Occurrence and ecology of the Open Bay Islands leech, *Hirudobdella antipodium*

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Abstract

The terrestrial leech *Hirudobdella antipodium* is endemic to the Open Bay Islands (South Westland). Searches of the largest island (Taumaka) were made in November 1994, January 1995, and June 1995, for populations of the leech. *H. antipodium* were once abundant in and around sooty shearwater burrows, but appear to have become severely restricted in abundance, possibly due to predation by introduced weka. Extensive searches on Taumaka failed to find any remnant populations other than that discovered in 1987. Aspects of their ecology, and options for the protection of this species are discussed.

1. Introduction

> *'Then thou art perhaps an expert on the leech?' asked Zarathustra; 'and thou investigatest the leech to its ultimate basis, thou conscientious one?' 'O Zarathustra', answered the trodden one, 'that would be something immense; how could I presume to do so!'*
>
> F. Nietzche, *Thus spake Zarathustra* (*c.* 1883)

New Zealand has eight genera of terrestrial and freshwater leeches (Arhynchobdellida: Hirudinidae, Erpobdellidae) (Rhynchobdellidae: Glossiphonidae), with eleven known species (Mason 1976). Two of these genera, *Hirudobdella* and *Ornithobdella*, are endemic to New Zealand, being found on the Open Bay Islands (Figure 1), the Snares, and Solander Islands. They are terrestrial rather than aquatic, and are thought to feed largely on the blood of seabirds. The subfamily Ornithobdellida is represented in Australia by the genus *Aethobdella*, which is also terrestrial and feeds on the blood of birds.

There has only been one record of a terrestrial leech on mainland New Zealand. A leech similar in all respects to *H. antipodium*, except for the position of the male genital pore, was discovered by R.R. Forster in 1948 under a log in Caswell Sound, Fiordland, 170 km south-west of the Open Bay Islands.

The Open Bay Islands leech *Hirudobdella antipodium* (Figure 2) was brought to scientific notice in February 1903 when Mr W. Dunlop and Dr Leonard Cockayne made a brief visit to Taumaka, the larger of the Open Bay Islands (Cockayne 1904). Dunlop was searching for weta in sooty shearwater (titi, *Puffinus griseus*) burrows when a leech bit him on the wrist. "Fortunately Mr Dunlop is keenly interested in natural history, and he carefully withdrew his hand and found a leech attached thereto" (Benham 1904). Further searches found six more leeches and some cocoons.

Weka (*Gallirallus australis*) were introduced to the Open Bay Islands sometime between 1905 and 1912, and were believed to have eradicated the leeches (Stirling and Johns 1969). Stirling and Johns (1969) did not find any

leeches, and considered that weka were also responsible for the paucity of ground dwelling invertebrates. They suggested that removal of the weka was justified on these grounds.

However, a population of the leeches was rediscovered (January 1987, relocated in March 1988 and January 1992) under a large glacial erratic boulder ("the rock") in the water-logged nests of Fiordland crested penguins (Tawaki, *Eudyptes pachyrhynchus*). No other populations were found.

Suggestions by the Department of Conservation that weka be eradicated were met with concern by the Maori owners of Taumaka and Popotai. There were two reasons for this: the islands belong to Poutini Ngai Tahu and not the crown, therefore the crown had no right to dictate what happened on the islands; and it was indicated that Maori had released weka onto the islands and were, therefore, not supportive of them being eradicated.

The purpose of this study was to resurvey under the rock to establish whether leeches were still present, survey likely habitat for other populations, and review the scientific literature. Options for the protection of the leeches are discussed.

2. Study site

The Open Bay Islands — Taumaka and Popotai — (43° 50′ S, 168° 53′ E) are about 5 km offshore of the Okuru River mouth, near Haast, South Westland. Taumaka is approximately 660 m long and 260 m wide, and Popotai is approximately 400 m long and 200 m wide (Figure 1). They are separated by a narrow channel.

