

A new species of *Gallicolumba*: Columbidae from Henderson Island, Pitcairn Group

Trevor H. Worthy¹ and Graham M. Wragg²

Abstract A new species of ground dove in the genus *Gallicolumba* is described from abundant material from late Pleistocene to Holocene age deposits of natural and midden derivation on Henderson Island in the Pitcairn Group, South Pacific Ocean. Osteological characters suggest that it was most closely related to *G. stairi* and *G. rubescens*. Relatively enlarged leg elements and reduced wing elements suggest that this dove was facultatively flightless.

Keywords Columbidae; *Gallicolumba* new species; Henderson Island; Pitcairn Group

INTRODUCTION

Henderson Island of the Pitcairn Group is one of the most remote islands in Oceania. At 24°22'S, 128°18'W, it is about 177 km east-north-east of the high volcanic island of Pitcairn, and 200 km east of Oeno and 360 km west of Ducie, the two low atolls of the group (Fig. 1). Henderson Island, with an area of about 37 km² and a maximum height above sea level of 33 m is a raised atoll whose outer rim is the ancient reef and the lower inner region the elevated floor of the lagoon.

Henderson Island was discovered by the Spaniard Pedro Fernandes de Quiros in 1606; it was then uninhabited and has not been settled since that time (Benton & Spencer 1995; Wragg 1995a). The island has attracted many scientific investigations, beginning as early as 1825 with *HMS Blossom*, but the most significant in terms of duration of investigation and scope of studies was the Sir Peter Scott Commemorative Expedition to the Pitcairn Islands 1991–1992 (Spencer & Benton 1995). As part of this multidisciplinary expedition, extensive archaeological and some palaeontological investigations were made (Weisler 1994, 1995; Wragg & Weisler 1994; Wragg 1995a,b).

A prehistoric human presence was discovered on Henderson Island in 1971 as cultural strata including burials in several sites (Fosberg et al. 1983; Sinoto 1983). Until then the island had been assumed to have a pristine biota that was unmodified by human influence, though the presence of the Pacific rat *Rattus exulans* should have suggested otherwise. Steadman & Olson (1985) studied 303 bird bones recovered from Sinoto's excavations and reported a fauna dominated by seabirds. Of the few landbirds, they reported two species of pigeon: *Ducula* cf. *aurorae* or *D.* cf. *pacifica* based on a few wing elements, and *Ducula* cf.

¹Palaeofaunal Surveys, 2A Willow Park Drive, RD 11, Masterton, New Zealand.
Email: twmoa@wise.net.nz

²350c Great South Road, Papakura, Auckland, New Zealand.

galeata based on two partial tibiotarsi and a mandibular fragment. The only species of pigeon now on Henderson Island is a small fruit dove *Ptilinopus insularis*, and, thus, Steadman & Olson (1985) documented apparent human-caused extinctions on this “uninhabited” island. Schubel & Steadman (1989) reported another 2795 bird bones from Henderson, including a fragmentary tarsometatarsus that they referred to *Gallicolumba*. This bone (USNM 388744) was described as about the size of *G. nui* of the Marquesas, but more similar to the smaller *G. erythroptera* in “its more smoothly curved, shallower proximomedial margin of the shaft, the presence of a lateral *foramen vascularium proximale*, and the shallower *fossa infracotylartica dorsalis*” (Steadman 1992).

Excavations during the Pitcairn Islands Scientific Expedition of 1991–1992 resulted in a collection of some 42 213 bird bones (Wragg 1995a). About 42 1-m² testpits were excavated in 11 of the 28 identified archaeological sites and one natural site (T12). The bird bones were sorted from the recovered materials by Weisler, and initial identification was made by Wragg (Wragg & Weisler 1994). Wragg & Weisler (1994) listed four extinct landbirds, including a Columbidae n. gen et n. sp., *Ducula* n. sp., and *Gallicolumba* n. sp., of which latter taxon they figured cranial, leg, and wing elements. They commented that the heavily constructed bill and legs of this new species showed specialisation towards a more terrestrial life. Wragg (1995a) provided more detail indicating 210 bones of the new *Gallicolumba* from 10 sites, one of which was the natural site. Excavations in many of the archaeological sites penetrated through the cultural horizons and many bones of the extinct taxa, including the new *Gallicolumba*, were found in precultural contexts. Polynesians occupied Henderson for some 600 years commencing sometime in the period 1300–1000 ¹⁴C yr BP, but certainly by about AD 1050 (Weisler 1995). Precultural horizons dated up to 13 420 ¹⁴C yr BP (OxA-5910), with this oldest date being on bones of the extinct *Gallicolumba* (Wragg 1995b; Hedges et al. 1997).

An extensive fossil record of birds has now been described from many islands in the Pacific, and often up to half of the species present are extinct, for example, in the Marquesas (Steadman 1989a; Steadman & Rolett 1996), Easter Island (Steadman 1995), Hawaiian Islands (James & Olson 1991; Olson & James 1991), Society Islands (Steadman 1989a), Samoa (Steadman 1994), Niue (Steadman et al. 2000), the Tongan and Cook Island groups (Steadman 1989a, 1993, 1995), New Caledonia (Balouet & Olson 1989), and in Fiji (Worthy 2000, 2001). Amongst the extinct taxa are many species of columbids (Balouet & Olson 1987, 1989; Steadman 1989a,b, 1992, 1997; Worthy 2001). The purpose of the present contribution is to describe the extinct *Gallicolumba* from Henderson Island.

METHODS

Locations of the excavated sites 1, 3, 5, 6, 7, 8, 10, 11, 12, 21, 22, T12 from which the material was derived are shown in Weisler (1995, fig. 2) and Wragg (1995b, fig. 2.1). Site nomenclature used in those publications is followed here and on specimen labels. All sediment was screened with 6.4 mm mesh sieves and selected samples fine-screened with 1.5 or 3.2 mm meshes (Wragg & Weisler 1994).

The following abbreviations are used throughout the text. AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, United Kingdom (formerly British Museum (Natural History)); CM, Canterbury Museum, Christchurch, New Zealand; FM, Fiji Museum, Suva, Fiji; LACM, Natural History Museum, Los Angeles County, California, USA; MNZ, Museum of New Zealand Te Papa Tongarewa (formerly National Museum of New Zealand, Dominion Museum, and Colonial Museum), Wellington, New Zealand; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; USNM, United States National Museum, Smithsonian Institution,

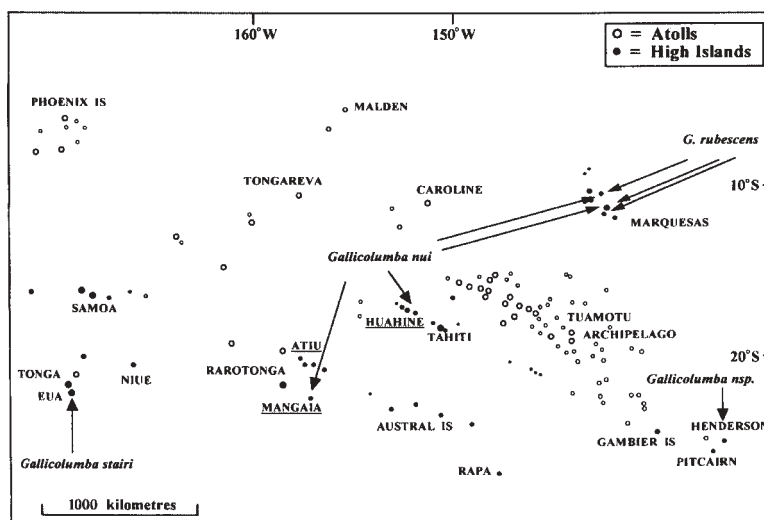


Fig. 1 Location of Henderson Island in the South Pacific Ocean and the distribution of both extant and fossil populations of *Gallicolumba* species within the area shown. *G. erythroptera* is known from those islands whose name is underlined. *G. stairi* is extant on islands in the Samoa, Tonga, and Fiji archipelagos.

Washington DC, USA; UWBM, University of Washington Thomas Burke Memorial Washington State Museum, Washington, USA.

The following abbreviations apply to single and plural usage of the elements. Acet, acetabular part of pelvis; cmc, carpometacarp; cor, coracoids; cran, crania; fem, femora; fib, fibulae; frags, fragments; hum, humeri; imm, immature; juv, juvenile; mand, mandibles; pel, pelvis; phal, phalanges; pmx, premaxillae; pt, part; quad, quadrates; rad, radii; sac, synsacra; scap, scapulae; skel, skeleton; stern, sterna; tmt, tarsometatarsi; tt, tibiotarsi; and vert, vertebrae. When listing material, bones are sometimes identified as left (L) or right (R) elements. L or R prefixed by p, s, or d indicates proximal, shaft, or distal part of the element, respectively, e.g., pR fem means the proximal part of a right femur.

Anatomical nomenclature for specific bone landmarks follows Baumel & Witmer (1993). Some common terms are abbreviated as follows: *proc.* for *processus*; *artic.* for *articularis*.

