Takaka Fossil Cave – a stratified Late Glacial to Late Holocene deposit from Takaka Hill, New Zealand

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ABSTRACT: A rich terrestrial vertebrate fauna from the pitfall trap deposit of Takaka Fossil Cave on Takaka Hill, South Island, New Zealand, is described. Radiocarbon ages on moa bones bracket the onset of sedimentation in the site to between 12 361 and 11 354 ^{14}C yrs BP. *Euryapteryx geranoides* was in the Late Glacial moa fauna that predates the onset of sedimentation in the site, but was absent in younger faunas. The moa *Anomalopteryx didiformis* was present in the Late Glacial fauna as well throughout the Holocene. A total of 1633 bones from 25 species of birds and a further 895 bones of 154 individuals of vertebrates other than birds (two species of frog, one tuatara, three lizards, two bats, and a rat) were identified in the total recovered fauna. A well-preserved partial skeleton of Haast's eagle (*Harpagornis moorei*) of Late Glacial age had severe arthritis. Unusually small specimens of *Euryapteryx* were morphologically diagnosed as *E. geranoides*, and confirmed as such by mitochondrial DNA analysis. The molluscan fauna contained two aquatic, troglobitic hydrobiids and 29 taxa of land snails. While there is little change in species diversity between lower and upper layers, there are marked changes in relative abundance of some taxa that suggest the environment was drier in the early and middle Holocene than it was in the Late Holocene.

KEYWORDS: Late Glacial–Holocene, avifauna, molluscs, faunal change, Takaka Fossil Cave, Takaka Hill, New Zealand.

Introduction

Takaka Hill is a granite and marble range reaching elevations of 800–900 m that is aligned north–south between Motueka in the Tasman Bay lowlands to the east and Takaka Valley to the west. The hard crystalline marble is of Ordovician age, is highly cavernous, and supports extensive and deep cave systems. Vertical entrance shafts (tomos) are common features and vary from a few metres deep to the spectacular 170 m deep Harwoods Hole, itself an important fossil site. Surface streams on Takaka Hill are restricted to those that flow on the granite landscape, and they all sink at the granite–marble contact. Large areas of Takaka Hill lack streams, and surface catchments are generally restricted to dolines measuring some tens of metres in diameter. Soil cover on the karst is thin, especially so on the deforested areas, where substantial recent loss of soil is attested to by the presence of fences lying on bare rock, or skeletal root systems of trees covering rocks. Within the remaining forest, soils are deeper, but generally limestone karren protrudes everywhere.

Fossil deposits containing bird bones have been known from Takaka Hill since Owen (1883) described the type of
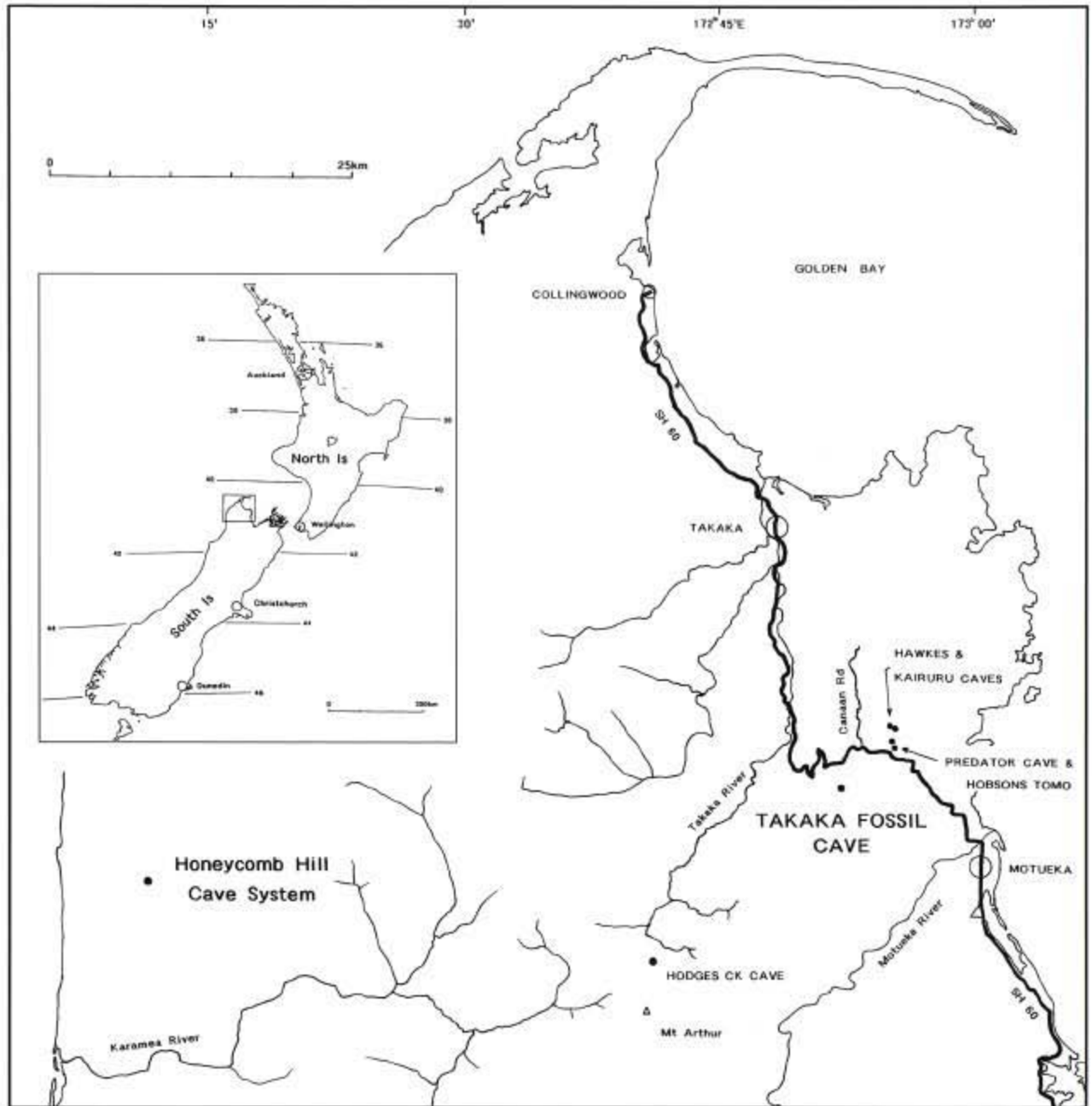
Fig 1. Location of Takaka Fossil Cave in the northwest Nelson district of South Island, showing important nearby fossil sites (filled circles), major geographic features, towns, and State Highway 60 (SH60).

Anomalopteryx parvus, now synonymised in *A. didiformis* (Owen). This and the later history of fossil discovery on Takaka Hill is described by Worthy & Holdaway (1994). For an introduction to the general physical setting, a summary of the Late Pleistocene conditions, and summaries of modern climate, vegetation, and fauna of Takaka Hill, the reader is also referred to Worthy & Holdaway (1994).

In most of the described fossil sites, bones have accumulated on the rocky floor of the caves, and generally have been unstratified surface features. The owl deposit in Predator Cave had a single deposit about 30 cm deep over c.1 m^2, but other owl deposits in Hawkes Cave and Kairuru were just shallow (<5 cm deep) surface features. Therefore, fossil deposits on Takaka Hill have generally not been able to be excavated

following stratigraphic features and thus a faunal history for the late Pleistocene–Holocene has only been inferred for a few taxa, mainly moa (Aves: Dinornithiformes) from a series of radiocarbon ages (Worthy & Holdaway 1994). Therefore, the discovery of a site containing bone-rich, fine, stratified sediment had the potential to provide significant new data on the faunal history of Takaka Hill. This paper describes the excavations and fauna from such a site discovered in 1998.

Site description

The cave, hereafter called Takaka Fossil Cave, is located in *Nothofagus* beech forest on Takaka Hill, about an hour's walk from the nearest access by 4WD vehicle at 41° 02' 32.5"S; 172° 52' 29.1"E or N26/994184, at about 800 m altitude (Fig 1). The cave entrance is in a small diameter (c. 20 m) doline at the foot of a rocky limestone slope. The entrance is about 3 m by 5 m in plan width at the surface and is a 10 m vertical drop to a floor from the lowest side. From the initial landing-floor, the cave floor slopes down at about 30° towards the west for about 5 m, then turns abruptly northwards and continues down slope for about 12 m. The passage starts at about 3 m wide and 10 m high and reduces in size to about 2 m wide by 5 m high at the foot of the slope. At the time of first investigation, the rockfall slope terminated out of daylight in a bone-covered, flat, silty floor about 2 m wide and 3 m long, upon which water dripped from a fissure in the roof (Fig 2). The water drained from the site via a hole against the wall on the true left side of the chamber. This hole was seen to extend down through sediment for at least 500 mm.

John Patterson and Arthur Freeman discovered the cave in August 1998 while they were prospecting for caves in the forested karst area south of the main road across Takaka Hill. Following one unsuccessful search earlier in 1999, John Patterson, Arthur Freeman, and THW relocated the cave on 8 August 1999 and marked a route to it. Upon initial examination, the potential significance of the site was immediately apparent, as it was the first THW had seen on Takaka Hill where a slope from a vertical shaft entrance led after a short distance to a flat floor on which bones and fine sediments had accumulated. While the moa accumulation was impressive with perhaps eight individuals apparent in the 2 by 3 m flat area (Fig 2), the drainage hole on the true left revealed a significant depth of potentially stratified sediments warranting excavation.