The bedrock consists of indurated, semi-crystalline contorted, Oligocene limestone with thin bands of muddy limestone (Mutch and McKellar 1964). This is capped with a sheet of glacial till, between 1.5 and 12 m deep and, in some areas, peaty soil. Several large glacial erratic boulders are scattered around Taumaka, and it is under one of these that the leeches were rediscovered.

The vascular vegetation on both islands is dominated by a dense tangle of kiekie *(Freycinetia banksii*), with mahoe (*Melicytus ramiflorus*) being the most abundant tree, and pate (*Schefflera digitata*) being common (Burrows 1972). The native climber pohuehue (*Muehlenbeckia australis*) is common in the canopy and on the edges of the kiekie mass. For a more detailed description of the vegetation see Burrows (1972).

Stirling and Johns (1969) list the avifauna, which includes Fiordland crested penguins, blue penguins (Korora, *Eudyptula minor*), fairy prions (Titi wainui, *Pachyptila turtur*), sooty shearwaters, spotted shags (Parekareka, *Stictocarbo punctatus*), and fernbirds (Matata, *Bowdleria punctata*). Other notable fauna include the endemic Open Bay Islands leech and Open Bay Islands skink

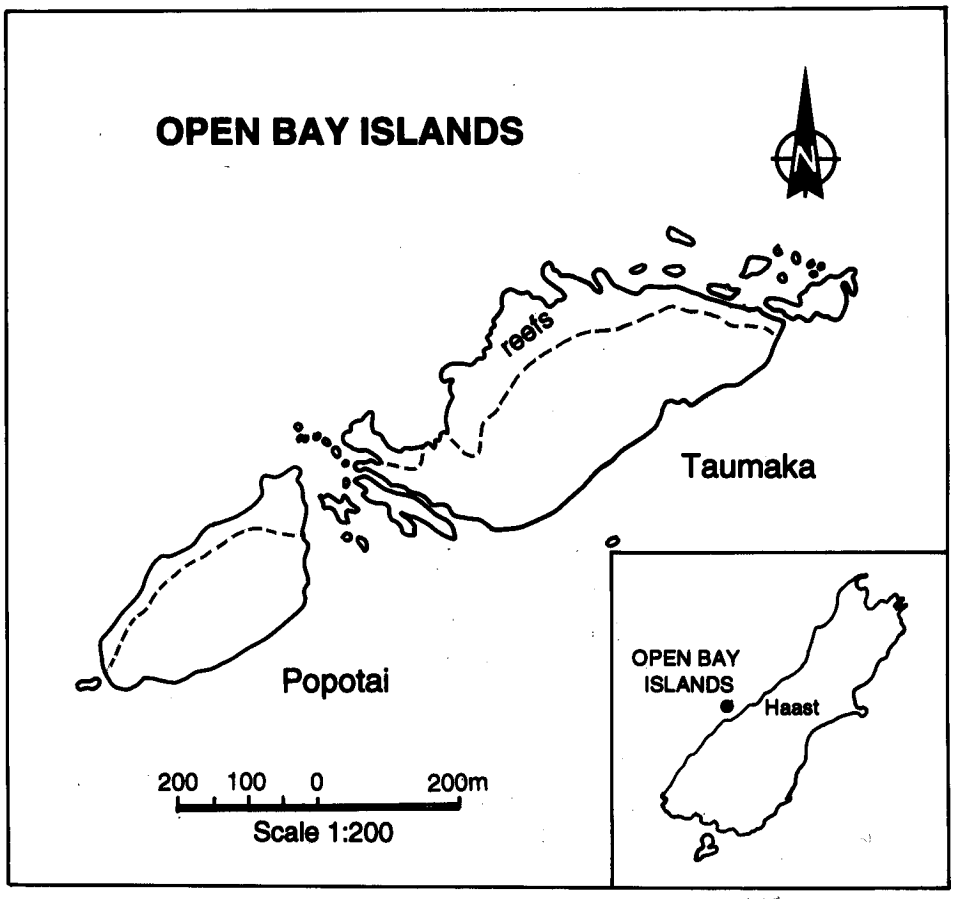

FIGURE 1. LOCATION OF THE OPEN BAY ISLANDS (TAUMAKA AND POPOTAI). THE LOCATION OF THE ROCK UNDER WHICH THE LEECH POPULATION IS FOUND IS NOT SHOWN FOR BIOSECURITY REASONS.

