Island differentiation of New Zealand's extinct mergansers (Anatidae: Mergini), with description of a new species from Chatham Island

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Abstract

Measurements of major bones from three island populations (New Zealand mainland, Auckland Islands, Chatham Island) of extinct mergansers presently known as *Mergus australis* indicate that birds from Chatham Island differed in size and proportion from those at Auckland Islands. The Chatham Island specimens were smaller overall, with a shorter skull, relatively shorter premaxilla, smaller sternum and keel, relatively shorter wing bones and a narrower pelvis. These differences support its taxonomic recognition as the new species, *Mergus milleneri*, described in this paper. Determining reliably the magnitude of the size differences of major bones between mergansers from mainland New Zealand and Auckland Islands or Chatham Island was not possible due to inadequate samples of these sexually dimorphic taxa. However, mainland mergansers may also have been smaller than Auckland Islands birds. Based on these measurements, Holocene fossils of mergansers on New Zealand's mainland therefore are considered to be *Mergus* sp. indeterminate and we recommend that *Mergus australis* henceforth be called the Auckland Islands Merganser.

Key words: Auckland Islands, Chatham Island, Merganser, *Mergus australis, Mergus milleneri*, new species, New Zealand.

When humans first settled in New Zealand, late in the 13th Century, a merganser (Anseriformes: Anatidae: Mergini) was present on mainland New Zealand (North, South and Stewart Islands) and on two nearby archipelagos: Chatham Islands, 800 km east of New Zealand, and Auckland Islands, 450 km to its south (Holdaway *et al.* 2001). Mergansers from New Zealand and Chatham Island did not survive initial human impacts, but those at Auckland Islands (islands visited briefly but not settled by Polynesians; Anderson 2005) persisted into the 19th Century before ultimately being exterminated (in 1902) by a flurry of specimen collecting (Williams 2012). Whereas Auckland Islands' mergansers are now represented by 27 skins and some bone specimens therefrom (Kear & Scarlett 1970; Williams 2012), those from New Zealand and Chatham Island are known only from bones retrieved from archaeological and/or natural deposits (Worthy 1998a,b, 2004; Millener 1999).

Mergansers from mainland New Zealand, Auckland Islands and Chatham Island are currently considered to be a single species *Mergus australis* (after Hombron & Jacquinot 1841), with Auckland Islands being the type locality (see Gill *et al.* 2010). However, two observations provide potential challenges to this classification. Livezey (1989) suggested that Auckland Islands' mergansers had reduced keels (carina sterni) and disproportionately short wing bones relative to other, and more vagile, merganser species and were on the verge of flightlessness. These interpretations of keel and wing bones, but not of flightlessness, were confirmed by Williams (2012). Millener (1999) commented that merganser bones he extracted from a natural deposit on Chatham Island seemed smaller than Auckland Islands specimens and may represent a different species. These two observations raise the hypothesis that mergansers of the wider New Zealand region may have responded to their isolation on separate archipelagos with morphometric changes, similar to those of New Zealand's brown-plumaged teals (*Anas chlorotis*, *A. aucklandica*, *A.nesiotis*; Williams *et al.* 1991) and each may warrant separate taxonomic recognition.

In this study we test the hypothesis that mergansers from all three populations in the wider New Zealand region were of similar size and body proportion, characteristics necessary to justify their aggregation as a single taxon. We would consider this hypothesis falsified if, statistically, the sizes or proportions of major skeletal elements from any one population were significantly different from one or both of the others.

Methods

Sources of samples

We measured all major merganser skeletal elements from New Zealand mainland (NZ), Auckland Islands (AI) and Chatham Island (CI) held in the collections of four museums: Otago Museum, Dunedin, New Zealand (OMNZ); Canterbury Museum, Christchurch, New Zealand (CMNZ); Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ); and Natural History Museum, Tring, England (NHMT) (see Appendix 1). The material included a coracoid bone (OR 23515) from Auckland Islands held at NMNZ not listed by Williams (2012). One NZ merganser femur held in the Auckland Museum, Auckland, New Zealand (LB10058) and a second at the Anthropology Department, Otago University, Dunedin (SRM BB324-01) were not sufficiently intact to allow accurate measurements. Four bones from NZ originally lodged in the collection of the Geology Department, Auckland University, Auckland, New Zealand and described by Millener (1981) as "an almost complete mandible (AU4834), and a coracoid, humerus and femur 'possibly of *Mergus*' (AU7868)" can no longer be located (N. Hudson, pers. comm. 2013).

All bones examined had sufficient location data to discriminate among the three geographic areas mentioned above. The NZ specimens, retrieved from both natural and archaeological sites, came from North Island (Ponui Island, Lake Poukawa, Mataikona, Paremata), South Island (Lake Grassmere/Marfells Beach, Oamaru, Cannibal Bay), and Stewart Island (Native Island, Old Neck) but their small number ultimately required us to combine all bones from NZ for our analyses. For CI bones a distinction was made between those recovered from a cave deposit (Te Ana a Moe (the cave of Moe): Simmons 1964; Millener 1999) and those recovered in dunes elsewhere on the island. No merganser bones have been retrieved from archaeological sites on Chatham Island. All AI bones were from birds shot between 1890 and 1902 (Williams 2012).

We also measured bones of Red-breasted Merganser *Mergus serrator* for comparative analyses. These specimens were from museums in Frankfurt, Basel, Vienna, Paris, Dublin, NHMT and NMNZ (see Appendix 1).

Sample sizes

No bones from either CI or NZ mergansers could be associated with any others as belonging to the same individual bird. Because the similar number of wing and leg bones and half that number of cranial elements from the CI cave site indicated that we were examining the remains of at least 51 individuals (based on tarsometatarsi) we separated their left and right wing and leg elements and measured whichever provided the larger dataset.

The AI sample comprised three almost complete skeletons of known sex (2♀, 1♂) and partial skeletons from two skins to which sex data were attached (1♀, 1♂); however, one (CMNZ 5176) is incorrectly sexed as a male (see Williams 2012: Appendix 1). Thus, we studied material from 4♀ and 1♂. Additionally, we examined coracoid bones and a single sternum of three mounted specimens registered as being AI females.

Overall, 92 measurements were obtained from unsexed NZ bones, 81 measurements from AI bones of known sex, 762 measurements of CI bones from the cave deposit, and 11 measurements of unsexed CI bones from dune deposits. Comparative data for *Mergus serrator* comprised 258 measurements from birds of known sex. Numbers of each bone measured and used in this study are provided in the summary statistics (Appendix 2).

Measurements

We used vernier callipers to measure wing and leg bones, sternum, pelvis and skull. Measurements, made (to 0.1 mm), were: skull length (maximum length from prominentia cerebellaris to tip of premaxilla), nares to tip (anterior edge of nares opening to tip of premaxilla), cranium post-orbital width (maximum width between left and right processus postorbitalis), cranium inter-orbital width (minimum dorsal width between the orbits), sternum length (maximum length taken along the midline, measured on the dorsal (visceral) surface), sternum anterior width (maximum width between the processus craniolaterali), sternum posterior width (maximum caudolateral width), carina sterni (keel) length (maximum chord length from apex carinae to margo caudalis), carina sterni (keel) area (determined from two–three thin plasticine impressions of the carina sterni, each subsequently scanned against 1 mm grid graph paper and measured to 1 mm^2, and the results averaged), coracoid(eum) length (maximum length from processus acrocoracoideus to angulus medialis), coracoid(eum) width (maximum width between processus lateralis and angulus medialis), humerus length (maximum length), ulna length (maximum length), carpometacarpus length (maximum length), pelvis length (length from anterior of ala preacetabularis ilii to rear of apex pubis), pelvis anterior width (maximum width between left and right ala preacetabularis ilii), pelvis posterior width (maximum width between left and right apex pubis), antitrochanter width (maximum width between left and right processus antitrochanter), femur length (maximum length parallel to shaft), tibiotarsus length (maximum length from proximal articular surface, i.e., excluding the crista cnemialis cranialis), and tarsometatarsus length (maximum length). Anatomical names are as described by Baumel *et al.* (1993). Mean values are given ± s.d. throughout.

The presence or absence of any conspicuous salt gland impression on the cranium above the orbit was also recorded, as depicted in Fig. 3.

Data recording, analyses and presentation

All measurements were recorded in MS Excel spreadsheets and an electronic record of these data has been deposited in NMNZ archives. Compilation of size-frequency distribution tables (in which most measurements are summarised in 1 mm (0.0–0.9) groupings) used the statistical analysis functions of MS Excel 2007. Measurements of AI specimens in all tables discriminate the single male (M) from all others, which are females. Non-parametric tests (Mann-Whitney U, Kruskall-Wallis) were performed using IBM SPSS Statistics v. 19.0.

The small sample sizes from AI (2–4 in most instances) largely precluded a statistical comparison of mean dimensions of bones from it and the other two populations. Our primary analytical approach, therefore, was to use the Mann-Whitney U test to determine the probability of the AI bones being drawn from the size-frequency distribution of bones from CI. A probability of ≤ 0.05 was taken to indicate a difference in size of the selected bone between the compared populations.

