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Soft-tissue specimens from pre-European extinct birds of New Zealand

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We provide the first complete review of soft tissue remains from New Zealand birds that became extinct prior to European settlement (c. AD 1800). These rare specimens allow insights into the anatomy and appearance of the birds that are not attainable from bones. Our review includes previously unpublished records of 'lost' specimens, and descriptions of recently discovered specimens such as the first evidence of soft tissues from the South Island goose (*Cnemiornis calcitrans*). Overall, the soft tissue remains are dominated by moa (with specimens from each of the six genera), but also include specimens from Finsch's duck (*Chenonetta finschi*) and the New Zealand owlet-nightjar (*Aegotheles novaezealandiae*). All desiccated soft tissue specimens that have radiocarbon or stratigraphic dates are late Holocene in age, and most have been found in the semi-arid region of Central Otago.

Keywords: *Aegotheles*; birds; *Chenonetta*; *Cnemiornis*; Dinornithiformes; extinct; feathers; moa; New Zealand; soft tissues

Introduction

The arrival of humans in New Zealand during the thirteenth century AD (Wilmshurst et al. 2008) spelled doom for the native avifauna. Approximately thirty species became extinct, or had become very rare, prior to the arrival of Europeans in 1769 (Bunce et al. 2009; Gill et al. 2010). While most of these species are known only from bones, rare specimens with preserved soft tissues provide an insight into how these birds appeared in life (e.g. Rothschild 1907; Rawlence et al. 2009) (Table 1, Supplementary file 5). Such specimens include two main types: (1) feather and skin impressions within fine sediments and coprolites (preserved dung), and (2) desiccated tissues that have been preserved by dry conditions at their sites of deposition. The excellent preservation of the latter led to them yielding some of the first proteins and DNA isolated from extinct birds (Cooper et al. 1992; Vickers-Rich et al. 1995).

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Supplementary data available online at www.tandfonline.com/10.1080/03036758.2012.704878
Supplementary file 1: Specimens of soft tissues from extant bird species of New Zealand; **Supplementary file 2:** Transcripts of paraphrased letters previously not available online; **Supplementary file 3:** Transcripts of paraphrased newspaper articles; **Supplementary file 4:** Moa feather colour patterns; **Supplementary file 5:** Specimens of soft tissues from pre-European extinct birds of New Zealand; **Supplementary file 6:** Radiocarbon dates of desiccated soft tissue remains; **Supplementary file 7:** Size of preserved moa feathers held in New Zealand and overseas museum collections; **Supplementary file 8:** Measurements of Finsch's duck *Chenonetta finschi* (Van Beneden, 1875) bones from Earnscleugh Cave held in Canterbury Museum (CMC), Christchurch

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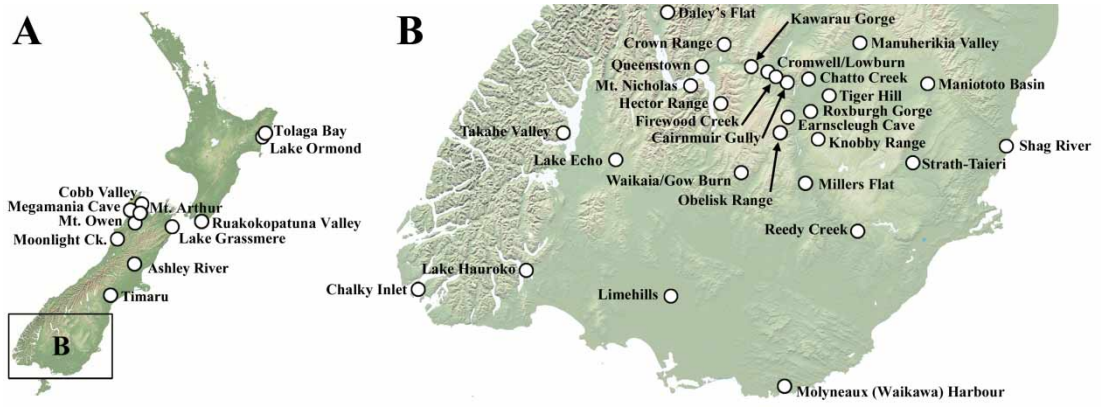

Figure 1 A, **B**, Localities mentioned in the text, including sites of pre-European extinct bird soft tissue specimens.

Specimens of preserved soft tissue from extinct New Zealand birds have been summarised by Anderson (1989a), and Worthy and Holdaway (2002). Here, we present the first complete review of all known specimens, outlining details of their discovery and subsequent analysis. In addition to well-known historically collected specimens, we present previously unpublished reports of soft tissue specimens, and provide the first description of soft tissues from the South Island goose (*Cnemiornis calcitrans* Owen, 1866). Not all examples of soft tissue preservation have reliable collection and historical data associated with them. In this review, we discuss only specimens with robust associated historical data, though many more are listed in Supplementary file 5. Also, we do not discuss the range of different feather types that have been found in dry crevices and rockshelter sediments, often in association with moa feathers. These include feathers from extant birds (Wood 2006, 2008a), but may also include feathers from pre-European extinct taxa. There are only three reported instances of desiccation in extant birds, from the Megamania and Nettlebed (Mount Arthur) cave systems (Fig. 1) (see Supplementary file 1 for further information).

Moa (Dinornithiformes)

South Island giant moa Dinornis robustus *Owen, 1846*

Tiger Hill

At Rattray's Store, Dunedin, on 14 January 1864, James Hector examined and measured the complete skeleton (albeit minus a few cervical vertebrae (Buller 1888)), of what is now known to be a female South Island giant moa. The specimen had been discovered by gold prospectors near Tiger Hill in the Manuherikia Valley, Central Otago (Hector 1864) (Fig. 1). Hector (1864) made measurements and notes on the condition of the remains, recording that 'mainly all the ligaments of the left knee are present . . . the fibula, the skin is also present and again on the foot of the same leg the sole of the foot and ligaments'. Buller (1888) noted that integument and feathers still adhered to the sacrum, and the interarticular cartilages were preserved. Dallas (1865) made the first description of moa feathers based on the specimen, noting an accessory plume comparable to those of emu (*Dromaius* spp.) and cassowary (*Casuarius* spp.), and that the feathers had 'barbs consisting of slender flattened fibres, bearing long silky and very delicate barbules, without any trace of barbicels'.

The circumstances surrounding the discovery of the specimen were outlined in a letter dated February 1864, from James Hector to Richard Owen (Owen 1866) (see Supplementary file 2). The bones were found after a shaft was dug into a river terrace composed of sand and gravel. Hector thought that the preservation of soft tissues was due to the favourable position of the remains within the surrounding matrix. However, it is more likely that the remains were found in a mica-schist cave or rock shelter, as fluvial river terrace sands or gravels are unlikely to preserve soft tissues (T. Worthy, pers. comm., 2008).

The original discoverers of the specimen also mentioned that the bones of four moa chicks were found beneath the skeleton (Buick 1931). This has never been verified (Wood 2008b).

The Tiger Hill specimen was subsequently purchased in New Zealand by Dr Gibson, who, while visiting England over the summer of 1863, had learnt that the Yorkshire Museum and Art Gallery (YMAG) desired to acquire moa and kiwi specimens for their collections. The *Dinornis* skeleton was forwarded to England, where it arrived at the Museum of the Yorkshire Philosophical Society (Allis 1865a,b). The skeleton was initially examined and described by T. Allis (Allis 1865a) and W. Dallas (Dallas 1865), and later taken to London for Owen to study (Owen 1866). Small amounts of soft tissues were preserved on a range of elements: cartilage attaching several ribs to vertebrae and sternal ribs to sternum; eight caudal vertebrae articulated by cartilage; the ligaments and interarticular cartilage preserved on the joints of one leg; the right inner toe phalanges attached to the tarsometatarsus by cartilage and with the skin from the sole of the foot attached (figured by Owen 1869); fragments of skin attached to a femur and fibula; and a large piece of skin with embedded feather bases on the pelvis (Allis 1865a; Owen 1866). Owen (1869) described the papillae on the sole of the foot as circular to pentahexagonal oblong in shape, covered in a thick epidermal layer as hard as horn. The specimen is housed in the YMAG (2004.20) (Supplementary file 5). Unfortunately, the majority of soft tissues described above have been separated from the specimen sometime in the past and are presumed lost (Isla Gladstone, pers. comm., 2011). YMAG has found no reference to when or why the separation was carried out.

Knobby Range

A right tarsometatarsus with phalanges, partial left tarsometatarsus, right tibiotarsus, left femur, and partial sternum from a presumably female *D. robustus* were collected by G.E. Allen on the 04 July 1874 from Galloway Station, Knobby Range, Central Otago (Fig. 1). The bones were found in a 'deep crevice among mica-shist rocks' (Hutton & Coughtrey 1875a; Buller 1888); '3 ft wide and 6 ft deep, and the bones were only partially covered by the rank grass growing up around them' (Buick 1931). Among the bones was a remarkably well-preserved foot, with dried skin, ligaments, and muscle adhering to the phalanges. The specimen was obtained by Julius von Haast, who forwarded it to Professor Milne-Edwards at the Museum of Natural History in Paris (Anon 1875). The specimen is currently held by Otago Museum (OM) (AV7476) (Supplementary file 5). The specimen has previously been figured in Anon (1875), Hutton & Coughtrey (1875a), and Worthy and Holdaway (2002). A radiocarbon date of 861 ± 30 yr BP was obtained for the specimen (Anderson et al. 2010) (Supplementary file 6). Desiccated muscle, not bone, was used to date the specimen, meaning the age could be biased by bacterial contamination introducing modern carbon into the sample (Geyh et al. 1974; Worthy 1989). In addition, depositional environment (dry versus damp) and collagen pretreatment (bulk versus ultrafiltration) will also bias the radiocarbon date (Bronk Ramsey et al. 2004a,b; Jacobi et al. 2006).