Measurements

All measurements were made by THW with Tesa[®] dial callipers and rounded to 0.1 mm. TL: greatest length, except for the coracoid, which was measured down the medial side. PW: proximal width in the lateromedial plane; femora were measured from the ball through the mid-depth point of the neck to the lateral side. SW: shaft width at mid length (unless otherwise stated) in a lateromedial plane. SD: shaft width in a dorsoventral plane. DW: distal width. Tibiotarsi PW: measured across the articular surface. Tibiotarsus PD: proximal depth from between the cnemial crests to the posterior side of the articular surface. Tarsometatarsi PD: proximal depth was measured as greatest proximal depth with one side of the callipers on the hypotarsus and the other across the anterior side of the cotylae. Tarsometatarsus DW is measured between the anterior part of the trochlea TII and TIV, rather than from the caudal process of TII to the side of TIV, which would be greater.

Comparative material

Sex, male (M) or female (F), is indicated after the catalogue number, where known. All material is from modern skeletons unless stated otherwise. Extinct taxa are indicated †.

Didunculus strigirostris (Jardine, 1845), tooth-billed pigeon, CM Av7160, Samoa.

Gallicolumba stairi (G. R. Gray, 1856), friendly ground dove, BMNH S/1975.3.3, F, Fiji; MVZ51708, M, Fiji. Fossil bones: MNZ S38223, 54 bones 6 individuals, Vatulele Island, Fiji.

G. rubescens (Vieillot, 1818), MVZ46017, F, Marquesas Is.

G. luzonica (Scopoli, 1786), MVZ53804, M, Aviary; LACM 89051, F, aviary; LACM 89050, M, aviary.

G. rufigula (Pucheran, 1853), LACM 106368, M, aviary.

G. criniger (Pucheran, 1853), LACM 89052, F, aviary.

G. beccarii (Salvadori, 1876), AMNH 7718, M, Torricelli Mountains, Papua New Guinea; USNM 615012, F, New Ireland, Papua New Guinea; UWBM 43037, M, Mount Missim, 1975 m, c.13 km north-east Wau, Morobe Province, Papua New Guinea.

G. jobiensis (A. B. Meyer, 1875), AMNH 6753, ?, Papua New Guinea.

Caloenas nicobarica Linnaeus, 1758, Nicobar pigeon, MNZ 22475, trunk skel, Wellington Zoo, New Zealand; USNM 292221, M, skel, Siam, Koh Tao; USNM 557085, F, skel, Halmahera Island, Moluccas.

Ptilinopus perousii Peale, 1848, many-coloured fruit-dove, FM 31, M, skel, Vitilevu, Fiji; FM23, M, skel, Vitilevu, Fiji.

Ptilinopus victor (Gould, 1871), orange dove, FM unreg., M, skel, Vanua Levu, Fiji; BMNH S/1975.3.1, M, Fiji.

Ptilinopus porphyraceus (Temminck, 1821), crimson-coloured fruit-dove, MNZ 16391, M, skel, Niue Island; THW colln skel, Niue Island.

Ptilinopus greyii Bonaparte, 1857, red-bellied fruit-dove, MNZ 22841, F, skel, Noumea, New Caledonia.

Ptilinopus rarotongensis Hartlub & Finsch, 1871, Cook Islands fruit-dove, MNZ 22463, two mixed individuals, Rarotonga.

Goura cristata Pallas, 1764, western crowned-pigeon, CM Av7110, skel, north-west New Guinea.

Microgoura meeki Rothschild, 1904, Choiseul pigeon †, AMNH 24959, cast R tmt.

Otidiphaps nobilis Gould, 1870, pheasant pigeon, USNM 614236, F, loc. ?, captive bird.

Columba vitiensis (Quoy & Gaimard, 1830), metallic pigeon. *C. v. vitiensis* FM26, F, skel, Mali Island, Vanua Levu, Fiji; *Columba v. griseogularis* USNM 560654, ?M, Batan Island, Philippines; *Columba v. castaneiceps* CM Av10293, M, Samoa.

Phaps chalcoptera (Latham, 1790), common bronzewing, CM Av7129, skel, Australia.

Ducula goliath (G. R. Gray, 1859), New Caledonian imperial pigeon, MNZ 22839, 3 mixed individuals, New Caledonia.

Ducula pacifica (Gmelin, 1789), Pacific pigeon, MNZ 16389A, F, trunk skel, Niue Island; THW colln (NHS19) skel, Niue Island; MNZ 25350 skel, Niue Island; MNZ 25351 skel, Niue Island; MNZ 25352 skel, Niue Island; MNZ 25353 skel, Niue Island.

Ducula latrans (Peale, 1848), Peale's imperial pigeon, FM 28, F, skel, Vanua Levu, Fiji; BMNH S/1975.3.4, M, skel, Fiji; BMNH S/1975.3.2, F, skel, Fiji.

Ducula galeata Bonaparte, 1855, Marquesan imperial pigeon, BMNH S/1975.9.5, F, skel.
Hemiphaga novaeseelandiae (Gmelin, 1789), New Zealand pigeon, Otago Museum Av1851, Dunedin, New Zealand.

SYSTEMATIC PALAEOLOGY

Class Aves

Order Columbiformes

Family Columbidae

The fossils described herein are referred to Columbidae (including *Raphus* and *Pezophaps*, see Kitchener (1993) and Shapiro et al. (2002)), because the tarsometatarsi have the following combination of characters: *fossa metatarsi I* large and deep, extending beyond the medial edge of the *facies dorsalis*; large *fossa parahypotarsalis medialis* bound by thin shaft anteriorly; shallow, narrow *fossa parahypotarsalis lateralis*; *crista medialis hypotarsi* largest and joined to *crista lateralis hypotarsi* posteriorly to enclose a single *canalis hypotarsi*; *trochleae metatarsi II* (TII) with marked medial inflection; *trochlea metatarsi III* width greater than anterior-posterior depth.

Gallicolumba Heck, 1849

The holotypical tarsometatarsus described below is referred to *Gallicolumba*, as it shares with the genus the following combination of characters: 1, straight elongate shaft that is flattened on the *facies dorsalis* distally; 2, *trochlea metatarsi IV* (TIV) has little lateral deflection; 3, the lateral and medial *foramina vascularia proximalia* are very small and of equal size; 4, *foramen vasculare distale* has a single distally directed opening to the plantar surface, not separate distal and plantar openings; 5, the anterior face of the *cotyla medialis* is not hooked anterodistally as it is in *Ducula* and *Ptilinopus*; 6, the *eminentia intercotylaris* is large.

The tarsometatarsus of *Hemiphaga*, *Ducula*, *Columba*, *Ptilinopus*, and *Phaps* are relatively shorter, and those of *Otidiphaps* relatively longer. *Goura* and *Microgoura*, while of similar proportions, are much bigger. The *foramen vasculare distale* has separate openings distally in the *incisura intertrochlear lateralis* and on the plantar surface in *Caloenas*, *Otidiphaps*, *Columba*, and *Didunculus*. The *foramina vascularia proximalia* are much larger in *Ducula*, *Columba*, *Ptilinopus*, and *Hemiphaga*.

Gallicolumba leonpascoi new species

ETYMOLOGY: The species is named after Leon Pasco, born 1959, who died climbing on Mt Aspiring, Southern Alps, New Zealand, in May 1987. Leon was a close friend of the Wragg family.

DIAGNOSIS: A *Gallicolumba* in which the tarsometatarsus is proportioned like that of *G. stairi* and is longer than in all species except *G. tristigmata*, *G. longitarsus*, and *G. nui* from which it differs in being relatively stouter. In addition, the species has relatively small wing elements that are of similar length to those of *G. stairi*.

HOLOTYPE: MNZ S40789, 1L tarsometatarsus. It is an adult bone that is a pale creamy colour with some brown streaking. It was reassembled from two pieces and is missing trochlea II (TII) and part of the plantar surface of TIV, and is slightly worn down the medial edge of the *fossa parahypotarsalis medialis*.

MEASUREMENTS OF THE HOLOTYPE: See Table 1.

TYPE LOCALITY: Henderson Island, Site 5, testpit 2, spit 14, 6 mm mesh. Collected by M. Weisler & G. Wragg during the Pitcairn Islands Scientific Expedition 1991–1992.

Table 1 Measurements of leg bones of *Gallicolumba leonpascoi*. Abbreviations as in Methods, and mc, medial condyle; mtf, metatarsal fossa.

