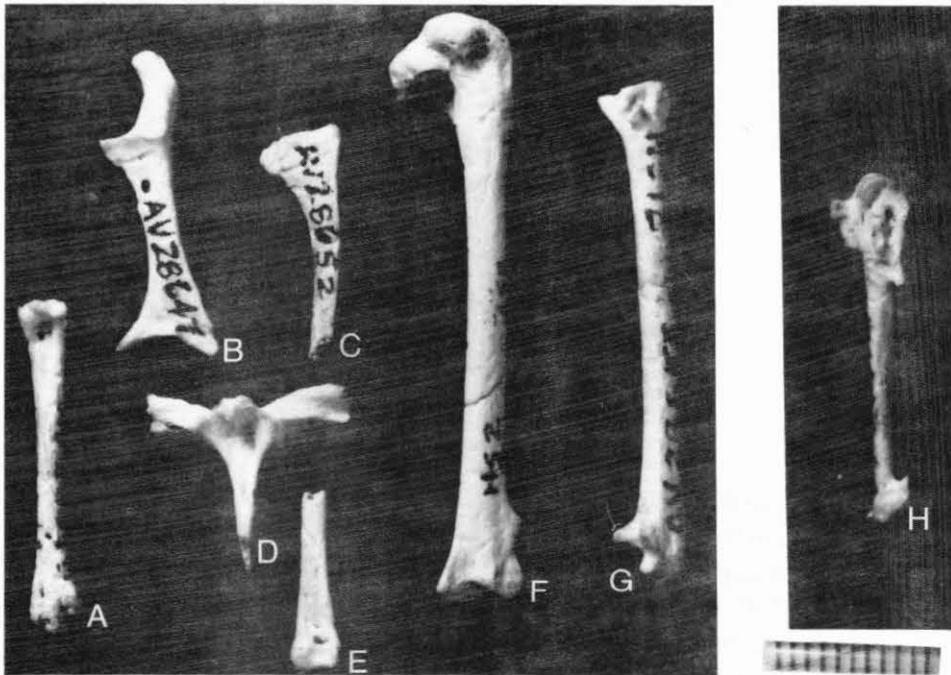


Fig. 2.6 *Pelecanoides* sp. from Mimiomoko Pocket: A, tarsometatarsus, AV28650; B, coracoid, AV28647; C, scapula, AV28652; D, sternum, AV28657; E, tibiotarsus (distal), AV28654; F, humerus AV28645; G, ulna, AV28653; and H, carpometacarpus, AV28648. Scale, each division equals 1 mm.

Measurements (in millimetres):

	Neural Canal		Centrum		Dorsoventral Diameter
	Height	Width	Length	Width	of Centrum Anterior End
Dorsal Vertebrae					
Rep. 439	1.0	1.3	1.5	0.6	0.7
Rep. 440	0.8	1.0	1.3	0.9	-
Caudal Vertebrae					
Rep. 441	-	-	1.4	1.0	0.8

Diagnosis: Many members of the family including this material distinguished from all other Cenozoic reptiles except some turtles and Sphenodon punctatus by amphicoelous vertebrae perforated for passage of notochord in adult (Romer, 1956). Distinguished from S. punctatus by presence of paired foramina subcentralia on amphicoelous forms (Hoffstetter and Gasc, 1969). Distinguished from amphicoelous dorsals of Chelonia by width of centrum greater than rather less than one-half the length.

Discussion: The lizard humeri mentioned previously are much too small to be conspecific with these gecko vertebrae. Owing to their fragmentary nature, it has not been possible to give meaningful measurements of these humeri. But comparison with a complete humerus of a modern skink (Leiolopisma infra-punctatus) together with a midshaft of a gecko (Hoplodactylus duvauceli) indicates how small the fossils are, probably no more than half the length of the modern specimens before being broken (see Fig. 2.3). The largest dorsal vertebrae associated with the modern gecko humerus figured here were only slightly larger than the Mimiomoko Pocket dorsal vertebrae (see Fig. 2.4). Because the epiphyses are fused to the diaphyses on the fossil humeri, they presumably belonged to adult individuals. Therefore, at Mimiomoko Pocket, there are gecko vertebrae the size of a modern specimen of H. duvauceli and humeri of a much smaller adult lizard.

Order ?cf. Apterygiformes

Family ?cf. Apterygidae

Material: ?Left phalanx 1, digit III (AV28667) (see fig. 2.5).

Measurements (in millimetres): Length (maximum), 14.6; maximum proximal width, > 6.6; maximum distal width, 4.6; maximum proximal depth, > 4.9; depth, internal condyle, 3.8; depth, external condyle, 3.9.

Diagnosis: Firm identification of this single phalanx is far from certain, but after careful comparisons across a broad range of avian families, AV28667 was most closely allied to the Apterygidae for the following reasons: in proximal view, proximal end of phalanx has convex sides where broadest part occurs somewhere between dorsal and ventral borders, not along either dorsal or ventral border; in ventral view, ventral shaft surface not grooved,

in fact over most of extent convex ventrally; area for attachment of flexor tendon on ventral surface at proximal end bulbous, protruding ventrally with two short, distinct ridges either side of midline present; in ventral view, proximal border of phalanx V-shaped, with proximalmost extension just about at mediolateral midpoint; phalanx expanded at both proximal and distal ends, with narrower shaft in between; external condyle extends slightly further distal than internal condyle.