'Alexandra Caves'

A pelvis and sternum from a *D. robustus* (OM AV3983), with small fragments of tissue

adhering, are listed as being from 'Alexandra Caves', and were collected by W. Allan in 1885 (OM register). Two bones of eastern moa (*Emeus crassus* (Owen, 1846)) are also attributed to this locality (see below). Worthy (1998a) noted that 'Alexandra Caves' is probably Earnscleugh Cave given the location and excellent preservation of these bones. However, while we believe that the *E. crassus* bones are probably from Earnscleugh Cave, we have uncovered evidence to suggest the *D. robustus* bones are from a different locality.

A previously unpublished letter dated 08 July 1885 (Allan 1885), from W. Allan of Alexandra South to T.J. Parker at OM (see Supplementary file 2), describes the discovery of a moa bone with soft tissue attached that was found among debris at the base of a pipeclay cliff. Allan thought the specimen originated from an erosion feature in the cliff as opposed to the clay itself. Attached to this letter, an unreferenced but apparently contemporaneous newspaper clipping (see Supplementary file 2) reports the discovery was made by Mr John Allan's son near Alexandra in a lacustrine clay and alluvial deposit on the banks of the Manuherikia River at Soloman's Face.

The name 'Solomon's Face' is no longer in common usage but the description of the site suggests it is likely to be cliffs near Galloway Bridge (J. Douglas, pers. comm., 2006). As Allan suggests to Parker, the bones would not have come from the Manuherikia Group sediments forming the cliff face, but from a late Holocene erosion feature (i.e. tomo or solution pipe) formed within them. Such features across Otago commonly hold moa bones (e.g. Chatto Creek; Worthy 1998a) and if conditions were dry enough could conceivably preserve soft tissues (e.g. feather impressions; Supplementary file 5). Parker obviously replied to Allan requesting more information about the find. A letter from Allan to Parker dated 27 July 1885 (Allan 1885) (see Supplementary file 2) states that it was likely that the bone originated from an erosion feature as the cliff face is full of caves and fissures. Allan suggested it is probable that the bone was washed into the erosion feature and was exposed when the cliff fall took place.

Ashley River

On the 25 January 1991, a University of Canterbury PhD student, Hugh Cowan, located a large landslide on the north limb of the Cust anticline in North Canterbury, which contained a partially exposed right tarsometatarsus (with articulated phalanges) of a presumably female *D. robustus*. The specimen is held by Canterbury Museum (CMC) (SB1). The site was on the south bank of the Ashley River just above its confluence with the Okuku River (New Zealand Fossil Record Number M34/f0296, 43°15′ 41″ S, 172°23′40″E (position reinterpreted using Google Earth from illustrations in Cowan 1992); Cowan et al. 1996). The remarkable thing about this leg is that it clearly shows the pattern of scales on both the tarsometatarsus and phalanges (Fig. 2). This patterning was in a blue crystalline substance that is probably the iron phosphate mineral vivianite that is known to form around bone in conditions of low pH and anoxia as the vivianite replaces the proteins in bone and scales (Thali et al. 2011). This is the first record of this type of soft tissue preservation in birds. Wood samples from this site were dated to 2300 ± 60 yr BP (NZ 7855) and 2270 ± 82 yr BP (NZ 7856) (Cowan et al. 1996).

Eastern moa **Emeus crassus** ***(Owen, 1846)***

Earnscleugh Cave

Earnscleugh Cave (Fig. 1) was first discovered by Europeans around 1869, when a goldminer's son stumbled upon an entrance en route to his father's gold claim (Fraser 1873). The boy and his father subsequently revisited the site and collected the neck of an *E. crassus*, still covered with skin and feathers (Fig. 3), which they sold to Dr Alexander Thomson of Clyde. Thomson

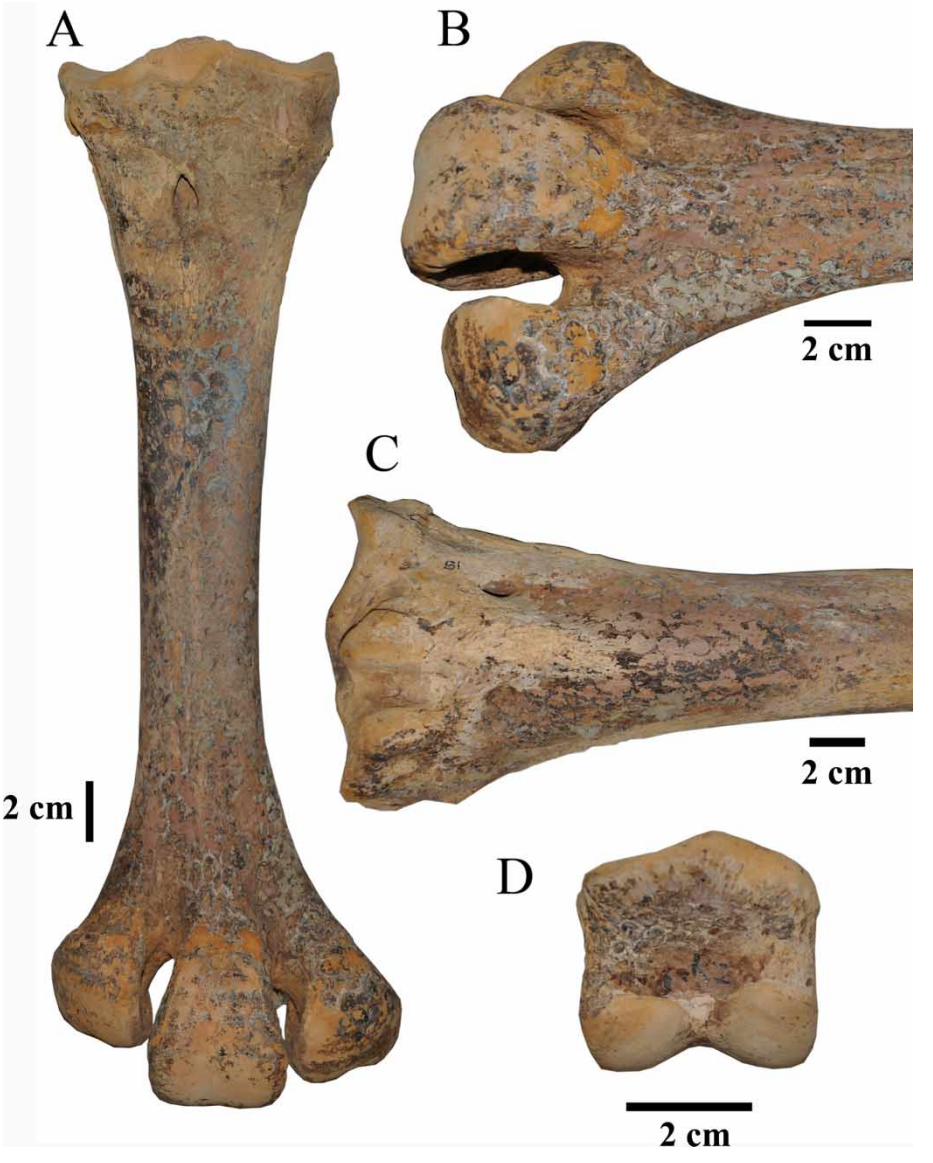

Figure 2 South Island giant moa (*Dinornis robustus* Owen, 1846) with mineralised skin impressions, Ashley River, Canterbury (CMC SB1). **A**, Right tarsometatarsus. **B**, Close up of distal right tarsometatarsus. **C**, Ventral side of proximal right tarsometatarsus. **D**, Underside of phalange. The blue crystalline substance is probably the iron phosphate mineral vivianite.

visited Earnscleugh Cave shortly thereafter, and collected some of the best preserved bone and soft tissue remains present in the cave, including a femur, fibula (Fig. 4), pelvis and sternum with fragments of soft tissues attached (Thomson 1871). They are all identified as *E. crassus*. Soon after visiting the cave, Thomson wrote to James Hector at the Geological Survey, Wellington, alerting him to the discovery. Following this correspondence, Hector wrote a short note to Owen on 28 October 1871 (see Supplementary file 2) stating that the

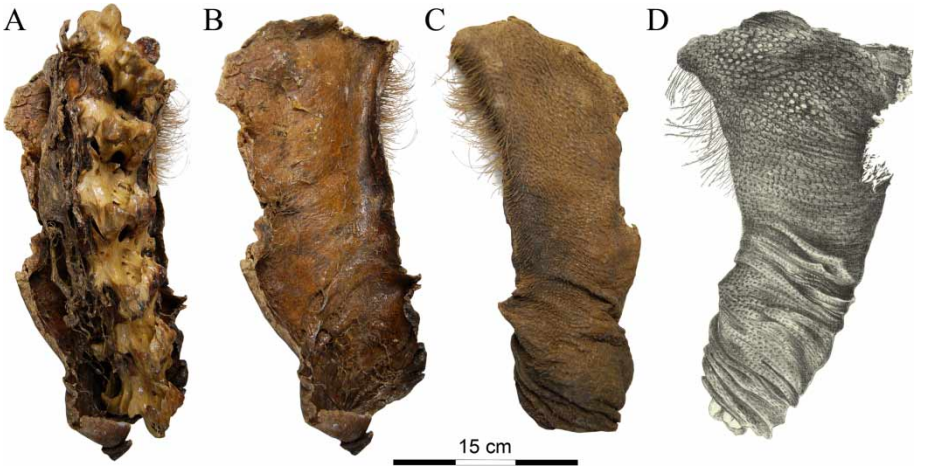

Figure 3 Desiccated neck of eastern moa (*Emeus crassus* (Owen, 1846)) collected from Earnscleugh Cave, Central Otago (OM AV7504): **A**, Articulated cervical vertebrae. **B**, Internal surface of skin. **C**, External surface of skin, showing preserved feather bases. **D**, Lithograph of same specimen from Hector (1872).

bird remains appear to have slid into the cave and included a complete skull with trachea attached, but also muscular tissue and fragments of skin (Owen 1879). The neck was sent to Dunedin, where it was drawn and described by Hector (Hector 1872), and it is still housed in OM (AV7504). The desiccated remains revealed that the neck of *E. crassus* did not have a dense covering of feathers (Hutton & Coughtrey 1875b) but had coarse skin with elevated papillae (Hector 1872).