Some of the bones from the surface of the rockfall slope were collected, as these would likely be trampled on

Fig 2. Photograph of the site of the excavation in Takaka Fossil Cave after L1 from Square 1A had been removed. The hollow where water then escaped down and that was found to contain L1 sediments to 300 mm depth is clearly seen on the left just beyond the excavated area with a *Dinornis giganteus* tibiotarsus poking up out of it. Square 1B encompassed that hollow across to the two *Dinornis* pelves. However, these and other bones outside of the excavation were left *in situ*. The tape is extended 50 cm.

subsequent trips. Of particular interest were bones of two individuals of very small yet adult *Euryapteryx geranoides* (Owen). They were the size of *Euryapteryx pygmaeus* Hutton and of an individual that THW had previously found in Kairuru Cave (Worthy 1992). Observed and left *in situ* on the slope were bones of an *Anomalopteryx didiformis* in an alcove at the top of the slope, and bones of two individual *Dinornis novaezealandiae* (Owen) near the base of the slope.

Methods

The site was excavated on the following dates. Approximate numbers of bags of sediment taken are listed, assuming each is about 15 kg, although sometimes two smaller bags would

in reality have been carried. Excavated fossils such as moa bones were extra to the sediment load indicated.

8 August 1999. THW, John Patterson, Arthur Freeman, Margaret Ives, and Rosie and Tom Ives. Bones from the rockfall slope were collected and a route was defined on the slope by tape.

18 March 2000. THW, Jeanette Winn, and Alison Pickford. Moa and other bones were collected from the true left side of the rockfall slope in the area where the two small *Euryapteryx* were found. Also, bones were collected from the surface 50 mm in the last metre of the slope before the flat area to create a working base. A 1 m by 0.5 m rectangle was set out on the sediment (Square 1A) so that one side abutted the foot of the slope and the left (facing downslope) edge, the cave wall. Sediment from Layer 1 over this area was collected, though the removal of Layer 1 (L1) from the drainage hole on the left side of the excavation was not completed. L1 sediments were reddish brown friable silts. All limestone clasts were discarded into the alcove on the right just up slope of the excavation (three bags of sediment carried home).

15 April 2000. THW, John Patterson, Rosemary and Katie Patterson, Aaron and Rowan Worthy, and Arthur Freeman. Sediment from Layer 2 in 50–100 and 100–200 mm spits from Square 1A was bagged for transport. The sediment had a uniform consistency of fine grey clay. Few bones were evident, so a test excavation of c. 200 by 200 mm was made below 200 mm depth that encountered moa bones at 500 mm depth. The test pit was expanded to 500 by 500 mm, and 500 mm deep in the right half of Square 1A, and the removed sediment stockpiled in an alcove just up the slope. This excavation revealed a semi-articulated skeleton of *Anomalopteryx didiformis* from which THW collected a femur and a tibiotarsus as vouchers and to do radiocarbon dating on. The bones were exceptionally well preserved (six bags sediment).

28 May 2000. THW, Travis Cross, John Richards, and Hamish McLauchlan expanded the excavation to 1 m² with the removal of L1 (c. 50 mm deep) from Square 1B. However, most of the area in 1B extending to about 300 mm from the left wall of the cave incorporated the drainage feature within which unconsolidated sediments of L1 were excavated to 300 mm deep without encountering L2 sediments. The fossils in Square 1B included many bones of *Dinornis novaezealandiae* and *D. struthoides* and the semi-articulated bones of an *Anomalopteryx didiformis*, which as it was the only so articulated moa on the site was the last moa to arrive there (eight bags sediment).

27 August 2000. THW, Terry, Anita, and Naomi Stanbridge, Clare Webster, Jim and Cory Palmer, and Aaron Worthy excavated the rest of L1 from Square 1B, finding a clay base in the drainage feature at –350 mm. Bones of a single kiwi were scattered through the whole 350 mm depth of L1 sediments in the erosion feature, confirming the observations made on site that these sediments were a single unit. The 50–150 mm depth range of L2 was excavated from adjacent to the drainage feature over the rest of Square 1B (c. 10 bags sediment).

3 September 2000. THW, Dion Richards, John Patterson, Alison Pickford, and John Richards excavated Square 1A from 150–300 mm and partly down to 500 mm around the moa, for which the radiocarbon age for of about 12,000 years had recently been obtained (c. 10 bags sediment).

23 November 2000. THW and Travis Cross excavated to the sediment base over the right half of Square 1A, finding a rockfall floor at about 600–700 mm, and eagle bones on this floor (c. four bags sediment).

25 November 2000. THW, Travis Cross, Terry Stanbridge, Mike Hadfield, and John Richards completed excavation to the rockfall base over ¾ of the square metre, recovering 38 bones of the eagle (c. 10 bags sediment).

7 December 2000. THW, Mike Hadfield, and Terry Stanbridge excavated the remainder of Squares 1A & 1B to the left wall down to the rockfall base. No eagle bones were found in this area, though a tibiotarsus was recovered from amongst rocks in the excavation wall that was the rockfall slope. An eagle femur was recovered on the original rockfall floor about 100 mm into the right wall in Square 1A at the foot of the entrance slope (c. six bags sediment).

9 December 2000. THW, John Patterson, and Alison Pickford extended Square 1A on the right by 300 mm width. Sediment from L1 was collected, but that from 50–500 mm was put into the alcove 3 m up the slope after obvious bones were extracted from it. An eagle ulna was found on the original cave floor in this area. The excavation was then extended from Square 1A towards the entrance into the foot of the entrance slope by c. 300 mm, but no eagle bones were found in the largely rock matrix. All basal sediments were retained for sieving. The last of the sediment in Square 1B was excavated from 300–500 mm depth, and the moa bones lying on the original floor in this area collected. (Left eight bags of sediment stashed for future hauling, c. six bags sediment taken home.)

27 December 2000. THW, Gavin Udy, and Jane Tansell set out to retrieve the last of the sediment and the equipment

used for entering the shaft and for the excavation. Since the previous trip, drip water had eroded the sediment in the face of the entrance slope a little beyond the limit of the previous excavation, exposing a perfect eagle femur and tibiotarsus. Further excavation resulted in the discovery of an eagle tarsometatarsus and associated phalanges that had been trapped behind a rock. Five bags of sediment were carried home (leaving three from 150–300 mm in Square 1B stashed). Sediment from the excavation face in the entrance slope left lying on the floor of the excavation should be processed if the site is further investigated.

All of the sediment (some 68 bags or c. 1020 kg) removed from the cave was backpacked for an hour back to the vehicles, and later washed through 6 mm and 2 mm sieves. The sieved sediments were then air-dried and all bones hand-picked by THW from them. Sediments were spread a teaspoon at a time in trays so that all grains were separated to facilitate bone detection. All fossil bones are catalogued in the Museum of New Zealand Te Papa Tongarewa within the series MNZ S38942–38944, 38981, 38988–39017, 39047–39088, and 39164–39270.

Samples of the sediments at various depths in the excavation were taken and forwarded to Dr Matt McGlone, Landcare, Lincoln, for pollen analysis. Unfortunately, pollen was only preserved adequately enough for counting in Layer 1, and it was dominated by rimu and beech and thus reflects the modern vegetation (pers. comm., M. McGlone 11 October 2001).

Six composite samples of molluscs were formed by amalgamation of shells from sediment samples from a range of depths below the present sediment surface in Takaka Fossil Cave. These have the following Museum of New Zealand station numbers N26200001 (0–50 mm), N26200002 (50–150 mm), N26200003 (150–300 mm), N26200004 (300–500 mm), N26200005 (450–550 mm), N26200006 (500–600 mm). Molluscs were extracted from the dried bulk sediment from which bones had already been sorted by DR.

Each sediment sample was soaked for a few hours in water in a plastic bucket, and then gently agitated. Floating material (mostly shells) was decanted over the lip of the bucket into a 3 mm mesh sieve above a 0.5 mm mesh sieve. After the shells were separated and set aside, the remaining mud was washed through the same two sieves, with intermittent water flow until all lumps of mud had disintegrated. Material that did not float was placed in an oblong plastic tray and dried, and shells were sorted from it by hand by DR with storkbill tweezers. All snails from each level were combined, dried thoroughly, then identified to species level.

Abbreviations and definitions

New Zealand institutions: MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington (formerly National Museum of New Zealand and Dominion Museum).

MNI (minimum number of individuals) was determined for each taxon at each site from the most frequent skeletal element (maximum of left or right side only) in the sample. In species lists, x/y = number of bones/MNI represented by the sample. In some instances 'x' is uncounted and is left as 'x', while the more important value for 'y' is determined. If 'x⁺' is used, it means more than the number given.

Skeletal elements and descriptive terms used (may be singular or plural as appropriate): acet, acetabular part of pelvis; cmc, carpometacarpus; cor, coracoid; cran, cranium; fem, femur; fib, fibula; frag, fragment; fur, furcula; hum, humerus; imm, immature; juv, juvenile; M, manus phalanx; mand, mandible; pel, pelvis; phal, phalange; pmx, premaxilla; quad, quadrate; rad, radius; sac, synsacrum; scap, scapula; stern, sternum; tmt, tarsometatarsus; tt, tibiotarsus; and vert, vertebra. When listing material, bones are sometimes identified as left (L) or right (R) elements. L or R prefixed by 'p', 's', or 'd' indicates 'proximal', 'shaft', or 'distal' part of the element, eg, pR femur means the proximal part of a right femur.

Measurements

Measurements were made to 0.01 mm with TESA® dial callipers, and rounded to 0.1 mm.

Identification

Bones were identified by THW. When necessary, comparisons were made with recent reference material, or previously validated fossil material, held in either the MNZ, or THW reference collections. Molluscs were identified by DR with reference to specimens in the MNZ collections.