Discussion: Some differences of unknown significance can also be seen between AV28667 and phalanx 1, digit III of the living kiwi Apteryx australis: AV28667 has a prominence, presumably for tendonal or ligamental attachment, along the medial part of the shaft near the proximal end, which A. australis (NMV B9127) does not possess: AV28667 also flares more broadly at the proximal end and has a more nearly parallel-sided shaft between distal and proximal ends; excavations on the medial and lateral sides of the internal and external condyles respectively are decidedly shallower in AV28667; and AV 28667 is only slightly greater than half the size of A. australis (where phalanx length = 23.2 mm for NMV B9127).

Further comparisons to other kiwi species (A. oweni, A. haasti) need be made before any final comment or assignment of this specimen should be attempted. On the basis of a single phalanx, however, any final assignment would have to be tentative, even once the above comparisons had been made.

Order Procellariiformes
Family Procellariidae

Material: Proximal end of right ulna (AV28662); distal end, right ulna (AV28663); dorsal fragment of right coracoid (AV28671), including most of bone to just ventral of coracoidal fenestra; proximal end of right tarsometatarsus with an abraded hypotarsus (AV28665) (see Fig. 2.5).

Measurements (in millimetres): Ulnae. AV28662, maximum width across cotylae, 6.2; maximum depth across cotylae and olecranon, 6.3; maximum depth of internal cotyla, 4.5; maximum depth of external cotyla, 3.5. AV28663, maximum width of distal end measured parallel with appropriate shaft surface, 6.6; maximum width across condyles, 4.1; depth of internal condyle, \bowtie 3.6; depth of external condyle, \bowtie 4.6; width of shaft just proximal to expansion for distal articular surfaces, 4.0; depth just proximal to expansion for distal articular surfaces, 2.9. Coracoid. AV28671, length from proximal most extension to procoracoid, 8.1; maximum width across procoracoid, \bowtie 5.2; anteriorposterior depth of coracoidal shaft at dorsal end, 4.4; anteroposterior depth of coracoidal shaft just dorsal to expansion for procoracoid, 3.7. Tarsometatarsus. AV28665, maximum width of proximal end, 4.5; maximum depth of internal calcaneal ridge from base of intercotylar process, \bowtie 4.7; length of internal calcaneal ridge @ 4.4.

Diagnosis and Discussion: Because of the incompleteness of the two ulnae of procellariiforms present in the Mimiomoko sample, which might even be opposite ends of the same bone, and the lack of comparative material of Pagodroma, Priocella, Bulweria among others, assignment of these specimens (AV28662 and AV28663) has been made only to family. Both ulnae represent birds the size of or slightly larger than Puffinus gavia, the Fluttering Shearwater, whereas the tarsometatarsus (AV28665) is from a much smaller procellariid. The coracoid fragment (AV28671) is slightly smaller than, although

perhaps within the size range of, P. gavia. Thus at least two, possibly three, taxa in the Procellariidae are present in the Mimiomoko avifauna.

ULNAE. The two ulna fragments were placed in Procellariidae because they possessed the following combination of character states: ulna not medio-laterally compressed, unlike that in Pelecanoididae; shaft triangular in cross-section near proximal end; olecranon elongate but projecting anconally, not proximally, and triangular in shape when viewed proximally, located only slightly mediad of mediolateral midpoint of proximal end; palmar surface of shaft near proximal end with two moderately deep channels, separated by a distinct ridge; cotylar surfaces oriented nearly perpendicular to palmar surface of shaft, not at all approaching same plane; proximal end of shaft (viewed palmarly) not expanded much to accommodate articular surfaces, thus not broadly splayed; shaft nearly straight, not highly curved in any view; on distal end, prominent process present lateral to tendinal groove, presumably for further stabilization of the tendon passing across this area; internal and external condyles not broadly separated from one another; carpal tuberosity an elongate, prominent process; distal end of shaft somewhat palmoanconally compressed (when viewed distally); in lateral view, little expansion over shaft width occurs at distal end; external condyle quite "squared off", not rounded, with about an equal, slight amount of expansion in both palmar and anconal directions; tendinal pit deep and located just distad of process on lateral side of tendinal pit.