One of the earliest surviving descriptions of Earnscleugh Cave is in a previously unpublished letter dated 27 November 1871, from Thomson to Dr T.M. Hocken of Dunedin (see Supplementary file 2), and is probably similar to the description that Thomson had sent Hector. Thomson visited the cave and found the remains of at least eight moa and fragments of eggshell. The cave is an irregular-shaped fissure in the mica-schist rock about 50 ft deep with two entrances and consists of multiple levels where bones were found buried under loose dirt. Thomson also highlights the finding of a complete skull with lower jaw and tracheal rings attached, and another nearby cave containing moa bones (Thomson 1871). Although the head has since been lost, the remaining bones with soft tissues are housed in OM (Supplementary file 5).

W. Fraser of Earnscleugh Station (on which the cave is located) also visited Earnscleugh Cave with his son around 1871–72 (Fraser 1873) and noted that the sediment in the cave was fine and dusty. He found several bones and some fine fragments of reddish-brown moa skin (Fraser 1873). F.W. Hutton, former director of the OM, visited Earnscleugh Cave twice over the summer of 1873–74 in the company of Dr Thomson (Hutton & Coughtrey 1875b). Hutton and Thomson collected a range of bird bones, dried skin and feathers of Finsch's duck (*Chenonetta finschi* (Van Beneden, 1875)). Hutton also sampled the cave sediment, which he forwarded to Professor J.G. Black (Professor of Chemistry and Mineralogy at University of Otago) with instructions to analyse it for any special properties for the preservation of soft tissues. However, Black found nothing unusual about the sediment (Hutton & Coughtrey 1875b). Earnscleugh Cave was rediscovered in 1993, and excavations the following year uncovered two moa feathers (Clark et al. 1996). Clark et al. described the cave more thoroughly, though Worthy (1998a) re-interpreted

Figure 4 Right femur and fibula of eastern moa (*Emeus crassus* (Owen, 1846)) with desiccated soft tissues attached (indicated by arrows), collected from Earnscleugh Cave, Central Otago (OM AV7503, AV7505).

the former study based on subsequent re-excavation of the site.

'Alexandra Caves'

A pelvis and sternum (OM AV7481, AV7482) of *E. crassus*, with tissue remnants still adhering to them, have also been discovered from 'Alexandra Caves'. As discussed above these remains were probably collected from Earnscleugh Cave given the location and excellent preservation of the bones. The pelvis (OM AV7482) is too large for the *E. crassus* femur from Earnscleugh Cave (OM AV7503; Fig. 4), so probably represents a second individual. This is supported by Hector (1872) quoting J.A. Thompson that there were at least eight moa in the Earnscleugh Cave deposit.

Upland moa Megalapteryx didinus *(Owen, 1883)*

Crown Range

A desiccated *M. didinus* was collected from a cave near Queenstown in 1878 (Oliver 1949) (Fig. 1). The exact location and circumstances of the discovery are not known, but the Otago Witness (19 October 1878, p. 4) (see Supplementary file 3) reported that the remains were 'discovered by two miners on the hills on the left bank of the Arrow River' (i.e. the Crown Range). Lydekker (1891) further states that it was found in a 'fissure-cave disclosed by a landslip'. A description of the specimen was given in the Tuapeka Times (23 November 1878, p. 2) (see Supplementary file 3), which reported that the head, legs and feet were complete. The desiccated tarsometatarsus was articulated and covered in muscle and skin, including the horny claws in all but two instances. The head included the tongue, eyeballs, and part of the neck and trachea. Buller (1888) reported that the trachea was enclosed and covered with dried integument, and the sclerotic ring in the eye was also present.

The specimen was purchased by H.L. Squires of Lawrence, who took it to England in 1878 and sold it to the Natural History Museum, London (NHM) in 1882 (Lydekker 1891; Parker 1893), where Owen designated it as the type specimen of *Dinornis didinus* Owen, 1883. Feather pits in the skin covering the skull indicated that the head was covered in small feathers (Oliver 1955), while the specimen also indicated that *M. didinus* had a muscular middle toe (Owen 1883). The specimen was first figured by Owen (1883), and formed the basis of an artistic reconstruction by Rothschild (1907). Parkes and Clark (1966) reconstructed the head and bill of *M. didinus* from the

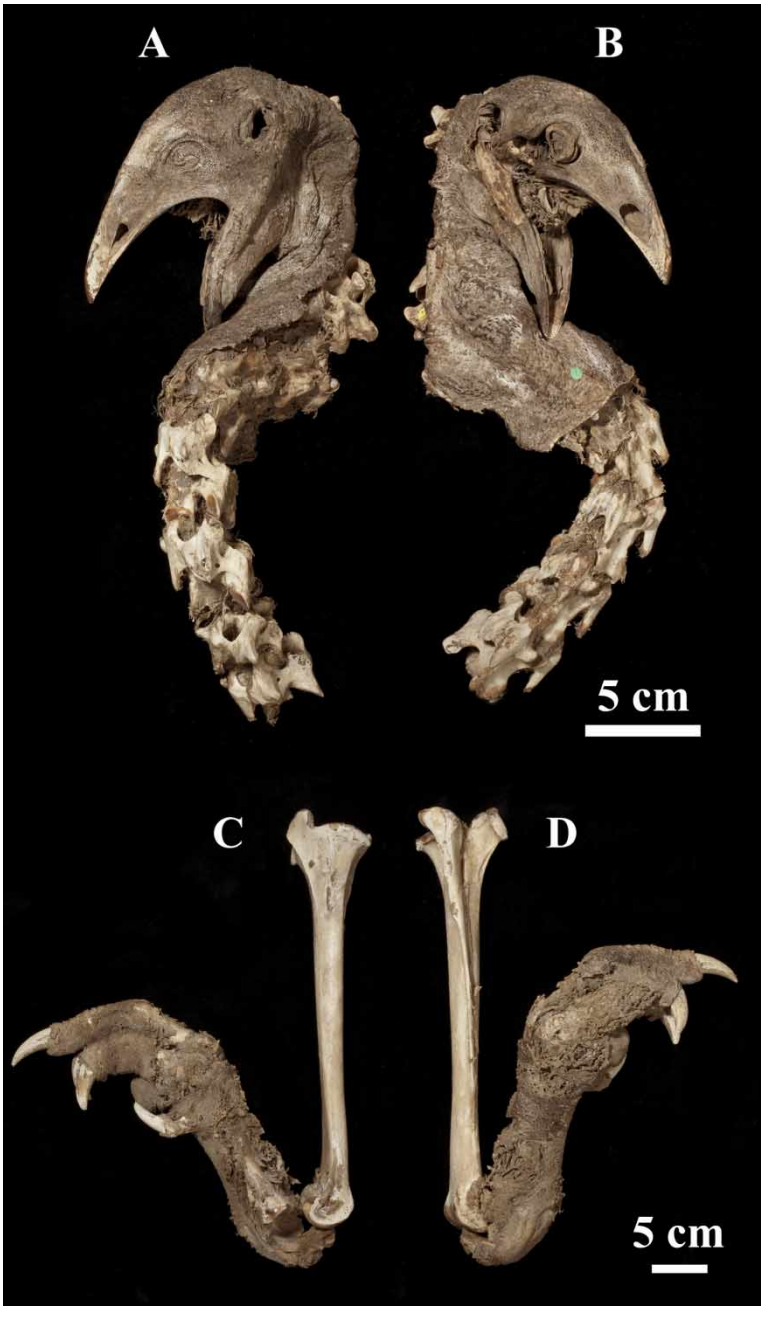

Figure 5 Desiccated type specimen of upland moa (*Megalapteryx didinus*) Owen, 1883)) (NHM A16), collected from Crown Range, Central Otago: **A-B**, Head and neck from left (**A**) and right (**B**) side. **C-D**, Right lower leg in medial (**C**) and lateral view (**D**). Photos courtesy of NHM.

lithograph by Owen (1883) of this specimen, with the conformation of the rhampotheca agreeing with that of other ratites. The specimen is housed in the NHM (Supplementary file 5) and is figured here as Fig. 5.

Waikaia

On 19 July 1894, Augustus Hamilton reported, to the Otago Institute, the discovery of a well-preserved leg of *M. didinus* (Fig. 6), complete with dried skin, muscle, ligaments, and feathers to the base of the ankle, in the Waikaia River catchment of the Old Man Range (Hamilton 1895) (Fig. 1). The specimen was probably lying half buried as the skin is better preserved on the lateral side (Oliver 1949; Fig. 6). It was found in a cave by gold prospector Peter McLeod (fide Oliver 1949). Although no date was given for the discovery, it was probably around December 1893 as there is an entry in the CMC accessions ledger for 14 February 1894 describing the accession of a *Megalapteryx* moa feather found in the Old Man Range in Christmas 1893 (these are probably CMC Av9341). The exact location of the cave is not known, and the specimen is often referred to as having come from either the Old Man Range, or Waikaia River catchment (Anderson 1989a; Worthy 1998a). However, it is possible to narrow down the location of cave, as Hamilton (1895) outlined the route he took to get there. He describes leaving his horse at 'an accommodation house known as Vernon's' before walking a further 3–4 miles (4.8–6.4 km) to a digger's hut, the cave only being a short distance from the hut, halfway up the steep side of a gorge. The 1892 directory of Otago and Southland lists an Edward Vernon of the Whitcombe Hotel, and Miller (1966) reports that Edward Vernon and his wife were the proprietors of the Whitcombe Hotel until they moved to Roxburgh in 1905. So, it is likely that the Whitcombe Hotel is what Hamilton referred to as 'Vernon's'. Whitcombe is located 14 km NNE of Waikaia. A 3–4 mile (4.8–6.4 km) radius around Whitcombe indicates the probable area in which the cave is located. From Hamilton's description of the cave as being in a steep, rocky gorge, it is most likely that he was travelling up the Gow Burn, northwest of Whitcombe. This would be con-

Figure 6 Desiccated leg of upland moa (*Megalapteryx didinus* (Owen, 1883)) (OM AV7474) from near Wakaia, northern Southland.

sistent with the reported climb following examination of the cave, to the tops and over to Gorge Creek (also known as Blue Creek) where a moa hunter campsite was discovered (Hamilton 1895; Anderson 1980). During Hamilton's visit numerous moa feathers were collected and these are now held in the collections of NMNZ, CMC and the NHM (Supplementary file 5). The leg is currently held by OM (Supplementary file 5). The feathers found with this specimen were mainly grey at the base, deepening to reddish brown at the tip, including a single purple feather (55 mm long and 5 mm wide); others were various shades of brown with lighter tips (Hamilton 1895; JRW, pers. obs.). This specimen and the specimen from Queenstown (described above) revealed that the legs of *M. didinus* were feathered to the base of the tarsometatarsus, presumably as an adaptation for coping with cooler temperatures and potential snow cover in its preferred upland habitat (Worthy 1989). Anderson et al. (2010) radiocarbon-dated desiccated muscle from the specimen and obtained an age of 631 ± 30 yr BP (Supplementary file 6). However, the young age on the soft tissue may reflect bacterial contamination introducing modern carbon into the sample (Geyh et al. 1974; Worthy 1989).