To appraise overall skeletal differences between populations and taxa we calculated the mean dimensions of selected bones from one population as a percentage of the mean of those from the population or taxon with which it was being compared. The associated 95% confidence interval was adjusted by that percentage. A significant difference in relative bone length is indicated when 95% confidence intervals do not overlap. We also compiled a logarithm-based ratio diagram, commonly referred to as a "Simpson diagram" (Simpson 1941; Göhlich & Mourer-Chauviré 2005) to depict differences in mean bone measurements from CI and NZ, converted to logarithms, as a ratio of those from AI. For example, we calculated $\log_{10}$ (mean CI) – $\log_{10}$ (mean AI) (= $\log_{10}$ (mean CI/mean AI)) to compare bones from CI and AI populations. Statistical variance associated with the mean measurement of each bone is not expressed.

To assess size-related proportional differences between populations and taxa we divided the mean dimensions of selected bones from each by its mean femur length (femur is the single bone best reflecting body mass; Campbell & Marcus 1992; Field *et al.* 2013). To recognise statistical variance associated with the mean values we required a $\geq$ 5% difference in the resulting statistic between populations and taxa to indicate a proportional difference.

Evaluation of Chatham Island cave sample

Chatham Island, the only island in the Chatham Islands archipelago on which merganser bones have been found, is dominated by an extensive barrier-bar lake (Te Whanga lagoon). A small single-chambered cave (Te Ana a Moe) lies near the base of a limestone cliff on the western shore of the lagoon (Simmons 1964). Millener (1999) described its entrance as being about 3 m above present lagoon level with its main fossil bird bearing sediment lying 0.6–1.5 m below the level of the cave's entrance. He recorded bird remains being most abundant in short (1–3 m) blind tunnels leading from the cave's 2 m-wide main chamber and obtained radiocarbon dates from those remains of 1150–3900 CAL BP. Considering the range of faunal specimens found (*e.g.* 17 land snail and 30 bird species), Millener (1999) suggested that the cave had acted as a pitfall trap.

The fortuitous aggregation of merganser bones appears to be a consequence of the cave having been used by mergansers as a nesting site, an interpretation supported by the copious amount of (unidentified) eggshell removed from the cave (now held at NMNZ) as well as a premaxilla (NMNZ S.30635) and a mandible (NMNZ S.27377) of merganser hatchlings. Other merganser species are hole-nesters (Cramp & Simmons 1977; Kear 2005) and females, not males, investigate and enter nest holes and undertake all incubation.

Extant merganser species are all sexually dimorphic in size; in general, linear dimensions of females are 6–10% smaller and weights 15–20% less than males, with little overlap of their dimensions or weights (Cramp & Simmons 1977; Kear 2005). Measurements of culmen and wing of male and female skins of AI mergansers recorded a 7–9% difference in size (Williams 2012: Appendix 2).

We examined the size-frequency distributions of lengths of premaxillae, humeri, ulnae, carpometacarpi, coracoids, sterna, femora, tibiotarsi and tarsometatarsi of the CI cave specimens (see Tables 1–4 and Table 7). The strictly unimodal distributions of all nine measurements examined indicate either there was no sexual size dimorphism in CI mergansers or, more likely, that all bones were from a single sex. Within the small sample of bones from non-cave sites on CI, measurements of some bones overlapped and others exceeded the ranges of those from the cave (Appendix 2).

The archive of these merganser bones at NMNZ included a large assortment of tracheal rings and syrinxes (the element where the trachea bifurcates) but not one ossified enlarged syrinx (bulla) characteristic of a merganser male (Johnsgard 1961). Syringeal bullae are common in caves throughout NZ where depositions of waterfowl (*e.g.* Finsch's Duck *Chenonetta finschi* (now extinct) and Brown Teal *Anas chlorotis*) have accumulated by pitfall (T.H. Worthy, pers. comm.).

We regard the CI cave adult *Mergus* bones as being all from females. These are referred to in the text as "CI cave" or "CI females", as distinct from "CI mergansers" or "CI bones" which cover all CI specimens irrespective of site.

Treatment of the New Zealand sample

The size-frequency distributions of merganser bones most commonly found in NZ (humerus, ulna, tibiotarsus, femur, coracoid) were all weakly bimodal (see Tables 2, 3 and 7) and extend above the ranges of the same bones retrieved from the CI cave site. We regard this sample as including birds of both sexes. We attempted an approximate differentiation of sex by separating each distribution into non-overlapping upper (male?) and lower (female?) samples such that their means differed by 7–9%, their standard deviations were similar, and their ranges were separated by ≥ 1 mm (Appendix 2). We used the resulting distributions for putative females to compare with those of females from AI and the CI cave sample.

We paid particular attention to the smallest bones in each set, mindful of Worthy's (2004) observation of potential confusion of *Mergus* bones with those of *Anas chlorotis*, *Aythya novaeseelandiae* and New Zealand fossil *Oxyura vantetsi*. In a few cases (identified in Appendix 1) we deliberately excluded outstandingly small "*Mergus*" bones from our analyses.

Results

Comparative sizes of bones

Skull

No intact skulls of NZ mergansers have been found, just two premaxillae and one cranium. Of the premaxillae (Table 1), one was smaller than any of three AI females and within the lower quartile of the measurements for CI cave premaxillae, while the other was the same size as the single AI male. All three AI female measurements were larger (1.7–6.0%) than the largest from the CI cave sample and the size-frequency distributions of these two samples were significantly different (Mann-Whitney $U = 0.0$, $P < 0.0005$). Similarly, the total lengths of two AI female skulls both exceed the largest of six intact CI cave skulls (Appendix 2). Thus, AI females had longer skulls and longer premaxillae than CI females (see Fig. 3).

Table 1: Size-frequency distribution of nares-tip lengths (mm) of premaxillae from New Zealand, Auckland Islands and Chatham Island mergansers. NZ = New Zealand; AI = Auckland Islands; CI cave = Chatham Island cave site; M = male.

Population	**Nares–bill tip length (mm)**										***n***
	31	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	
NZ		1								1	2
AI					1	1	1			1M	4
CI cave	2	6	15	20	3						46

The widths of 44 CI cave crania at the post-orbital process grouped tightly around the mean (27.7 ± 0.3 mm) and included only one specimen smaller than the two AI female crania, both of which were 27.2 mm (Appendix 2). The one AI male measurement (29.0 mm) exceeded all others. The NZ cranium (specimen CM 11532) had a width at the post-orbital process of 25.3 mm, conspicuously smaller than any skull of CI and AI mergansers.

The inter-orbital widths from 43 CI cave crania (mean = 6.1 ± 0.3 mm) included just four measurements smaller than the maximum (5.8mm) from three female AI crania (Appendix 2). The post-orbital/inter-orbital width ratio for CI cave crania (mean = 4.5 ± 0.2) differed sufficiently from that of two AI female measurements (mean = 4.9) as to suggest proportional differences in the crania of the two populations.

Salt gland impressions, conspicuous on all CI cave crania (see Fig. 3; also depicted in Fig. 13 of Millener 1999 and Fig. 7.2 of Worthy & Holdaway 2002), were discernible but inconspicuous on the AI crania.

Wing bones

Humerus. Whereas the lengths of 47 CI cave humeri differed by 3.9 mm between shortest and longest, the 16 humeri from NZ extended over twice that range and their size-frequency distribution (Table 2) strongly indicated the inclusion of both sexes. The size-frequency distribution of putative NZ females (range 65–68 mm) was not significantly different from the CI cave sample (Mann-Whitney $U = 232.5$, $P = 0.64$). The lengths of the two AI female humeri overlapped only the longer of the CI cave humeri and the distributions of these two samples were significantly different (Mann-Whitney $U = 3.5$, $P = 0.01$). The AI male humerus was approximately 5% longer than the longest of the CI and AI female humeri and of similar length to the longest NZ humerus.

Ulna. The lengths of two AI female ulnae exceeded the longest from the CI cave and the two size-frequency distributions (Table 2) were significantly different (Mann-Whitney $U = 2.5$, $P = 0.03$). The AI male bone was longer than any from New

Zealand. The size-frequency distribution of 14 NZ bones, however, was unlike that of humeri (Table 2) by including four bones shorter than any found on CI. As a consequence the size-frequency distribution of putative NZ female ulnae (range 48–53 mm) was significantly different from that of CI cave specimens (Mann-Whitney $U = 309.0$, $P < 0.0005$).

Carpometacarpus. Both AI female carpometacarpi were the length of the longest found on CI, and that of the single AI male was the same length as the longest of three bones found in NZ (Table 2). The size-frequency distributions of AI female carpometacarpi and those of CI cave were significantly different (Mann-Whitney $U = 2.0$, $P = 0.02$).