CORACOID. Although only a small fragment of the coracoid (AV28671) was preserved, it can be assigned to Procellariidae because of the following combination of character states: shaft of coracoid between procoracoid and dorsal end, when viewed medially, not deep anteroposteriorly and of equal depth from procoracoid to head, not increasing in dimensions in either direction; ventral border of coracohumeral surface, along which lies brachial tuberosity, forming straight line that is tilted slightly posteriorwards and not undercut; procoracoid well developed, pointing only slightly dorsally, but mainly medially, not primarily dorsally or anteriorly; procoracoid delicate and V-shaped, not broad or squared-off; coracoidal fenestra present and separated from, yet close to, medial margin of shaft; brachial tuberosity not elongate, pointing primarily medially; procoracoid and brachial tuberosity extending about an equal distance mediad; dorsal end of coracoid not noticeably pneumatized; area between brachial tuberosity and procoracoid broadly C-shaped with separation of two structures wide, neither closely apposed, and forming a nearly closed-O; glenoid facet decidedly more extensive in area than scapular facet, semicircular in shape, with straight side bordering medial margin of coracoid; glenoid facet not protruding abruptly beyond lateral margin of coracoidal shaft; in anterior view, dorsal end of coracoid not bulbous, but only slightly broader than shaft that occurs between procoracoid and dorsal end.

Of all the procellariid material available for comparison, the coracoid of Pterodroma seems most similar to AV28671. It should be noted again, however, that Priocella, Pagodroma, and Bulweria, all forms now known in the New Zealand region, were not available for comparison, so any of the following comments may need to be revised in light of further study involving these genera.

With coracoids of Pterodroma, AV28671 shares the following character states: distinct and prominent muscle scar present along medial border of coracoidal shaft just medial to coracoidal fenestra; in medial view, dorsalmost projection of coracohumeral surface at anterior end a distinct bulge with surface tilted gently ventrad towards posterior end; in same view, medial surface of shaft between coracohumeral surface and procoracoid not deeply excavated; viewed dorsally, coracohumeral surface compact, boxy, with medial and lateral margins parallel, posterior margin perpendicular to these, while anterior margin forms acute angles at intersection with medial and lateral margins; posterior end of coracohumeral surface protrudes as a distinct process; about size of Pterodroma mollis; slightly smaller, but perhaps even within the size range of Puffinus gavia.

TARSOMETATARSUS. The tarsometatarsus fragment (AV28665) was assigned to Procellariidae because it possessed the following combination of character states: three calcaneal ridges present, internal longer than external two; shaft deep, with marked channelling on anterior part; channelling present on posterior surface of shaft, but much shallower than that on anterior; internal calcaneal ridge set along internal border of shaft, not displaced towards mid-line of shaft; intercotylar prominence projecting far proximal of cotylae; proximal end not played broadly. Because the tarsometatarsus is only represented by the proximal moiety, and even that is rather worn, particularly in the area of the hypotarsus, it seems rather pointless to attempt assignment of this form, which is about the size of Halobaena caerulea (but definitely not that taxon), to any category more specific than Procellariidae.

Family Pelecanoididae

Pelecanoides sp.

Material: Sterna (AV28657, AV28658), fragments of anterior part including coracoidal sulci and most of the anterior margin of the keel with remainder of element completely eroded; scapulae, right (AV28651) and left (AV28652); coracoids, right (AV28646, AV28647), both lacking sternocoracoidal processes; humeri, right (AV28644, AV28645); ?radius, left (AV28661); ulnae, right (AV28653) and left (AV28659); carpometacarpii, right (AV28648) and left (AV28649); femur, right (AV28664), lacking proximal end but most of shaft and distal end present; ?tibiotarsus, right (AV28654); tarsometatarsus, right (AV28650) (see Fig. 2.6).

Measurements (in millimetres): See Table 2.1.

Diagnosis: the following diagnosis is appropriate at both familial and generic level, because Pelecanoides is the only genus in that family.

HUMERUS. Head palmoanconally compressed, not inflated or even smoothly rounded (P,H);¹ head deeply undercut in two areas that are separated by a pointed projection from the head instead of having a single, large undercut (P,H); bicipital crest forming an angle approaching 90° with internal margin of shaft, rather than a large, obtuse angle (P,H); deltoid crest not prominent, low (P,H); shaft markedly mediolaterally compressed, particularly near distal

1. P, Procellariidae; H Hydrobatidae. Initial given in parentheses after a character indicates those family(ies) which differ(s) in that character from the taxon being diagnosed.

Table 2.1 Measurements (in mm) of *Pelecanoides* from Mimiomoko Pocket, north Canterbury, N.Z. and modern species

Element/Measurement	Fossil Material		Recent Material			
			<u><i>P. urinatrix</i></u> Range	n	<u><i>P. georgicus</i></u> Range	n
CORACOID	AV28646	AV28647				
1. Length	23.7	21.4	22.9-25.8	14	21.2-22.8	3
2. Width across procoracoid	-	5.5	5.5-6.2	14	5.2-5.8	3
SCAPULA	AV28651	AV28652				
1. Width across head	6.3	6.2	6.4-7.0	14	5.9-6.7	2
HUMERUS	AV28644	AV28645				
1. Total length	44.0	41.8	41.7-45.6	16	38.6-41.7	3
2. Proximal width	8.8	8.7	9.2-11.8	16	8.6-9.3	3
3. Distal width	4.3	4.2	4.4-4.8	16	4.1-4.6	3
ULNA	AV28659	AV28653				
1. Total length	34.5	35.0	33.8-37.1	16	29.2-31.8	3
2. Proximal width	4.0	4.1	4.0-4.5	16	3.8-4.1	3
3. Distal width	4.8	5.1	4.7-5.7	16	4.3-4.6	3
CARPOMETACARPUS	AV28648	AV28649				
1. Length	24.7	24.1	23.7-26.7	15	21.4-22.2	3
2. Proximal width (across carpal trochleae to metacarpal I process)	5.5	5.8	5.7-6.3	15	5.5-5.6	3
TARSOMETATARSUS	AV28650					
1. Total length	24.3		24.9-28.8	13	21.9-23.4	3
2. Proximal width	3.8		4.2-5.1	13	3.9-4.2	3
3. Distal width	3.7		4.2-4.8	13	3.7-4.1	3
4. Minimum shaft width	1.8		1.7-2.3	13	1.4-1.8	3

