

The species has occasionally been seen on Norfolk Island, although the earliest collection cited by Green (1994) is dated only 1912. According to Green the species is absent from Lord Howe Island, being replaced there by *L. aemula*. The subsequent Flora of Australia treatment (Jacobs & Brown 2009) gives the opposite distribution, and seems wrong (e.g., Peter de Lange's AK 236426 from Norfolk I. is certainly *L. filiformis*).

The species has naturalized in South Africa and in the New World too. For example, the Flora of North America (Barkworth et al. 2007, p. 696) states that *L. filiformis* has been known from several localities in the USA, including "waste areas around a wool-combing mill", and that it is invading one of California's most unique and endangered habitats, the ephemerally wet "vernal pools".

For Great Britain, *L. filiformis* is recorded as "a casual of wool and esparto" (Ryves et al. 1996), that

is, the plant appears sporadically near woollen mills and paper mills, getting to these places as a seed-contaminant of the raw products. The wool presumably comes from Australia or New Zealand. The esparto grass (actually two species, *Stipa tenacissima* and *Lygeum spartum*) comes from North Africa and Spain, but so far there seems to be no record of *L. filiformis* wild in these countries.

### Appendix

Habitats of *L. filiformis* in the Auckland region, from label notes on specimens in the Auckland War Memorial Museum herbarium (AK): Clay roadside, sandflats at Waitakere River mouth, stable bare clay banks and clay-gravel talus near railway line, clay slopes above saltmarsh, damp fine scoria of quarry floor, by roadside ditch, long grass along fenceline, waste land, among *Juncus maritimus*, garden, low grass between graves, parking place gravel area, damp asphalt, between building and footpath, sand-dune lake margin, trackside, wetland near shore.

### References

- Barkworth, M.E. et al. (eds.) 2007: *Flora of North America*. Vol. 24. O.U.P.  
Burbidge, N. 1968: *Australian grasses*. Vol. 2. Angus & Robertson, Sydney.  
Edgar, E. 1995: New Zealand species of *Deyeuxia* P.Beauv. and *Lachnagrostis* Trin. (Gramineae: Aveneae). *New Zealand Journal of Botany* 33: 1–33.  
Edgar, E.; Connor, H.E. 2000: *Flora of New Zealand*. Vol. V. Manaaki Press, Lincoln.  
Green, P.S. 1994: *Flora of Australia*. Vol. 49. AGPS, Canberra.  
Hitchcock, A.S. 1922: The Grasses of Hawaii. *Memoirs of the Bishop Museum* 8(3). Honolulu.  
Jacobs, S.W.L. 2001: The genus *Lachnagrostis* (Gramineae) in Australia. *Telopea* 9: 439–448.  
Jacobs, S.W.L.; Brown, A. J. 2009: *Lachnagrostis*. Flora of Australia, Vol. 44A: 174–190. ABRS/CSIRO, Melbourne.  
Ryves, T.B.; Clement, E.J.; Foster, M.C. 1996: *Alien Grasses of the British Isles*. BSBI, London.  
Trinius, C.B. 1820: *Fundamenta Agrostographiae*. J.G. Huebner, Vienna.  
Veldkamp, J.F. 1982: *Agrostis* (Gramineae) in Malesia and Taiwan. *Blumea* 28: 199–222.

---

## Truffles of New Zealand: a discussion of bird dispersal characteristics of fruit bodies

Ross E Beaver<sup>1,3</sup> and Teresa Lebel<sup>1,2</sup>

Truffle and truffle-like fungi typically have an indehiscent fruiting body, which does not open to release the spores. Associated with this feature, the spores are usually not actively released from the spore-bearing structure, whether an ascus or a basidium (Theirs 1984, Kendrick 2000). The fruiting bodies may be below ground (hypogeous), or produced at (emergent) or above (epigeous) the substrate surface. Many species either lack or have a very reduced stipe, but in some the fruiting body may resemble mushrooms in general morphology, complete with cap and stipe. Not unexpectedly for a biological group defined by the absence of characters, truffles are a phylogenetically diverse

assemblage including Ascomycota, Basidiomycota and Glomeromycota.

New Zealand has perhaps 170–200 species of truffles, mostly Basidiomycota but including a dozen or more Ascomycota, and four to five Glomeromycota. Taxonomically the species are poorly known, with about half described and various nomenclatural puzzles with those that have been named. A few, such as *Rhizopogon luteolus*,

---

<sup>1</sup> Landcare Research, Private Bag 92170, Auckland, New Zealand

<sup>2</sup> Royal Botanic Gardens Melbourne, Private Bag 2000, South Yarra, Victoria, Australia

<sup>3</sup> Deceased 3 June 2010

*Melanogaster ambiguous* and *Tuber* species, have been introduced along with their ectomycorrhizal pine and oak hosts. Present knowledge indicates that the indigenous species are mostly endemic but some are shared with Australia and a few extend even further afield (Segedin & Pennycook 2001, Orlovich & Cairney 2004).