Coracoid. AI female coracoids were generally larger than those from CI cave and the size-frequency distributions of both lengths and widths (Table 3) were significantly different (length: Mann-Whitney $U = 0.0$, $P < 0.0005$; width: Mann-Whitney $U = 26.0$, $P = 0.005$). However, they were similarly proportioned (mean length/width ratios: AI = 2.61 ± 0.06; CI cave = 2.58 ± 0.06; Mann-Whitney $U = 74.0$, $P = 0.19$; Fig. 1). NZ coracoid bones were narrower than all others and their mean length/width ratio (2.89 ± 0.08) conspicuously different from the other two populations (overall Kruskall-Wallis test $\chi^2_2 = 19.46$, $P < 0.0005$, AI *vs.* NZ, Mann-Whitney $U = 0.0$, $P = 0.004$; NZ *vs.* CI cave, Mann-Whitney $U = 0.0$, $P < 0.0005$). The size-frequency distribution of lengths of putative NZ female coracoids (range 39–42 mm) was different from that of CI cave (Mann-Whitney $U = 52.5$, $P = 0.001$) and the bones conspicuously narrower (Mann-Whitney $U = 0.0$, $P < 0.0005$; Fig. 1). Figure 1 also depicts the larger size of the AI male coracoid bone and suggests that the NZ sample similarly included one larger male.

Sternum and keel

No sternum of a NZ merganser has been found and, on CI, none other than those in the cave deposit.

Sternum length and width. The size-frequency distributions of AI female and CI cave sternum lengths were significantly different (Mann-Whitney $U = 0.00$, $P = 0.001$). So too were their distributions of sternum posterior widths (Mann-Whitney $U = 1.5$, $P = 0.02$) but sternum anterior widths were not (Mann-Whitney $U = 52.5$, $P = 0.46$, n.s.; Table 4). Thus, AI females had longer and posteriorly wider sterna than CI females. The single AI male's sternum was 10 mm (15%) longer than the longest CI female and 7% longer than the longest AI female. Its anterior sternum width was 5% wider than the widest CI female and 11% wider than the widest AI female (Appendix 2).

Keel length and area. Lengths of keels on four AI female merganser sterna averaged 14% longer than those from CI cave (Mann-Whitney $U = 0.0$, $P = 0.001$; Appendix 2) and respective size-frequency distributions of their lengths did not overlap (Table 5). The longest keel, of an AI male, exceeded the longest from CI cave by 20% and the longest AI female by 7%.

Although the keel areas of two (of four) AI females were smaller than the two largest from CI cave, the mean keel area of AI

Table 2: Size-frequency distribution of wing bones lengths (mm) from New Zealand, Auckland Islands and Chatham Island mergansers. NZ= New Zealand; AI = Auckland Islands; CI cave (largest sample from one side used = right humeri, left ulnae, right carpometacarpi); CI dune = from other Chatham Island sites; M = male.

Population	**Humerus length (mm)**									***n***
	64	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	
NZ		5	1	1	2	2	1	1	3	16
AI				1	1				1M	3
CI cave	3	9	16	17	2					47
CI dune							2			2

Population	**Ulna length (mm)**										***n***
	48	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	
NZ	1	1	1	1	3	1	1	1	4		14
AI							1	1		1M	3
CI cave				2	9	20	12				43
CI dune				1							1

Population	**Carpometacarpus (mm)**								***n***
	35.5–35.9	**36.0–36.4**	**36.5–36.9**	**37.0–37.4**	**37.5–37.9**	**38.0–38.4**	**38.5–38.9**	**41.0–41.4**	
NZ				2				1	3
AI							2	1M	3
CI cave	1	1	7	16	11	3	1		41
CI dune	1								1

females was 11% larger than CI females (Appendix 2, Table 9) and the size-frequency distributions of the two groups differed significantly (Mann-Whitney U = 6.0, P = 0.01; Table 5). However, the mean (± s.d.) keel area/keel length ratios were

Table 3. Size-frequency distribution of coracoid lengths and widths (mm) from New Zealand, Auckland Islands and Chatham Island mergansers. NZ = New Zealand; AI = Auckland Islands; CI cave = left coracoids from Chatham Island cave site; CI dune = from other Chatham Island sites; M = male.

Population	**Coracoid length (mm)**												***n***
	37	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	
NZ			1	4		3	1	2	1				12
AI								5				1M	6
CI cave					2	11	28	6					47
CI dune	1		1						1				3

Population	**Coracoid width (mm)**												***n***
	13.5–13.9	**14.0–14.4**	**14.5–14.9**	**15.0–15.4**	**15.5–15.9**	**16.0–16.4**	**16.5–16.9**	**17.0–17.4**	**17.5–17.9**	**18.0–18.4**	**18.5–18.9**	**19.0–19.4**	
NZ	2	3	2			1							8
AI							2	2	1			1M	6
CI cave					3	21	20	3					47

similar (AI = 6.60 ± 0.38, CI cave = 6.80 ± 0.44; t_{22}= 0.42, P = 0.43, n.s.), indicating they were similarly proportioned.

Keel length and area relative to sternum length. Lengths of keels of AI females, relative to their sternum lengths, were slightly longer (mean 3%) than CI females and their apex carinae projected slightly further forward of the sternum. The size-frequency distributions of keel length/sternum length ratios (Table 6) were significantly different (Mann-Whitney U = 8.0, P = 0.005) and the means also (AI = 1.21 ± 0.01, CI cave = 1.18 ± 0.02; t_{32} = 2.93, P = 0.006).

Despite this difference however, keel area/sternum length ratios were very similar (AI female mean = 8.01 ± 0.33, CI cave mean = 8.05 ± 0.52; t_{22} = 0.23, P = 0.83, n.s.).

Overall, the sterna of CI female mergansers were shorter and posteriorly narrower than those of AI female mergansers and had keels that were shorter and less forward projecting.

Leg bones

Femur. There was complete overlap in the size ranges of femora from all three

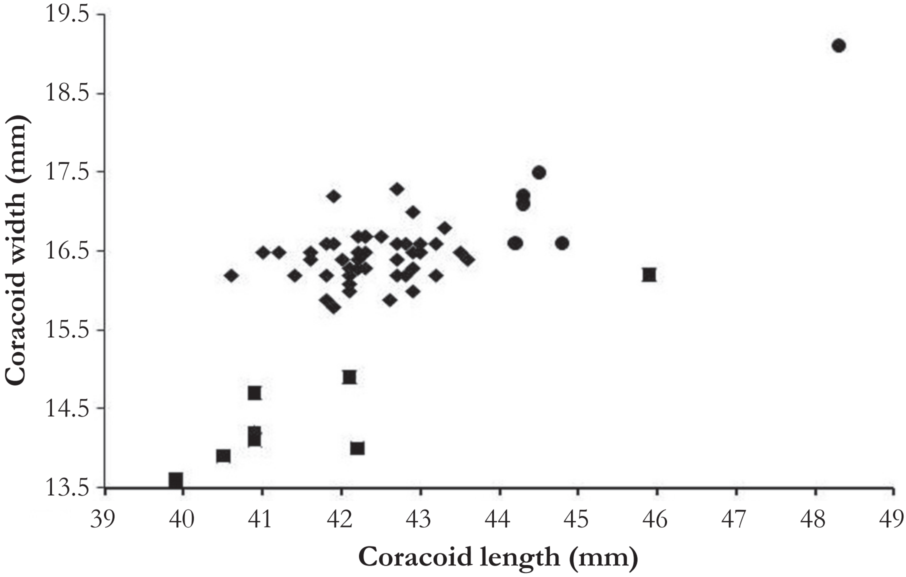

Figure 1. Scatterplot of lengths and widths of merganser coracoid bones. ● = Auckland Islands, ■ = New Zealand, ♦ = Chatham Island. The largest Auckland Islands specimen is from a male. The largest New Zealand specimen is similarly proportioned to all other New Zealand coracoid bones and may also be from a male.

populations (Kruskall-Wallis test $\chi^2_2 = 3.47$, $P = 0.18$, n.s.) (Table 7) and despite the NZ sample presumably including both sexes, its size-frequency distribution was not different from the CI cave sample (Mann-Whitney U = 288.0, $P = 0.09$, n.s.). However, the size-frequency distribution for the putative New Zealand females (40–41 mm) was significantly different from that of the CI females (Mann-Whitney $U = 0.0$, $P < 0.0005$).

Tibiotarsus. Most NZ tibiotarsi were similar in length to those from CI, but some were longer (Table 7). The lengths of the two female AI tibiotarsi were within the range of CI females.

Tarsometatarsus. There was complete overlap in tarsometatarsus measurements from all three populations (Kruskall-Wallis test $\chi^2_2 = 2.96$, $P = 0.23$, n.s.; Table 7) and the distributions of the CI and AI samples did not differ (Mann-Whitney $U = 12.0$, $P = 0.07$, n.s.).

Pelvis

The pelves of CI females appeared conspicuously small. The two AI pelves were both longer than those of CI females (Table 8) and the size-frequency distributions of the two populations were significantly different (Mann-Whitney $U = 0.0$, $P = 0.004$). Similarly, the three AI female antitrochanter widths all exceeded those from CI cave and the means of the two samples (Appendix 2) were significantly different ($t_{36} = 9.57$,

Table 4. Size-frequency distribution of sternum lengths and their anterior and posterior widths (mm) from Auckland Islands and Chatham Island mergansers. AI = Auckland Islands; CI cave = Chatham Island cave site; M = male.