(*Oligosoma* "Open Bay Islands"), Open Bay Islands gecko (*Hoplodactylus* "Open Bay Islands"), and large numbers of fur seals (*Arctocephalus forsteri*).

Exotic mammals, including rats (*Rattus* spp.), mice (*Mus musculus*), and possums (*Trichosurus vulpecula*), are absent from the islands and precautions are taken by Department of Conservation staff and other scientists visiting the islands, to avoid introducing them.

James (1928) reported that weka were released onto the islands on several occasions by Mr James Molley, part owner of a steamer that traded in South Westland; however there is an alternative view (see below).

FIGURE 2. OPEN BAY ISLANDS LEECH
Hirudobdella antipodium.

3. Methods and results

I first visited Taumaka from 14 to 16 November 1994, with Glenn McDonald (Field Centre Manager, Haast). The first day was spent locating the rock, and exploring the island looking for potential sites to examine more closely. We briefly examined the area of tussock where Dunlop and Cockayne first found the leeches. There were a few shearwater burrows in the area where leeches were discovered (Cockayne 1904), and the peat was heavily compacted, as noted by Stirling & Johns (1969) and Burrows (1972).

We spent the 15 November actively searching under the rock (Figure 3) and in other likely locations, such as damp or wet caves inhabited by Fiordland crested penguins, and other seabird burrows. There were several Fiordland crested penguins in residence under the rock, and it was very damp (with small trickles of running water), muddy, and smelly. We did not find anything resembling the leech found in 1992. Discussion with GMcD, and re-reading Cockayne (1904) confirmed that all leeches found in the past had been located in January or February. This was optimistically hoped to be a reason for not finding any leeches. I decided to come back in January for further survey. The following day (16 November) was spent in further searches under the rock and other seabird burrows, just in case.

The second visit was from 23 to 25 January 1995. The weather was drizzly, and searching under the rock was a very wet affair. I found one leech in the wet mud, under branches and a large number of Fiordland crested penguin feathers (it was moulting season). We took this leech back to the hut for photographing. We resurveyed the areas identified last time as being potential leech habitat (caves and tunnels with Fiordland crested penguin nests, and titi burrows). We did not find anything, but noted weka poking around in the accessible tunnels and caves.

The morning of 24 January was spent searching in penguin shelters near the boat landing site, blue penguin burrows near the hut, and in titi and fairy prion nests under kiekie. It was very wet, and we did not find any leeches. In the

FIGURE 3. ENTRANCE TO "THE ROCK".

afternoon we revisited the rock. Water was flowing in the spot where I found the leech the day before. I searched this spot again anyway, but did not find anything. I then looked under a branch in a relatively dry spot at the top end, and found three leeches attached. Two were large (approximately 5–7 cm extended), and one was small (approximately 1.5 cm extended, and 0.5 cm across widest point). I returned the leech collected the day before.

The third visit was on 22 June 1995 when I flew across to Taumaka for one day. I searched under the rock and found one leech deep in an old nest of sticks. I left it there and did not search any further. Conditions under the rock were very dry, and there were no Fiordland crested penguins present (having left for sea early in March; Warham 1974) or any fur seal pups.