Close examination of this specimen by JRW showed that a small bare patch on the lateral side of the upper left tibiotarsus was an area of active moult (Fig. 7). The area was covered in newly emerging feather tips, about 1 cm long. It was notable that these feathers are a brighter rufous brown than the surrounding feathers, indicating that the surrounding feathers had faded significantly. This may be explained by (1) the bird being late in its moult cycle with complete body moult imminent; (2) the longer, more exposed feathers having faded since the specimen's discovery and unearthing; (3) 'shock moult'. Body moult in living ratites is poorly described but 'shock moult' is well documented especially in kiwi (Marchant & Higgins 1990). The localised nature of the bare area and its location on an area likely to be prone to trauma suggests that this is indeed 'shock moult' that must have occurred some weeks before the individual's demise. This is the first documented evidence of moult in moa.

Cromwell

In 1943 W. Oliver (Director of the Dominion Museum, now National Museum of New Zealand Te Papa Tongarewa, NMNZ),

Figure 7 Moulting of upland moa (*Megalapteryx didinus* (Owen, 1883)) (OM AV7474) from near Wakaia, northern Southland.

purchased, for the sum of £5, a remarkably well-preserved *M. didinus* from D.W. Simpson of Tākaka (Vickers-Rich et al. 1995). The specimen consisted of a complete head and neck with desiccated eye, dried skin and muscle, but had no feathers attached (first figured by Oliver 1949). The first nine cervical vertebrae were articulated with the cranium, attached by muscle and skin. The rest of the skeleton consisted of a pelvis, articulated left femur, left tibiotarsus and left fibula joined by ligaments, left tarsometatarsus with one phalanx of digit two joined by ligament, sternum, vertebrae, right femur and ribs (Vickers-Rich et al. 1995). The specimen had apparently been discovered near Cromwell, Central Otago (Fig. 1), though the date of discovery is not known. Through unknown circumstances the specimen had ended up in the possession of D.W. Simpson's great-grandfather, James Campbell (Oliver 1955; Vickers-Rich et al. 1995). It would be unusual if the discovery of such a specimen was unreported at the time, although there may be a relationship with the report of a well-preserved moa skeleton found near Lowburn, Central Otago, in 1887 (see description later in this review). The Cromwell specimen is housed in NMNZ (S.400) and is figured in Vickers-Rich et al. (1995) and Trusler et al. (2010). Vickers-Rich et al. (1995) gave a detailed description of the cranial and stapedial morphology, and the DNA and collagen content of the specimen. They further described the structure of two major ligaments and ten cranial muscles, including some of the jaw muscles. Their conclusions were subsequently discussed by Livezey and Zusi (2006), who disagreed with Vickers-Rich et al.'s (1995) interpretation of two superficial jaw muscles originating from the temporal fossa identified as m. adductor mandibulae (externus rostralis) and m. adductor mandibulae (external caudalis). Two radiocarbon dates for the Cromwell specimen are 646 ± 95 and 690 ± 120 yr BP (Supplementary file 6).

Lake Hauroko

Forrest (1987) recorded that the Clifden ranger station, western Southland, held the pelvis, ribs and five vertebrae of a little bush moa (*Anomalopteryx didiformis* (Owen, 1844)), the vertebrae being held together by gristle and skin. The specimen was reported to have been found by K. Hamilton at Lake Hauroko, Fiordland, in 1975 (Forrest 1987) (Fig. 1). Anderson (1989a) stated that the specimen was held in the Southland Museum and Art Gallery (SMAG), from personal communication with R. Beck, the then Director of the museum. However, the specimen was not mentioned by Worthy (1998b) in a review of Quaternary fossil specimens from Southland, despite Worthy reviewing all such material held in the museum. We have made further enquiries and have confirmed that the specimen is now presumed lost, although new information about its discovery and movements were obtained and are outlined here.

Following its discovery, the Southland Times (7 January 1975, p. 3) published an article reporting the find of a moa pelvis made by W. Norman, L. Mennell, R. Rooney and R. Winsloe. We examined the photograph accompanying the article and suggest the remains are likely to be from a small *M. didinus* based on the shape of the pelvis (see Worthy & Holdaway 2002). The pelvis was taken to SMAG, where R. Beck confirmed it was a moa, although a specific identification was not made. W. Norman contacted the National Park Board ranger, K. Hamilton at Clifden, with the aim of making further investigations at the site of discovery.

The rock shelter was located near the shore of Lake Hauroko, just north of Mary Island, approximately 30 m from the shore and just below a steep cliff (K. Hamilton, pers. comm., 2009). Hamilton and his son returned to the rock shelter and found the articulated vertebrae and ribs. R. Beck inspected the bones and conducted further excavations of the rock shelter but no more remains were found. The

bones were sent away for further inspection, before being returned to the Clifden ranger station and stored under glass, along with several other unassociated artefacts.

Following the closure of the New Zealand Forestry Service, the Clifden ranger station was sold and the remains disappeared. K. Hamilton reported that they were sent to the Forestry Service headquarters at Te Anau (now the Te Anau Department of Conservation area office), but B. Mannix and R. Montgomery (pers. comm., 2008), the rangers who preceded K. Hamilton at the ranger station, thought the specimen was moved to Tuatapere. The Tuatapere office of the Forest Service had moa bones and artefacts in a display case, and these were apparently left there when the building was sold (R. Montgomery, pers. comm., 2008).

A previous unsuccessful attempt to find the remains was conducted by L. Sanson (pers. comm., to NJR). He ascertained that the Clifden ranger station had also displayed some moa bones, which belonged to a local farmer. When the ranger station was closed, all the moa bones held there were returned to the farmer, possibly including the desiccated remains.

Mount Owen

In January 1987, members of the New Zealand Speleological Society discovered the remains of a small *M. didinus* in the junction of Blowhole and Whalesmouth Caves, Mount Owen, northwest Nelson (Worthy 1989; NMNZ S.23808) (Fig. 1). The remains consisted of a right mandible, vertebrae, ribs, pelvis, left and right tibiotarsus, left and right fibula, right tarsometatarsus, left and right phalanges, left femur and tracheal rings (Worthy 1989). Most of the bones had preserved soft tissue attached to them. The specimen was discovered within an area exposed to a strong draft between Blowhole and Whalemouth Caves. The left tarsometatarsus and phalanges had preserved muscles, pads, and skin on the dorsal surface, although the horny claws of the terminal phalanges were missing. A large piece of muscle and skin with feather pits was also collected. The majority of soft tissue on the proximal right tarsometatarsus was present. Tissue was also present on the right tibiotarsus and right fibula, dorsal surface of pelvis (muscles and connective tissue), ribs, and vertebrae. Loose fragments of muscle and a few fragmentary feathers were also found in association with the specimen. This specimen has been figured in Worthy (1989), and Worthy and Holdaway (2002). Radiocarbon ages of 3350 ± 70 yr BP and 2120 ± 310 yr BP were obtained from bone and soft tissue respectively (Supplementary file 6). The younger age on the soft tissue may reflect bacterial contamination introducing modern carbon (Geyh et al. 1974; Worthy 1989).

Heavy-footed moa Pachyornis elephantopus *(Owen, 1856)*

Hector Mountains

In 1884 the lower leg of *P. elephantopus*, with dried skin and tendons, was discovered in Central Otago (Fig. 8). Reports on the exact site where the specimen was found vary. F.W. Hutton reported that it had been found in the Remarkable Mountains near Queenstown (Hutton 1892). Anderson (1989a) placed the specimen in the adjoining Nevis District. Buller (1888) queried the finder of the specimen and stated that it was discovered in 1884 by Mr W.J. Branford in a cave in the Hector Ranges, Otago. The tarsometatarsus was partially covered in integument and underlying desiccated tendons. Two phalanges were also articulated to the tarsometatarsus by desiccated tendons. The specimen is housed in the Cambridge University Zoology Museum (CZD) (Supplementary file 5) and includes a left tarsometatarsus with phalanges and skin attached, and a sternum. The collection locality data reads 'Hector Range, Nevis, Otago, New Zealand' (M. Lowe, pers. comm., 2008) (Fig. 1). Buller (1888) submitted a photograph of the specimen to Owen, who identified it as *Dinornis*

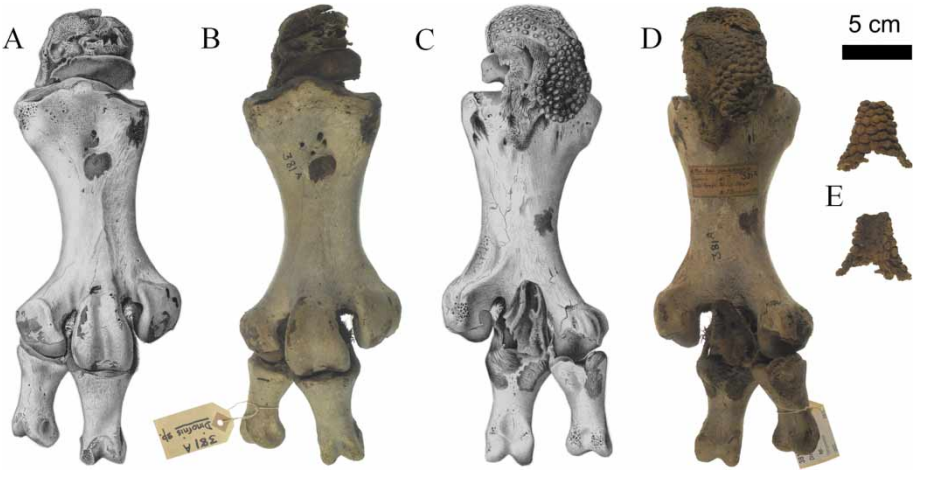

Figure 8 Desiccated skin and muscle tissue on tarsometatarsus and phalanges of heavy-footed moa (*Pachyornis elephantopus* (Owen, 1856)) collected from Hector Ranges, Otago (CZD 381.A). A comparison of photographs (B, D and E) taken in 2008 with lithographs (A and C) from Buller (1888). Photos courtesy of CZD.

elephantopus Owen, 1856 (the original name of *P. elephantopus*).