Population	**Sternum length (mm)**									***n***
	60–61	**62–63**	**64–65**	**66–67**	**68–69**	**70–71**	**72–73**	**74–75**	**76–77**	
AI						2	2		1M	5
CI cave	1	10	13	7						31

Population	**Sternum anterior width (mm)**								***n***
	40	**41**	**42**	**43**	**44**	**45**	**46**	**47**	
AI		1	2	1				1M	5
CI cave	1	4	5	10	9	3	2		34

Population	**Sternum posterior width (mm)**								***n***
	42	**43**	**44**	**45**	**46**	**47**	**48**	**49**	
AI				1		3		1M	5
CI cave	2	3	10	12	1				28

$P < 0.0001$). However, anterior pelvis widths from the two populations entirely overlapped (Table 8).

Posterior pelvis widths were widest in CI females (AI mean 47.4 ± 0.5 mm; CI mean 49.1 ± 1.6 mm) but three of the CI measurements were conspicuously larger than all others, suggesting the ischia were splayed during preservation in the cave deposit. Excluding these three measurements the mean CI cave posterior pelvis width was 48.9 ± 1.5 mm, which was not significantly different from the AI female mean width ($t_{26} = 1.80$, $P = 0.084$, n.s.). However, with or without these three measurements, the posterior pelvis width/antitrochanter width ratios differed significantly between the two populations (Table 8). Their size-frequency distributions did not overlap, and the means of the two samples (three widest CI measurements excluded) were significantly different ($t_{27} = 6.93$, $P < 0.0001$). The width ratios from the three CI females with the

Table 5. Size-frequency distribution of keel (carina sterni) length (mm) and area (mm^2) from Auckland Islands and Chatham Island mergansers. AI = Auckland Islands; CI cave = Chatham Island cave site; M = male.

Population	**Keel length (mm)**													***n***
	69–70	**71–72**	**73–74**	**75–76**	**77–78**	**79–80**	**81–82**	**83–84**	**85–86**	**87–88**	**89–90**	**91–92**	**93–94**	
AI							1		1	2			1M	5
CI cave	2		7	17	5									31

Population	**Keel area (mm^2)**									***n***
	426–450	**451–475**	**476–500**	**501–525**	**526–550**	**551–575**	**576–600**	**601–625**	**626–650**	
AI					1	1	1	1	1M	5
CI cave	1	2	5	2	5	3	1			19

conspicuously larger posterior pelvis widths were three of the four highest, also suggestive of possible distortion.

Comparative size and proportional relationships

Relative skeletal size

Comparison of Auckland Islands and Chatham Island females. Based on mean dimensions (Appendix 2), major skeletal elements of CI mergansers were generally smaller than those of AI female mergansers, most by 3–6%, although sternum lengths differed by 10%, as did keel lengths and areas (Table 9, Fig. 2). Mean wing bone lengths also differed by about 3%. Differences in pelvis length, and width at the antitrochanter, indicate the CI merganser had a significantly shorter and narrower pelvis, but which may have been wider posteriorly. As a consequence, posterior width/antitrochanter width ratios differed. However, leg bones were of similar size.

Comparison of Chatham Island and New Zealand putative females. The lengths of ulnae from NZ putative females were shorter than those of CI females, but not so the humeri (Table 9). Additionally, NZ coracoid bones were conspicuously narrower distally. The legs of NZ putative females may have been shorter than CI mergansers.

Comparison of Auckland Islands and New Zealand putative females. Although mean

Table 6. Size-frequency distributions of keel length / sternum length ratios and keel area / sternum length ratios for Auckland Islands and Chatham Island mergansers. AI = Auckland Islands; CI cave = Chatham Island cave site. M = male.

Population	**Keel length/sternum length ratio**											***n***
	1.13	**1.14**	**1.15**	**1.16**	**1.17**	**1.18**	**1.19**	**1.20**	**1.21**	**1.22**	**1.23**	
AI							1		2	1	1M	5
CI cave	2		2	1	5	10	7	1	3			31

Population	**Keel area/sternum length ratio**									***n***
	7.0–7.24	**7.25–7.49**	**7.50–7.74**	**7.75–7.99**	**8.0–8.24**	**8.25–8.49**	**8.50–8.74**	**8.75–8.99**	**9.0–9.24**	
AI			2		1M	2				5
CI cave	1	3	3	1	4	3	2	1	1	19

lengths of main wing and leg bones of NZ putative female mergansers were all shorter that AI females (Table 9), sample sizes from both populations were too small to confirm any difference statistically. Despite uncertainty which accompanies our discrimination of sex for the NZ sample (see Methods), coracoid dimensions alone suggest AI birds were conspicuously larger.

Comparison with Mergus serrator *females.* Female mergansers from all three New Zealand region populations were smaller than *M. serrator* females (Table 9, Fig. 2). While skulls (of AI birds) and pelvic bones (of both AI and CI) were comparable in size to those of *M. serrator*, wing bones and sternal elements were considerably smaller (10–20%), indicating a much smaller overall body size.

The conspicuously diminished sternum and keel characteristics of female AI and CI mergansers also provide other relative differences. Mean keel length/mean sternum length ratios (*M. serrator* = 1.32 ± 0.04, *n* = 8; AI = 1.21 ± 0.02, 4; CI cave = 1.18 ± 0.02, 31) emphasise a difference in the extent of the apex carinae projecting forward of the sternum. Similarly, mean keel area/mean sternum length ratios (*M. serrator* = 9.32 ± 0.4, *n* = 5; AI = 8.01 ± 0.4, 4; CI = 8.05 ± 0.5, 19) emphasise a relative diminution in pectoral muscle mass of the Antipodean forms and, thus, their diminished flight capabilities.

Leg bones, especially femora, were only

Table 7. Size-frequency distribution of leg bone lengths (mm) from New Zealand, Auckland Islands and Chatham Island mergansers. NZ= New Zealand; AI = Auckland Islands; CI cave = Chatham Island cave site (left femur, right tibiotarsus, left tarsometatarsus); CI dune = other Chatham Island sites; M = male.

Population	**Femur length (mm)**						***n***
	40	**41**	**42**	**43**	**44**	**45**	
NZ	1	6	3	3	2	1	16
AI			2	1		1M	4
CI cave		1	20	21	2		44
CI dune	1	1		1	1		4

Population	**Tibiotarsus length (mm)**							***n***
	69	**70**	**71**	**72**	**73**	**74**	**75**	
NZ	3	1		4		3	1	15
AI		1		1				2
CI cave		9	9	13	14	2		47
CI dune	1							1

Population	**Tarsometatarsus length (mm)**							***n***
	38	**39**	**40**	**41**	**42**	**43**	**44**	
NZ	2	1	1	1			1	6
AI			1	1				2
CI cave	5	18	25	3				51

slightly smaller than those of *M. serrator*, perhaps indicating a more "terrestrial" habit (*e.g.* exploiting smaller and shallower stream habitats) for the Antipodean populations. The pelves of *M. serrator* and CI mergansers were of similar width and their posterior/antitrochanter width ratios did not differ (*M. serrator* = 1.86 ± 0.11, n = 6; CI = 1.92 ± 0.013, 26; t_{30} = 1.8, P = 0.08, n.s.).

Table 8. Size-frequency distribution of pelvis measurements (mm) and ratio of widths from Auckland Islands and Chatham Island mergansers. * Posterior measurements (52.6, 54.2, 54.6 mm) and the derived width ratio may indicate distortion. AI = Auckland Islands; CI cave = Chatham Island cave site; M = male.

Population	**Length (mm)**						***n***
	80–81	**82–83**	**84–85**	**86–87**	**88–89**	**≥ 90**	
AI				1	1	1M	3
CI cave	12	10	3				25

Population	**Anterior width (mm)**					***n***
	16	**17**	**18**	**19**	**≥ 20**	
AI			2	1M		3
CI cave	3	11	11	1		26

Population	**Antitrochanter width (mm)**									***n***
	23	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	
AI						2	1		1M	4
CI cave	1	7	18	9						35

Population	**Posterior width (mm)**							***n***
	45	**46**	**47**	**48**	**49**	**50**	**>51***	
AI			2	1	1M			4
CI cave	1	1	5	7	5	7	3	29

Population	**Posterior/antitrochanter width ratio**						***n***
	1.6	**1.7**	**1.8**	**1.9**	**2.0**	**2.1**	
AI	3 + 1M						4
CI cave		1	9	10	7*	1*	28

Table 9. Mean (± 95% confidence intervals, *n*) percentage size relationships of selected skeletal elements of Chatham Island cave and putative female New Zealand mergansers, and *Mergus serrator* females, relative to those of Auckland Islands female mergansers. All data from Appendix 2 ([a] = significant size difference between AI and CI; [b] = significant size difference between CI and NZ; * = excluding three longest measurements, see Table 8).