end (P, H); viewed distally, distal end square, not rectangular in outline (P, H); brachial depression shallow, not deep (P); development of attachment for pronator brevis slight (H); olecranal fossa deeply excavated, forming deep pit in distal end (F);² entepicondyle projects far ventrally (F).

ULNA. Prominent process projecting dorsal to olecranon and lying between cotyla (P, H); entire bone markedly mediolaterally compressed, rather than being more gently rounded in cross-section (P, H); robust process projecting dorsodistally and lying lateral to tendinal groove (less well developed in most P, H).

CARPOMETACARPUS. Process of metacarpal I elongate proximodistally but abbreviate dorsoventrally, giving a "snub-nosed" appearance (P, H); deep, elongate excavation present on internal surface of head just dorsal to attachment for pisiform process (P, H); attachment of pisiform process not prominent, only slightly indicated (prominent in most Pu);³ lacking or with only slight development of indentation in dorsal margin of internal carpal trochlea (F); entire proximal end and shaft markedly compressed dorsoventrally (P, H).

TARSOMETATARSUS. Intercotylar prominence not as well developed as that in most Procellariidae; posterior surface of shaft planar and oriented at nearly right angle to lateral and medial shaft surfaces, not tiled otherwise or rounded (P); distal end does not flare much beyond nearly parallel medial and lateral margins of shaft (most P, although Daption approaches this condition); posterior surface between trochleae highly excavated (most P).

STERNUM. Deep excavation present at base of manubrial spine (P, H); flange present along ventral margin of coracoidal sulcus at lateral edge (H); in ventral view, angle formed at manubrial spine by margins of two coracoidal sulci large, obtuse, approaching 180°, not 90° or less (meaning that ventral ends of coracoids articulating here are directed mediolaterally, rather than anteromedially-posterolaterally (P)).

CORACOID. Brachial tuberosity not protruding far medially, and thus head of coracoid more in line with main shaft axis (P, H); procoracoid not protruding far dorsally, and thus entire medial margin of shaft and head between brachial tuberosity and procoracoid much less highly curved (P, H); coracoid much more slender and elongate than in Hydrobatidae, not flaring into broad sternocoracoidal process as far proximally as in Hydrobatidae, thus flaring only very near distal end, and producing a straight lateral margin over much of coracoidal length (H); width of sternal facet about equal to width across proximal end of bone at level of procoracoid, not decidedly more (H).

SCAPULA. Proximal articular facet dumbbell-shaped with slight expansions at both medial and lateral ends, rather than being broadest laterally (H) or having a marked medial constriction as well as a marked lateral expansion (Pu).

Discussion: Although several bones (femur, tibiotarsus, and radius) other than those diagnosed above have been tentatively assigned to Pelecanoides, they have not been diagnosed due to incompleteness and thus some uncertainty of their identity. The single femur lacks a proximal end and thus is difficult to assign with any high certainty. As with most of the hind limb elements, the

1. F, Fulmarinae; see footnote 1 on previous page.

3. Pu, Puffininae; see footnote 1 on previous page.

tibiotarsus is rather generalized and assigned to the Pelecanoididae primarily on the basis of size and proportions, a most unsatisfactory basis.

Assignment of the Pelecanoides from Mimiomoko Pocket to any one of the living species, based on the modern samples available in this study is problematical. Three of the living species listed in Peters (1931) were unavailable for comparison. No consistent qualitative differences can be found to allow distinction of the two modern New Zealand species from one another or the Mimiomoko form(s). Based on a limited modern sample, Pelecanoides urinatrix and P. georgicus can be distinguished in many cases on the basis of size, P. georgicus being consistently smaller. For some bony elements there is overlap in size, where only specimens on either extreme can be confidently assigned to one or the other species (see Table 2.1). As Table 2.1 illustrates, the Mimiomoko Pelecanoides do not consistently fit into either species. Certain measurements fall only within the range of P. urinatrix (coracoidal length, ulnar length, ulnar distal and proximal widths, carpometacarpal length). Other measurements fall only within the range of P. georgicus (scapular width, proximal and distal humeral widths, distal tarsometatarsal width). Yet some measurements fall within the range of overlap of P. georgicus and P. urinatrix (width across procoracoid, humeral length, proximal ulnar width, proximal carpometacarpal width, minimum tarsometatarsal shaft width). One measurement (tarsometatarsal length) lies intermediate between those of the two extant species, and another (proximal tarsometatarsal width) is smaller than measurements of both species.