MNZ S	Element	Tmt TL	Tmt L mc to mtf	Tmt PW	Tmt PD	Tmt PD mc	Tmt SW	Tmt SW at mtf	Tmt DW	Tmt L mc to mf/TL	Tmt PW/TL	Tmt SW/TL	Tmt DW/TL
40839	R tmt	40.28	27.55	8.23	7.82	3.88	3.72	4.16	8.60	0.68	0.20	0.09	0.21
40844	L tmt	43.54	30.70	8.40	8.00	3.93	3.58	3.76	8.86	0.71	0.19	0.08	0.20
40789	L tmt	44.20	30.79	8.72	2.23	4.15	3.73	3.96		0.70	0.20	0.08	
40795	dR tmt							4.00	8.50				
MNZ S	Element	Fem L	Fem PW	Fem SW	Fem DW	Femur depth mc	Femur depth lc	Tib TL	Tib PW	Tib SW	Tib DW	Tib depth mc	Tib depth lc
40832	L fem	44.15	8.26	3.52	8.60	5.36	6.60						
40832	pR fem		8.05										
40828	dR fem				8.20	6.10	6.60						
40828	dL fem				8.25	6.10							
40854	pL fem		8.00										
40854	pR fem		7.95										
40840	L tt												
40842	dR tt							69.28	6.83	3.28	7.80	6.85	6.33
40857	dR tt										7.46	6.53	
											7.74		

PARATYPES: MNZ S40844, 1L tarsometatarsus, Henderson Island, Site 10, testpits 3, spit 7, 6 mm mesh; MNZ S40839, 1R tarsometatarsus, Henderson Island, Site 10, testpit 1, from infilled burrow in precultural sediments (labelled spit 50), 6 mm screen, both collected by M. Weisler & G. Wragg, 1991–1992. MNZ S40839, while adult and more complete and less worn, is judged to have a deformed medial cotyla that is displaced somewhat anterodistally from the normal condition. MNZ S40844 is subadult with incomplete ankylosis of the distal tarsal bone with the fused metatarsals, though it is judged that adult length and width has been attained.

REFERRED MATERIAL: The following material is certainly referable to *Gallicolumba leonpascoi*.

Site 1: testpit 1, spit 10, 6 mm mesh, MNZ S40776, 1R cor; testpit 1, spit 10, 3 mm mesh, MNZ S40778, 1R metatarsal; testpit 1, spit 11, 3 mm mesh, MNZ S40779, dR ulna; testpit 2, spit 3, 3 mm mesh, MNZ S40777, L metatarsal.

Site 3: testpit 1, spit 6, 6 mm mesh, MNZ S40781, dL tmt.

Site 5: testpit 1, spit 8, 3 mm mesh, MNZ S40782, 1L metatarsal; testpit 1, spit 12, 6 mm mesh, MNZ S40784, 1pL cmc; testpit 1, spit 13, 6 mm mesh, MNZ S40785, anterior stern; testpit 1, spit 15, 6 mm mesh, MNZ S40786, 1L cmc; testpit 2, spit 13, 6 mm mesh, MNZ S40787, 1L scap; testpit 2, spit 14, 6 mm mesh, MNZ S40788, pt mand; testpit 3, spit 6, 6 mm mesh, MNZ S40790, 1pR cmc; testpit 8, spit 3, 6 mm mesh, MNZ S40792, 1dL tmt; testpit 9, spit 7, 6 mm mesh, MNZ S40793, 1dR hum; testpit 10, spit 7, 6 mm mesh, MNZ S40795, 1dR tmt; testpit 10, spit 8, 6 mm mesh, MNZ S40796, R acet pel, 1pR hum, R M2.1, 1dL fem frag; testpit 11, spit 3, 6 mm mesh, MNZ S40798, 1dR fem; testpit 11, spit 5, 6 mm mesh, MNZ S40799, 1R scap; testpit 16, spit 3, 6 mm mesh, MNZ S40802, 1 anterior stern; testpit 15, spit 4, 6 mm mesh, MNZ S40801, 1dL cor.

Site 6: testpit 1, spit 7, 6 mm mesh, MNZ S40803, 1pR cmc; testpit 1, spit 11, 3 mm mesh, MNZ S40804, 1pR cor; testpit 1, spit 12, 3 mm mesh, MNZ S40805, pmx, pt mand; testpit 1, spit 13, 3 mm mesh, MNZ S40806, R metatarsal; testpit 1, spit 14, 6 mm mesh, MNZ S40808, 1L scap; testpit 2, spit 11, 6 mm mesh, MNZ S40814, R M2.1; testpit 2, spit 8, 6 mm mesh, MNZ S40810, 1pL ulna; testpit 2, spit 10, 6 mm mesh, MNZ S40813, 1dL tmt; testpit 2, spit 10, 3 mm mesh, MNZ S40812, 1L metatarsal; testpit 2, spit 11, 3 mm mesh, MNZ S40815, 1dR rad; testpit 3, spit 4, 6 mm mesh, MNZ S40816, R cmc.

Site 7, testpit 1: spit 1, 3 mm mesh, MNZ S40818, 1pL cmc; spit 6, 6 mm mesh, MNZ S40821, R M2.1; spit 7, 3 mm mesh, MNZ S40822, pmx, L M2.1, L M2.2.

Site 8: testpit 1, spit 2, 6 mm mesh, MNZ S40823, 1pL cmc.

Site 10: testpit 1, spit 6, 6 mm mesh, MNZ S40826, 1R hum; testpit 1, spit 7, 6 mm mesh, MNZ S40827, 2R scap; testpit 1, spit 8, 6 mm mesh, MNZ S40828, 1L hum; MNZ S40828, 1dL 1dR fem; MNZ S40828, 2R scap; MNZ S40828, pt mand; MNZ S40828, 1R cmc; testpit 1, spit 50 (= burrow), 6 mm mesh, MNZ S40832, 1L 1pR fem; MNZ S40831, 1L cor; MNZ S40840, 1L juv tt with attached astragalus, 1R astragalus; MNZ S40841, 3L ulna; MNZ S40836, LR rad juv; MNZ S40833, 2L hum; MNZ S40837, 1R scap; MNZ S40834, 1 pmx; MNZ S40834, 1L side mand; MNZ S40835, LR acet of pel; MNZ S40835, sac; MNZ S40838, pt skull, frontals and pmx; testpit 1, spit 50 (= burrow), 3 mm mesh, MNZ S40830, metatarsal, 1 pmx, R M2.2; testpit 2, spit 4, 6 mm mesh, MNZ S40842, 1dL tt adult; testpit 2, spit 6, 6 mm mesh, MNZ S40843, 1L 1dL hum.

Site 11: testpit 3, spit 4, 6 mm mesh, MNZ S40847, 1R hum; testpit 3, spit 5, 6 mm mesh, MNZ S40848, 1L 1R ulna; testpit 3, spit 6, 6 mm mesh, MNZ S40849, 1R tmt juv, 1L cmc juv, 1L rad juv, sac, LR acet of pel; testpit 5, spit 4, 6 mm mesh, MNZ S40850, 1L ulna.

Site 21: testpit 1, spit 1, 6 mm mesh, MNZ S40851, anterior stern.

<i>G. longitarsus</i>	NCP100 Holotype (Balouet & Olson 1989)	51.6	8.1	8.1	3	7.9	0.157	0.058	0.153
<i>G. nui</i>	BPBM 176000 (Balouet & Olson 1989)	51.5	9	9	3.9	9.6	0.175	0.076	0.186

Table 3 Measurements of femora (Fem) and tibiotarsi (Tib) of species of *Gallicolumba*. Abbreviations as in Methods, and mc, medial condyle; lc, lateral condyle. Data for *G. tristigmata* are mean (range) *n*.

Species	Catalogue no.	Fem L	Fem		Femur		Tib TL	Tib PW	Tib SW	Tib DW	Femur depth mc	Femur depth lc	Tib TL	Tib PW	Tib SW	Tib DW	Tib depth mc	Tib depth lc	Tib TL/Fem TL	Tib DW/TL	
			PW	SW	DW	DW															mc
<i>G. beccarii</i>	AMNH 7718	27.21					45.03														
<i>G. beccarii</i>	USNM 615012	27.59					41.84														
<i>G. beccarii</i>	UWBM 43037	27.74	4.58	1.94	4.4	3.12	45.06	3.92	1.75	3.71	3.86	3.44	3.71	3.92	1.75	3.71	3.86	3.44	0.616	0.082	
<i>G. criniger</i>	LACM 89052	40.23	7.7	3.3	7.25	5.28	61	6.7	3.08	6.3	6.16	5.4	6.3	6.7	3.08	6.3	6.16	5.4	0.660	0.103	
<i>G. jobiensis</i>	AMNH 6753						49.23														
<i>G. luzonica</i>	MVZ53804	36.22	6.47	3	6.58	4.87	55.15	5.75	2.4	5.3	6.02	5.1	5.3	5.75	2.4	5.3	6.02	5.1	0.657	0.096	
<i>G. luzonica</i>	LACM 89051	35.7	6.74	3.08	7	4.82	55.65	6.1	2.7	5.96	5.77	5.14	5.96	6.1	2.7	5.96	5.77	5.14	0.642	0.107	
<i>G. luzonica</i>	LACM 89050	39.8	7	3.04	6.9	5	60.9	6.05	2.82	5.77	6	5.32	5.77	6.05	2.82	5.77	6	5.32	0.654	0.095	
<i>G. rufigula</i>	LACM 106368	32.7	5.85	2.9	6.34	4.3	51.27	5.04	2.37	4.78	5.33	4.66	4.78	5.04	2.37	4.78	5.33	4.66	0.638	0.093	
<i>G. rubescens</i>	MVZ46017	27.4	4.9	2.16	5	3.42	43.72	4.6	2	4.36	4.68	3.8	4.36	4.6	2	4.36	4.68	3.8	0.627	0.100	
<i>G. stairi</i>	MVZ51708	38.54	7.75	3	7.16	5.55	61	59.25	2.66	5.8	6.44	5.67	5.8	6.4	2.66	5.8	6.44	5.67	0.650	0.098	
<i>G. stairi</i>	NHM S/1975.3.3	34.2	6.7	2.8	6.4	5.7	51.9	5.7	2.5	5.3				5.7	2.5	5.3			0.659	0.102	
<i>G. tristigmata</i>	USNM (Balouet & Olson 1989)	41.5 (39.5– 42.7)	7.9 (7.5– 8.1)	3.1 (3.0– 3.2)	7.4 (6.9– 7.8)	5.6 (5.9)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)	6.3 (6.0– 6.8)
<i>G. longitarsus</i>	Balouet & Olson 1989, NCP101	45.4 <i>n</i> = 4	9.4 <i>n</i> = 4	3.8 <i>n</i> = 4	9.4 <i>n</i> = 3	6.7 <i>n</i> = 4	7.3 <i>n</i> = 3	9.4 <i>n</i> = 4	3.8 <i>n</i> = 4	9.4 <i>n</i> = 3	6.7 <i>n</i> = 4	7.3 <i>n</i> = 3	9.4 <i>n</i> = 4	3.8 <i>n</i> = 4	9.4 <i>n</i> = 3	6.7 <i>n</i> = 4	7.3 <i>n</i> = 3	9.4 <i>n</i> = 4	3.8 <i>n</i> = 4	9.4 <i>n</i> = 3	6.7 <i>n</i> = 4