Nomenclature

The nomenclature and higher taxonomy of birds advocated in the *Checklist of the Birds of New Zealand* (Turbott 1990) as modified by Holdaway *et al.* (2001) is followed. Mollusc nomenclature follows Spencer *et al.* (in press).

Anatomical nomenclature follows Baumel *et al.* (1993), with English translations used after the first reference.

The geological periods referred to here are: Holocene beginning at 10 000 ^{14}C yrs BP, the time since the end of the most recent cold stage; the Otira Glaciation, the most recent New Zealand glaciation, which lasted from about 70 000 to 15 000 ^{14}C yrs BP. It is broadly equivalent to the Wisconsinan–Weichselian or Marine Oxygen Isotope stages 4–2. The Last Glacial Maximum (LGM) is taken as the period from c. 25 000 to 15 000 ^{14}C yrs BP, and the Late Glacial (Termination 1) is the period of rapid climatic and vegetational change from 15 000 to 10 000 ^{14}C yrs BP (eg, Newnham *et al.* 1999). These divisions better reflect the major episodes of vegetation history than does use of the term Aranuian (Suggate 1978), which covers all the time from 14 000 years to the present.

Radiocarbon dating

Radiocarbon dating of bones was done by the Rafter Laboratory of the Institute of Geological and Nuclear Sciences at Lower Hutt. The surfaces of all samples were dremmeled to remove surface coatings and dirt. The remaining sample was then crushed and sieved to <450 µm, then demineralised in 0.5 *M* HCl while stirred at room temperature for 1 h to extract the collagen. The collagen was then gelatinised in 0.01 *M* HCl under N_2 at 90°C for a minimum of 16 hours. The gelatin fraction was combusted, and the CO_2 was reduced to a graphite target and dated using accelerator mass spectrometry (AMS). Dates are reported as conventional radiocarbon ages, based on the Libby T½ of 5568 yrs, uncorrected for secular variation, in years before present (^{14}C yr BP), where present is CE 1950. The Rafter Radiocarbon Laboratory, using the most recent available terrestrial bidecadal calibration curve, provided calibrated dates in calendar years before present (CAL BP) within the present calibration range.

Results

Site taphonomy

Most fossils in Takaka Fossil Cave have a pitfall origin, with individuals having fallen down the entrance shaft and then been trapped in the cave. The fauna is thus characterised by flightless birds such as various moa, kiwi (*Apteryx* spp.), kakapo (*Strigops habroptilus*), and acanthisittid wrens. The absence of greenstick fractures indicates the length of the fall into the cave was insufficient to break the leg bones of any of the moa in the site. The presence of an individual

Haast's eagle (*Harpagornis moorei*) suggests that this eagle was lured into the cave by the presence of a moa trapped in the cave, and having swooped down into the cave was unable to escape. At the time of its entrapment in the Late Glacial, forest probably did not grow around the cave entrance and moa trapped within would have been visible from the air.

The fact that many of the bones of small species, such as parakeets (*Cyanoramphus* spp.), South Island robin (*Petroica australis*), bellbird (*Anthornis melanura*), brown creeper (*Mohoua novaeseelandiae*), acanthisittid wrens, and bats (*Mystacina* spp.), either have greenstick fractures or are digested to various degrees indicates that they were deposited by an avian predator (for example, see Worthy 2001). These taxa were principal prey of laughing owl (*Sceloglaux albifacies*) at other sites on Takaka Hill (Worthy & Holdaway 1994, 1996) and this owl is assumed to be the predator responsible for the presence of the bones of most of them in Takaka Fossil Cave. The presence of crevices and niches in the roof of the entrance passage would provide either suitable roosting or nesting sites. The combined taphonomic origins of pitfall and predator have resulted in the relatively diverse assemblage.

Among the first bones to be deposited in the cave were those of several moa and the Haast's eagle, which accumulated on a rockfall floor in the final chamber. They were then weathered and worn to various degrees by exposure to trampling feet and dripping water, as is particularly well shown by the eagle bones, before burial in clays. The bones or parts thereof that were within crevices between limestone blocks were well preserved, but if they protruded from the floor they were broken or damaged. The eagle carcass apparently came to rest near the base of the rockfall slope and it is evident that as it decomposed its leg bones dropped down between the large rocks that supported the base of the rockfall slope. The head, body, and wings dropped to the floor of the final chamber and were spread about by trampling of other birds and/or water, and the surviving parts were all within crevices between the floor rocks. So, for example, only the left, rear quarter of the eagle skull was preserved where it lay in a triangle between rocks; the rest was planed off by trampling and or water flows.

Excavation stratigraphy

The stratigraphy revealed by the excavation shows three main phases to fossil deposition in the terminal chamber. The first was when bones were deposited in the late Pleistocene on a rockfall floor at c. 550–650 mm depth in the excavation.

Mainly moa and the eagle bones survive from this phase. Smaller bones (ribs, vertebrae) had penetrated the rocks for about 200 mm, but below this level there was neither silt nor bones between the rocks.

Secondly, Layer 2, composed of grey silty clays, enveloped the rocks and bones on the old floor in laminated sediments that extended to within 50 mm of the surface. Because of the size of the bones and of the rock clasts, the sediment from 500 mm to the base was excavated as a unit. In an effort to detect faunal change, the rest of L2 was excavated in spits, which were amalgamated into the units 50–150 mm, 150–300 mm, and 300–500 mm. These silty clay sediments have an allochthonous origin, having been washed into the cave from the land above. Similar silts can be observed in water runnels on the ground surface in the karst above the cave. Several sets of articulated bones were found in this layer, including the *A. didiformis* at 500 mm depth, and an *Aptornis* foot at 300–500 mm on the edge of the excavation. The latter is presumed to have penetrated the clay while the bird was alive and so the rest of the bird will be lying above it in the stratigraphic sequence: a mandible was in the 50–150 mm level. Therefore, it is probable that the rest of this bird's bones lie outside the area of Squares 1A & 1B.

The third phase resulted in 50 mm of friable red-brown silts being deposited to form L1. These sediments then gained a flat, clean, and washed surface by water dripping on them except where the water drained out of the chamber down the left wall. Here a hole formed deep into Layer 2 sediments that later was mostly back-filled with Layer 1 sediments. These Layer 1 sediments are interpreted as being of autochthonous origin as the insoluble weathering products of limestone from the cave roof and walls. Such deposition is relatively slow, though the rate is dependent on available moisture.

Radiocarbon ages

Five radiocarbon ages were obtained on bones from Takaka Fossil Cave (Table 1).

The *Anomalopteryx didiformis* in L1 that was the last moa to enter the excavation site had a radiocarbon age of 1576±60 ^{14}C yrs BP (NZA13547). The *Dinornis novaezealandiae* whose bones rested on the boundary between L1 and L2 was 3761±60 ^{14}C yrs BP (NZA13548). Therefore, L1 was deposited over the last 3761 ^{14}C yrs BP, though little or no sediment was deposited in the last 1500 years. The *A. didiformis* that was essentially articulated at 500 mm depth

was 11 354±60 ^{14}C yrs BP (NZA11614). The *Euryapteryx geranoides* individual that lay on the base of the excavation on the original rock floor with the eagle skeleton and other moa skeletons was 12 361±65 ^{14}C yrs BP. The position of the bones upon which the last two dates were obtained indicates that deposition of the grey clays of L2 commenced between 12 361 and 11 354 ^{14}C yrs BP.

Of the two small *Euryapteryx* individuals found on the rockfall slope, one was adult and the other subadult. Both were represented mainly by leg bones, with vertebrae, ribs, and phalanges noticeably absent. A sternum, probably of the adult, was located at 300–500 mm depth against the cave wall in the excavation. The adult bird gave a radiocarbon age of 12 450±656 ^{14}C yrs BP (NZA13267). This date is consistent with parts of the skeleton being located at near 500 mm depth in the excavation, and indicates that bones on the surface of the rockfall slope could have ages spanning from the present to over 12 000 ^{14}C yrs BP.

The supplementary data obtained with the radiocarbon ages indicates the bones were very well preserved. The percentage collagen values that ranged from 13 to 39% are high and together with the C:N ratios of 2.8–2.9 indicate that the radiocarbon ages are probably reliable (Stafford *et al.* 1988; Stafford *et al.* 1991). This very good preservation in bones up to 12 000 ^{14}C yrs BP is attributable to the stable and cold depositional environment. With no connection to further passages to cause air movement and as the site is in forest at about 800 m altitude, it would have had a relatively constant temperature (presently about 8°C) and also have had constant humidity.

Molluscan fauna

Twenty-nine land mollusc taxa and two freshwater species were recorded from the sediment samples taken from the excavation in Takaka Fossil Cave (Table 2). Several taxa are known but undescribed, and in many cases form part of a species complex as indicated in the following taxonomic notes by DR.

Family HYDROBIIDAE

The two species of freshwater snails in the Takaka Fossil Cave samples are both members of the gastropod family Hydrobiidae. The *Opacuincola* specimens resemble *O. caeca* Ponder 1966, but differ in that the teleoconch whorls are more weakly convex and the spire is slightly taller than specimens of *O. caeca* from the type locality (Gorge Creek

Cave), which is in a separate catchment to the north on the Takaka massif, and from the Riwaka River resurgence, which is the likely outlet for water entering Takaka Fossil Cave. The spire is highest in specimens from the lower layers (450–550 mm and 500–600 mm).

Horatia is currently known from one species in New Zealand (*Horatia nelsonensis* Climo 1966) from only the type locality (the Riwaka River resurgence). The single specimen from the uppermost layer of cave sediment differs from specimens from the Riwaka resurgence (MNZ) by being larger and in having a lower spire and a weak but distinct peripheral angulation. The New Zealand hydrobiids are currently being revised (M. Haase, in prep).