Measurements that are only in the range of the larger Pelecanoides urinatrix tend to be the length measurements of bones, whereas width measurements tend to more closely approximate P. georgicus, thus, perhaps suggesting the presence of a third species with more slender elements, but tending to be about the same overall size as P. urinatrix. Perhaps, however, if modern samples were larger, the Mimiomoko form would simply reside in that intermediate "no-man's land" where P. urinatrix and P. georgicus cannot be distinguished. For the moment, then, the Mimiomoko material will be assigned only to Pelecanoides sp.

Family Rallidae

Gallirallus cf. minor (? = australis)

Material: Left carpometacarpus (AV28672); left radius (AV28656); left proximal and distal fragments of ulna (AV28660 and AV28655) (See Fig. 2.7).

Measurements (in millimetres): Carpometacarpus. See Table 2.2. Radius. Total length, 28.6; width of proximal end, 3.9; width of distal end, 3.4; maximum palmoanconal depth of proximal end, 2.3; minimum shaft width, 1.2. Ulnae Fragments. Proximal end, maximum width, 4.4; maximum depth 4.1. Distal end, maximum width, 4.4; maximum depth, 4.1.

Diagnosis: CARPOMETACARPUS. Placed in the Rallidae because of the following combination of character states: neither trochlea extending markedly further proximal than the others; trochleae not compressed proximodistally with respect to depth of proximal end (= distance across internal condyle and process of metacarpal I); deep pit present between and at distal

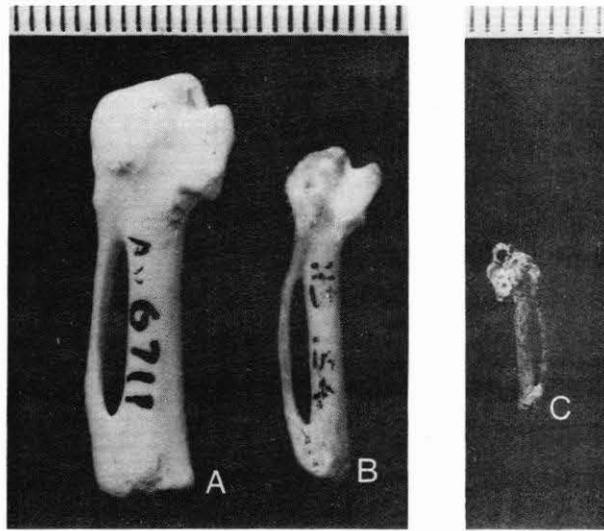


Fig. 2.7 Carpometacarpi of fossil Rallidae from the New Zealand region. A, Diaphorapteryx hawkinsi, AV6711; B, Gallirallus cf. minor, AV28672, from Mimiomoko Pocket; and C, Capellirallus karamu, AV20615. Scale, each division equals 1 mm.

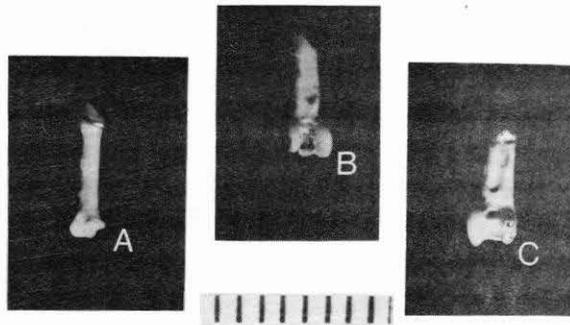


Fig. 2.8 Passeriform birds from Mimiomoko Pocket: A, Ulna (distal), AV28669. Distal tibiotarsi: B, AV28668; and C, AV28670. Scale, each division equals 1 mm.

bases of external and internal trochleae, just proximal to where metacarpal III joins remainder of bone; metacarpal III originating proximally primarily off metacarpal II rather than from base of carpal trochleae; process of metacarpal I broad (or elongate) proximodistally, not narrow and not tremendously elongate; ligmental attachment of pisiform process set back towards metacarpal III, not set towards base of metacarpal I process; intermetacarpal tuberosity that in some avian groups approaches or joins metacarpal III lacking; in cross-section, metacarpal II has rounded outlines, not angular; facet for digit II extending further distad than that for digit III; metacarpal III closely opposed to metacarpal II, not broadly bowed away from it, thus making the intermetacarpal space relatively narrow; metacarpals II and III fused distally over broad area (elongate proximodistally).

RADIUS. Considered rallid because of the following combination of character states: in proximal view, shape of humeral cotyla rectangular; cotyla compressed palmoanconally, not mediolaterally; small capital process present, triangular in shape. Bicipital tubercle located very near proximal end, merging directly into it, not displaced distally; distal end slightly, not broadly splayed; splaying, although slight, beginning near proximodistal midpoint of shaft so that shaft not parallel-sided over distal half; distal end not highly curved palmarly; in palmar view, distal end not deeply undercut, distal margin of radius rounded (curved), not straight; in distal view, scapholunar facet not extremely slender palmoanconally, particularly inflated on side of ligamental prominence, while either side tapers to a point; expansion palmarly and anconally about equal; shaft of radius rather rounded, not highly compressed; shaft short and straight, not significantly curved in any direction.