Little bush moa Anomalopteryx didiformis *(Owen, 1844)*

Lake Echo

In 1980 a partially desiccated articulated skeleton of *A. didiformis*, with skin and feather bases attached, was discovered by J.R. Murdoch in a cave near Lake Echo, western Southland (Forrest 1987) (Fig. 1). The specimen was found on the floor of the cave, and was protected from the prevailing westerly winds and rain. The remains were collected by L. Williams, M. Forrest, A. Naylor, D. Humphries, and J. Murdoch on 11 July 1980, and consisted of a fully articulated vertebral column, ribs and pelvis, with in situ left and right femora held together with dried skin, flesh and cartilage. A large fragment of skin with small, light yellowish brown feathers covered the pelvis. Other associated remains included a complete articulated cranium covered in skin with a large number of small feathers, desiccated eyes and sclerotic rings; articulated left tibiotarsus, left fibula and left tarsometatarsus with most of the phalanges attached by skin and ligaments; right tibiotarsus; and a right tarsometatarsus with most of the phalanges attached, some with the terminal phalanges present. Two loose pieces of skin with attached feathers were also found. The largest piece had a thick covering of feathers with aftershafts/accessory plumes. Fragments of moa eggshell were also found within the vicinity of the body (Forrest 1987). The specimen has been radiocarbon dated to 623 ± 28 yr BP (Bunce et al. 2009) (Supplementary file 6). The remains are housed in SMAG (Supplementary file 5).

Moa feathers

The first description of moa feathers was by Dallas (1865), based on feathers preserved in association with the Tiger Hill *D. robustus* skeleton. Since this seminal publication we estimate that the total number of loose moa feathers found now exceeds 1065 (Table 1, Supplementary file 5). Many more are present on desiccated flesh from Waikaia, while feather bases are present on the flesh from Crown Range, Earnscleugh Cave and Lake Echo. However, few feathers have reliable collection and historical data associated with them (Supplementary file 5), and few can be identified to species (see *Moa plumage* below).

The literature relating to moa feathers is extensive, yet consists almost exclusively of short descriptions of individual or small associations of feathers. The lack of a consistent pattern of size and colour was commented on by Anderson (1989a). Perceived colour can change depending on the observer, illumination (Villafuerte & Negro 1998), and fading, leading to an overwhelming variety of colours and patterns described in the literature (see Supplementary file 4). There are many slight variations in descriptions of moa feathers (including the same feather). They have been variously described as brown to black, usually with the tip either lighter (e.g. white) or darker in colour, though some are white, with rare claims of purple or blue feathers.

Both double- and single-shafted feathers have been recorded, comparable to accessory feather plumes in ostrich and emu (Dallas 1865). Evidence of where these may have been located on moa is provided by in situ feathers on desiccated specimens. Double-shafted feathers were present on the upper leg of *M. didinus* but smaller feathers on the tarsometatarsals were single-shafted (Owen 1883; Hutton 1892). Bases of double-shafted feathers were preserved on the *D. robustus* pelvis from Tiger Hill (Dallas 1865), and the neck of *E. crassus* from Earnscleugh Cave (Fig. 3).

Moa feathers of a range of sizes have also been noted and can be summarised as up to 207–230 mm in length (see Supplementary file 7 for historical and new data) and up to c. 37 mm in width, depending on what part of the body they come from and whether the fore or aftershaft was measured.

Worthy and Holdaway (2002) note that feathers attributed to moa and possibly excavated from Monck's Cave (housed in SMAG) are the longest known; up to 230 mm. However, we question the identity and origin of these specimens. The feathers were obtained by L. Esler c. 1990, from A. Green of Gore, Southland. Green reportedly collected the feathers from a cave in Southland or Central Otago, but could not remember the exact location (L. Esler, pers. comm., 2009). No moa feathers were reported in descriptions of archaeological material from Monck's Cave or Moa Bone Point Cave, both in Sumner, Christchurch (Haast 1875; Meeson 1890; Buick 1937). Also, supposed moa feathers from a Māori cloak in Hawkes Bay museum are similar to the SMAG specimens, yet DNA analysis revealed they were emu feathers (Heaslop 2007). Although the SMAG feathers could well be moa, due to their anomalously large size compared with all other known moa feathers we would advise caution until DNA tests prove their identity.

Moa plumage

Several accumulations of moa feathers have been identified to species (mostly *M. didinus*), providing an insight into moa plumage. Below we discuss those with reliable morphological information. Feathers preserved on the desiccated *M. didinus* from Crown Range were grey at the base, deepening to reddish brown at the tip, while those from Wakaia were various shades of brown with lighter tips (Hamilton 1895). A. Hamilton also collected 600–700 moa feathers from the same locality, and several more from caves nearby, with the same colour pattern, that are undoubtedly *M. didinus* (Many of these are in NMNZ and CMC. Seven are in the NHM; Buick 1931).

Additional moa feathers that are probably attributable to *M. didinus* were found in an archaeological site in a limestone rockshelter (Shelter A) on the southeast end of Takahe Valley, Fiordland. The feathers, figured in Vickers-Rich et al. (1995), were the same colour pattern as the Crown Range feathers and were found in association with archaeological *M. didinus* bones, with traces of desiccated flesh, and Māori artefacts (Duff 1952a,b). Māori occupation of the overhang dates from the fourteenth century AD (O'Regan 1992), although the putative moa coprolites are significantly older at 2538 ± 95 yr BP

(NZA-15997) (95.4% 2750 – 2348 cal. yr BP, ShCal 04 via OxCal) (Horrocks et al. 2004).

Genetic research by Rawlence et al. (2009) has shown that several isolated feathers from Central Otago rockshelters (Roxburgh Gorge B, C, and Sawers) (Supplementary file 5) also belong to *M. didinus*. The feathers were tan to light brown at the base, grading to dark brown to black at the tip. The three different feather colour patterns in *M. didinus* suggest that this species had a relatively plain, but slightly streaky and speckled plumage.

Rawlence et al. (2009) also identified moa feathers from Roxburgh Gorge B and Sawers rockshelters to *D. robustus*, *P. elephantopus* and *Euryapteryx gravis* (Owen, 1870) (Supplementary file 5). This is the only record of soft tissue preservation in *Eurypateryx*. The feathers of *Euryapteryx* were tan to light brown at the base, grading to dark brown to black at the tip (Australian Centre for Ancient DNA (ACAD) samples 7151, 7155). Feathers taken from the neck of the desiccated *E. crassus* (Fig. 3) from Earnscleugh Cave (housed in Clyde Museum; CV 1976.456.1) are of similar colour. The research also identified a single short feather from *P. elephantopus* that was dark brown to black for the basal two thirds and white at the tip (held by Central Stories Museum, Alexandra (ALEX), A06.49.18). This colour pattern is similar to *M. didinus* feathers from Waikaia, and shows that speckled plumage was not unique to *M. didinus*.

There is extensive overlap in plumage types between different moa species. The multiple plumage types within species could represent feathers of different colour on the same individual, or differences between sexes or growth stages (Rawlence et al. 2009).

Fossil feather impressions

In addition to moa feathers preserved by desiccation, there are two instances where they have been preserved as fossil impressions in sediment. Impressions of three moa feathers were discovered by Hill (1889) in lacustrine sediments at Lake Ormond near Gisborne. Two were described as being '4 inches' (c. 100 mm) long with the ends missing, and the third about '2.5 inches' (c. 64 mm) long (Hill 1889). The age of these impressions was reported by Hill (1889) to be Pliocene, although the sediments have since been revised as mid Pleistocene (c. 620 ka) (Kennedy & Alloway 2004). The impression of a moa feather was also found in silt adjacent to a *D. robustus* tarsometatarsus at Chatto Creek, Central Otago, in 2004 (Wood 2008b), although a direct association with the bone could not be made.

Specimens not attributed to species

Alexandra district flesh

A specimen collected from the Alexandra district is known only from a description in a letter (Hector 1872) from W.A. Low to J. Hector dated 18 October 1871 that states W. Low obtained some desiccated bird flesh partially covered in down and feather shafts. The date of the letter suggests the possibility that the specimen was from Earnscleugh Cave.

Limehills skin

A piece of moa skin was found at Limehills, Southland (R. Beck, pers. comm., in Anderson (1989a)). The skin is currently on display in SMAG.