4. Discussion

There were concerns raised in 1969 that weka, which had been introduced to the Open Bay Islands, had eradicated the endemic leech *Hirudobdella antipodium*, as well as reducing the abundance of other ground invertebrates and preying on birds eggs (Stirling and Johns 1969). This was the first call to remove weka from the island[1] to restore its natural biodiversity. However a small leech population was rediscovered in 1987 under a large glacial rock. Resurveys in 1988, 1992, and 1994 confirmed that this population was still in

[1] However the New Zealand Native Bird Protection Society did approach the Department of Internal Affairs to transfer weka back to mainland south Westland to infuse "new blood and improve the breed there", as they were becoming rare (James 1928). Weka are now absent from most of south Westland.

existence, although the small numbers found and the lack of other known populations raised concerns for its viability.

While the surveys we conducted in 1994 did not find any evidence of other populations, it has been suggested that leeches occur at sites other than the rock. Fresh scars observed on the ankles[2] of blue penguins from Taumaka may indicate that the leeches are still present in bird burrows (Rod Morris, TVNZ, pers. comm.). Our inability to find them may be due to their absence from the sites searched, or because our method of survey was inappropriate. However the first leeches recorded on Taumaka (Benham 1904) were found by searching a shearwater burrow by hand, as we did.

Regardless, a small population of the leeches has remained under the rock since at least 1969. That they are still breeding is indicated by the presence of the small leech found in January 1995. How long this population can remain viable is not known. While there is a ready source of blood, and the leeches are protected from predation, population genetic theory would predict that extinction is inevitable through factors such as inbreeding depression.

This is a moot point, however (see discussions in Caughley 1994, Wallis 1994, Gilpin 1996), and inbreeding may also be a feature of terrestrial leech ecology. Richardson (1979) notes that terrestrial leech habitats can be small, giving 30 m × 2 m as an example, and that populations are usually discontinuous within their range, being separated by distances of up to 50 km. If the population under the rock is the only remaining population, then they are existing in a habitat of approximately 5 m × 2 m. However as noted, it has not yet been confirmed whether it is the last population.

4.1 CLASSIFICATION OF *Hirudobdella antipodium*

The classification of leeches is based primarily on the morphological differences in the mouthparts, reflecting the diversity of feeding habits among the various species (Sawyer 1986). The subclass Euhirudinea is comprised of two major orders, Arhynchobdellida and Rhynchobdellida. Both groups feed on blood, but they obtain it in fundamentally different ways. Arhynchobdellids have jaws armed with teeth, with which they bite the host. They protect against the initial clotting of the blood by secreting a non-enzymatic polypeptide, hirudin, which specifically inhibits the clotting enzyme thrombin; the medicinal leech *Hirudo medicinalis* L. is found in this order. Rhynchobdellids possess a tubular proboscis which they insert into the body of the host.

H. antipodium is a member of the primarily predaceous group of species, Distichodontia. In this group the jaw is relatively rudimentary and functions as a supplementary grasping and tearing organ. The name Distichodontia arises from the jaw of most species bearing coarse, blunt denticles arranged in two irregular rows (Sawyer 1986). The jaws of *H. antipodium* are tall and long, and lie on a short bulbous pharynx (Mason 1976).

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[2] A leech removed from the island by the author was noted to feed on or around the ankle of a captive Fiordland crested penguin and a shag. This left slight scarring on the leg of each bird.

Phylum:	Uniramia
Subphylum:	Clitellata
Class:	Hirudinea (Lamarck, 1818)
Subclass:	Euhirudinea
Order:	Arhynchobdellida (Blanchard 1894)
Family:	Hirudinidae (Whitman, 1886). Revised. Distichidont series
Subfamily:	Ornithobdellinae (Richardson 1969)
Genus:	*Hirudobdella* (Goddard, 1910)
	Hirudobdella antipodium (Benham, 1904)

The leech discovered by R.R. Forster under a log in Caswell Sound, 170 km south-west of the Open Bay Islands was similar in all respects to *H. antipodium* except for the position of the male genital pore. Mason (1976) described and named this new species *H. benhami*. She originally considered the position of the genital pore significant enough to raise a new genus, but because the type locality was so close to the location of *H. antipodium*, and there was only one specimen and record, she did not do so. The significance of the location of the genital pore is that *H. antipodium* would be unable to copulate with *H. benhami*.