Site T12 (a palaeontological site): testpit 1, spit 1, MNZ S40853, 1R metatarsal, LR M2.2, 1L scap, 1pR hum frag, 1pR cor, 1R fib, testpit 1, spit 2, MNZ S40854, 1pL 1pR fem, 1dL ulna, 1R metatarsal, testpit 2, spit 1, MNZ S40855, L M2.2, testpit 3 spit 1, MNZ S40856, L M2.1, 1R cmc, skull frag, pmx, L acet of pel, testpit 4, spit 1, MNZ S40857, 1L1R metatarsal, 1pL ulna, 1R cmc, 1dR tt, 1R acet of pelvis, 1dL hum.

The following material is probably referable to *Gallicolumba leonpascoi*.

Site 1: testpit 1, spit 10, 3 mm mesh, MNZ S40778, pedal phal LII.1, RIV.2; testpit 1, spit 11, 3 mm mesh, MNZ S40779, pedal phal III.2.

Site 3: testpit 1, spit 6, 3 mm mesh, MNZ S40780, pedal phal RIV.1, RIII.1.

Site 5: testpit 1, spit 9, 3 mm mesh, MNZ S40783, ungual phal, pedal phal ?II.2; testpit 1, spit 12, 6 mm mesh, MNZ S40784, pedal phal IV.1; testpit 2, spit 14, 6 mm mesh, MNZ S40788, pedal phal ?II.2, 4 vert, skull frag; testpit 6, spit 4, 6 mm mesh, MNZ S40791, pt fur; testpit 10, spit 6, 6 mm mesh, MNZ S40794, pedal phal RII.1; testpit 13, spit 8, 3 mm mesh, MNZ S40800, pedal phal L or R III.3.

Site 6: testpit 2, spit 9, 3 mm mesh, MNZ S40811, pedal phal RIII.2; testpit 2, spit 10, 3 mm mesh, MNZ S40812, ungual phal, pedal phal LR IV.1; testpit 1, spit 12, 3 mm mesh, MNZ S40805, pedal phal I.1 juv.; testpit 1, spit 13, 3 mm mesh, MNZ S40806, pedal phal ?IV.3, III.3; testpit 1, spit 14, 3 mm mesh, MNZ S40807, pedal phal ?LIV.2; testpit 1, spit 17, 3 mm mesh, MNZ S40809, pedal phal LIV.1; testpit 102, spit 50, 3 mm mesh, MNZ S40817, pedal phal LI.1.

Site 7: testpit 1, spit 5, 3 mm mesh, MNZ S40819, pedal phal LIV.1, ?III.3; testpit 1, spit 6, 3 mm mesh, MNZ S40820, pedal phal LIII.1; testpit 1, spit 7, 3 mm mesh, MNZ S40822, pedal phal RII.1, III.1, ungual phal.

Site 8: testpit 3, spit 8, 3 mm mesh, MNZ S40824, ungual phal; testpit 3, spit 9, 3 mm mesh, MNZ S40825, pedal phal III.3.

Site 10: testpit 1, spit 8, 6 mm mesh, MNZ S40828, 2 cranial frags, 1L palatine, 2 vert; testpit 1, spit 50 (burrow), 6 mm mesh, MNZ S40829, pt fur; testpit 1, spit 50 (burrow), 3 mm mesh, MNZ S40830, ungual phal, pedal phal III.3, L M1.1 (alula).

Site 11: testpit 2, spit 4, 6 mm mesh, MNZ S40845, pedal phal III.2; testpit 2, spit 5, 6 mm mesh, MNZ S40846, pedal phal III.1; testpit 5, spit 4, 6 mm mesh, MNZ S40850, skull frag.

Site 21: testpit 1, spit 2, 3 mm mesh, MNZ S40852, pedal phal RI.1.

Site T12: testpit 1, spit 1, MNZ S40853, pedal phal 2L2R IV.1, LII.1, RIII.1, RIII.2, RIV.2, I.1, 2R radiale, ungual phal; testpit 1, spit 2, MNZ S40854, pedal phal I.1, II.1, III.1, IV.2, IV.3, ungual phal; testpit 2, spit 1, MNZ S40855, pedal phal RI.1, ?II.2, RIII.2; testpit 3, spit 1, MNZ S40856, pt fur, R radiale, pedal phal RII.1, 3L I.1, RIII.1, LIV.2; testpit 4, spit 1, MNZ S40857, pedal phal IV.4.

The following additional material referable to *Gallicolumba leonpascoi* was used for radiocarbon dating (Hedges et al. 1997).

Site 6, testpit 1, spit 10: 1L ulna, no collagen, no date, Wragg (1995b, fig. 3.22.2).

Site 6, testpit 1, spits 10 & 11: 2R metatarsal, 1dL rad, 1 fib, phalanges, $13\,420 \pm 340$ ^{14}C yr BP (OxA5910), Wragg (1995b, fig. 3.22.7).

Site 6, testpit 1, spits 15 & 16: pt stern, L cor, L metatarsal, LM2.1, 3 pedal phalanges, 2320 ± 60 ^{14}C yr BP (OxA6018), Wragg (1995b, fig. 3.22.11).

Site 6, testpit 1, spit 17: L rad, 2 pts ant stern, pt dR tmt, dRpR rad, no collagen, no date, Wragg (1995b, fig. 3.22.4).

Site 10, testpit 1, spit 50 (burrow): R acet of pelvis, 1885 ± 55 ^{14}C yr BP (OxA6019), Wragg (1995b, fig. 3.22.12).

Description and comparison

Tarsometatarsus (Fig. 2)

Tarsometatarsi of *G. leonpascoi* at 40–44 mm long are larger than all extant taxa except *G. tristigmata*, which it overlaps in length (Tables 1 and 2; Appendix 1). Among extinct taxa, both *G. longitarsus* of New Caledonia (Balouet & Olson 1989) and *G. nui* of the Marquesas and the Cook Islands (Steadman 1992, 1997) were larger. However, tarsometatarsi of *G. leonpascoi* are more robust than those of *G. nui* (Steadman 1992), and much more so than those of *G. tristigmata* and *G. longitarsus* (Table 2; Balouet & Olson 1989). The tarsometatarsus of *G. leonpascoi* differs further from that of *G. nui* in that the proximomedial margin is concave not convex and the lateral *foramen vascularium proximalium* is about half the size of its medial counterpart. In the diagnosis of *G. nui*, the lateral foramen is described as smaller than in *G. longitarsus* (Steadman 1992, p. 330), but Steadman (1992, p. 343) stated that the Henderson tarsometatarsal fragment (USNM 388744) “resembles that of *G. erythroptera* rather than that of *G. nui* in ... the presence of a lateral *foramen vascularium proximalium*”, inferring that *G. nui* lacks one, as it would appear from the figured holotype (Steadman 1992, fig. 2A). This may be an aberration of the individual bone, but it seems that the lateral foramen is either much reduced or closed and the medial one relatively more enlarged than in *G. leonpascoi*.