ULNAE. Assigned to the Rallidae because of the following combination of character states: Proximal end. Olecranon a broad-based, triangular process, not narrow; in proximal view, proximal end triangular in shape; external cotyla not projecting abruptly laterad, margins nearly, if not entirely, straight, not irregular in outline; external and internal cotyla extending about same distance palmarly, one not projecting decidedly further than the other; no proximally projecting processes present on proximal end, palmar to olecranon; in lateral view, external cotyla highly recurved proximally, giving hook-like appearance to cotylar margin; in palmar view, proximal articular surface somewhat undercut, shaft not gradually merging into proximal end; prominence for anterior articular ligament not well developed; proximal end of shaft significantly mediolaterally compressed. Distal end. Carpal tuberosity low and rounded, not slender and prominent, not forming narrow process that projects distally; distal part of shaft compressed somewhat mediolaterally; external condyle short proximodistally and lacking any processes on lateral side; in lateral view, external condyle smoothly rounded, not flattened distally; distinct tendinal pit present on palmar edge of external condyle; no marked excavations present on palmar surface of shaft at proximal base of internal condyle; in distal view, distal end triangular in shape, gradually diverging from a carpal tuberosity apex, lacking irregular outlines or abrupt changes in directions of the margins; in distal view, groove between internal and external condyles, particularly on anconal surface, not deep.

Discussion: When compared with bones of other rails, both fossil and recent, from New Zealand and nearby islands, AV28672 appears to most closely approach the morphology of Gallirallus. The Mimiomoko carpometacarpus is a short, robust element (see Table 2.2) with an enlarged proximal end relative to the remainder of the bone. This combination of characters rules out inclusion of this form in Porphyrio (P. porphyrio), Rallus (R. pectorallis, philippensis), Porzana (P. pusilla, P. tabuensis), Gallinula (G. tenebrosa, G. chloropus), Fulica (F. atra, F. chathamensis [= Nesophalaris prisca]), Tri-bonyx ventralis, and probably T. hodgeni (names of rails of New Zealand follow Olson, 1975). On the other hand, the Mimiomoko carpometacarpus is not nearly so robust as is that of Diaphorapteryx hawkinsi, which is only slightly more elongate. The Mimiomoko bone is twice the size of Capellirallus karamu and further differs in having a more angular outline of the internal carpal trochlea, not being smoothly curved over much of its circumference, having a much more prominent proximal metacarpal I process, and having metacarpal III originate off the shaft of metacarpal II rather than smoothly grading into the base of the carpal trochleae. It differs from Notornis mantelli in being less than half the size, in that the proximal end of the Mimiomoko bone is much less dorsoventrally compressed, and in that the pisiform process is much more prominent. Although approximately the same size, the Mimiomoko Gallirallus differs from the Chatham Island G. (= Nesolimnas) dieffanbachii in that metacarpal III originates proximally off metacarpal II and not off the base of the carpal trochleae and is thus relatively shorter; metacarpal II is more robust; the carpal trochleae appear to be more enlarged relative to the rest of the bone; and the facet for digit II is much more dorsoventrally compressed.

In all the above-mentioned characters, the carpometacarpus of Gallirallus australis and that from Mimiomoko Pocket are identical. The only differences between the two that can be noticed are: AV28672 is somewhat smaller than any of the G. australis in our measured sample, and the long axis of the metacarpal I process of AV28672 is not shifted as far proximally as in most G. australis.

Because of the modifications of the forelimb associated with loss of flight so common in rails, bones of the wing are of limited use in determining relationships within many of the Rallidae. Certainly the rallid carpometacarpus and radius from Mimiomoko Pocket indicates a bird of at least reduced flying ability. The carpometacarpus shows the greatest number of similarities to Gallirallus australis, but is smaller than any we have been able to measure (see Table 2.2). Perhaps if Gallirallus minor is indeed distinct from G. australis (see Olson, 1975, for a discussion of this problem), the Mimiomoko rallid belongs in the former species. This question, as Olson (1975) points out, is yet to be resolved, however. Thus, for the present, until more comprehensive work is carried out on New Zealand fossil rails, assignment of the Mimiomoko rail material will tentatively be made to Gallirallus cf. minor.

Order Passeriformes

Material: Distal end of left ulna (AV28666); two distal ends of right tibiotarsi (AV28669, AV28670); distal end of left tibiotarsus (AV28668) (see Fig. 2.8).