4.2 ECOLOGY OF TERRESTRIAL LEECHES

The majority of leeches live in fresh or salt water, however a small number of species are amphibious or truly terrestrial. The terrestrial leeches tend to be in the order Arhynchobdellida, with the Hirudinidae being the most advanced of these.

Terrestrialism requires specific physiological adaptations and behaviours for water conservation. Sawyer (1986) discusses these in detail. In summary these include a specialised haemocoelomic system with lateral hearts and dissolved haemoglobin, an albuminotrophic embryo which is typically deposited out of water, the ability to tolerate high levels of desiccation for periods of time, and the ability to decrease the concentration of water in the urine.

Behaviourally, terrestrial leeches live in damp if not wet habitats, and tend to be most active after rain when the substrate is moist, although they are capable of rapid movement over dry surfaces (Sawyer 1986). Richardson (1979) describes typical terrestrial leech habitat as being a forested area or forested fringe, with a gently sloping floor providing rapid run-off during rain, and free from standing water. Several Open Bay Island leeches were observed to hang underneath branches out of the flowing and pooling water during rain, suggesting avoidance. Not unexpectedly, the only leech found during a dry period, when penguins and seal pups were absent, was several inches below the surface in a mass of sticks and mud.

Physiological factors limiting terrestrial leeches to damp environments include the need to keep the skin moist, and because they excrete ammonia rather than uric acid as their main nitrogenous waste product, they require relatively large quantities of water for its dispersal and elimination.

World-wide, mammals play a disproportionate role in the feeding biology of sanguivorous leeches, owing to the fact that they are the class most richly endowed with erythrocytes (Sawyer 1986). New Zealand's sanguivorous leeches are however another example of species evolving in the absence of mammals, with *H. antipodium* and *O. edentula* feeding on bird blood.

All vertebrate species in a habitat may be attacked by the leeches, however they normally restrict themselves to one vertebrate class. The availability of vertebrate blood tends to be limited or sporadic in most habitats. For example, adult Fiordland crested penguins arrive on the Open Bay Islands early in July to breed. Adults and fledglings then leave in late November, spending 60–80 days at sea before returning in February to moult. They then leave again early in March to return in July (Warham 1974). Because of this many leeches have adapted to feeding on other sources of food. For terrestrial species this may include other invertebrates such as worms (Sawyer 1986).

I believe that, because of the habits of New Zealand birds, *Hirudobdella* and *Ornithobdella* may feed opportunistically on animal groups other than birds, including perhaps worms and frogs. The location of the one specimen of *H. benhami* provides further circumstantial evidence of this, as it was found under a log, distant from any nesting birds.

Digestion of a blood meal over a period of months may also enable them to survive the vagaries of blood supply. In laboratory conditions the medicinal leech *Hirudo medicinalis* were able to take up to 2–9 times their body weight in blood, with digestion taking several months to a year (Dickinson and Lent 1984, Lent and Dickinson 1987, 1988). Lent and Dickinson (1987) found that medicinal leeches took approximately half an hour to reach total satiation, although Elliot and Tullett (1992) considered it likely that in the wild, leeches would detach or be detached from the host long before they are satiated. *Hirudobdella* and *Ornithobdella* feeding on nesting birds may however be able to feed to satiation before detaching.

4.3 REPRODUCTION

Leeches are hermaphroditic, having both male and female gonads. The reproductive ducts have relatively fixed positions (Barnes 1981); cf. *H. antipodium* and *H. benhami* male pore 2.5 annuli anterior to usual position for hirudinid leeches.