Family PUNCTIDAE

The two specimens identified as *Paralaoma* sp., one from 300–500 mm and one from 450–550 mm, closely resemble *Paralaoma thomsoni* (Suter, 1917), particularly specimens from Hawke's Cave, nearby on the Takaka Hill. These and some other undescribed *Paralaoma* species are commonly found as fossils in cave entrances.

Family CHAROPIDAE

The specimens of *Allodiscus* sp. A would be usually identified as *Allodiscus granum* (Pfeiffer, 1857). Two species of similar appearance have extant populations on Takaka Hill (and elsewhere), and it is yet unclear which if either is *A. granum*.

Specimens of *Allodiscus* sp. B are commonly identified as *Allodiscus tessellatus* Powell, 1941 in collections, with which they share the same chequered colour pattern, a circular white area in the centre of the base, and similarly sinuous riblets. However, compared to living specimens from the central North Island (ie, including the type locality), Takaka Fossil Cave specimens are much smaller and flatter, with more evenly spaced ribs. They are similar to specimens from Paturau but have consistently much closer riblets on the teleoconch. *Allodiscus* sp. B is evidently endemic to the Takaka Hill area and is part of a species complex.

Allodiscus sp. C is a member of a species complex that includes *Allodiscus tullia* (Gray, 1850). Similarly, *Allodiscus* sp. D is part of a species complex that includes *Allodiscus venulatus* (Pfeiffer, 1857).

Allodiscus sp. E would usually be identified as *Allodiscus planulatus* (Hutton, 1883), which name has been used for *Allodiscus* specimens with an adult diameter of about 3

mm. However, all of the known specimens, other than the type material and topotypes, form a complex of undescribed species (Climo & Mahlfeld 1998).

Cavellia sterkiana (Suter, 1891) is a variable species and it is uncertain whether the Takaka Fossil Cave specimens form merely part of this variation, which seems more likely, or are a distinct undescribed species.

The single specimen of *Flammulina* sp. from the topmost layer does not match well any known *Flammulina* species, described or undescribed.

While there were no clear presence/absence type taxon changes between Layer 1 and Layer 2 (samples 2, 3, 4, and 5 in Table 2), relative frequency data for several taxa showed marked changes between the layers. Species that markedly increased in frequency through time (from Layer 2 to Layer 1) were *Allodiscus* n. spp. A and D, *Cavellioropa moussoni*, *Mocella spelaeus*, *Pseudegestula worleyi*, and *Suteria ide*. Species that markedly decreased in frequency through time (from Layer 2 to Layer 1) were *Allodiscus* n. spp. C and E, *Cavellia anguicula*, *Fectola trilamellata*, and punctid n. sp. 50.

Avifauna

A total of 1633 bones from 25 species of birds and a further 895 bones of 154 individuals of vertebrates other than birds (two species of frog, one tuatara, three lizards, two bats, and a rat) were identified in the total recovered fauna from Takaka Fossil Cave (Table 3). This diversity is a minimum, as it is probable that parakeets and wrens (*Xenicus* spp.) would each have been represented by more than one species, but no attempt was made to determine species in these genera. Also the taphonomic features on many of the small bones indicates they were deposited by an avian predator presumed to have been the laughing owl, which species can thus be added to the total fauna.

Identity of the *Euryapteryx* taxon

The two individuals identified as *Euryapteryx geranoides* that were found on the rockfall slope (MNZ S39016, 39017) were unusually small (Table 4). While one was sub-adult in terms of ossification, the adult length of the bones had been attained.

The cranium associated with S39016 has the following combination of features that clearly identify it as *E. geranoides* (Worthy 1992): there is wide gap between the *crista temporalis* and *crista nuchalis transversus* (lambdoidal ridge); viewed dorsally, the medial edges of the *fossa temporalis* are

straight and diverge anteriorly slightly (not highly concave); the width between the *proc. postorbitali* is slightly greater than that between the *os squamosi* (not markedly so); the *rostrum parasphenoidale* is compressed and ridged ventrally; neither the *prominentia cerebellaris* (which is not inflated) nor the *condylus occipitalis* protrude caudally of a line connecting the *proc. paroccipitali*, which are rounded posterolaterally; the *lamina parasphenoidalis* has well-developed mamillar tuberosities caudally with a deep groove between them; the part of the *os squamosum* that forms the dorsal border of the *recessus tympanicus dorsalis* does not extend as a ridge across the *proc. zygomaticus*.

The sternum (pt S39016) has features that identify it as *E. geranoides* (Worthy 1992): the body is longer (135 mm) than wide (91 mm caudad of *proc. costalis*), and lacks deep pneumatic hollows dorsally beside the *proc. craniolateralis*; it lacks *sulci articularis coracoideus*; the *proc. craniolaterali* are well developed laterally to provide a maximum width of 140 mm.

The leg bones of both individuals have the characteristic features of *E. geranoides* (Worthy 1988; Worthy & Holdaway 2002). The individual in the base of the excavation (S38942) was also a subadult as the patella was not completely fused to the tibiotarsus, but adult length had been attained. This individual was of more usual size for the species.

The femur has a stout, straight shaft, lacking large pneumatic fossae proximally, either on its ventral or dorsal face; the *impressio ansae m. iliofibularis* (ectocondylar fossa) lies anterior of the *fossa poplitea*; in dorsal view, the *condylus lateralis* is angled away from the line of the shaft (is not subparallel); ventrally, the *trochanter femoris* (trochantal ridge) does not extend to the *facies artic. acetabularis*; the shaft is not compressed lateromedially, rather is wider than deep.

The tibiotarsus has a long *crista fibularis* (fibula crest) (26.3% total length) with the medulloarterial foramen situated adjacent to its distal end (usually in *Euryapteryx* it lies proximal of that point); the anterior facies beside the fibula crest is flat (not highly convex caused by a buttress-like extension of the *crista cnemialis lateralis* (ectocnemial ridge) as in *Pachyornis*); the distal end is not greatly expanded medially and in anterior view, the medial edge of the shaft grades into the *condylus medialis* (not stepped down to it).

The tarsometatarsus is short and stout with its length 1.92 times its distal width; anteriorly *trochlea metatarsi III* arises at a low angle from the shaft; the *crista lateralis* and *crista medialis hypotarsi* (hypotarsal ridges) are of approxi-

mately equal height; viewed proximally, the depth of the bone across the mid-third of proximal width in the *area intercotylaris* is constant (not increasing medially), with the anterior surface that forms the margin of the intercotylar area a flat anterior-facing plane opposite the hypotarsal ridges (not with the intercotylar area deepening medially so that the anterior surface appears to be facing somewhat laterally); this flat anterior surface below the intercotylar area results in the depth of the proximal end being only a little over half (58%) total width (compared to about 75% in *Pachyornis*, *Emeus*); in medial view, the high (anterior-most) point of the *trochlea metatarsi II* (endotrochlea) is level with the low (distal-most) point; in anterior view, the medial margin of the endotrochlea is sharply angled and this angle is distal to the proximal wall of the *incisura intertroclear medialis*.

All the above features indicate these specimens are referrable to *Euryapteryx geranoides*, albeit small individuals.

Alan Cooper (The Henry Wellcome Ancient Biomolecules Centre and Department of Zoology, University of Oxford, United Kingdom) extracted and analysed mitochondrial DNA, sequencing two fragments from the control region and the protein-coding sequences CO1 and ATP 8, from S39016. He found no differences from sequences obtained in studies of typical-sized *E. geranoides* from both Seatoun (MNZ S465) on the Wellington coast and Cheviot swamp (CM SB237) in North Canterbury (A. Cooper pers. comm., March 2002). This analysis of the mt DNA of one of the small specimens from Takaka Fossil Cave supports its identification as *E. geranoides*.

Moa fauna

At least 30 individual moa are represented in the total fauna from Takaka Fossil Cave (Table 3). There are differences in the distribution of species over time. While five species of moa are present in the total fauna, the Holocene-aged deposits contain only three: *Anomalopteryx didiformis*, *Dinornis novaezealandiae*, and *D. struthoides*. *Dinornis novaezealandiae* was not in the Late Glacial deposits, although both *A. didiformis* and *D. struthoides* were. The three individuals of *A. didiformis* on the base of the excavation included two juveniles and one adult (MNZ S39010-12). They must be older than 11 354 ^{14}C yrs BP (NZA11614) though are possibly younger than 12 361 ^{14}C yrs BP (NZA13266), but nevertheless are of Late Glacial age.

Radiocarbon ages indicate that the *Euryapteryx geranoides* on the surface of the rockfall slope (S39016) and the

large subadult (S38942) in the base of the excavation are of Late Glacial age. The other *Euryapteryx* on the rockfall slope (S39017) is assumed to be of similar age, as like S39016, only the most robust bones of the skeleton survive: vertebrae, ribs, and even the pelvis were not evident. A single juvenile left femur (S39074) from 300–500 mm in the excavation cannot be of the two individuals on the rockfall slope, as each have their left femur. Moreover, it is of a different size to the two individuals below it in the excavation, and so represents another bird. The presence of a single bone in the excavation is explained best by the carcase having decayed higher on the rockfall slope, and the bone having been secondarily moved downslope by the combined actions of water, gravity, and moa trampling. It would therefore be at least as old as the *A. didiformis* found about the same level (NZA11614), and so is of Late Glacial age. The two individual *E. geranoides* on the excavation base are older than the *A. didiformis* at 500 mm (NZA11614), so are also of Late Glacial age. Therefore, all the *E. geranoides* individuals are of Late Glacial age.