The tarsometatarsus of *G. leonpascoi* has proportions like that of *G. stairi* and *G. rubescens* (Table 2), and shares with those taxa a similarly strongly grooved dorsal surface to TIV. The tarsometatarsus of *G. erythroptera* is markedly smaller. The tarsometatarsus of *G. beccarii* is very much smaller, more elongate, has a poorly demarcated *fossa metatarsi I*, but has a dorsally grooved TIV. Tarsometatarsi of *G. luzonica* and *G. rufigula* also have relatively narrower proximal and distal ends but the TIV is not deeply grooved on its dorsal surface. Tarsometatarsi of *G. criniger*, while having a similar length and distal and proximal dimensions to *G. stairi*, and a dorsally grooved TIV, differ in having a much thicker shaft. In *G. criniger*, the *fossa parahypotarsalis medialis* is relatively larger yet the *fossa metatarsi I* is relatively smaller compared with *G. leonpascoi*.

In *G. leonpascoi*, *G. beccarii*, *G. stairi*, and *G. rubescens* the *cotyla lateralis* and *cotyla medialis* are nearly level with each other, whereas in *G. rufigula*, *G. criniger*, and *G. luzonica* the lateral cotyla is farther distad. In *G. leonpascoi*, *G. rubescens*, and *G. stairi*, more than half the width of the lateral cotyla overhangs the side of the shaft, contributing to a markedly flared proximal end. That it does not in the paratype MNZ S40839 is considered an abnormality in this individual due to the anterodistal rotation of the medial cotyla. In *G. beccarii*, the lateral cotyla overhangs the shaft, but to a lesser degree than in *G. stairi*. In *G. criniger*, the lateral cotyla does not overhang the side of the shaft, and it is only slightly overhung in *G. luzonica* and *G. rufigula*.

In *G. leonpascoi*, *G. stairi*, and *G. beccarii*, the depth of the hypotarsus is greater than the depth of the medial cotyla, whereas it is slightly less in *G. rubescens*, *G. rufigula*, *G. luzonica*, and *G. criniger*.

In *G. leonpascoi* and *G. stairi*, the *crista plantaris medialis* is thin dorsoventrally and is undercut proximally below the medial cotyla by the deeply excavated *fossa parahypotarsalis medialis* that extends distally to about mid length. In *G. luzonica* and *G. rufigula*, the *crista plantaris medialis* is thicker dorsoventrally with a rounded medial margin and the *fossa parahypotarsalis medialis* shallower proximally. In *G. leonpascoi* and *G. stairi*, the proximal half of the medial profile of the shaft is concave, whereas it forms a straight line below the

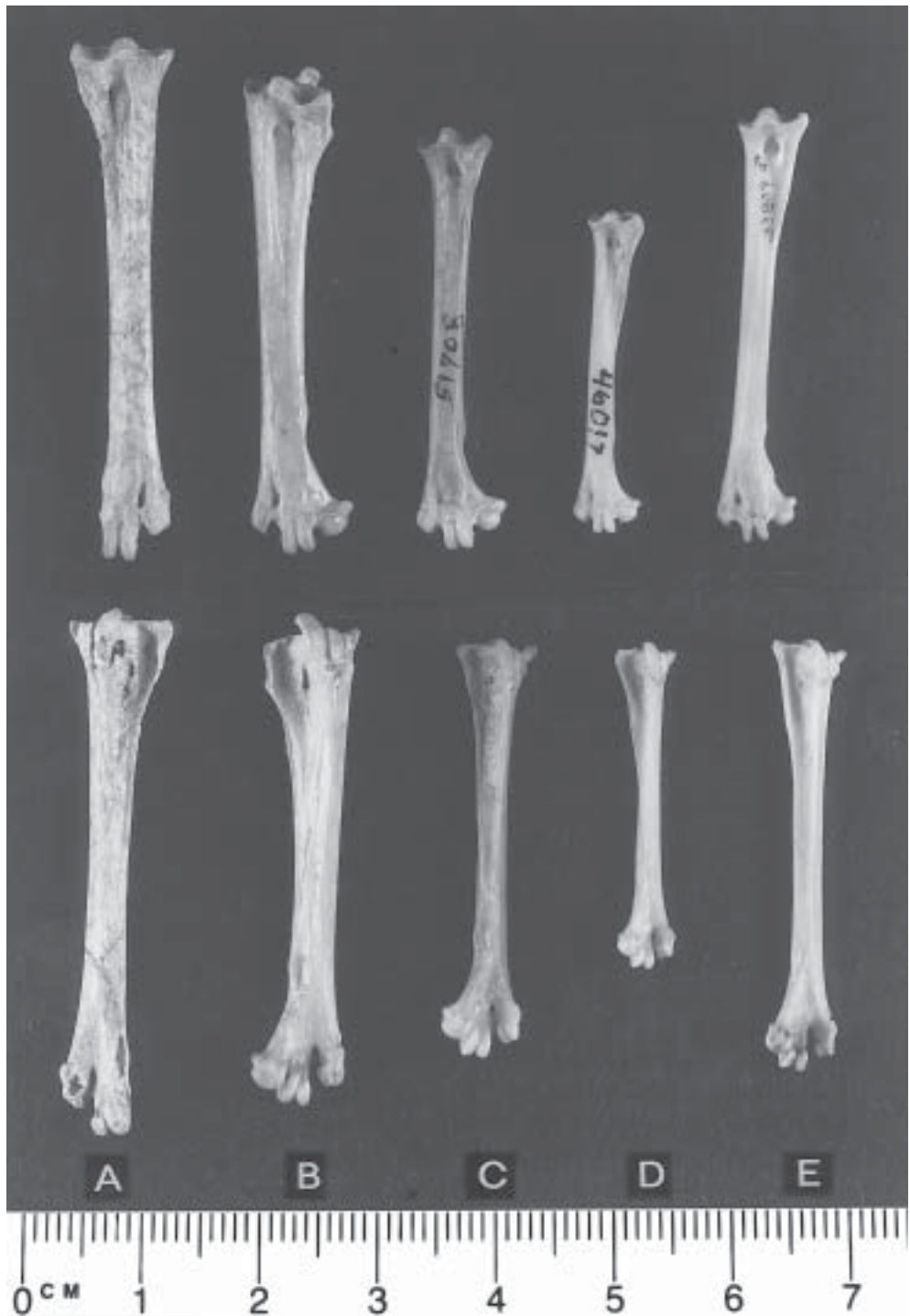


Fig. 2 *Gallicolumba* tarsometatarsi in dorsal view (upper and plantar view (lower), left element (A) and right elements (B–E). A, *G. leonpascoi*, holotype, MNZ S40789; B, *G. leonpascoi*, paratype, MNZ S40839; C, *G. stairi*, MVZ 51708; D, *G. rubescens*, MVZ 46017; E, *G. luzonica*, MVZ 53804.

cotyla in *G. luzonica*, *G. criniger*, and *G. rufigula*, and the *fossa parahypotarsalis medialis* extends noticeably past mid length. In *G. beccarii*, the *fossa parahypotarsalis medialis* is small, and while not excavated deeply proximally is bound dorsally by a thin *crista plantaris medialis*, and it does not extend as far as the mid-length point and the medial profile is straight. In *G. criniger*, where the tarsometatarsus is of similar length to that of *G. stairi*, the *fossa parahypotarsalis medialis* is much broader and is about twice as large due to excavation laterally and expansion medially of the *crista plantaris medialis*.

In *G. leonpascoi*, *G. nui*, and *G. stairi*, the *foramen vascularia proximalia medialis* is larger than its lateral counterpart, whereas the lateral foramen is larger in *G. rufigula* and *G. rubescens*, or they are of equal size in *G. beccarii*, *G. luzonica*, and *G. criniger*. Above the proximomedial side of the medial foramen in *G. leonpascoi* there is a low elongate ridge, one of the *impressiones retinaculi extensorii*, which is stouter and more prominent in *G. stairi*. In *G. stairi*, *G. leonpascoi*, *G. beccarii*, *G. rufigula*, and *G. rubescens*, the medial foramen forms the medial border of the *fossa infracotylaris dorsalis* or the top edge of the *sulcus extensorius*, with the *facies* medial to it and the *tuberositas m. tib. cranialis* being directed medially. In contrast, in *G. luzonica* and *G. criniger* the *sulcus extensorius* is wider and extends proximally as a separate groove medially of the *tuberositas m. tib. cranialis* and the crest medial to the medial foramen. The latter crest is thus seated deeper in the fossa below the cotyla and overhangs the medial foramen, partially occluding it. As a result, the *facies* below the medial cotyla is directed anteriorly, not medially.

The tarsometatarsus of *G. leonpascoi* has flattened trochleae like *G. beccarii*, *G. stairi*, and *G. rubescens*, so that in plantar view T2 overlaps T3 by about 50% of depth (in *G. luzonica*, *G. rufigula*, *G. criniger*, T2 is totally distad of T3).

In *G. leonpascoi* and in *G. rubescens*, the proximal plantar surface on trochlea IV is slightly hooked proximodistally, whereas it is not in *G. stairi*, *G. beccarii*, *G. rufigula*, *G. luzonica*, or *G. criniger*.

In summary, the tarsometatarsus of *G. leonpascoi* is most similar to that of *G. stairi* or *G. rubescens*.