Arhynchobdellids deposit cocoons, each containing about 5–10 small eggs, in damp soil or beneath rocks and sticks. Most leeches have an annual reproductive cycle, breeding in spring and maturing the following year. From scant evidence *H. antipodium* may also follow this annual pattern. Dunlop and Cockayne found empty cocoons in January (Benham 1904), and in this study I found a small leech in January, with other larger leeches.

4.4 WEKA ON TAUMAKA AND POPOTAI

Just who released weka on to Taumaka and Popotai, when they were released, and where they came from, are contentious issues. In 1928, Eric James reported:

> "[I]n years gone by, in the days when the steamer *Jane Douglas* was trading regularly to South Westland, the part owner of the vessel, Mr James Molley, on several occasions secured a number of Maori-hens (wekas), and liberated them on Open Bay Islands, off Okuru. These native birds have multiplied exceedingly, and at present the island is over-run with them. There are probably more Maori-hens on this island than in the whole of South Westland at present."
>
> *New Zealand Fishing and Shooting Gazette* 1 July 1928

However, when the West Coast Conservancy prematurely announced plans to eradicate the weka, the owners of the islands protested. Apart from the fact that the Crown did not own the islands, it was stated that Ruera Te Naihi took weka to the islands some 90 years ago, and they were therefore taonga.

It is likely that weka have had an effect on the abundance of leeches on Taumaka. The behaviour of terrestrial leeches would make them particularly susceptible to predation by weka, as they will move overland, particularly during or following rain (Sawyer 1986). For example, two leeches were observed moving through dead *Olearia colensoi* leaves, and one other was found climbing up the side of a wooden bird transfer box on Kaimahou Island[3] (Titi Island group, south-west of Stewart Island).

The effects of weka on the leeches, lizards, invertebrates, and birds on the Open Bay Islands can only be inferred. Stirling and Johns (1969) commented on the paucity of ground dwelling invertebrates and suspected that this could be due to weka, although no quantitative measurements were ever made. They also noted weka eating eggs from a shags nest and suspected that they may do the same with penguin eggs. Skeel (1974) noted in a study of spiders on Taumaka that weka were responsible for the loss of almost 3000 trap nights of samples through overturning traps and eating the contents.

There is further anecdotal evidence of the effects of weka on the islands fauna and flora. In my visits to the islands I have observed the remains of fairy prion chicks outside of their burrows, with only the sternum and wings remaining. I cannot be sure whether weka killed them or merely scavenged birds that were already dead. I have also observed the weka consuming the fruits (tawhera) of the kiekie. Kiekie fruit are very rarely seen on mainland New Zealand, due to predation by possums. The endemic Open Bay Island skink has only ever been able to be relocated under cover of corrugated iron adjacent to the research hut, where they are inaccessible to weka.

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[3] This is the first official record of leeches from any of the titi islands, although Maori frequently find them there when muttonbirding (R. Morris, pers. comm.). Two live specimens were collected by Jane Sedgely, Pete McLelland and Brian Rance and sent to this author.

5. Conclusions

Despite predictions of their extinction, a small population of Open Bay Islands leeches still remains on the island: no more than 5 individuals have been found at any one time. Just how long this population will remain viable is not known. I suggest that, unless efforts are made to protect and enhance the population, the endemic *Hirudobdella antipodium* will become extinct from the island. Protective measures could include removing the weka from the islands, providing weka proof exclosures, and/or establishing an *ex situ* population of the leeches.

Hirudobdella antipodium may also be found on the adjacent mainland (as was *H. benhamii*), although there is no guarantee of this. They have never been specifically looked for (a common cause of rarity) and it is likely that, if found by chance, their significance would not be realised. For example, the leeches recently found on the Kaimahou Islands have long been known to Maori muttonbirders (R. Morris, TVNZ, pers. comm.).