This fauna lacks *Megalapteryx didinus*, which species was dated to LGM faunas elsewhere on Takaka Hill (Worthy & Holdaway 1994). Neither *Pachyornis australis* nor *P. elephantopus* were confirmed to be present in Takaka Fossil Cave, though the latter is relatively common in LGM faunas elsewhere on Takaka Hill, eg, Kairuru and Hawkes Caves. However, the single bone referred to a juvenile *Pachyornis* from the rockfall slope is likely to be of Late Glacial age, as were the small *Euryapteryx geranoides* bones from there.

Non-moa fauna

Nine non-passerines other than moa are present in the Takaka Fossil Cave fauna, though a tenth, laughing owl (*Sceloglaux albifacies*), can be inferred from the taphonomy of some remains. Relatively few kiwi (*Apteryx* spp.) were present in this site, which is attributed to the obvious nature of the large diameter entrance: pitfall sites with small cryptic entrances often have abundant kiwi and weka (*Gallirallus australis*) bones (pers. observ. THW). There are several individuals of a large kiwi, either *Apteryx australis* or *A. haastii*, although the individual from Layer 1 has been confirmed as a member of the brown kiwi clade by analysis of its mt DNA (David Lambert and Lara Shepherd, pers. comm. 2003). The smaller little spotted kiwi (*A. owenii*) was not present in the fauna despite being common in other sites on Takaka Hill (Worthy & Holdaway 1994). The bones of Finschs duck (*Chenonetta finschi*) found on the Rockfall

slope (S39194) and those from 0–50 mm in the excavation (S39172) do not include any common elements and may be from a single individual. A Holocene age for the specimen, as indicated by its presence in L1, is supported by its measurements. The carpometacarpus at 45 mm long is 69% of the femur length (65.1 mm), a ratio smaller than seen in any Late Glacial and older populations (Worthy 1997). Other individuals from Hobsons Tomo and Hawkes Cave on Takaka Hill had humeri lengths similar to specimens of Glacial age, and such an age was confirmed by radiocarbon dating of one of the Hobsons Tomo birds (Worthy & Holdaway 1994), so the Takaka Fossil Cave specimens indicate that *C. finschi* was present on Takaka Hill during both the Glacial and Holocene periods.

The Takaka Fossil Cave Haast's eagle (*Harpagornis moorei*) is the fourth individual to be discovered on Takaka Hill. Like the others, it lived there during the Late Glacial to LGM period (Worthy & Holdaway 1994). Nowhere is Haast's eagle known to have been present when closed canopy forests occupied the landscape (Worthy 1999; Worthy & Holdaway 2002). An interesting feature of the Takaka Fossil Cave individual is that it had osteoarthritic growths affecting two major joints. In the right wing, the proximal ulna was affected on the olecranon and around the dorsal cotyla particularly, as was the corresponding distal humerus above the dorsal condyle. Second, the distal right tibiotarsus was markedly affected on the anterior and medial surfaces, as was the proximal right tarsometatarsus on the anterior facies below the cotyla (Fig 3).

Gruids were rare in the deposit, with only two species present. Weka, as mentioned above, were relatively rare compared to their abundance in sites in other tomos on Takaka Hill. While there are few bones of the large gruid *Aptornis defossor*, at least two individuals are represented. The articulated leg bones at 300–500 mm in L2 indicate a bird died in the final chamber of the cave, and that before it did so it pushed at least one leg down to this depth in the clay deposits. A single mandible was found in the 50–150 mm spit of L2, suggesting this may be the depth at which the rest of the skeleton lies. As the foot bones were found on the edge of the excavation, it is likely the rest of the bird lies in the unexcavated area. Yet a cranium was found relatively high on the rockfall slope about 8 m distant. For these to be the same individual would require the actions of a scavenger, but transport of the cranium, the largest element in an *Aptornis* skeleton, up a steep slope is not likely. Therefore, it appears that at least one of these *Aptornis*
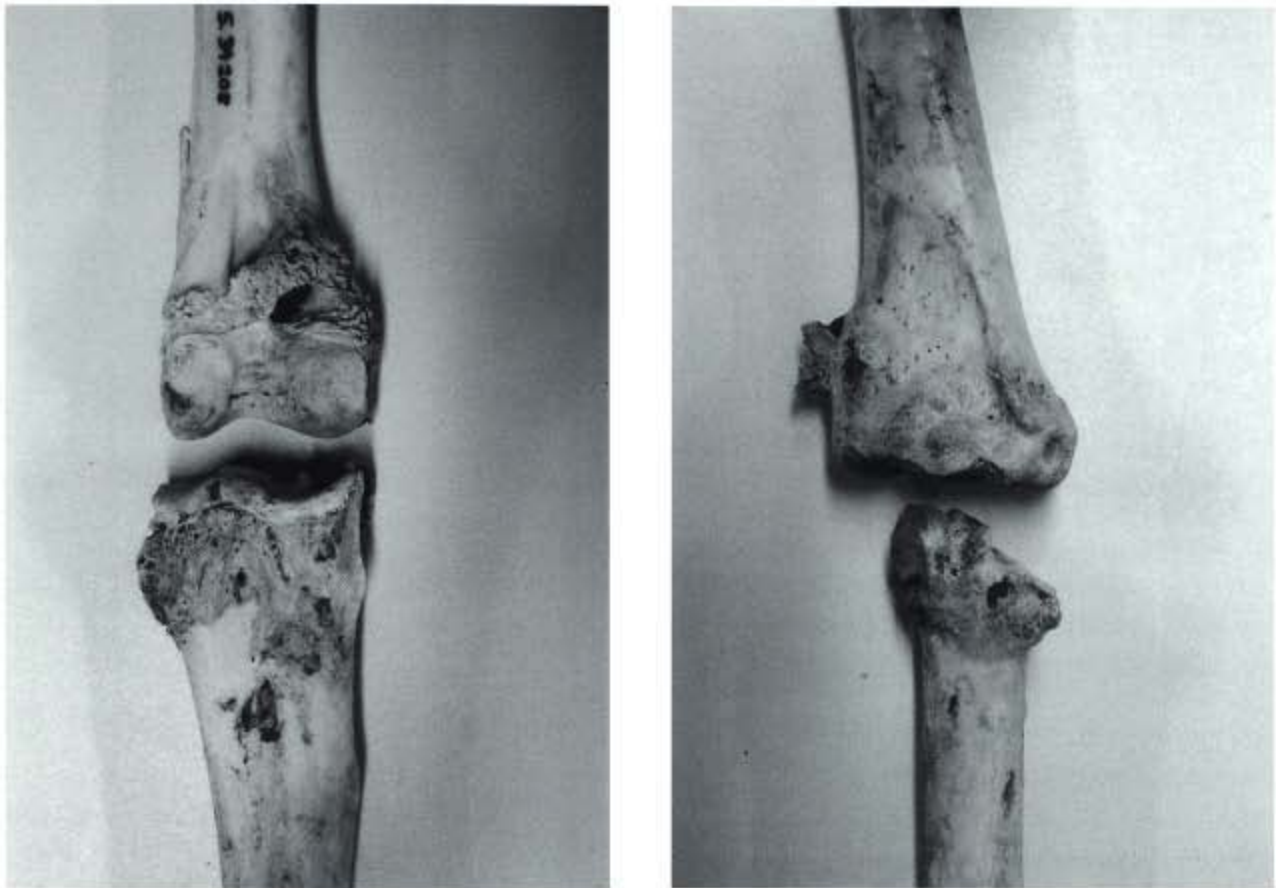
Fig 3. Photograph of the right distal tibiotarsus and proximal tarsometatarsus (left) and the right distal humerus and proximal ulna (right) of Haast's eagle *Harpagornis moorei* MNZ S39208 showing the osteoarthritic growths.

died between 11 354 (NZA11614) and 3761 (NZA13548) ^{14}C yrs BP, which ages bracket the articulated feet and the mandible. This mid- to early-Holocene occurrence on Takaka Hill is the youngest date for *Aptornis* there.

As in most sites on Takaka Hill, kakapo (*Strigops habroptilus*) was common and was present in deposits of all ages in Takaka Fossil Cave. Only a single kaka (*Nestor meridionalis*) was present and kea (*N. notabilis*) was absent, although the latter has been recorded from sites on Takaka Hill before (Worthy & Holdaway 1994) and are still seen in the area (pers. observ. THW). Parakeets (*Cyanoramphus* spp.) are relatively common in the fauna, and the taphonomic features on the bones indicate they are there as the result of having been prey of laughing owls. Owlet nightjars (*Aegotheles novaezealandiae*) are common in Takaka Fossil Cave, probably as a result of a combination of things: the distribution of their remains in other caves is suggestive that they often roosted in caves and hence died in them (Worthy

& Holdaway 2002), but they were also a favoured prey of the laughing owl (Worthy & Holdaway 1996).

Eleven species of passerines are present in Takaka Fossil Cave with most individuals being one of four acanthisittid wrens. Some of these were demonstrably the prey of laughing owls, but the terrestrial habits of bush or rock wrens (*Xenicus* spp.), Stephens Island wren (*Traversia lyalli*), and the Stout-legged wren (*Pachyplichas yaldwyni*) would have predisposed them to having been pitfall trapped, which some undoubtedly were. The other passerines, yellowhead (*Mohoua ochrocephala*), brown creeper (*M. novaeseelandiae*), grey warbler (*Gerygone igata*), South Island robin (*Petroica australis*), bellbird (*Anthornis melanura*), and South Island saddleback (*Philesturnus carunculatus*), probably were all prey of laughing owls judging by the digested nature of many of their bones. The South Island kokako (*Callaeas cinerea*) is represented necessarily only by two birds, one in the uppermost layer and one in the lower layer. The rarity of

South Island kokako in Takaka Fossil Cave supports the ob-
servations of Worthy & Holdaway (1994), who found them
to be relatively less abundant on Takaka Hill than at lower
elevations, eg, Honeycomb Hill Cave in the Oparara.