Skin impressions in moa coprolites

In the past decade several deposits of moa coprolites have been discovered in the Otago region (Wood 2008b; Wood et al. 2008, 2011). A few of the coprolites hold skin impressions from the lower leg or foot of a moa, made before the dung had dried and hardened (Fig. 9). Eight such specimens are known from Sawers rockshelter in the Roxburgh Gorge (ALEX), and one from Daley's Flat in the Dart River Valley (currently held by Landcare Research, Lincoln, to be deposited in CMC). One of the specimens from Sawers rockshelter

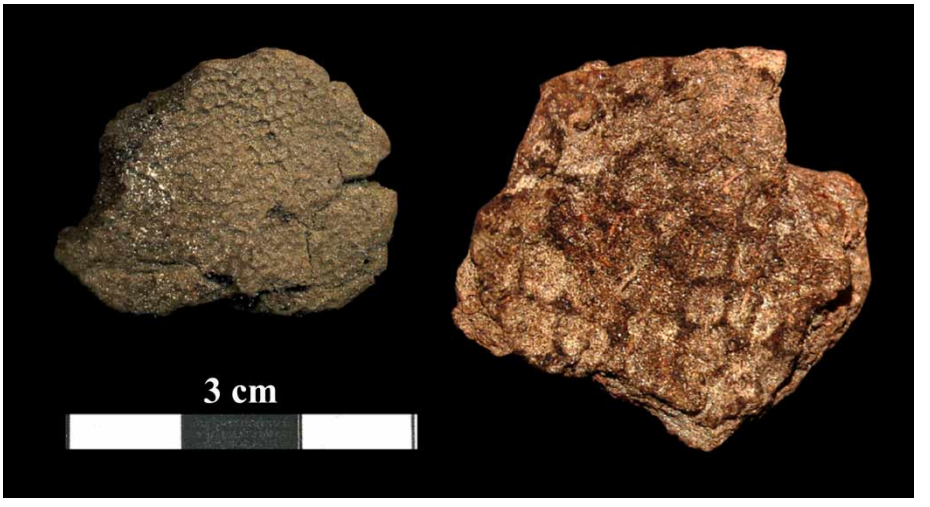

Figure 9 Moa leg and foot skin impressions in coprolites from Sawers' rockshelter, Roxburgh Gorge, Central Otago (ALEX).

has what appears to be the entire toe print of a smaller bird, perhaps a moa chick, or another bird species that may have once used the shelter.

Associations with human artefacts

It seems likely that garments of moa skin may have existed but none have survived (Orbell 2003). A narrow strip of moa skin, '3 inches' (c. 76 mm) long, and with five or six double-shafted feathers, sewn over a seam into a Māori cloak made predominantly of weka skins, was found in a Māori burial cave at Strath-Taieri, Otago, in 1892 (Hamilton 1893; Buick 1931; Anderson 1989a), and is widely cited as the only definite evidence of moa feathers and skin in an archaeological context (e.g. Hamilton 1895; Vickers-Rich et al. 1995). The feathers were poorly preserved and detached from the skin upon examination (Hamilton 1893). The specimen was attributed to *M. didinus* (Hamilton 1895; Anderson 1989a), based on similarities with feathers on the preserved leg from a cave near Waikaia, but this has not been verified by DNA analysis. Given the extensive overlap in feather morphology and colour within moa (Rawlence et al. 2009), this specimen could represent any number of moa species.

While visiting the NHM in the mid-1870s, J. Hector examined New Zealand artefacts in the 'Christy Collection', and discovered possible moa feathers attached to the top of a Taiaha and a paua and iron fish hook (Hector 1877; Owen, 1879). Hector collected one of the feathers and brought it back to New Zealand (Bay of Plenty Times, 21 October 1876, p. 2) (see Supplementary file 3) but we have not been able to trace this. Owen (1879) examined the feathers on the artefacts and determined that the ones on the Taiaha were more similar to kiwi feathers, yet were longer ('5.2 inches'; c. 130 mm) than known kiwi feathers. The feathers on the fishhook were too poorly preserved to allow identification (Owen 1879).

In 1970 P. Coutts excavated the floor of a cave (SP1) in Chalky Inlet, Fiordland, and recovered 445 feathers (in association with European artefacts) of which three were identified as moa (species indeterminate) (Coutts 1972) and subsequently confirmed by F.C. Kinsky (at NMNZ). The moa feathers were from a layer which, as Anderson (1989b) noted, contained many European items. Coutts (1972) interpreted this layer as indicating occupation

of the site by Māori in contact with sealers during the early nineteenth century. The date of SP1, and the fact that moa probably became extinct prior to European settlement (Tennyson & Martinson 2007), raises questions about the identity or age of the feathers. Ian Smith of the University of Otago provided some subsequent observations about SP1: it is a dry cave, which has a deep and complex occupation history and was presumably used repeatedly since the early prehistoric period through to the historic era, although recent historical evidence suggests that the European items discovered at SP1 were left by European sealers rather than Māori (Smith 2002). With frequent re-use of the cave, subsequent stratigraphic disturbance is highly likely. Therefore it is probable that the association of 'moa' feathers with European artefacts cannot be considered robust evidence of contact between moa and Europeans (I. Smith, pers. comm., 2009). In conclusion, the only confirmed soft tissue specimen that we consider to be primarily associated with a human artefact is the Strath-Taieri moa skin (see also section below on misidentified specimens).

Unverified specimens

There are several records of preserved soft tissues on moa bones that cannot be verified because the specimens were neither described in detail nor illustrated and they are not clearly locatable today. These specimens are outlined below.

Molyneaux Harbour

Mr Meurant, a Māori interpreter employed by the government, in 1823 saw desiccated moa flesh at Molyneaux Harbour and a moa leg bone covered in desiccated flesh and sinew (Ohinemuri Gazette, April 1902, Volume 12, Issue 952, p. 2) (see Supplementary file 3). Although Molyneaux is the historic name for the Clutha River and the district of South Otago, Molyneaux Harbour was a name erroneously assigned to the area now known as Waikawa Harbour, South Otago.

Central Otago flesh

A portion of bird skin with adhering feathers was sent to Vincent Pyke from W. Robinson and was thought to be moa. V. Pyke obtained the skin from Mr Mouat, via an acquaintance who found it at Reedy Creek in a narrow gully (Bruce Herald, 20 July 1865, p. 3) (see Supplementary file 3).

North Otago

It was reported by the North Otago Times (19 April 1867, p. 2) (see Supplementary file 3) that Mr George Sumpter had a large collection of moa bones, several of which still retained desiccated flesh. It was believed that the bones were discovered on the property of Mr Peter Miller. The preservation may have been similar to the Ashley River *D. robustus* specimen (Fig. 2).

Lowburn

The only known description of this specimen is from a short paragraph in the Tuapeka Times (16 July 1887, p. 2) (see Supplementary file 3) which states that some rabbiters working on Mr Cowan's property opposite Lowburn found a complete moa skeleton. The skeleton was well preserved with brown feathers still adhering to the head. The description of the specimen seems consistent with a skeleton of *M. didinus*; however, we could find no record of what happened to it. We suggest that it could be the specimen from Cromwell (NMNZ S.400). Lowburn is located approximately 4 km north of Cromwell.

Moonlight Creek

In 1893, P.J. O'Regan visited Moonlight Creek in the Grey Valley, West Coast, and reports that moa bones were found in spoil heaps excavated by miners deepening a tail race.

The bones were 'in an excellent state of preservation; in fact, the claws and scales were still intact on the leg bones' (O'Regan in Buick, 1931) (see Supplementary file 2). The presence of scales suggests a similar type of preservation to the Ashley River *D. robustus* specimen (Fig. 2).

Timaru

The Press (30 July 1895, p. 4) (see Supplementary file 3) reports that a moa skeleton with feather impressions was discovered embedded in papa (clay or mudstone) in a road cutting near Timaru.

Shag River Mouth

In a description of animal remains from Māori middens at the mouth of the Shag River, Otago, Hutton (1876) reports that a 'piece of skin of some animal was found at a depth of about two feet', but provides no indication as to its identity. Anderson (1989a) lists the specimen as a piece of moa skin measuring c. 2.5 cm width and 4 cm long, based on field notes by the finder, B.S. Booth.

Millers Flat

There are unconfirmed reports of desiccated moa flesh (along with confirmed reports of partial moa eggs and a probable moa chick) from Millers Flat, Central Otago, discovered by John Shaw (a rabbiter for the rabbit board in the 1950–60s) and Bill Dakker (J. Shaw, pers. comm., 2011). Both parties had explored the hills around Teviot and knew of one cave with a complete moa foot in it. Given the number of rock outcrops in the vicinity that have the chance to preserve soft tissue and coprolites, this area requires further investigation.

Misidentified and miscellaneous specimens

Some remains initially reported as preserved moa soft tissues were later disproved. A supposed specimen of feathery hairs and moa skin found in the Mareburn Creek, near Hyde, Otago, was subsequently identified as small fibrous plant roots (Otago Witness, 20 November 1890, p. 23) (see Supplementary file 3). Māori artefacts discovered by rabbiters in a rock shelter near Thomson's Gorge, Central Otago, were reported to include bits of moa feathers; however, these were later thought to be kiwi feathers (Otago Witness, 4 August 1892, p. 20) (see Supplementary file 3).

In March 1943, a collection of feathers was donated by A.S. Milne of Wanaka, Central Otago, to the OM. The collection includes several long, brown, moa feathers. Although no record exists of where the feathers were collected, it is likely, given the distribution of other known feather sites, that they were collected from a cave or rock shelter somewhere in the Wanaka, or wider Central Otago district. Associated with these moa feathers are five small violet-tipped contour feathers (OM AV10357; two have been used in the analyses below). The identity of these feathers was not able to be determined through visual inspection alone, as their colouration did not match the plumage of any extant, or recently extinct, New Zealand bird. However, the museum label with the feathers indicated that they had been found with the moa feathers, prompting further investigation. A radiocarbon date (Wk24513) on one of these feathers returned an age of 115 ± 30 yr BP (calibrated confidence ranges: 95.4%, AD 1757–1950), suggesting it is most likely post-European and reflects a mistaken association with the moa feathers. DNA analysis of the feathers (ACAD, sample A3505) has revealed they are from an undetermined kingfisher species, most closely allied with south-east Asian and central American taxa (J. Austin, pers. comm., 2007). Kingfisher feathers were often used in Chinese clothing and art, and the feathers may therefore represent use of the cave by a Chinese goldminer during the Otago goldrush.

Figure 10 **A**, Dissected terrace at Moa Farm, Maniototo Basin, Central Otago, showing location of the South Island goose (*Cnemiornis calcitrans* Owen, 1866) specimen with soft tissue impressions. **B**, Plaster jacket encasing the sediment block containing the leg bones and soft tissue impressions.