While leeches may not have the public appeal of colourful birds or the liquid-amber eyed fur seal, they are a distinctive and unique part of New Zealand's biodiversity, a taonga, and require protection.

Any conservation management to protect the leech and the biodiversity of the Open Bay Islands will need to be done with the consent and co-operation of the islands Maori owners. The Department of Conservation recognises the Tino Rangatiratanga of Poutini Ngai Tahu over Popotai and Taumaka, and seeks to meet its Section 4, and Section 6 obligations (Conservation Act 1987) to protect the values of these islands.

6. Recommendations

- The owners of Popotai and Taumaka should be invited to discuss with the Department of Conservation ways of protecting the indigenous biodiversity of these islands.
- Surveys of mainland sites should be carried out, focusing on the nesting colonies of Fiordland crested penguins between Haast and Fiordland. This should include the site where *H. benhami* was found.
- The population under the rock should be regularly monitored, preferably every 2 years, during January or early February.
- A captive population of *Hirudobdella antipodium* should be established, so as to be able to repopulate the island, should the island population become extinct.

7. Acknowledgements

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8. References

Barnes, R.D. 1980. Invertebrate Zoology. 4th ed. Holt-Saunders International Editions, Tokyo.

Benham, W.B. 1904. On a new species of land leech (*Hirudo antipodium*) recently discovered in New Zealand. *Transactions and Proceedings of the New Zealand Institute* 36: 185–192, pl. 8.

Burrows, C.J. 1972. The flora and vegetation of Open Bay Islands. *Journal of the Royal Society of New Zealand* 2: 15–42.

Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63: 215–244.

Cockayne, L. 1904. Notes on the vegetation of the Open Bay Islands. *Transactions and Proceedings of the New Zealand Institute* 37: 368–377.

Dickinson, M.H. and Lent, C.M. 1984. Feeding behaviour of the medicinal leech, *Hirudo medicinalis* L. *Journal of Comparative Physiology A* 154: 449–455.

Elliot, J.M. and Tullett, P.A. 1992. The medicinal leech. *Biologist* 39(4): 153–158.

Gilpin, M. 1996. Forty-eight parrots and the origins of population viability analysis. *Conservation Biology* 10: 1491–1493.

James, E. 1928. *New Zealand fishing and shooting gazette*. July edition.

Lent, C.M. and Dickinson, M.H. 1987. On the termination of ingestive behaviour by the medicinal leech. *Journal of Experimental Biology* 131: 1–15.

Lent, C.M. and Dickinson, M.H. 1988. The neurobiology of feeding leeches. *Scientific American* 258: 78–83.

Mason, J. 1976. Studies on the freshwater and terrestrial leeches of New Zealand. 2. Orders Gnathobdelliformes and Pharyngobdelliformes. *Journal of the Royal Society of New Zealand* 6: 255–276.

Mutch, A.R. and McKellar, I.C. 1964. Sheet 19 Haast (1st ed.). *Geological map of New Zealand* 1:250 000. N.Z. D.S.I.R.

Richardson, L. R. 1979. On two land-leeches labelled as from New Zealand (Hirudinea: Haemadipsoidea). *Tuatara* 24: 41–48.

Sawyer, R.T. 1986. Leech biology and behaviour. Clarendon Press, Oxford. Vol. 1–3. 1065 p.

Skeel, M.E. 1974. An ecological analysis of the Arachnida of Open Bay Islands, New Zealand. *Journal of the Royal Society of New Zealand* 4: 39–46.

Stirling, I. and Johns, P.M. 1969. Notes on the bird fauna of Open Bay islands. *Notornis* 16: 121–125.

Wallis, G.P. 1994. Population genetics and conservation in New Zealand: a hierarchical synthesis and recommendations for the 1990s. *Journal of the Royal Society of New Zealand* 24: 143–160.

Warham, J. 1974. The Fiordland crested penguin *Eudyptes pachyrhynchus*. *Ibis* 116: 1–26.