Table 2.2 Measurements (in mm) of Rallidae from Mimiomoko Pocket, north Canterbury, N.Z., and extant or fossil rails from the Australasian, mainly New Zealand, region

Taxa	Measurements of Carpometacarpi				
		Proximal width	Width across distal end (from tuberosity of metacarpal II to facet for digit III)	Length of metacarpal I	Minimum width of metacarpal II
AV28672	22.2	6.5	> 3.6	4.3	2.3
<u>Capellirallus karamu</u> (AV20615) (r)	@ 11.1	3.4	-	@ 2.8	@ 1.2
<u>Diaphorapteryx hawkinsi</u> (n=3)	25.1-28.1	9.5-10.6	6.2-6.8	6.2-6.9	3.3-3.6
<u>Fulica atra</u> (n=14 for length; 1 for others NMV W4573 (l))	39.1-45.0	8.1	4.4	5.2	2.8
<u>Fulica chathamensis</u> (CSIRO-BS1657) (l)	46.9	10.7	6.4	6.7	3.8
<u>Gallinula tenebrosa</u> (NMV W6821) (l)	38.4	7.8	4.1	4.8	2.4
<u>Gallirallus australis</u> (n=7)	25.8-27.9	6.9-7.6	4.3-4.8	5.4-6.7	2.6-2.8
<u>Gallirallus dieffenbachii</u> (CSIRO-BS1660) (r) ²	21.8	> 6.1	@ 3.9	> 3.6	1.9
<u>Notornis mantelli</u> (DM17177) (cast, l)	45.4	10.9	5.9	7.4	3.9
<u>Porphyrio porphyrio</u> (NMV W6813) (l)	50.9	9.2	5.4	6.2	3.2

(contd.)

Table 2.2 (contd.)

	Length	Proximal width	Width across distal end (from tuberosity of metacarpal II to facet for digit III)	Length of metacarpal I	Minimum width of metacarpal II
<u>Porzana pusilla</u> (NMV W5552) (l)	13.7	2.9	1.8	2.0	1.1
<u>Porzana tabuensis</u> (NMV W6866) (l)	15.2	3.2	1.8	1.8	1.2
<u>Rallus pectoralis</u> (NMV B11094) (l)	19.1	4.3	2.4	2.6	1.4
<u>Rallus philippensis</u> (NMV B5234) (r)	27.3	5.7	3.3	3.6	2.1
<u>Tribonyx ventralis</u> (NMV W6814) (l)	40.2	8.0	4.6	4.9	2.9

- 1 Left Element
2 Right Element

Measurements: See Table 2.3.

Diagnosis: The following diagnoses are appropriate only to the ordinal level. More refined diagnoses were not attempted owing to lack of availability of a complete suite of skeletal material of New Zealand passeriform families. The combination of character states, and not necessarily any single character, is diagnostic.

ULNA. Small size; papillae of secondaries well developed as prominent knobs; carpal tuberosity slender, coming to a point internally, not squared off as in Alcedinidae or bulky as in Cuculidae, and not projecting primarily distally as in Turnicidae; distal radial impression deep; shaft near distal end straight, lacking any curvature between it and distal end; in distal view, distal articular surface neither extremely deep nor mediolaterally compressed; lateral to external condyle lies short flange producing deep channel between it and external condyle for passage of tendon.

TIBIOTARSI. Small size; condyles deep and of subequal depth and length; in lateral and medial views, margins of condyles describing a half circle; condyles subparallel to long axis of shaft, not angled, and not displaced to one side of shaft; in distal view, condyles nearly subparallel, only slightly diverging anteriorly; condyles projecting far anterior to shaft but only slightly posterior; supratendinal bridge "broad" proximodistally (elongate), lying nearly, if not, perpendicular to long axis of shaft; intercondylar fossa well excavated but raised area present connecting proximal ends of condyles on anterior surface; distal opening of tendinal canal located centrally, not noticeably laterally or medially displaced, opening just proximal to bar connecting condyles.

Discussion: As many as three different kinds of passeriforms may be represented by the 3 tibiotarsi, but much better comparative material is needed to ascertain that those few differences noted cannot be matched by variability within one species. AV28668 has a more slender shaft and is the smallest of the three tibiotarsi; the long axes of the distal condyles are twisted at a slight angle laterad of the long axis of the shaft, thus not lying parallel with it; it thus differs from AV28670 with which it shares a broad (proximodistally) supratendinal bridge. AV28670 and AV28669, although very similar in size, differ in that AV28670 has a very broad supratendinal bridge while AV28669 has a much narrower one. Additionally, the tendinal canal is centrally located in AV28669 but displaced laterally in AV28670.

In size AV28668 is comparable to that of Zosterops lateralis (the Silvereye), while AV28669 and AV28670 are somewhat larger. The ulna (AV28666), on the contrary, is markedly smaller than that of Z. lateralis. Thus, unless limb proportions of the fossil form are distinctly different than those exhibited by Z. lateralis (and they well could be), as many as 3 or 4 different species of passeriforms could be represented in the Mimiomoko sample.