Waterfowl (Anseriformes)

South Island goose Cnemiornis calcitrans *Owen, 1866*

Maniototo

A South Island goose skeleton associated with soft tissue impressions in the surrounding sediment was discovered by JRW at Moa Farm, 10 km southwest of Ranfurly, Central Otago (NZMG coordinates 2274000/5554250) in 2008 (Figs. 1 and 10). The specimen is housed in CMC (Av41297). In April 2008 phalanges from the right foot were collected from the ground surface by JRW, and a sediment block containing the remainder of the specimen was collected in May 2008. The remains consisted of articulated bones of the right leg distal of the femur (Fig. 11). Most of the skeleton had already been eroded and destroyed; however, both humeri were recovered approximately 3 m below the in situ bones. These were the only other bones discovered. The bones were situated within a terrace composed of both horizontally bedded and cross-bedded sands and silts, but are likely to have been incorporated into reworked sediments in a manner identical to that suggested for Holocene bones at nearby Chatto Creek (Worthy 1998a). Impressions of skin and feathers were preserved in the fine silty sediment surrounding the lower leg bones (Fig. 11). Due to the crumbly nature of the sediment, the impressions were preserved by consolidating the sediment with cyanoacrylate glue. The impressions reveal that the skin on the foot of *C. calcitrans* was relatively rough, with large papillae (Fig. 11).

Finsch's duck Chenonetta finschi *(Van Beneden, 1875)*

Earnscleugh Cave

Hutton and Coughtrey (1875b) reported finding *C. finschi* wing bones retaining portions of skin and feathers under several inches of sand in Earnscleugh Cave. Preserved soft-tissue remains from Earnscleugh Cave at CMC (Worthy 1998a) include: skin fragments with attached tracheal rings and cricoid (Av5340) (Fig. 12); an articulated coracoid and scapula (Av6394); articulated radius, carpometacarpus and digits (Av6398); and an articulated radius and ulna (Av6399) with attached tendons and desiccated flesh (Fig. 13) (see Supplementary file 8 for measurements of these bones). In 2006, a small pit was excavated in the base of Earnscleugh Cave, examining sediments that had probably been reworked downslope during early excavations in the cave (Wood 2008b). Numerous feathers, all mostly faded, were recovered, some of which may be attributable to *C. finschi* (Supplementary file 5).

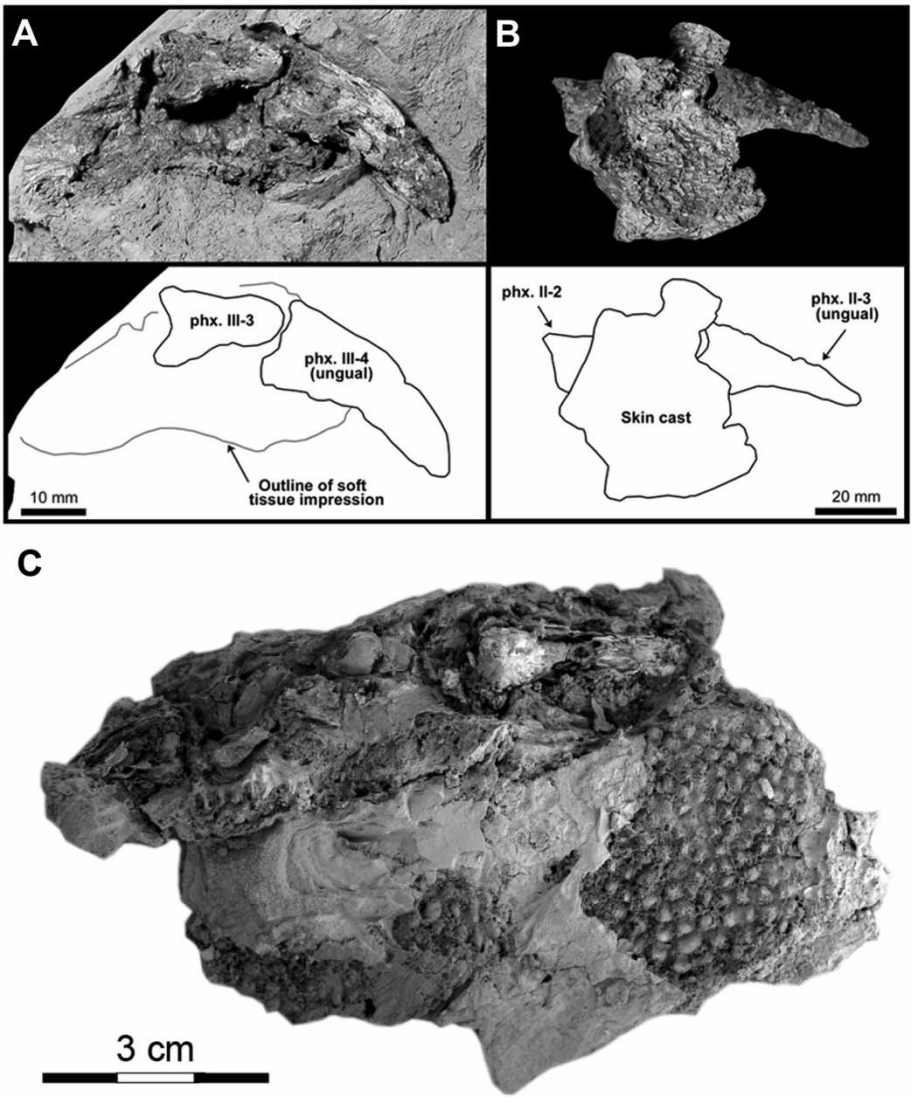

Figure 11 **A**, In situ terminal phalanges of right middle toe, showing outline impression of soft tissue pad on the bottom of the foot. **B**, Terminal phalanges of right medial toe showing the characteristic spur-like ungual. Overlaying the bones is a latex cast of the skin impression from the sediment around these bones. **C**, Block of sediment associated with South Island goose (*Cnemiornis calcitrans* Owen, 1866) specimen from Moa Farm, Maniototo Basin, Central Otago. A poorly preserved phalanx is visible at the top right, and positive casts of the foot skin can clearly be seen on the right, with small sections also visible in the lower centre and lower left.

Waikaia

At least six feathers thought to be from *C. finschi* are housed in NMNZ (S.44746). The feathers are from a bolus (from a collection of 14) that also contains fur and has been partly pulled apart. The feathers are silvery-greyish and most have dense vermiculations but at least one is a more even grey with a black spot at each distal corner (Fig. 14). They are up to 37 mm long. They are very similar to the feathers on the breast of male Australian wood ducks (*Chenonetta jubata* (Latham, 1802)).

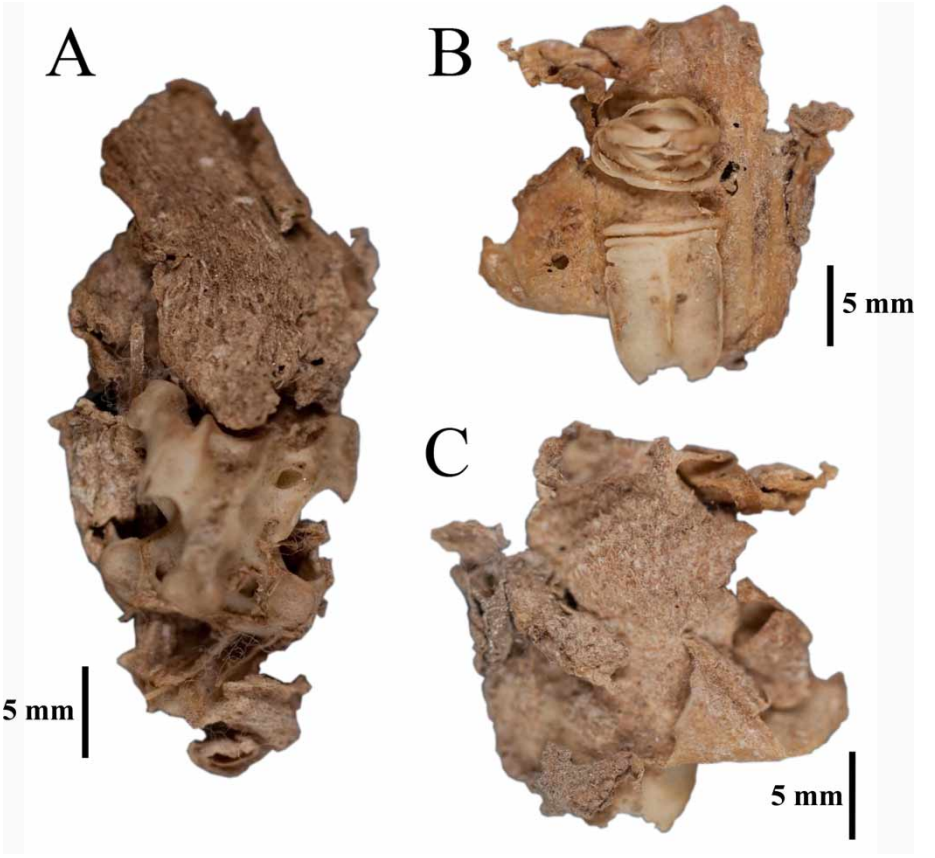

Figure 12 Finsch's duck (*Chenonetta finschi* (Van Beneden, 1875)) desiccated bones and soft tissues from Earnscleugh Cave (CMC Av25340). **A**, Articulated neck vertebrae with associated soft tissue. **B, C**, Skin associated with the cricoid.

The pellets are labelled as being probably collected by A. Hamilton in about 1893 from Waikaia – the site that contained the feathered *M. didinus* leg (OM AV7474). In Hamilton's (1895) description of this cave he reports that there were numerous moa, weka (*Gallirallus australis*) (Sparrman 1786), morepork (*Ninox novaeseelandiae novaeseelandiae*) (Gmelin 1788) and parakeet (*Cyanoramphus* sp.) feathers as well as a large number of owl pellets, suggesting occupation of the cave over an extended period. It seems likely that this description is of the pellets now held by NMNZ, but the location of some of the described remains are unknown; for example, there are no parakeet feathers from the site present in NMNZ collections.