Femur (Fig. 3)

The femur of *G. leonpascoi* is stout and larger than any extant species of *Gallicolumba* (Tables 1 and 3; Appendix 1) and is narrowest at mid length; there is no excavation mediadorsally under the *crista trochanteris*; the trochanter is not raised much above the *facies articularis antitrochanterica*; the *fossa poplitea* is deep; the *impressio ansae m. iliofibularis* is swollen and elevated from the shaft proximodistally, but not so much above the shaft between it and the popliteal fossa. The single described specimen of the extinct *G. longitarsus* is slightly longer and, uniquely within *Gallicolumba*, has a pneumatic foramen on the anterior face of the trochanter (Balouet & Olson 1989). The femur of *G. nui* is undescribed.

In *G. stairi*, the shaft is slender and has the same diameter over the middle 50% of femur length; the femur is also not excavated mediadorsally under the trochanter; the *impressio ansae m. iliofibularis* is elevated above the area between it and the popliteal fossa. The femora of *G. rubescens* and *G. beccarii* are much smaller but are shaped like that of *G. stairi* except that the shaft is narrowest at mid point.

The femur of *G. rufigula* has a robust shaft that is narrowest at mid length; the trochanter is excavated and undercut mediadorsally; and the *impressio ansae m. iliofibularis* is not markedly raised above the area between it and the popliteal fossa.

In *G. luzonica* and *G. criniger*, the shaft is robust and narrowest at mid length; there is no excavation under the trochanter mediadorsally but the area laterad of the popliteal fossa is elevated as in *G. rufigula*.



Fig. 3 *Gallicolumba* left femora in dorsal view (upper and ventral view (lower). **A**, *G. leonpascoi*, MNZ S40832; **B**, *G. stairi*, MVZ 51708; **C**, *G. rubescens*, MVZ 46017; **D**, *G. luzonica*, MVZ 53804.



Fig. 4 *Gallicolumba* left tibiotarsi in anterior view. A, *G. leonpascoi*, adult distal end, MNZ S40842; B, *G. leonpascoi*, juvenile, MNZ S40840; C, *G. stairi*, MVZ 51708; D, *G. rubescens*, MVZ 46017; E, *G. luzonica*, MVZ 53804.

Tibiotarsus (Fig. 4)

One adult distal end of a tibiotarsus referred to *G. leonpascoi* allows comparisons with other taxa. It is larger than any extant species of *Gallicolumba* (Table 1). It is referred to *Gallicolumba* by the similar depth:width proportion of the condyles (*Ducula*, *Columba*, and *Ptilinopus* are much wider than deep). The lateral side of the *sulcus extensorius* lacks the sharp ridge of *Ducula*. It differs from *G. rubescens* and *G. stairi*, apart from its larger size, in having a much larger tubercle in the middle of the *condylus medialis*. *G. beccarii* has a small tubercle on the medial condyle. The species *G. rufigula*, *G. luzonica*, and *G. criniger* lack a tubercle in the middle of the medial condyle. The juvenile tibiotarsus indicates a total length of c. 70 mm.

Humerus (Fig. 5)

Humeri of *Gallicolumba* have a more pedicellate *proc. supracondylaris dorsalis* than in *Ptilinopus*; the *fossa pneumotricipitalis* has a large pneumatic foramen in it (small in *Ptilinopus*, *Ducula*); dorsal surface of *crista deltopectoralis* is concave (flat in *Ptilinopus*,

concave in *Ducula*); the *incisura capitalis* is partially bridged by a low ridge at the end opening towards the *margo caudalis* (low ridge not present in *Ptilinopus*).

The humerus of *G. leonpascoi* has all the above features of *Gallicolumba* and is similar in length to that of *G. stairi* (Tables 4 and 5; Appendix 1). However, it is much smaller proximally with the *crista bicipitalis* ending distally not much beyond a point level with the angle of the *crista deltopectoralis* (*crista bicipitalis* markedly distad of the angle of the *crista deltopectoralis* in *G. stairi*), and has a relatively thinner shaft and distal end. The *fossa brachialis* is well defined, oval in shape, and lies entirely in the ventral half of the bone and the *epicondylus ventralis* is more acutely pointed. Humeri of *G. luzonica* have similar proportions to those of *G. stairi* and differ only slightly with a more well-marked brachial fossa, and a less acute *epicondylus ventralis*. Humeri of *G. rufigula* and *G. criniger* are

Table 4 Wing bone measurements of *Gallicolumba leonpascoi*. Abbreviations as listed in Methods.

MNZ S	Part	Hum TL	Hum PW max.	Hum PW from dorsal tubercle	Hum SW	Hum SD	Hum DW	Hum depth of dorsal condyle
40857	dL hum						8.14	4.95
40833	L hum	37.68	12.94	10.62	3.50	2.96	8.52	5.00
40833	L hum	35.71	12.50	9.93	3.56	2.92	8.28	4.90
40826	R hum	37.38		10.82	3.60	2.94	8.53	5.03
40828	L hum	37.77	13.29	10.66	3.52	3.03	8.53	5.00
40843	L hum	37.58		10.63	3.64	2.94		
40843	dL hum						8.07	5.10
40793	dR hum						8.28	
40847	R hum	35.50	12.75	10.37	3.40	3.18	8.36	5.07

MNZ S	Part	Ulna TL	Ulna PW	Ulna SW (dorso-ventral)	Ulna DW max.	Cmc TL	Cmc PW	Cor med L	Cor sternal W	Rad TL
40841	L ulna	41.50	5.30	2.55	4.60					
40841	L ulna	40.00	5.21	2.50	4.75					
40841	L ulna	41.40	5.25	2.50	4.92					
40850	L ulna	38.35	4.95	2.56	4.66					
40848	L ulna	38.83	5.21	2.52	4.75					
40848	R ulna	39.05	5.19	2.54	4.74					
40779	dR ulna				4.91					
40857	pL ulna		5.26							
40836	R rad									37.40
40836	L rad									37.18
40849	L rad									33.10
40831	L cor							28.43	6.66	
40856	R cmc					22.64	6.27			
40818	pL cmc						6.82			
40816	R cmc					22.70	6.50			
40828	R cmc					24.22	7.03			
40786	L cmc					23.76	6.90			
40823	pL cmc						6.61			
40849	L cmc					21.95	6.10			
40857	R cmc					24.00	6.86			



Fig. 5 *Gallicolumba* humeri (upper) in caudal view (A, B, F, G left element; E right element), and left ulnae (lower) in dorsal aspect. A, B, G, *G. leonpascoi*, MNZ S40833; C, D, *G. leonpascoi*, MNZ S40841; E, H, *G. stairi*, MVZ 51708; F, I, *G. rubescens*, MVZ 46017; G, J, *G. luzonica*, MVZ 53804.

relatively shorter and more robust than that of *G. luzonica* but are otherwise similar. Humeri of *G. beccarii* and *G. rubescens* are very much smaller (Table 5).

Ulna (Fig. 5)

In *Gallicolumba*, the olecranon is very rounded (pointed in *Ptilinopus*). The ulna of *G. leonpascoi* is about as long as that of *G. stairi* and is similarly slender, whereas those of *G. rufigula*, *G. criniger*, and *G. luzonica*, are all stout (Tables 4 and 5; Appendix 1). On the caudal surface, dorsal to the olecranon, is a groove that forms a marked notch anterior to the cotyla, best seen in medial view. A similar notch is present in *G. beccarii*, *G. rubescens*, and *G. stairi*, but in *G. rufigula*, *G. criniger*, and *G. luzonica* the “groove” is much shallower.

Table 5 Measurements of wing elements of species of *Gallincolumba*, abbreviations as in Methods.

Species	Catalogue no. or reference	Hum TL	Hum PW max.	Hum PW ex dorsal tub	Hum SW	Hum SD	Hum DW	Hum depth dorsal cond	Hum TL/Fem TL
<i>G. beccarii</i>	AMNH 7718	24.52							0.901
<i>G. beccarii</i>	USNM 615012	25.9							0.939
<i>G. beccarii</i>	UWBM 43037	24.87	8.7	7.45	2.56	2.12	5.95	3.63	0.897
<i>G. criniger</i>	LACM 89052	37.82	15.2	12.7	4.36	3.7	10.2	5.95	0.940
<i>G. luzonica</i>	MVZ 53804	35.2	12.9	10.96	3.96	3.5	8.75	5.3	0.972
<i>G. luzonica</i>	LACM 89051	34.86	13.25	11.35	4.02	3.6	8.87	5.7	0.976
<i>G. luzonica</i>	LACM 89050	36.26	13.52	11.62	4.14	3.52	9.34	5.8	0.911
<i>G. rufigula</i>	LACM 106368	32.02	12.8	10.85	3.76	3.13	8.36	5.22	0.979
<i>G. rubescens</i>	MVZ 46017	28.2	9.55	7.9	2.5	2.16	6.45	3.86	1.029
<i>G. stairi</i>	MVZ 51708	36.8	14.06	12.03	4.0	3.27	9.1	5.34	0.955
<i>G. stairi</i>	NHM S/1975.3.3	34.0	10.3		3.85		8.2		0.994