Population/ Bone	**Auckland Islands**	**Chatham Island**	**New Zealand**	***Mergus serrator***
Skull length	100 ± 0, 2	94.6 ± 1.5, 6		99.3 ± 3.1, 4
Nares-tip	100 ± 4.0, 3	92.3 ± 0.7, 46[a]		100.0 ± 1.1, 4
Post-orbital width	100 ± 0, 2	104.1 ± 0.3, 44		103.0 ± 0.2, 8
Inter-orbital width	100 ± 0.6, 3	115.1 ± 0.1, 43		115.0 ± 0.2, 7
Humerus length	100 ± 0, 2	97.4 ± 0.4, 47[a]	97.2 ± 1.4, 9	121.8 ± 2.4, 9
Ulna length	100 ± 0, 2	97.4 ± 0.4, 43[a]	93.4 ± 2.6, 8[b]	125.5 ± 2.0, 10
Carpometacarpus length	100 ± 0, 2	96.9 ± 0.5, 41[a]		128.3 ± 1.9, 6
Coracoid length	100 ± 0.5, 5	95.5 ± 0.5, 46[a]	92.8 ± 1.7, 8[b]	119.8 ± 2.1, 9
Coracoid width	100 ± 2.7, 5	96.5 ± 0.5, 46[a]	83.5 ± 1.4, 7[b]	113.5 ± 0.5, 8
Sternum length	100 ± 1.0, 4	89.0 ± 0.8, 31[a]		114.1 ± 1.1, 11
Sternum anterior width	100 ± 1.6, 4	100.5 ± 1.1, 34		112.0 ± 1.5, 12
Sternum posterior width	100 ± 2.4, 4	94.9 ± 0.7, 28[a]		110.8 ± 1.7, 10
Keel length	100 ± 5.0, 4	87.5 ± 0.7, 31[a]		124.9 ± 2.1, 9
Keel area	100 ± 6.5, 4	89.8 ± 3.1, 19[a]		132.5 ± 17.4, 5
Femur length	100 ± 0, 2	100.2 ± 0.4, 44	96.3 ± 1.3, 7[b]	103.7 ± 0.8, 10
Tibiotarsus length	100 ± 0, 2	101.0 ± 0.5, 47	95.8 ± 1.9, 7	108.4 ± 1.5, 7
Tarsometatarsus length	100 ± 0, 2	97.8 ± 0.5, 51		105.4 ± 1.0, 9
Pelvis length	100 ± 0, 2	93.6 ± 0.5, 25[a]		
Pelvis anterior width	100 ± 0, 2	97.8 ± 1.6, 26		
Antitrochanter width	100 ± 1.3, 3	88.5 ± 0.7, 36[a]		88.2 ± 0.5, 9
Pelvis posterior width	100 ± 1.6, 3	103.3 ± 0.6,26*		97.0 ± 1.5, 9

Size-related skeletal proportions

Size-standardised measurements (i.e. mean bone lengths divided by mean femur length) were used to appraise proportional differences in skeletal elements of the three Antipodean populations and *M. serrator* (Table 10). These data indicate that AI mergansers had longer skulls than CI

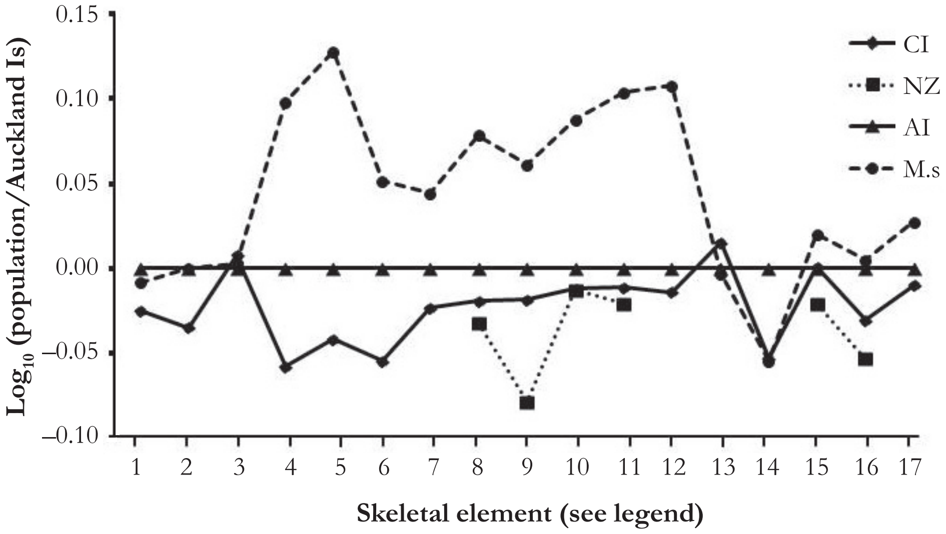

Figure 2. Ratio diagram depicting log differences in mean dimensions of selected *Mergus serrator* (M.s.), Chatham Island female (CI) and New Zealand putative female (NZ) merganser skeletal elements relative to those of Auckland Islands female (AI) mergansers. The vertical distance between points of the same element is proportional to the ratio of their actual dimensions. Skeletal elements compared are, in order: Skull = total skull length (1), nares to tip (2), post-orbital width (3); Sternum = keel length (4), keel area (5), sternum length (6), sternum posterior width (7); Wing = coracoid length (8), coracoid width (9), humerus (10), ulna (11), carpometacarpus (12); Pelvis = posterior width (13), antitrochanter width (14); and Leg = femur length (15), tibiotarsus length (16), and tarsometatarsus length (17). For further explanation of diagram see Methods. Data derived from Table 9; variance estimates not depicted.

because of their more elongate premaxillae, and that relative to *M. serrator* females, mergansers from all three Antipodean populations had reduced pectoral and sternal elements. CI female mergansers had a proportionately shorter coracoid and sternum than AI female mergansers, perhaps indicating a reduced flying ability, and differing pelvic proportions also. The limited data for NZ putative female mergansers indicate a clear reduction in the pectoral girdle relative to *M. serrator* females and hint at a possible difference from the CI and AI populations.

Discussion

Comparison of female mergansers from Auckland Islands and New Zealand

Our analyses have not established statistically significant differences between bone lengths of female mergansers from AI and NZ, with the exception of coracoids (Fig. 1, Fig. 2). Testing for possible differences between these two populations has been hampered by the paucity of bones from both, and especially by the absence of sterna from NZ. That differences in skeletal

Table 10. Size-related proportional relationships of selected skeletal elements of female mergansers from Auckland Islands, Chatham Island and New Zealand (putative females), and *Mergus serrator*. All data from Appendix 2. Mean length of selected skeletal element is divided by mean femur length from the same population/taxon. * = differ from AI by >5% († = mean length excludes three longest measurements, see Table 8).

Population/ Skeletal element	**Auckland Islands**	**Chatham Island**	**New Zealand**	***Mergus serrator***
Skull length	2.40	2.27*		2.30
Nares-tip	0.85	0.79*		0.82
Post-orbital width	0.62	0.64		0.61
Inter-orbital width	0.12	0.14*		0.14
Humerus length	1.59	1.55	1.61	1.87*
Ulna length	1.28	1.28	1.24	1.55*
Carpometacarpus length	0.90	0.87		1.11*
Coracoid length	1.03	0.99	1.00	1.20*
Coracoid width	0.40	0.37*	0.34*	0.43*
Sternum length	1.67	1.49*		1.84*
Sternum anterior width	0.99	0.98		1.07*
Sternum rear width	1.10	1.04*		1.17*
Keel length	2.00	1.75*		2.41*
Keel area	13.40	12.00*		17.10*
Tibiotarsus length	1.67	1.68	1.66	1.74
Tarsometatarsus length	0.95	0.93		0.97
Pelvis length	2.05	1.91*		
Pelvis anterior width	0.42	0.41		
Antitrochanter width	0.67	0.59*		0.57*
Pelvis posterior	1.10	1.14†		1.03

characteristics may exist, however, are hinted at by the minimum lengths of all NZ bones, except femur, being shorter than those from AI. The smaller NZ coracoid bones hint at a relatively weaker pectoral apparatus. The putative NZ females were more similar in size and proportion to females on CI than AI, but we cannot rule out the possibility that larger NZ females were mis-diagnosed by our methodology. Maximum lengths (likely to be of adult males) of humeri and ulnae from NZ were similar to the single AI male (Appendix 2).

The NZ sample, by amalgamating bones from North, South and Stewart Islands, is drawn from a 13° latitudinal range and may mask any possible north-south size gradient expected under both Bergmann's (Mieri & Dayan 2003) and Allen's rules (Nudds & Oswald 2007) and demonstrated by other New Zealand waterfowl, for instance *Hymenolaimus malacorhynchos* (see Marchant & Higgins 1990; Godfrey *et al.* 2003) and *Anas chlorotis* (see Matthews 1936; Marchant & Higgins 1990).

Comparison of female mergansers from Auckland Islands and Chatham Island

Our comparative measurements of female merganser bones from AI and CI recorded significant size differences (Tables 1–9) and proportional differences (Table 10) between these two populations. Mergansers from CI were smaller birds (Table 9) with differing skull, sternal and pelvic proportions (Table 10, Fig. 2), and we consider these differences, in combination, sufficient to establish the CI merganser as a taxon distinct from *M. australis* at Auckland Islands. We propose that it be recognised as a new species.

Systematics

Order Anseriformes

Family Anatidae Leach, 1819

Mergus Linnaeus, 1758

Mergus milleneri **Williams & Tennyson, sp. nov.**

VERNACULAR NAME: Chatham Island Merganser.