Some 18 indigenous passerines have been recorded
from Takaka Hill previously, nearly the full complement of
those known in the South Island prehistorically (Worthy &
Holdaway 1994). Apart from New Zealand pipit (*Anthus
novaeseelandiae*) and fernbird (*Bowdleria punctatus*), which
have special habitat requirements (open grassland and
scrubland), and so would not be expected in Takaka Hill's
Holocene forests, Takaka Fossil Cave lacks fantail (*Rhipidura
fuliginosa*), tomtit (*Petroica macrocephala*), tui (*Prosthemadera
novaeseelandiae*), South Island piopio (*Turnagra capensis*),
and New Zealand crow (*Corvus moriorum*). The absence of
the first four of these species is probably due to the small
size of the predator-accumulated sample, as all were com-
mon on the hill prehistorically, though the piopio is extinct
now. The crow is a species generally associated with open
environments such as coastlines and eastern areas during the
Holocene, but deforestation in the Pleistocene allowed it to
live in western regions then (Worthy & Holdaway 2002).
Its absence from Takaka Fossil Cave probably relates to the
absence of a sufficiently extensive LGM fauna.

A notable taxon missing from the fauna is the long-
billed wren (*Dendroscansor decurvirostris*), the rarest bird in
New Zealand late Quaternary deposits. Three specimens of
this species were recorded from Hobsons Tomo on Takaka
Hill in a shallow deposit that was as old as at least 14,000
^{14}C yrs BP. Its absence from the extraordinarily rich fauna of
Predator Cave indicates the species was probably not present
in the vicinity at any time in the Holocene, so Worthy &
Holdaway (1994) postulated that it lived in the shrublands
that typified LGM and Late Glacial landscapes on Takaka
Hill. It was hoped that a rich deep stratified deposit would be
found to test this hypothesis, but it seems that the stratified
record for Takaka Fossil Cave does not extend deep enough
in time to do so. However, the absence of the long-billed
wren from the Holocene sediments once again suggests that
Holocene *Nothofagus* beech forests were not the habitat of
this enigmatic wren.

The herpetofauna comprises just six taxa: two frogs
(*Leiopelma* spp.), a tuatara (*Sphenodon*), and three lizards
with geckos (*Hoplodactylus* spp.) abundant. As is usual for
pitfall traps in higher rainfall districts of the South Island
such as on Takaka Hill, both *Leiopelma markhami* and *L.*

hamiltoni were common, and probably fell into the cave.
The abundance of smaller *Hoplodactylus* species is attributed
to them having been prey of the laughing owl. While the
two records of tuatara from Takaka Fossil Cave double the
number of records from Takaka Hill, the local rarity of the
species is confirmed.

The mammal fauna includes both Recent mystacinid
bats known from New Zealand, although the smaller lesser
short-tailed bat (*Mystacina tuberculata*) is much more com-
mon than the larger greater short-tailed bat (*M. robusta*). This
is probably a function of the relative abundance of either
species to the laughing owl, as in the laughing owl deposit
in nearby Predator Cave, the lesser short-tailed bat was about
twice as abundant as the greater short-tailed bat (Worthy &
Holdaway 1994). A single individual of the Pacific rat (*Rattus
exulans*) was present in the L1 sediments within the drainage
feature, and is probably at most a few hundred years old.

Discussion
Period of deposition

The late Pleistocene is marked by the coldest part of the
Last Glacial Maximum (LGM) at about 19 000 ^{14}C yrs BP,
with glacial conditions continuing to about 15 000 ^{14}C yrs
BP, followed by a period of rapid climatic and vegetational
change to about 10 000 ^{14}C yrs BP, termed the Late Glacial
(Hellstrom *et al.* 1998; Newnham *et al.* 1999). These global
climatic events have been associated previously with marked
changes in the distribution of certain species in the New
Zealand avifauna (eg, Worthy & Holdaway 1993, 1994,
2002; Worthy 1994, 1999).

The avifaunas in different regions reacted differently,
according to variations in the local expressions of these global
climate changes. Therefore, an understanding of the regional
events associated with the climate changes is necessary to
place the Takaka Hill story in perspective. 14 000 ^{14}C yrs
BP marked the commencement of organic sedimentation
(peats) in inland and western South Island sites, and reaf-
forestation of Taranaki and western South Island took place
13 000–12 000 ^{14}C yrs BP (McGlone 1988). At Dew Lakes,
just east of Nelson, Dodson (1978) analysed a pollen record
that dated from 10 430 ^{14}C yrs BP. At that time a forest
dominated by *Podocarpus* and *Dacrydium* species was already
established. However, *Nothofagus fusca*-type pollen rapidly
rose to prominence in the record and remained high there-
after. This same pattern was documented by Moar (1971)

from a pollen record at Tophouse, Nelson Lakes, where a single radiocarbon age of 7820 ^{14}C yrs BP marks the beginning of *Nothofagus fusca*-type pollen dominance and the rapid decline in abundance of *Phyllocladus*.

A few kilometres southwest of Takaka Hill, valley glaciers and ice caps were present in the area around Cobb Valley over the LGM. Singer *et al.* (1998) documented pollen profiles from three sites in Cobb Valley spanning the period of 17 120 ^{14}C yrs BP to the present and recorded a vegetation succession as follows, though key changes in the vegetation were undated. Herbs and grasses dominated at 17 000 ^{14}C yrs BP. As these declined in significance shortly afterwards, the low tree/shrub *Phyllocladus* peaked in abundance, possibly at about 13 200 ^{14}C yrs BP (15 904–15 578 CAL yrs BP), as indicated by NZA6325 from Lake Sylvester (LS1). A subsequent decline in *Phyllocladus* was matched by a rise in *Halocarpus* and fuscasporites-type pollen, probably mountain beech (*Nothofagus solandri* var. *cliffortioides*). The rise to prominence of *Phyllocladus* in the pollen record correlates well with the period of rapid change in Hellstrom *et al.*'s (1998) δ^{13}C record. The subsequent attainment of peak δ^{13}C values about 14 000 CAL yrs BP, which remained high through the Holocene, may thus correlate with the attainment of significant levels of *Nothofagus* pollen in the Cobb record.

The radiocarbon ages indicate the faunal deposit in Takaka Fossil Cave is about 12 500 ^{14}C yrs old at maximum, which places it in the midst of the Late Glacial period. The two dates (NZA11614, NZA13266) bracket the onset of sedimentation in the site, suggesting silts began to be deposited in the period about 12 000 to 11 500 ^{14}C yrs BP, or about 14 800 to 13 450 CAL yrs BP. This period coincides more or less perfectly with the attainment of Holocene δ^{13}C levels and δ^{18}O levels in stalactites on nearby Mt Arthur (Hellstrom *et al.* 1998). The δ^{13}C levels reached in speleothems in Mt Arthur at this time were correlated with establishment of substantial vegetation above the sites (Hellstrom *et al.* 1998), and with the establishment of forest in other parts of central New Zealand (McGlone 1988). The initiation of the deposition of silt in Takaka Fossil Cave in this same period is best explained by an increase in rainfall, which has been otherwise invoked for the simultaneous increased proportions of rimu (*Dacrydium cupressinum*) in lower altitude forests (McGlone 1988), resulting in increased erosion of the thin soils on the poorly vegetated karst.

The landscape on Mt Arthur under which the speleothem ED1 was formed is at 800–900 m (Hellstrom *et al.*

1998), and thus is a little higher than the altitude around Takaka Fossil Cave. Lack of speleothem deposition in ED1 between 73 000 and 16 000 CAL yrs BP implies that substantial vegetation was lacking above the cave during this period and that the treeline was depressed to below 800 m over the LGM (Hellstrom *et al.* 1998). However, growth of ED1 after 16 000 CAL yrs BP suggests that vegetation should have been present around Takaka Fossil Cave after that time. However, the plateau around Takaka Fossil Cave is largely bare rock now under a cover of *Nothofagus* and *Libocedrus* forest. Except in depressions, soils are very shallow or absent, and this factor probably resulted in a considerable delay to the re-establishment of taller shrub and tree vegetation cover in the area. Thus a mosaic of forest and scrub probably established first, with a slow spread of forest over the bare ground.

Molluscan fauna and ecological implications

The presence of the two hydrobiids in Takaka Fossil Cave reflects living populations in the site. *Horatia* has only been found living in the dark zone of a cave in flowing water. *Opacuincola* species are also aquatic and found only in caves. They are not threshold or seepage dwellers but rather obligate troglobites and so probably lived in the pool that is on top of the site and that is fed by a drip from the ceiling.

All land molluscs in the site would have lived either in the doline catchment about the cave entrance, on the vertical walls of the shaft, or in the litter accumulated at the foot of the shaft. Dead shells would then have been washed by percolation water and/or fallen down the slope to eventually be incorporated in the sediments accumulating in the excavation site. The doline has a diameter of about 30 m at most, so all shells can be considered to be of local origin.

Punctids are poorly represented in Takaka Fossil Cave, more so than in samples from most limestone caves. This is unexpected as typically there are similar numbers of punctid and charopid species in rich samples taken in unmodified bush. Some of this lack of diversity could be explained by the minimum mesh size of 2 mm used for the initially washing of the sediment taken from the cave as many punctids are smaller than 2 mm. But many specimens collected are smaller than 2 mm and many punctids are bigger than 2 mm, so other factors must be at work. Most punctids are leaf-dwellers, so their shells would have to come from the forest above the cave rather than from litter in the shaft itself. Also, their shells tend to be more fragile than those of charopids so their

scarcity in the excavation may be the result of taphonomic factors – their shells may not have survived the trip down the entrance and down the 30 m slope to the preservation site.