Species	Catalogue no. or reference	Ulna TL	Ulna PW	Ulna (dorso-ventral)	Ulna SD	Ulna DW max.	Ulna TL/Fem TL	Cmc TL	Cmc PW	Cmc DW	Cmc TL/Fem TL	Cor med L	Cor sternal W
<i>G. beccarii</i>	AMNH 7718							16.9			0.637	21.44	
<i>G. beccarii</i>	USNM 615012	30.86						17.58			0.598	20.35	4.6
<i>G. beccarii</i>	UWBM 43037	30.0	3.66	1.74	2.07	3.54	1.081	16.6	4.7	3.45	0.605	31.35	8.84
<i>G. criniger</i>	LACM 89052	44.94	6.6	2.85	3.74	5.6	1.117	24.35	8.11	6.7			
<i>G. jobienis</i>	AMNH 6753	40.43						23.31					
<i>G. luzonica</i>	MVZ 53804	40.88	5.7	2.7	2.91	5.06	1.129	24.16		6.14	0.667	28.23	8.1
<i>G. luzonica</i>	LACM 89051	41.18	6.14	2.65	2.9	5.32	1.154	23.4	7.4	6.24	0.655	28.78	8
<i>G. luzonica</i>	LACM 89050	43.16	6.5	2.7	3.0	5.48	1.084	24.72	7.3	6.3	0.621	29.5	6.92
<i>G. rufigula</i>	LACM 106368	37.8	5.2	2.43	2.78	4.5	1.156	21.8	6.74	5.55	0.667	25.96	7.14
<i>G. rubescens</i>	MVZ 46017	32.14	4.14	1.92	2.24	3.7	1.173	18.96	5.26	4.34	0.692	21.18	5
<i>G. stairi</i>	MVZ 51708	43.56	5.7	2.53	2.65	5.24	1.130	24.24	7.64	6.1	0.629	30.2	7.7
<i>G. stairi</i>	NHM S/1975.3.3	40.2	5.5	2.5		4.8	1.175	23.15	6.65		0.677	27.65	

The depth of the *condylus ventralis ulnaris* is less than the width from the ventral condyle to the *tuberculum carpale* in *G. stairi* and *G. rubescens*, about equal in *G. beccarii*, but distinctly greater in *G. rufigula*, *G. criniger*, and *G. luzonica*. In *G. leonpascoi*, these measurements are about equal, as the carpal tuberculum is not as extended ventrally and not as pointed as in *G. stairi*.

Another feature of the ulna of *G. leonpascoi* is that only the distal 4 papillae are obvious. In ulnae of *G. stairi* and *G. rubescens*, the distal-most 5 are prominent, and in *G. beccarii*, *G. rufigula*, *G. criniger*, and *G. luzonica*, 7 are obvious.

Carpometacarpus (Fig. 6)

In *Galllicolumba*, the *proc. extensorius* is prominent and directed proximo-laterally, the *proc. pisiformis* is robustly buttressed caudally, the proximal synostosis between the metacarpals is short, and the central section of the *os metacarpale minus* is rotated to partly face ventrally in its mid section. The carpometaacarpus of *Galllicolumba* has a wider *spatium intermetacarpale*, effected by a wider distal end, than has *Ptilinopus*.

There is a poorly developed *proc. intermetacarpalis* in *Galllicolumba*, which in *G. leonpascoi* is centred on the mid point of the intermetacarpal space, as in *G. rubescens*, and similar to *G. stairi* where it is located just above the mid point. In *G. beccarii*, *G. rufigula*, *G. luzonica*, and *G. criniger* it is located in the proximal half of the intermetacarpal space.

Galllicolumba leonpascoi has a reduced proximal end compared with other species, so while the whole element is of similar length to that of *G. stairi*, the proximal width is less (Tables 4 and 5; Appendix 1). In all species of *Galllicolumba*, the internal rim of the *trochlea carpalis* ends abruptly proximad to the minor metacarpal at a point about level with the distal margin of the pisiform process, as it does in *Ducula*. It slopes gradually to the minor metacarpal in *Ptilinopus*. The distal edge of the internal rim is just proximad to the *proc. alulae*, in most *Galllicolumba* species, whereas in *G. leonpascoi*, the distal edge of the internal rim is markedly proximal to the alular process as a result of the reduced size of the carpal trochlea.

Coracoid (Fig. 6)

Coracoids of *Galllicolumba* are characterised by the *proc. acrocoracoideus* being non-pneumatic (large pneumatic foramen in *Ptilinopus*), the dorsal surface of the sternal end has pneumatic fossae within a large sulcus on the *proc. medialis* and smaller fossae on the *proc. lateralis*, and the *facies articularis clavicularis* is notched, with the ventral lobe longest and overhanging the *sulcus m. supracoracoidei* to form a distinct hook. The dorsal lobe is expanded dorsally so that in medial aspect it overhangs the *cotyla scapularis* (much less developed in *Ducula* and *Ptilinopus*). The *proc. procoracoideus* is relatively larger in *Galllicolumba* than it is in *Ducula* or *Ptilinopus*.

The coracoid of *G. leonpascoi* is broadly similar to other species of *Galllicolumba*, but is a bit smaller than that of *G. stairi* and is relatively more slender (Tables 4 and 5; Appendix 1). The lateral margin forms a thin flange above the lateral process that merges with the shaft before mid length; the *impressio m. sternocoracoidei* is shallower and similar to that of *G. stairi*, with small foramina medially and laterally. The *angulus medialis* is produced as an acute point. The procoracoid extends as a lobe towards the ventral lobe of the clavicle articular facet, but does not extend above the *cotyla scapularis*.

In *G. stairi* and *G. rubescens*, the margin above the lateral process extends as a thin flange to about 50% of the distance to the shaft mid-length point, whereas it extends to mid length in *G. beccarii*, *G. luzonica*, *G. criniger*, and *G. rufigula*.



In *G. stairi*, *G. beccarii*, and *G. rubescens* the medial angle is drawn to an acute point as in *G. leonpascoi*, whereas in *G. luzonica*, *G. criniger*, and *G. rufigula* the medial surface of the shaft nearly forms a right angle with the *facies artic. sternalis*. These three taxa differ further in that the margin above the medial angle is drawn into a narrow flange, whereas the shaft is rounded at this point in *G. stairi*, *G. rubescens*, and *G. leonpascoi*. However, in *G. beccarii*, the margin above the medial angle is a narrow flange.

The procoracoid extends above the scapular cotyla in *G. luzonica*, *G. criniger*, and *G. rufigula*, partially closing the gap between it and the *proc. acrocoracoideus*, whereas in *G. stairi*, *G. beccarii*, and *G. rubescens* the *proc. procoracoideus* does not extend above the cotyla *scapularis*.

Summary

The foregoing comparisons show that *Gallicolumba leonpascoi* had bones most similar to those of *G. stairi*, with some similarity to *G. rubescens*. The latter is substantially smaller and its skeleton is modified reflecting its reduced flight ability. Taxa such as *G. luzonica*, *G. rufigula*, *G. criniger*, and *G. tristigmata* differ from *G. leonpascoi* in many ways, as predicted from the more distant relationships these taxa have to *G. stairi*, indicated by Goodwin (1967, fig. D11).

RADIOCARBON DATING

Radiocarbon ages on several bones of *G. leonpascoi* were reported by Hedges et al. (1997) and support the field observations that most bones of this species were either in the lowermost archaeological horizons or in the still lower precultural sediments (Wragg 1995b). One sample (comprised of 13 phalanges, 2 metatarsals, a partial radius, and a partial fibula (OxA-5910) (see Wragg 1995b, fig. 3.22), from Site 6, testpit 1, spit 10), was, at $13\,420 \pm 340$ ^{14}C yr BP, one of the oldest radiocarbon dates for bones from a Pacific island. Another sample (comprised of a left coracoid, 3 phalanges, a metatarsal, a sternal fragment, and a left alar phalanx M2.1 (OxA-6018) from Site 6, testpit 1, spits 15 and 16) was 2320 ± 60 ^{14}C yr BP. Such ages from pooled specimens give an average of the carbon derived from collagen contributed by each specimen, and small poorly preserved bones may contribute nothing to the date, which will be most affected by the better preserved elements. Thus, these ages probably indicate a minimal age for at least one of the contributing bones in each sample, and it is probable that a large element (coracoid) in the second sample (OxA-6018) contributed most to the age. That these ages differ greatly, and are inverted with respect to the location of the samples in the stratigraphy, is probably explained by the combination of differential preservation of the bones pooled in the sample, with the smaller specimens unlikely to contribute any collagen (two other samples from Site 6 failed to have enough collagen to date (Wragg 1995b, fig. 3.22.2, 3.22.3); and the inversion of the key carbon contributors by the extensive burrowing caused by crabs and petrels in the site. Despite the uncertainties, it suggests that Site 6 may preserve a record back to the Late Pleistocene period.