TYPE LOCALITY: The cave Te Ana a Moe, Chatham Island, Pacific Ocean (Holocene age).

DISTRIBUTION: Chatham Island.

ETYMOLOGY: The species epithet is a noun in the genitive case honouring Dr Philip Ross Millener (former Curator of Fossil Birds at NMNZ) who collected most of the fossil Chatham Island *Mergus* material referred to in this paper, including all specimens from Te Ana a Moe.

HOLOTYPE: NMNZ S.29496.3 – Skull (Fig 3A), collected by P.R. Millener, 20 February 1991, sample 93/91. Sex female.

MEASUREMENTS OF HOLOTYPE: Complete skull: cranium + premaxilla length 99.2 mm, nares to tip 34.8 mm, width at post-orbital process 27.7 mm, inter-orbital width 6.2 mm.

PARATYPES: NMNZ S.32198.4 – sternum (Fig. 4A), collected by P.R. Millener & N.H. Hyde, 15 February 1992, sample 152/92, sex female. NMNZ S.32198.6 – pelvis (Fig. 4B), collected by P.R. Millener & N.H. Hyde, 15 February 1992, sample 152/92, sex female. Both collected in Te Ana a Moe, Chatham Island.

MEASUREMENTS OF PARATYPES: NMNZ S.32198.4, sternum: length carina sterni 76.5 mm; sternum length (basin length, pila coracoidea to caudal margin) 63.0 mm; anterior width 43.8 mm; posterior width 45.7 mm; carina sterni area 543 mm^2. NMNZ S.32198.6, pelvis: length 84.9 mm, anterior width 17.7 mm, posterior width 47.7 mm, width at antitrochanter 25.8 mm, posterior width/antitrochanter width = 1.85.

NON-TYPE SPECIMENS EXAMINED: See Appendix 1.

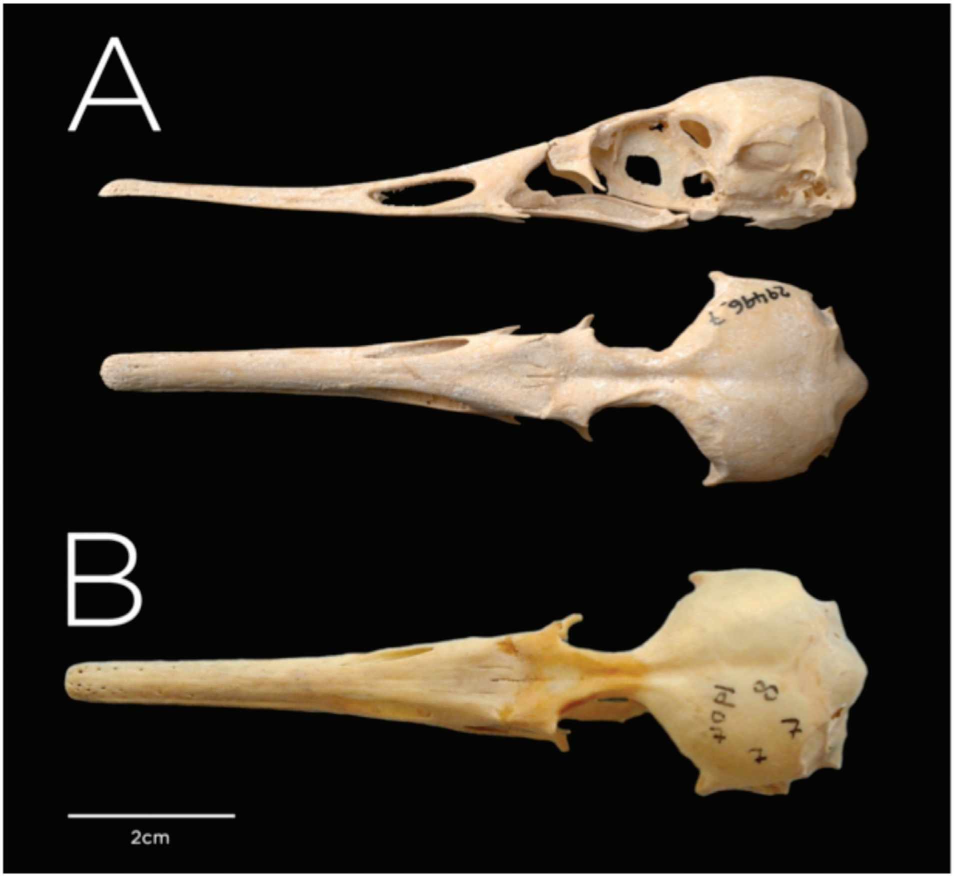

Figure 3. A = Lateral and dorsal views of Holotype (NMNZ S.29496.3, female) of Chatham Island Merganser *Mergus milleneri*; B = dorsal view of female Auckland Islands Merganser *Mergus australis* skull (NHMT 1904.8.4.4).

DIAGNOSIS: Compared with *M. australis* (AI) the skull has a shorter premaxilla, a broader inter-orbital width, and larger, more conspicuous, salt gland impressions. Proportionately, the skull and premaxilla are shorter but the inter-orbital width is greater. The humerus, ulna, carpometacarpus and coracoid are shorter and the coracoid absolutely and proportionately narrower. The sternum differs by being absolutely and proportionately narrower posteriorly, shorter, with the carina sterni less forward projecting, shorter, and of smaller area. The pelvis is absolutely and proportionately shorter, and narrower between the processus antitrochanter. The pelvis has a posterior width/antitrochanter width ratio > 1.7, whereas for *M. australis* this ratio is 1.6. The new species differs from all other *Mergus* species by smaller

Figure 4. Dorsal and lateral views of paratypes of Chatham Island Merganser *Mergus milleneri*. A = sternum (NMNZ S.32198.4, female) ; B = pelvis (NMNZ S.32198.6, female).

size and reduced pectoral and sternal elements.

REMARKS: We recognise the size and proportional differences between the Chatham Island Merganser and mergansers from the Auckland Islands as being small but many, indicative of prolonged geographic separation, and indicative of a response to local environmental conditions. The taxonomic distinction we propose is an example of allopatric speciation (Price 2008) and the species-level status is conferred under the phylogenetic species concept (*sensu* Cracraft 1983; McKitrick & Zink 1988). Although our discrimination of putative females in the New Zealand sample suggests there may be a size distinction between mergansers from AI and NZ, we have been unable to validate the difference statistically, other than for coracoids, because of small comparative sample sizes, the possibility of a geographic size cline in NZ birds, and the uncertainty of our sexing of the NZ bones. We suggest that the New Zealand population should be considered *Mergus* sp. until subsequent mensural and/or genetic distinctions provide clarity. Therefore, we suggest that the vernacular name of mergansers from Auckland Islands revert to 'Auckland Islands Merganser', as the name 'New Zealand Merganser' *sensu* Gill *et al.* (2010) is no longer appropriate.

Island differentiation

It is not a novel prospect that populations of a merganser established in the New Zealand region should have differentiated mensurably from each other upon colonising the isolated Auckland Islands and Chatham Island. Many New Zealand avian taxa have done so following dispersal to these, and to other neighbouring archipelagos or islands (*e.g.* kaka *Nestor* sp., pigeon *Hemiphaga* sp., pipit *Anthus novaeseelandiae* subsp., banded dotterel *Charadrius bicinctus* subsp.). Most of the land and freshwater birds present on the Chatham Islands prior to human arrival have been identified as taxa mensurably differentiated from congeners on mainland New Zealand (Gill *et al.* 2010) with consequent endemism being recognised at both species and subspecies level (Miskelly 2008). The Chatham Islands archipelago is sufficiently distant (800 km) and sufficiently large (966 km^2) to have intercepted and retained not just species dispersing downwind from New Zealand but also direct from Australia (*e.g.* Tennyson 1998). Descendents of some successful colonists (for instance *Prosthemadera novaeseelandiae chathamensis*, *Hemiphaga chathamensis*, *Bowdleria rufescens*, *Fulica chathamensis*, *Gallirallus dieffenbachii*), conform to the "island rule" by being larger than their mainland forebears (see Marchant & Higgins for data; Clegg & Owens 2002; Lomolino 2005).

None of Chatham Island's recent or contemporary duck species (notably *Anas chlorotis*, *A. gracilis*, *A. rhynchotis*, *A. superciliosa*, *Aythya novaeseelandiae*) have been examined to determine mensural differences from populations in New Zealand. However, Tennyson & Millener (1994) and Worthy & Holdaway (2002) have suggested that two undescribed Holocene fossil waterfowl (a shelduck *Tadorna* sp. and a swan *Cygnus* sp.) may be of distinctly different size from congeners in New Zealand and warrant taxonomic distinction. Molecular analyses have detected mtDNA haplotypes unique to the Chatham Island population of *A. superciliosa* (see Rhymer *et al.* 2004) and determined that the large, extinct Chatham Island duck (*Pachyanas chathamica*) is a sister taxon to *A. chlorotis* (see Mitchell *et al.* 2014).