Paralaoma thomsoni and several similar undescribed species are generally uncommon. They are usually found as fossils in sediment within cave entrances but the micro-habitat in which they prefer to live is unknown.

Phrixgnathus celia Hutton, 1883 and punctid n.sp. 50 are widespread in the North and South islands and are usually associated with undisturbed leaf litter in mature native forests. *Phrixgnathus celia* lives mostly in relatively dry leaf litter. Its relative abundance is similar throughout the cave section, indicating that it was little affected by environmental changes that caused the differing sedimentation regimes. Punctid n.sp. 50 is usually found in damp or muddy habitats (DR pers. observ.). That both species are numerous in all layers suggests that they may live in deep and permanently damp litter in the base of the cave entrance shaft where conditions may be quite stable relative to in the adjacent forest.

Members of the Charopidae are mostly forest litter and log dwellers. Five species of *Allodiscus* are present in the fauna, and all are strongly limestone associated and are often found just inside cave entrances. Ecological correlates among related species suggest the following habitat preferences (Solem *et al.*, 1981): *Allodiscus* n.sp. A – moist areas in early decay, and cavities in fibrous matter among rocks; *Allodiscus* n.sp. B – under logs and in wet litter; *Allodiscus* n.sp. E – on the ground surface under rotten logs. That the two species (*Allodiscus* n.sp. A and *Allodiscus* n.sp. D) markedly increased in relative frequency from Layer 2 to Layer 1, while species *Allodiscus* n.sp. C, and to a lesser extent *Allodiscus* n.sp. B and *Allodiscus* n.sp. E, decreased in relative frequency from Layer 2 to Layer 1, may indicate a change from drier to wetter environmental conditions.

Cavellia anguicula (Reeve, 1852) is common under leaves in drier leaf litter throughout the southern North Island and the northern South Island of New Zealand, and usually occurs on the fringe of native bush. Its marked decline in relative abundance from Layer 2 to Layer 1 suggests the environment when Layer 2 was being deposited was relatively drier.

Charopa coma (Gray, 1843), *Fectola trilamellata* Climo, 1978, and *Mocella spelaeus* (Climo, 1971) are often present in cave talus, frequently in large numbers, in the Takaka Hill area. *Mocella spelaeus* has been recorded only from limestone caves, but the other two species are common

under shallow leaf litter layers in indigenous forest on Takaka Hill, and elsewhere, where daylight has access. All three species declined in abundance from Layer 2 to Layer 1, possibly indicating that the canopy has become more complete in recent times, so reducing the light levels on the forest floor. Such changes would also parallel an at least seasonally dry litter becoming wetter on average.

Cavellioropa moussoni (Suter, 1890) increased in relative abundance from Layer 2 to Layer 1. This species appears to be a facultative calciphile, as it is usually found in limestone cave talus, often in large numbers, and only occasionally has it been found living under logs, typically as lone specimens.

Cavellia marstoni (Climo, 1969) is restricted to Takaka Hill and nearby areas to the west of the Waimea Plains. This species is commonly found in areas where scrub persists, and also appears to tolerate drier areas. Its low numbers in Layers 1 and 2 of Takaka Fossil Cave probably reflect the presence of either a forest or tall scrub vegetation, as predicted by regional pollen records for the period these layers were deposited (see above), rather than a short scrub in the cave surrounds. *Cavellia sterkiana* (Suter, 1891) appears only in Layer 1, and is usually associated with the cryptozoic layer (between leaves and soil) in a relatively moist litter regime.

The very low numbers of specimens of either *Flammulina* species suggests the surrounding environment was relatively unsuited to them and precludes any indication of habitat change over time. *Flammulina zebra* is a spectacularly flammulated species often associated with grass clumps, a habitat that is rare in the cave vicinity at present and likely to have been so over the 12 000 years in which Layers 1 and 2 were deposited.

Huonodon hectori (Suter, 1890) lives in tree forks or leaf axils (Solem *et al.*, 1981), being rarely found alive in ground litter, so its rarity in these samples would appear to indicate merely that overhanging trees with suspended litter were probably not very close to the cave entrance.

Huonodon pseudoleiodon (Suter, 1890) is a generalist species that lives in wet but not slimy litter, and is commonly seen on the underside of logs in any stage of decay (Solem *et al.*, 1981). It usually avoids limestone, accounting for its rarity in these layers.

The remaining charopids and rhytidids are common in undisturbed dry bush and scrub on the Takaka Hill today. The absence of *Georissa purchasi* (L. Pfeiffer, 1862) from the samples is notable, as it is abundant in short shrubby vegetation or forest fringes throughout New Zealand. Its rarity in

all layers in Takaka Fossil Cave suggests such habitat has been absent about the cave for the last 12 000 years.

Species that are not usually associated with limestone are the two *Huonodon* species and *Phacussa hypopolia* (Pfeiffer, 1853), so their only occasional occurrence in these samples would indicate conditions were not favourable for them around or in the cave entrance. They are all usually associated with deeper acidic twiggy leaf litter.

As far as we are aware, this is the first documentation of changes over time in the relative frequency of species in New Zealand land molluscan faunas. However, with some 897 known taxa (Spencer *et al.* in press), New Zealand, for its area, has the richest land molluscan fauna in the world, and so land mollusca have great potential to document environmental changes over time. In general, the terrestrial molluscan fauna suggests that a tall scrub to forest vegetation has been around the entrance of Takaka Fossil Cave for the last 12 000 years. However, there are strong indications that the environment when Layer 2 was being deposited (about 12 000–3700 ^{14}C years BP) was drier than in the subsequent period of the late Holocene.

Avifaunal change

The species composition of the moa faunas from various depths indicates faunal change in this group over the period of the Late Glacial to the Holocene. The site lacks a fauna from the LGM stage of the Pleistocene, but includes at least some species from the Late Glacial, some of which are likely to have been present during the LGM. The Late Glacial moa fauna includes *Euryapteryx geranoides*, probably *Pachyornis* sp., *Dinornis struthoides*, and *Anomalopteryx didiformis*. The first three were known elements of the Late Glacial and Glacial faunas of Takaka Hill (Worthy & Holdaway 1994), but *A. didiformis* was not. The previous oldest individual of *A. didiformis* on Takaka Hill was 8274±72 ^{14}C yrs BP from Kairuru Extension (Worthy & Holdaway 1994). The data from Takaka Fossil Cave indicate *A. didiformis* was resident on Takaka Hill in the Late Glacial about 12 000 ^{14}C yrs BP. This could be predicted from the ^{13}C isotope data on nearby Mt Arthur that indicates substantial vegetation cover would have developed on Takaka Hill about this time. Whether or not the presence of *E. geranoides* actually overlaps that of *A. didiformis* in time cannot be determined from the available data, as the bones of both species were scattered on the Late Glacial floor of the cave. However, it might be expected that they would, as the habitat around the cave would have

been an ecotone between forest and open scrubby habitat for a period.

The presence of small examples of *Euryapteryx* on Takaka Hill has been somewhat of a puzzle since Hutton (1891) first described *Euryapteryx pygmaeus* based on a pair of tarsometatarsi that survive in the MNZ as S24322. They were reassessed by Worthy (1992) and their synonymy with *E. geranoides* supported. A partial skeleton with tarsometatarsi of similar size that included other skeletal elements was described by Worthy (1992) and referred to *E. geranoides*. These small individuals have not been dated, so whether they were coeval with the typical larger ones known to be of LGM age on Takaka Hill (Worthy & Holdaway 1994) or whether they were of Holocene age and were a small geographic form was unknown. The Takaka Fossil Cave specimens allow partial resolution of this problem as they confirm that both small and larger individuals coexisted on Takaka Hill in the Late Glacial. So it is likely that the small forms on Takaka Hill represent the smallest end of a size range that includes birds of similar size to those found elsewhere in the South Island, such as lowlands of Canterbury (Worthy 1992).

The presence of a Haast's eagle in Takaka Fossil Cave in the Late Glacial is consistent with its known distribution in areas where vegetation mosaics of shrubland, grassland, and forest existed (Worthy 1999, Worthy & Holdaway 2002).

The rest of the vertebrate fauna shows no evidence of faunal change over the period sampled. No bones of taxa smaller than the moa and eagle can be certainly allocated to the period before sedimentation began in the final chamber as bones deposited then will have been mixed with the bones arriving with the first sediments of L2. All would be mixed within the upper rocks of the floor at that time. Such smaller taxa, where there are several individuals present, appear equally likely to occur at any depth within the excavation and thus exhibit no evidence of faunal change for the period of the last 12 000 ^{14}C yrs. They therefore essentially document the well-vegetated Holocene conditions for Takaka Hill. We still lack a good stratified record by which to document the small bird fauna of the Glacial period on Takaka Hill and the associated changes over the LGM and through to the Holocene.

Acknowledgements

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Table 1. Radiocarbon ages obtained from moa bones in Takaka Fossil Cave. NZA, Rafter Laboratory number; R, sample number; CRA, conventional radiocarbon age; ^{13}C, value for carbon isotope ^{13}C; % collagen is the percentage by weight of the sample that remained after acid demineralization and includes the bone proteins plus lipids and other non-collagenous bone material; %N is percentage nitrogen; d15N, value for nitrogen isotope ^{15}N; and C:N is ratio of total carbon to total nitrogen.