Owlet nightjars (Aegothelidae)

New Zealand owlet nightjar* Aegotheles novaezealandiae *(Scarlett, 1968)

The articulated tarsometatarsus and phalange, with desiccated muscle attached, of *A. novaezealandiae* were discovered by Diane Cooper in a cave near Magnesite Quarry, Cobb Valley, northwest Nelson in December 1984. The phalange was used in a DNA analysis that suggested *A. novaezealandiae* was sister to *A. savesi* of New Caledonia (Dumbacher et al. 2003). The tarsometatarsus and some adhering tissue are housed in the Waitomo Caves Museum (WCM) (18374, formerly WO139).

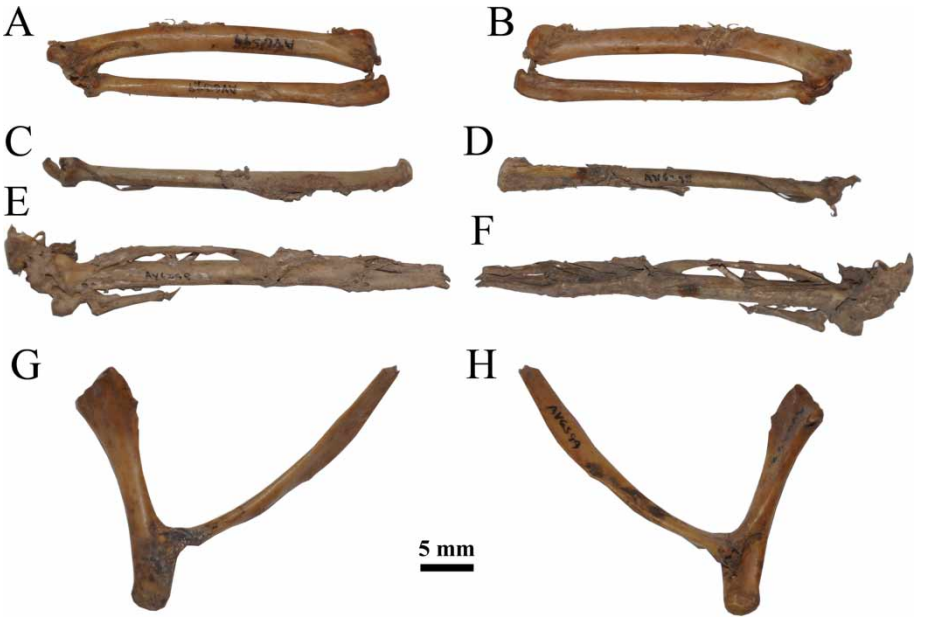

Figure 13 Finsch's duck (*Chenonetta finschi* (Van Beneden, 1875)) bones and desiccated soft tissues from Earnscleugh Cave. **A**, **B**, Ulna, radius (CMC Av6399). **C**, **D**, Radius (CMC Av6398). **E**, **F**, Distal wing tip (carpometacarpus, P1, P2) (CMC Av6398). **G**, **H**, Joined coracoid and scapula (CMC Av6394).

Figure 14 Feathers, probably of Finsch's duck (*Chenonetta finschi* (Van Beneden, 1875)), from a cave near Waikaia (NMNZ S.44746). Photos courtesy of NMNZ.

In addition to the Magnesite Quarry specimen, a 'wing, supposedly of a caprimulgid, was found on the West Coast in the 1960s but has been lost' (Worthy & Holdaway 2002). Tennyson and Martinson (2007, p. 154) further state that the specimen was found in Haast Pass. However, this claim requires further clarification. All skeletal remains of *A. novaezealandiae* date to prehistoric times (Holdaway 1999), though there are plausible mid-nineteenth-century records of a kingfisher-sized owl from the upper Rangitata before the introduction of little owls that may be *A. novaezealandiae* (Potts 1882). The only confirmed record of mummified *A. novaezealandiae* remains comes from Magnesite Quarry. In the absence of any evidence to support this Haast Pass record we do not accept it as valid.

Discussion

Faunal representation

Of the 30 species of pre-European extinct birds (Bunce et al. 2009; Gill et al. 2010), evidence for soft tissues exists for just nine (Table 1). Six of these species, and the majority of specimens, are of moa. This is perhaps not surprising, as moa often dominate cave and rock shelter deposits, and would have used dry shelters as roosting and nesting sites (Wood 2008a). Of the

Table 1 Summary of soft tissue remains from pre European extinct birds of New Zealand. Full details are provided in Supplementary file 5.

Order	Species	No. specimens (excl. feathers)	No. attributed feathers	Geographic region
Dinornithiformes	South Island giant moa (*Dinornis robustus*)	4	>20	North Canterbury, Central Otago
	Eastern moa (*Emeus crassus*)	6	>9	Central Otago
	Upland moa (*Megalapteryx didinus*)	6	>4	Northwest Nelson, Otago, Fiordland
	Heavy-footed moa (*Pachyornis elephantopus*)	1	2	Central Otago
	Little bush moa (*Anomalopteryx didiformis*)	1	Unknown no.	Southland
	Stout legged moa (*Euryapteryx curtus*)	0	2	Central Otago
	Unidentified	13	c. 1065	East Cape, Wairarapa, Marlborough, Otago, Fiordland, Southland
	Unverified	7	Unknown no. incl. feather impressions	West Coast, South Canterbury, Otago
Anseriformes	South Island goose (*Cnemiornis calcitrans*)	1	Feather impressions	Central Otago
	Finsch's Duck (*Chenonetta finschi*)	5	>20	Central Otago
Apodiformes	New Zealand owlet nightjar (*Aegotheles novaezealandiae*)	1	0	Northwest Nelson

other taxa represented by desiccated remains, Finsch's duck was probably a cavity nester (Worthy & Holdaway 1994) and may also have favoured dry sheltered sites. Owlet nightjars are also cavity nesters (Brigham 1998).

Taphonomy and age of desiccated specimens

The discovery of moa bones with soft tissues attached prompted suggestions as to the possibility that these were geologically young specimens and that moa may have survived until very recent times (Travers 1876). However, Hutton (1892) realised that all the specimens at that time had been found within a relatively small geographic region (Central Otago), and that the specimens were probably not old but represented exceptional preservation conditions due to the aridity of that region. This view has been vindicated by radiocarbon dating of moa specimens with desiccated soft tissues (Supplementary file 6), as none are anomalously young with regard to the extinction of moa soon after Polynesian settlement (Holdaway & Jacomb 2000; Rawlence & Cooper in press). However, all of the dated Central Otago desiccated specimens are less than 1000 years old. Six Central Otago rockshelters (Firewood Creek B, Kawarau Gorge, Cairnmuir Gully B, Sawers, Roxburgh Gorge B; see Wood 2008a; Wood & Walker 2008) have moa feathers excavated from discrete radiocarbon dated stratigraphic layers. The oldest of these (Roxburgh Gorge B) has a date of 2928 ± 100 yr BP. The late Holocene age of all these specimens reflects what is known about climate change in the region; the El Niño Southern Oscillation (ENSO) intensified during the mid-late Holocene (Marchant & Hooghiemstra 2004), and was operating at its present intensity by about 3000 yr BP, resulting in the mid-late Holocene aridification of Central Otago (McGlone et al. 1992; McGlone & Moar 1998; Gomez et al. 2004; Donders et al. 2005). The relationship between desiccated remains and aridity or soil dryness is also evident within stratigraphic sequences from individual rockshelters, where feathers, coprolites, and desiccated plant remains are often only present in the uppermost layers (< 40 cm depth) and not in lower layers, which are often relatively damp (Wood 2008a).

The Mount Owen *M. didinus* leg returned an older date than the Central Otago specimens (Supplementary file 6); however, the taphonomy of this specimen differs as well. Instead of preservation due to a regionally dry climate, the Mount Owen leg was desiccated by a constant breeze caused by drafting between two cave entrances (Worthy 1989). It is likely this process may also have contributed to the preservation of soft tissues in Earnscleugh Cave, which also has multiple entrances creating a chimney effect that dried the cave (Clark et al. 1996; Worthy 1998a).

Conclusion

This study provides the first comprehensive review of soft tissue specimens of pre-European extinct birds of New Zealand, building upon lists of previous authors (Anderson 1989a; Worthy & Holdaway 2002). The specimens reviewed here include many with vague or conflicting locality data, which we have attempted to refine. We have also reviewed the identifications of some specimens. Of the 30 avian species that went extinct before European colonisation, soft tissue remains have been documented for only nine of these species. The majority of records are from moa (all six genera and six of the nine currently recognised species) and almost all are from the South Island. Further excavations of caves and rockshelters in the North Island may result in additional soft tissue finds and genetic characterisation of unassigned soft tissue remains in museum collections should increase the number of species represented.

The soft tissue and feathers documented in this paper have provided unique information that has allowed scientists to attempt reconstructions of the musculature (Vickers-Rich et al. 1995) and external appearances of the extinct birds of New Zealand (e.g. Tennyson &

Martinson 2007; Rawlence et al. 2009). Moa for example exhibited a wide range of feather sizes (up to 207 mm in length and c. 37 mm in width) and colour patterns. Our review shows that soft tissue specimens are rare and provide vital information for understanding extinct species. As such soft tissue specimens need to be carefully preserved and cared for.

Supplementary files

Supplementary file 1: Specimens of soft tissues from extant bird species of New Zealand
Supplementary file 2: Transcripts of paraphrased letters previously not available online.
Supplementary file 3: Transcripts of paraphrased historical newspaper articles.
Supplementary file 4: Moa feather colour patterns.
Supplementary file 5: Specimens of soft tissues from pre-European extinct birds of New Zealand.
Supplementary file 6: Radiocarbon dates of desiccated soft tissue remains.
Supplementary file 7: Size of preserved moa feathers held in New Zealand and overseas museum collections.
Supplementary file 8: Measurements of Finsch's duck *Chenonetta finschi* (Van Beneden, 1875) bones from Earnscleugh Cave held in Canterbury Museum (CMC), Christchurch

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