Many waterfowl (especially *Anas* sp. in the 400–800 g weight range), once established on remote southern islands, have become smaller than their source congeners (*e.g. Anas marecula, A. eytoni, A. aucklandica, A. nesiotis*) and some flightless (Lack 1970; Weller 1980; Mourer-Chauviré *et al.* 1999). McNab (1994a,b) considered this to be an energy conservation response in the face of increased intra-specific competition. The diminished wing bone lengths and sterna of mergansers from Auckland Islands and Chatham Island relative to *M. serrator* may be evidence of this "island" response. Their lesser flight capability (Livezey 1989) could also imply an ecology that featured year-round site fidelity and small foraging ranges for all New Zealand region mergansers.

For mergansers, Chatham Island may have provided a very different environment from New Zealand and, particularly, from Auckland Islands. It is, presently, a low flat island of recent (~2.5 mya) emergence with 350,000 years of peat accumulation and a shoreline of contrasting exposed cliff and rock-strewn sections (south and southwest), extensive sand-floored protective bays (west and east) and a broad northern shoreline with both sand and rock seafloors (Campbell 2008; Schiel 2008). Most of the island's northern, eastern and western shorelines are flanked by low barrier dunes. Modern (from 6500 years ago) Chatham Island has many small lakes, small slow peat-stained rivers draining the southern "uplands", and the dominating barrier-bar lake (Te Whanga lagoon), which comprises 20% of the island's area. A freshwater fish fauna of nine species (Bott 2008) could have offered mergansers lacustrine and riverine fare. If mergansers occupied coastal margins (as the presence of fossil merganser bones in coastal dunes implies) they were likely to have been widely dispersed and foraging over a largely featureless sand seafloor, a distinct contrast to habitats occupied on Auckland Islands (Williams 2012). Mergansers exploiting Te Whanga Lagoon (as their retrieval from Te Ana a Moe implies) similarly would have foraged over a shallow, macrophyte-laden sandfloor below windswept waters. Stable isotope analyses indicate a predominantly marine-sourced (lagoon or sea) diet for mergansers recovered from Te Ana a Moe whereas mergansers at Auckland Islands had a mixed freshwater and marine-sourced diet (Williams *et al.* 2012). Thus, the influences that may have induced change in skeletal size and proportion in Chatham Island mergansers are most likely to reflect a feeding environment which contrasted with that at Auckland Islands and, possibly, mainland New Zealand.

Phylogeographic considerations

Phylogeographic questions highlighted by our appraisal of size differences of mergansers in the New Zealand region include:

1) Did the Auckland Islands and Chatham Island populations arise from the same geographic source? Because mergansers on mainland New Zealand extended over 13° of latitude, clinal changes in body dimensions might be expected. The two island populations, if derived from widely-separated areas of New Zealand, may have been established by birds already of differing size.

2) Was dispersal and settlement a one-off event? The ability of waterfowl to cross significant ocean gaps to reach and establish in New Zealand and on its nearby islands (*e.g.* Rhymer *et al.* 2004; Williams *et al.* 2006; Gill *et al.* 2010) suggests merganser dispersal to the island archipelagos was unlikely to have been a one-off event. Repeat dispersal and settlement events are likely to have left a genetic rather than a mensural footprint.

A wider perspective recognises the presence of a merganser in the geographically isolated New Zealand region as a biogeographic conundrum. From where did it come? For example:

3) Were New Zealand's mergansers the consequence of trans-hemispheric dispersal and, thus, an isolated relative of an extant northern-hemisphere

congener such as *M. squamatus* or *M. merganser*, as suggested by Humphrey (1955) and reiterated by Johnsgard (1965) and Kear & Scarlett (1970)? Contemporary trans-hemispheric movements of waterfowl in the Asia-Pacific-Australasia region (Williams *et al.* 2006; Gill *et al.* 2010) are scant.

4) Alternatively, is there a closer phylogenetic relationship with the only other extant southern hemisphere merganser, *M. octosetaceus*? Downy ducklings of these two species are more similar in colour and patterning to each other than to any northern merganser (see Kear 2005). Livezey (1989) suggested "*M. australis* is a member of a basal grade of comparatively small, southern hemisphere mergansers; the Brazilian Merganser (*M. octosetaceus*) branched next and is the sister-group to the larger, more derived, northern hemisphere species of *Mergus*."

Solovyeva & Pearce (2011) used molecular analysis to further resolve phylogenetic relationships of northern hemisphere mergansers. The questions posed above are potentially resolvable by similar means should mtDNA be extracted from the remains of all three New Zealand *Mergus* populations.

Establishing the nearest living relative of New Zealand's mergansers may elucidate a rarely-evidenced route for avifaunal colonisation of New Zealand. Identifying relationships and divergence times between all three New Zealand *Mergus* populations will help inform waterfowl dispersal and establishment on New Zealand's surrounding archipelagos, especially when viewed alongside the pattern of divergence and dispersal Mitchell *et al.* (2013) reported for New Zealand's brown-plumaged teals and Chatham Island's extinct duck *Pachyanas chathamica*.

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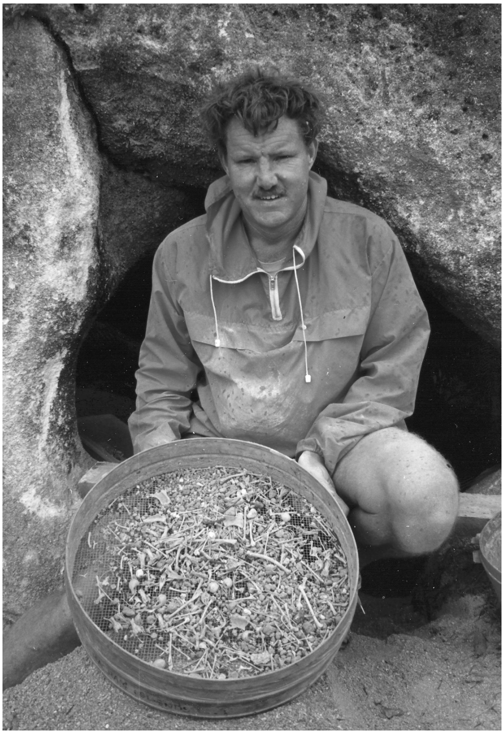

Photograph: Former Museum of New Zealand Curator Dr Philip Millener, after whom *Mergus milleneri* is named. Along with his colleague Noel Hyde, he excavated Chatham Island's spectacular Te Ana a Moe cave deposit of fossil bird bones (shown), retrieving bones from 9 marine and 21 terrestrial and freshwater species, including the collection of *Mergus* bones analysed in this study. (Photograph by N.H. Hyde).

Appendix 1: Institutional source and specimen number of all *Mergus* bones examined.

I. Bones of Chatham Island Merganser. Most Museum of New Zealand specimen numbers refer to multiple bones, each of which has a unique subsidiary number.

Canterbury Museum, Christchurch, New Zealand: Non-cave specimens. AV27501, AV29860.
Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand: Non-cave specimens. S.26362, S.27743, S.28456, S.29534, S.30828, S.31176, S.31259, S.31298, S.35277. Cave specimens. S.27140–27142, S.27144, S.27145, S.27147–27158, S.27520, S.29183, S.29231, S.29702, S.29713, S.29477, S.29478, S.29496, S.29677, S.29689, S.29749, S.30046, S.30052, S.30080, S.30110, S.30126, S.30136, S.30234, S.30243, S.30276, S.30284, S.30618, S.30627, S.30634, S.31634, S.31700, S.31756–31758, S.31777, S.32093, S.32094, S.32109, S.32198, S.44360, S.44361, S.45516, S.45517–45519, S.45521, S.45523–45528.

II. Bones of New Zealand mainland (North Island, South Island, Stewart Island) mergansers. Some Museum of New Zealand specimen numbers refer to multiple bones, each of which has a unique subsidiary number.

Canterbury Museum, Christchurch, New Zealand: AV11532, AV11600, AV13496, AV13512, AV13648, AV13649, AV21264, AV24919, AV26397, AV26398, AV33852, AV33853, AV36201, AV37112, AV37117, AV37125, AV37328.
Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand: S.2363, S.22131, S.22168, S.22169, S.33294–33297, S.35437, S.35947, S.36845, S.37217, S.38954, S.43865, S.43873, S.44466.
Note: Two femora (S.33294.2, S.35947.8) and three tibiotarsi (S.33294.1, S.33295, S.37217.2) were conspicuously smaller than all others and were excluded from analyses.

III. Bones of Auckland Islands Merganser.

Canterbury Museum, Christchurch, NZ: AV1582, AV5176, AV7157.
Museum of New Zealand Te Papa Tongarewa, Wellington, NZ: OR23515.
Otago Museum, Dunedin, NZ: AV1110.
Natural History Museum, Tring, United Kingdom: 1904.8.4.2, 1904.8.4.3, 1904.8.4.4.