NZA	R	CRA	Error	^{13}C	%Collagen	%N	d^{15}N	C:N	Species	Notes
11614	26109/5	11354	60	-22	13	14.4	5.6	2.8	*Anomalopteryx didiformis*	500 mm depth
13266	26510/1	12361	65	-22.2	23	14.3	1.8	2.8	*Euryapteryx geranoides*	Base of excavation. Large individual
13267	26510/2	12450	65	-23.2	39		2	2.8	*Euryapteryx geranoides*	Rockfall slope
13547	26546/1	1576	60	-22	27.3	20.2	4.4	2.8	*Anomalopteryx didiformis*	Last moa on site
13548	26546/2	3761	60	-23.3	17	17.2	0.4	2.9	*Dinornis novaezealandiae*	Base of Layer 1 (-50 mm)

Table 2. List and frequency of land and freshwater snails found in Takaka Fossil Cave by excavation unit. Each *Powelliphanta* protoconch, with or without attached teleoconch remnant, was counted as a single individual. NZS2000 = New Zealand Species 2000 (Spencer et al. in press).

Species; station N2620000n; n=mm. below surface:	1 0–50	2 50–150	3 150–300	4 300–500	5 450–550	6 500–600	1%	2,3,4,5%	6%
Alladiscus n.sp. A	16						2.89	0.62	0.00
Alladiscus n.sp. B	4						0.72	1.39	0.00
Alladiscus n.sp. C	7	1	18	15	4	3	1.26	5.86	4.11
Alladiscus n.sp. D	54	4	1	7	6	5	9.75	2.78	6.85
Alladiscus n.sp. E	14			4	24		2.53	4.32	0.00
Cavellia anguiculus (Reeve, 1852)	56	2	15	78	61	25	10.11	24.07	34.25
Cavellia marstoni (Climo, 1969)	8	1		1		3	1.44	0.31	4.11
Cavellia cf. *sterkiana* (Suter, 1891) (?)	2						0.36	0.00	0.00
Cavelliorepa mousoni (Suter, 1890)	28	1	1	7	2	1	5.05	1.70	1.37
Charopa coma (Gray, 1843)	11	1	3	11	9	3	1.99	3.70	4.11
Fectola trilamellata Climo, 1978	27	6		40	40	6	4.87	13.27	8.22
Flammulina zebra (Le Guillou, 1842)	3						0.54	0.00	0.00
Flammulina n.sp.	1						0.18	0.00	0.00
Huonodon hectari (Suter, 1890)			1		1		0.00	0.15	0.00
Huonodon pseudoleiodon (Suter, 1890)							0.00	0.15	0.00
Mocella elliottae (Climo, 1969)	2		1	1		1	0.36	0.31	1.37
Mocella spelaeus (Climo, 1971)	48		9	1	6		8.66	2.47	0.00
Panacharopa chrysaugeia (Webster, 1904)	1						0.18	0.00	0.00
Phacussa hypopolia (Pfeiffer, 1853)				3	4		0.00	1.08	0.00
Pseudegestula worleyi (Powell, 1928)	78	2	12	23	25	1	14.08	9.57	1.37
Suteria ide (Gray, 1850)	26	1	2	4	3	3	4.69	1.54	4.11
Charopidae sp. 94 (NZS2000)	3		7		9	1	0.54	2.62	1.37
Charopidae sp. 161 (NZS2000)	18	1	4	5	4		3.25	2.16	0.00
Paralaoma thomsoni (Suter, 1917)				1	1		0.00	0.31	0.00
Phrixgnathus celia Hutton, 1883	22	1	7	10	17	1	3.97	5.40	1.37
Punctidae sp. 50 (NZS2000)	13	1	9	25	29	7	2.35	9.88	9.59
Powelliphanta hochstetteri (Pfeiffer, 1862)	15	2	4	5	10	4	2.71	3.24	5.48
Rhytida greenwoodi (Gray, 1850)					3		0.00	0.46	0.00
Rhytida meesoni Suter, 1891	26	2	2	2	6	7	4.69	1.85	9.59
Honatia sp.	1						0.18	0.00	0.00
Opacuncola sp.	70		1	2	2	2	12.64	0.77	2.74
N=1275. Individual column totals:	554	27	98	252	271	73	100.00	100.00	100.00

Table 3. List of all the bones from Takaka Fossil Cave excavations. Faunas are arranged in columns for various depths in the site as follows: RF slope is the fauna collected from the surface of the rockfall slope between the entrance and the excavation at the base of the slope; 0–50, etc. represents depth units in mm within the excavation; MNI is minimum number of individuals; NISP is number of bones.

Species		RF slope NISP	RF slope MNI	0–50 NISP	0–50 MNI	50–150 NISP	50–150 MNI	150–300 NISP	150–300 MNI	300–500 NISP	300–500 MNI	500 to base NISP	500 to base MNI
Moa sp.		0	0	16	0	5	0	0	0	17	0	0	0
Anomalopteryx didiformis	Little Bush Moa	7	2	198	5	0	0	53	3	39	2	32	3
Pachyornis sp. juv.	Moa	1	1	0	0	0	0	0	0	0	0	0	0
Euryapteryx geranoides	Stout legged moa	16	2	0	0	0	0	0	0	1	1	43	2
Dinornis struthoides	Slender moa	0	2	42	2	0	0	0	0	0	0	104	3
D. novaezealandiae	Large Bush moa	x	2	140	2	0	0	0	0	0	0	0	0
Apteryx australis/haastii	Kiwi, large species indet	0	0	70	1	0	0	0	0	3	2	6	2
Apteryx spp. juv.		0	0	39	1	0	0	2	1	0	0	0	0
Chenonetta finschi	Finsch's duck	5	1	8	1	0	0	0	0	3	1	0	0
Harpagornis moorei	Haast's eagle	0	0	0	0	0	0	0	0	0	0	69	1
Gallirallus australis	Weka	0	0	0	0	1	1	0	0	1	1	1	1
Aptornis defossor	Adzebill	1	1	0	0	0	0	0	0	30	1	0	0
Strigops habroptilus	Kakapo	53	8	69	3	8	1	10	1	21	2	23	2
Nestor meridionalis	Kaka	0	0	0	0	0	0	0	0	0	1	1	1
Cyanoramphus spp.	Parakeet	2	1	27	3	5	2	11	1	9	2	7	2
Sceloglaux albifacies	Laughing owl	XXX	1	XXX	3	XXX	2	XXX	2	XXX		XXX	3
Aegotheles novaezealandiae	Owlet nightjar	4	1	23	2	6	2	4	1	12	4	13	3
Acanthisitta chloris	Rifleman	0	0	15	2	5	1	5	1	13	2	24	5
Xenicus sp.	Wren	5	3	65	5	8	2	19	2	39	5	35	3
Traversia lyalli	Stephens Is wren	0	0	6	2	2	1	1	1	6	1	4	2
Pachyplichas yaldwyni	Stout-legged wren	0	1	6	3	4	2	0	0	9	2	2	1
Mohoua ochrocephala	Yellowhead	1	0	8	2	1	1	1	1	3	1	6	1
Mohoua novaeseelandiae	Brown creeper	0	0	0	1	0	0	0	0	1	1	0	0
Gerygone igata	Grey warbler	0	0	0	0	5	1	0	1	7	1	0	0
Petroica australis	South Island robin	6	3	16	2	5	5	4	1	2	3	7	2
Anthornis melanura	Bellbird	0	0	1	1	5	3	2	1	2	1	6	1
Callaeas cinerea	South Island kokako	1	1	3	1	0	0	2	0	5	0	3	1
Philesturnus carunculatus	South Island saddleback	0	0	0	0	0	0	0	0	0	0	1	1
TOTAL		102	27	753	39	55	19	113	16	223	35	387	37
TOTALS												1633	173

Species		RF slope NISP	RF slope MNI	0–50 NISP	0–50 MNI	50–150 NISP	50–150 MNI	150–300 NISP	150–300 MNI	300–500 NISP	300–500 MNI	500 to base NISP	500 to base MNI
Sphenodon sp.	Tuatara	0	0	2	1	0	0	0	0	1	1	0	0
Leiopelma hamiltoni	Hamilton's frog	3	2	195	7	93	7	37	4	55	5	50	5
Leiopelma markhami	Markham's frog	3	2	12	2	14	2	4	1	4	2	6	1
Hoplodactylus sp.	Gecko	0	0	108	13	18	2	15	3	60	8	43	6
Hoplodactylus duvaucelii	Duvaucel's gecko	0	0	3	1	0	0	0	1	0	0	0	X
Skink	Skink	0	0	2	1	0	0	3	1	2	1	6	1
Mystacina tuberculata	Lesser short tailed bat	0	0	22	5	26	6	41	8	19	3	23	5
Mystacina robusta	Greater short tailed bat	0	0	4	1	0	0	0	1	2	1	0	0
Rattus exulans	Pacific rat	0	0	19	1	0	0	0	0	0	0	0	0
TOTAL		6	4	367	32	151	17	100	17	143	21	128	13
TOTALS												895	104

Table 4. Measurements (mm) of *Euryapteryx geranoides* bones from the three Takaka Fossil Cave individuals.

| | MNZ Catalogue numbers | | |
	S39016	S39017	S38942
Femur Length	230	c. 220	277
Femur PW	78	61	104
Femur SW	33	33	42
Femur DW	91	91	111*
Tibiotarsus Length	373	390	498
Tibiotarsus PW	106	107	129
Tibiotarsus SW	31	32	39
Tibiotarsus DW	67	64	77
Tarsometatarsus Length	167	170	205
Tarsometatarsus PW	71	69	82
Tarsometatarsus SW	38	37	45
Tarsometatarsus DW	87	82	106