Bias of Mimiomoko Sample

The sample of bones from Mimiomoko Pocket by no means represents all, or even nearly all, elements present in a vertebrate skeleton. To demonstrate this, Table 2.4 is a tabulation of the tetrapod sample by major categories of elements. Owing to the small sample size, only broad groupings of elements were tabulated. Many elements used in this tabulation were too fragmentary

Table 2.3 Measurements (in mm) of Passeriformes from Mimiomoko Pocket, north Canterbury, New Zealand

ULNA	AV28666		
1. Width across condyles	1.6		
2. Depth of external condyle	1.2		
3. Width of shaft at base of external condyle	0.8		
TIBIOTARSUS	AV28668	AV28669	AV28670
1. Width across distal end of condyles	-	2.4	2.2
2. Depth of internal condyle	@ 1.9	@ 2.3	-
3. Depth of external condyle	-	2.3	-
4. Length of internal condyle	-	1.7	-
5. Length of external condyle	-	2.0	1.9

Table 2.4 Tetrapod Elements Represented at Mimiomoko Pocket

	Rib	Skull and Mandible	Vertebrae	Limb Girdles	Limbs	Phalanges
Reptilia						
Number	3	4	7	4	21	25
% of reptiles	4.7	6.3	10.9	6.3	32.8	39.1
Bird						
Number	0	1	6	16	28	29
% of birds	0	1.3	7.5	20.0	35.0	36.2

to be identified more precisely other than as bird or reptile, hence the discrepancy between the number of specimens listed in the systematics section and enumerated here. Of the 199 bones or bone fragments in the tetrapod sample, 55 could not be identified to either Class or element.

Perusal of Table 2.4 reveals a marked bias towards rod-shaped over spherical or disc-shaped elements. This is strikingly evident in the case of the limb girdle elements. Among the reptiles, these elements are primarily disc-shaped and occur infrequently in the sample. By contrast, birds have many rod-shaped limb girdle elements such as the clavicle, scapula, and coracoid and these occur three times as frequently as in the reptilian case. Such post-mortem sorting on the basis of shape was most likely owing to mechanical action by either flowing water or wind.

Conclusions

Except for the possible presence of a kiwi, the tetrapod sample from Mimiomoko Pocket could be duplicated on Stephens Island in Cook Strait, New Zealand, today. Before the drastic alteration of the mainland New Zealand fauna by the exotic rodents and carnivores introduced by man, this same suite occurred there as well.

The sample appears to represent an accumulation in a shallow cave or burrow. The best represented taxa in the sample are the very ones to be expected in burrows where the tuatara and seabirds live alongside one another at the present time. Between the death of the tetrapods and their final burial, either wind or flowing water brought about mechanical sorting of the bones so that rod-shaped elements were preferentially preserved over spherical or disc-shaped ones.

Tuatara had disappeared from mainland New Zealand by 200 years ago. With this in mind together with the fact that none of the tetrapods introduced by man are represented in the collection from Mimiomoko Pocket, it is likely to be still older, possibly more than one thousand years. The high concentration of collagen in the bones argues against a significantly greater age than that.

Mimiomoko Pocket was originally believed to be conformable within the Miocene Double Corner Shell-beds. Primarily the presence of an unexpectedly large concentration of collagen in the tetrapod bones makes this interpretation now unacceptable. Without that critical piece of evidence, the site would still be regarded as Miocene. Unfortunately, the tetrapods themselves as yet do not provide a safeguard to prevent a similar error in the future. Without some well dated pre-Pleistocene fossil tetrapod assemblages as standards for comparison, it is unreasonable to rule out a pre-Pleistocene age for a modern-looking suite of terrestrial vertebrates. Small tetrapods in New Zealand may have been allied with living genera by the Miocene or even earlier in the Tertiary. Modern genera of birds and reptiles elsewhere in the world frequently have records extending well back into the Tertiary, quite in contrast to the mammals where only a few living genera are known before the Pliocene.

Afterward

The original impetus for two of us (TR & PR) to work on this project was the possibility that it represented the first pre-Pliocene terrestrial vertebrate fauna in New Zealand. New Zealand has a unique potential to test the ideas of MacArthur and Wilson (1967) on the relationship between island area and faunal diversity over an extended period of geologic time. The almost continuous record there of terrestrial sediments from the Cretaceous to the Holocene has the potential for yielding tetrapod remains (Rich, 1975).

The limited diversity of the New Zealand tetrapod fauna is owing in part, no doubt, to its long isolation from other land masses since the Cretaceous (Griffiths and Varne, 1972). However, a second factor could have had a long term effect on the diversity of the fauna. During the Landon (Oligocene), a widespread marine transgression occurred that probably reduced New Zealand to an archipelago of less than one-third its present area (Stevens, 1973). Indirect evidence of a decrease in diversity at this time is furnished by the marked turnover in the New Zealand flora during the Oligocene (Fleming, 1963). In light of this "Atlantis Factor" in New Zealand's history, beyond assuming that the highly endemic groups were present, only the discovery of pre-transgression fossil assemblages will provide an adequate basis for a characterisation of the tetrapod fauna there prior to the Oligocene.

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Mr. Robert Suddarth, Geosciences Department, Texas Tech University, drafted Fig. 2.2.

Mrs. Mary Lee Vickers and Miss Kayelene Voege skillfully typed the manuscript.

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