IV. Bones of *Mergus serrator*.

Naturmuseum Senckenberg, Frankfurt, Germany: 1943, 7821, 7825, 7845.
Naturhistorisches Museum, Basel, Switzerland: 1200, 1543, 7730.
Museum Nationale d'Histoire Naturelle, Paris, France: 1996/39.
National Museum of Ireland, Natural History, Dublin, Ireland: 1927.6.1, 1932.13.1, 2004.79.26.
Naturhistorisches Museum, Vienna, Austria: 4456, 4457, 4827, 8639, 8704.
Natural History Museum, Tring, United Kingdom: 1898.2.12.5, 1930.3.24.240, 1930.3.24.242, 1930.3.24.633, 1997.78.1.
Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand: OR12707.

Appendix 2: Summary statistics of measurements of merganser bones from New Zealand, Auckland Islands and Chatham Island (cave, dune), and of Red-breasted Merganser *Mergus serrator*.

New Zealand measurements are of all bones (both sexes combined) followed by putative (?) females and putative (?) males determined as described in Methods. Chatham Island dune measurements are of all bones (both sexes combined). Chatham Island cave measurements are of females. All measurements in mm. Abbreviations: Tsk = total skull length; N-t = nares to rostrum tip; Pop = cranium post-orbital process width; Iow = cranium inter-orbital width; Hum = humerus length; Uln = ulna length; Cmc = carpometacarpus length; Col = coracoid length; Cow = coracoid width; Stv = sternum visceral(dorsal) length; Sta = sternum anterior width; Stp = sternum posterior width; Kel = Keel (carina sterni) length; Kea = Keel (carina sterni) area (mm^2); Fem = femur length; Tbt = tibiotarsus length; Tmt = tarsometatarsus length; Pel = pelvis length; Pea = pelvis anterior width; Pep = pelvis posterior width; Ant = process antitrochanter width; s.d. = standard deviation; *n* = sample size.

New Zealand

All bones	**N-t**	**Hum**	**Uln**	**Cmc**	**Col**	**Cow**	**Fem**	**Tbt**	**Tmt**
Mean	36.5	68.5	53.2	38.6	42.3	14.5	42.6	71.2	40.2
s.d.		2.7	2.7	2.3	1.9	0.8	1.5	2.9	1.8
Maximum	40.4	72.4	56.8	41.3	45.9	16.2	45.0	75.4	43.2
Minimum	32.5	65.3	48.8	37.2	39.9	13.6	40.0	66.6	38.6
Median		68.1	53.0	37.4	42.1	14.1	43.8	72.0	39.6
n	2	16	14	3	12	8	16	15	6

?Females									
Mean		66.5	51.3		41.2	14.2	41.3	68.5	
s.d.		1.2	1.7		0.9	0.4	0.57	1.5	
Maximum		68.1	53.3		42.2	14.9	41.7	70.3	
Minimum		65.3	48.8		39.9	13.6	40.0	66.6	
Median		65.7	51.8		40.9	14.1	41.3	69.2	
n		9	8		8	7	7	7	

?Males									
Mean		71.0	55.8		44.6	16.2	43.7	73.6	
s.d.		1.5	0.8		0.9	–	0.9	1.3	
Maximum		72.4	56.8		45.9	–	45.0	75.4	
Minimum		69.0	54.6		43.8	–	42.9	72.0	
Median		71.7	56.1		44.3	–	43.8	74.2	
n		7	6		4	1	9	8	

Auckland Island

Females	**Tsk**	**N-t**	**Pop**	**Iow**	**Hum**	**Uln**	**Cmc**	**Col**	**Cow**	**Stv**	**Sta**
Mean	103.1	36.6	27.2	5.3	68.4	54.9	38.5	44.4	17.0	71.8	42.5
s.d.		0.8		0.5				0.2	0.4	0.5	0.5
Maximum	103.6	37.3	27.2	5.8	68.9	55.0	38.5	44.8	17.5	72.3	43.1
Minimum	102.6	35.8	27.2	4.8	67.8	54.7	38.5	44.2	16.6	71.2	41.9
Median		36.6		5.2				44.3	17.1	71.8	42.4
n	2	3	2	3	2	2	2	5	5	4	4
Male (1)	109.9	40.2	29.0	5.4	72.1	57.7	41.0	48.3	19.1	77.1	47.7

Females	**Stp**	**Kel**	**Kea**	**Fem**	**Tbt**	**Tmt**	**Pel**	**Pea**	**Pep**	**Ant**
Mean	47.1	85.9	575	42.9	71.5	40.8	87.9	18.2	47.4	28.8
s.d.	0.8	3.1	27						0.4	0.2
Maximum	47.9	88.5	601	43.1	72.1	41.2	89.7	18.4	48.0	29.0
Minimum	45.9	81.5	545	42.6	70.9	40.4	86.0	18.0	47.0	28.7
Median	47.3	86.7	576						47.1	28.7
n	4	4	4	2	2	2	2	2	3	3
Male (1)	49.6	94.8	628	45.4			94.9	19.3	49.9	31.2

Chatham Island cave

Females	**Tsk**	**N-t**	**Pop**	**Iow**	**Hum**	**Uln**	**Cmc**	**Col**	**Cow**	**Stv**	**Sta**
Mean	97.5	33.8	27.7	6.1	66.6	53.5	37.3	42.4	16.4	63.9	42.7
s.d.	1.4	0.5	0.3	0.3	0.9	0.8	0.6	0.7	0.3	1.5	1.3
Maximum	99.2	35.2	28.3	6.5	68.3	54.9	38.8	43.6	17.3	67.0	45.5
Minimum	95.7	31.3	26.7	5.2	64.4	51.6	35.8	40.6	15.8	60.7	40.0
Median	97.8	34.1	27.7	6.2	66.6	53.6	37.3	42.3	16.4	63.9	42.8
n	6	46	44	43	47	43	41	46	46	31	34

Females	**Stp**	**Kel**	**Kea**	**Fem**	**Tbt**	**Tmt**	**Pel**	**Pea**	**Pep**	**Ant**
Mean	44.7	75.2	516	43.0	72.2	39.9	82.3	17.8	49.4	25.5
s.d.	0.8	1.6	37	0.6	1.1	0.7	1.1	0.7	2.0	0.6
Maximum	46.0	78.3	577	44.1	74.0	41.8	85.0	19.3	54.6	26.5
Minimum	42.4	69.4	447	41.8	70.0	38.4	80.7	16.4	45.3	23.9
Median	44.8	76.0	516	43.1	72.3	40.0	82.1	17.9	49.2	25.6
n	28	31	19	44	47	51	25	26	29	35

Chatham Island dunes

All bones	Hum	Uln	Cmc	Col	Fem	Tbt
Mean	70.7	51.7	35.5	41.0	43.2	69.9
s.d.				4.3	1.1	
Maximum	70.8			45.7	44.2	
Minimum	70.6			37.4	41.7	
Median				39.9	43.8	
n	2	1	1	3	3	1

Mergus serrator

Females	Tsk	N-t	Pop	Iow	Hum	Uln	Cmc	Col	Cow	Stv	Sta
Mean	102.4	36.6	27.4	6.1	83.3	68.9	49.4	53.2	19.3	81.9	47.6
s.d.	3.2	1.1	0.3	0.2	3.0	2.6	1.9	2.7	0.6	1.6	2.4
Maximum	105.5	37.7	27.7	6.4	89.9	73.9	52.6	56.9	20.1	84.7	50.1
Minimum	98.2	35.5	27.1	5.9	81.4	64.7	46.7	49.2	18.1	79.2	45.3
Median	102.8	36.3	27.3	6.0	82.7	68.7	49.1	52.4	19.2	81.6	47.2
n	4	4	8	7	9	10	6	9	8	11	12
Males											
Mean	108.4	40.4	30.0	6.6	89.7	73.8	52.2	58.7	20.5	91.0	54.9
s.d.	3.7	2.1	0.8	0.3	1.5	1.4	0.8	2.0	0.8	3.0	2.5
Maximum	110.7	42.8	31.1	7.1	91.2	76.2	52.8	60.7	21.6	94.8	58.6
Minimum	104.2	38.5	29.2	6.2	87.6	72.2	51.2	56.0	19.8	86.3	52.3
Median	110.3	40.1	29.7	6.6	90.3	73.7	52.4	58.8	20.3	91.7	54.0
n	3	4	5	5	7	7	4	5	5	8	7

Females	Stp	Kel	Kea	Fem	Tbt	Tmt	Pep	Ant
Mean	52.2	107.3	762	44.5	77.5	43.0	46.0	25.4
s.d.	2.5	2.6	15	1.3	1.9	1.4	2.4	0.8
Maximum	57.7	110.9	771	48.0	81.9	45.4	49.6	27.1
Minimum	48.4	103.1	740	43.7	76.4	41.4	43.6	24.6
Median	52.3	108.5	769	44.7	76.8	42.7	45.6	25.2
n	10	9	5	10	7	7	9	9
Males								
Mean	58.0	121.7	982	47.7	82.7	46.9	47.9	27.4
s.d.	2.4	1.8	80	1.4	1.2	1.0	2.2	1.6
Maximum	60.5	123.4	1090	49.2	84.2	48.4	49.8	29.3
Minimum	54.8	118.7	876	45.9	81.5	45.6	44.7	25.7
Median	57.8	122.1	981	47.5	82.1	46.7	48.8	26.8
n	7	5	5	5	6	6	5	5