◀ **Fig. 6** *Gallicolumba* left coracoids in dorsal view (upper), ventral view (middle), and carpometacarpus in ventral view (lower). **A, B**, *G. leonpascoi*, MNZ S40831; **C**, *G. leonpascoi*, MNZ S40828; **D–F**, *G. stairi*, MVZ 51708; **G–I**, *G. rubescens*, MVZ 46017.

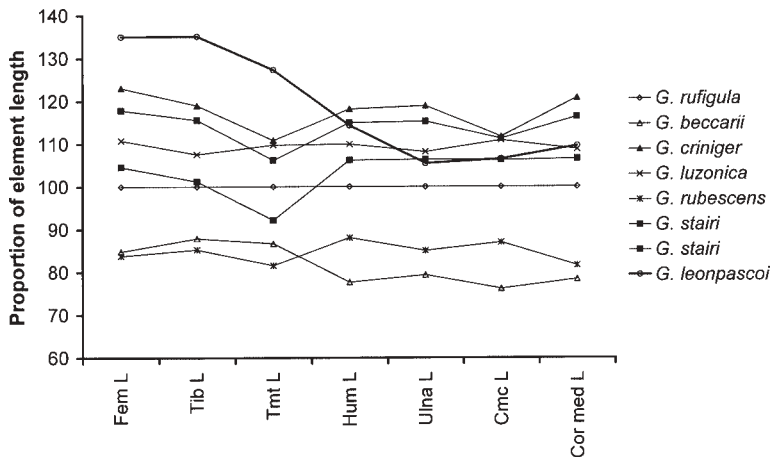


Fig. 7 A ratio diagram comparing *G. leonpascoi* with selected species of *Gallicolumba*. The average-sized volant *G. rufifigula* is taken as the standard, so its elements are plotted as 100%, with elements of the other taxa plotted as proportions of it. Thus, species with lines below the horizontal line are smaller and those above larger. If all species had equal proportions lines would be parallel. The comparison clearly shows that the wing and pectoral girdle elements of *G. leonpascoi* are much reduced from their expected size given leg bone size and the lines for *G. criniger* or *G. stairi*. Specimens used: *G. rufifigula* LACM 106368, *G. beccarii* UWBM 43037, *G. criniger* LACM 89052, *G. luzonica* MVZ 53804, *G. rubescens* MVZ 46017, *G. stairi* MVZ 51708, *G. stairi* NHM S/1975.3.3, and for *G. leonpascoi* the mean of the lengths in Tables 1 and 2.

DISCUSSION

The three known extinct species of *Gallicolumba*, *G. leonpascoi*, and *G. nui* of the Marquesas (Steadman 1992, 1997), and *G. longitarsus* of New Caledonia (Balouet & Olson 1989), are also the largest species in the genus. Steadman (1992) referred bones to *G. nui* from the Society Islands and the Cook Islands but these groups lie considerably to the south-west of the Marquesas. The presence of the well-defined *G. leonpascoi* on Henderson Island, an equal distance from the Marquesas to the south-east, and its relatively rapid derivation as a species, raises the possibility that the few specimens of a limited variety of elements referred to *G. nui* from the Society and the Cook Islands (Steadman 1992) may be from a distinct, similar-sized, island derivative.

The recognition of *G. leonpascoi*, combined with the known geological history of Henderson Island, provides another example of near flightlessness occurring over a known and relatively short amount of time (see also Worthy 1988; Slikas et al. 2002). In comparison with its closest relatives (*G. stairi* and *G. rubescens*) and all other extant species of *Gallicolumba*, *G. leonpascoi* has markedly reduced wing elements and heavily constructed leg bones, indicating markedly reduced powers of flight. Length of leg elements plotted in a ratio diagram (Fig. 7) clearly indicate that the bird is bigger than its extant congeners and that its wing elements are considerably shorter than predicted if its proportions were consistent with those of other congeners. Endemic forms cannot have become established on Henderson while it was a low atoll as it would have been regularly over-washed by cyclones and tsunamis, so a continued avian biota would rely on regular dispersal events. However, Henderson Island has been sufficiently elevated above sea level for the last 380 kyr (Blake 1995) through which populations of terrestrial species may have persisted. With the reasonable

assumption that the flighted precursor to *G. leonpascoi* was regularly re-invading the pre-uplifted Henderson Island after such local extinction events as tsunami, it is likely that a population of ground doves was present on Henderson from the earliest stages of its uplift, and that 380 kyr is therefore the maximum available time in which this distinct species evolved. In this comparatively short time it became much larger than its ancestor, a bird presumed to be similar to *G. stairi*, and lost much of its volant ability. Similarly, the Henderson rail *Porzana atra*, became a distinct taxon in the same short length of time, and other distinct rails, e.g., *Porzana palmeri*, have evolved in as little as 125 kyr (Slikas et al. 2002). These examples suggest that evolution of such distinctive forms as the various large flightless insular rails, e.g., New Zealand's South Island takahe *Porphyrio hochstetteri*, might therefore have taken only a few hundred thousand years at most.

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Appendix 1 Measurements of fossil *G. strairi* from Vatulele Island, Fiji. Abbreviations as in Methods, and mc, medial condyle; lc, lateral condyle; mtf, metatarsal fossa.

	Tmt L		Tmt PD		Tmt SW at		Tmt DW	
	Tmt TL	mc to mtf	Tmt PW	Tmt PD	Tmt SW	mtf	Tmt DW	
Mean	30.42	21.95	6.22	6.01	2.75	3.00	6.37	
Standard Error	0.415	0.846	0.123	0.122	0.098	0.068	0.102	
Standard Deviation	0.587	1.465	0.302	0.322	0.219	0.168	0.227	
Minimum	30.0	20.8	5.8	5.5	2.5	2.8	6.1	
Maximum	30.8	23.6	6.6	6.3	3.0	3.2	6.6	
Count	2	3	6	7	5	6	5	
Femur								
	Fem L	Fem PW	Fem SW	Fem DW	Femur depth mc	Femur depth lc	Tib TL	Tib PW
Mean	34.33	6.47	2.83	6.41	4.74	5.48	52.42	5.75
Standard Error	0.348	0.106	0.044	0.096	0.085	0.131	1.385	–
Standard Deviation	0.853	0.298	0.140	0.254	0.209	0.293	1.959	–
Minimum	33.5	6.2	2.6	6.2	4.6	5.2	51.0	5.8
Maximum	35.3	7.1	3.1	6.7	5.1	5.9	53.8	5.8
Count	6	8	10	7	6	5	2	1
Tib depth								
	Fem L	Fem PW	Fem SW	Fem DW	Femur depth mc	Femur depth lc	Tib TL	Tib PW
Mean	34.33	6.47	2.83	6.41	4.74	5.48	52.42	5.75
Standard Error	0.348	0.106	0.044	0.096	0.085	0.131	1.385	–
Standard Deviation	0.853	0.298	0.140	0.254	0.209	0.293	1.959	–
Minimum	33.5	6.2	2.6	6.2	4.6	5.2	51.0	5.8
Maximum	35.3	7.1	3.1	6.7	5.1	5.9	53.8	5.8
Count	6	8	10	7	6	5	2	1
Ulna								
	Hum TL	Hum PW max.	Hum PW via dorsal tubercle	Hum SW	Hum SD	Hum DW	Hum dorsal condyle	Ulna TL
Mean	36.03	13.62	11.09	3.99	3.35	8.72	5.12	41.86
Standard Error	0.471	0.252	0.282	0.097	0.111	0.263	0.147	0.669
Standard Deviation	0.942	0.505	0.690	0.256	0.272	0.527	0.329	1.771
Minimum	34.6	13.1	10.4	3.7	2.9	8.0	4.8	39.7
Maximum	36.7	14.3	12.2	4.5	3.7	9.2	5.5	44.5
Count	4	4	6	7	6	4	5	7
Ulna SW								
	Hum TL	Hum PW max.	Hum PW via dorsal tubercle	Hum SW	Hum SD	Hum DW	Hum dorsal condyle	Ulna TL
Mean	36.03	13.62	11.09	3.99	3.35	8.72	5.12	41.86
Standard Error	0.471	0.252	0.282	0.097	0.111	0.263	0.147	0.669
Standard Deviation	0.942	0.505	0.690	0.256	0.272	0.527	0.329	1.771
Minimum	34.6	13.1	10.4	3.7	2.9	8.0	4.8	39.7
Maximum	36.7	14.3	12.2	4.5	3.7	9.2	5.5	44.5
Count	4	4	6	7	6	4	5	7
Coracoid								
	Cmc TL	Cmc PW	Cor med L	Cor sternal W	Rad TL	Rad DW	Ulna PW	Ulna DW
Mean	23.48	6.89	28.82	7.28	37.79	3.45	5.62	2.64
Standard Error	0.498	0.117	0.579	0.257	0.668	0.066	0.112	0.049
Standard Deviation	0.997	0.261	1.418	0.574	1.336	0.131	0.317	0.155
Minimum	22.0	6.5	27.0	6.8	36.2	3.3	5.2	2.4
Maximum	24.3	7.1	30.5	8.0	39.3	3.6	6.1	2.9
Count	4	5	6	5	4	4	8	10