Here we discuss extant and extinct dispersal agents, and four different features of truffle fruiting bodies, epigeous habit, colour, developmental visual flags, and distinctive odours, in relation to the potential for bird dispersal as a unique selection pressure in the evolution and retention of this fruiting body form in New Zealand.

### **Dispersal agents**

If the fruiting bodies of these fungi do not open even at spore maturity, how do the spores get around? Undoubtedly some fruiting bodies are transported intact during mass soil movement. In other instances, the fruit bodies may be broken open by soil movement or animal damage and the spores released to be transported by air and water. In the case of *Tirmania* and truffle *Agaricus* species from deserts and arid regions, the intact fruiting body is eroded on emergence from the soil and spores are blown by the wind (Alsheik & Trappe 1983, Lebel 2013). Molluscs and insects, including truffle flies, also feed on the fruiting bodies and will incidentally carry spores a short distance (Hammond & Lawrence 1989, Lawrence & Milner 1996, Houston & Bougher 2010).

However, do truffle-like fungi rely on these mechanisms for dispersal especially over longer distances? The basic axiom of the animal dispersal hypothesis is that animals eat the fruiting body and defecate the spores, or at least a proportion of them, intact and viable in their droppings (Kotter & Farentinos 1984, Lamont et al. 1985, Claridge *et al.* 1992, Cazares & Trappe 1994, Colgan & Claridge 2002). Obvious parallels exist with the dispersal of fleshy-fruited plants by fruit-eating animals (Howe 1986, Levey *et al.* 2002, Matias *et al.* 2010). In North America and Europe, although placental mammals such as chipmunks, squirrels, voles, and mice are particularly implicated (Maser et al. 1978, Blaschke & Baumler 1989, Frank *et al.* 2006, Schickmann *et al.* 2012), some larger mammals such as pigs and deer (Boudier 1876, Cazares & Trappe 1994, Nunez *et al.* 2013) have also been documented as eating truffle fruiting bodies. In Australia and Papua New Guinea marsupials such as potoroos, bandicoots, bettongs, and possums (Claridge & Cork 1994, Abell *et al.* 2006, Vernes & Lebel 2011) along with placental rats (Carron *et al.* 1990, Vernes & McGrath 2009), and macropods such as kangaroos and wallabies (Vernes & Trappe 2007, Vernes 2010, Danks 2011) are known truffle dispersers.

A major conclusion of these studies is that a close 3-way interrelationship exists between mycorrhizal trees (especially conifers, oak, and beech in the Northern Hemisphere, and eucalypts, casuarinas and southern beech in Australia), truffle-like fungi (with mostly different genera in the two regions), and small mammals. The trees depend on the fungus for mycorrhiza formation, the animals use the fungi as food, and the fungus depends on small mammals for dispersal (Trappe & Maser 1977, Maser *et al.* 1978, Malajczuk et al. 1987). Pirozynski and Malloch (1988) point out that these same mammals also disperse seed and thus may concomitantly disperse host and fungus. While most truffle-like fungi are known or suspected mycorrhiza-formers with trees and shrubs, some are saprophytes living on decaying matter. In the case of the saprophytes, there may well be survival value for the fungus in being dispersed in a nutrient-rich faecal pellet, but little is known.

### **New Zealand bird fauna – extinct and extant**

New Zealand presents an immediate problem to the hypothesis that mammals disperse truffle-like fungi. Prior to human contact, less than a thousand years ago (Wilmhurst & Higham 2004), the only land mammals were some three species of bats. Nevertheless, New Zealand boasted a diverse vertebrate fauna, dominated by birds but also including reptiles in addition to the bats. It is becoming increasingly apparent that birds occupied at least loosely some niches occupied by mammals in the rest of the world (Atkinson & Greenwood 1989, Clout & Hay 1989). Could it be then, that these vertebrates, especially birds, dispersed the spores of truffle-like fungi?

Extinction of about half of the New Zealand bird fauna since human contact (Holdaway 1989, Duncan & Blackburn 2004), and rarity of the remaining species, makes it difficult to assess their role in forest dynamics in general and dispersal of truffles in particular (Gill *et al.* 2010). However, several features of the bird fauna and truffle flora allow the hypothesis to be plausibly advanced.

Truffles in New Zealand occur primarily in forests. The forest bird fauna comprised some 100 species and included many flightless and poorly flighted species. The generalised feeding patterns of these species are known from direct and indirect sources (Holdaway 1989, Wood et al. 2008, Lee *et al.* 2010). They included foliage browsers and forest floor omnivores. Of particular note was the presence of nine species of moa (large ratites), the largest of which weighed over 250 kg (Gill *et al.* 2010). Other extinct forest floor species included Finch's duck, several species of snipe and the adzebill. Still extant but in much depleted numbers are three species of kiwi, characterised by a deep probing bill with external nares at the tip of the beak, the takahe (a large rail which lived in the forests

but is presently reduced to tussock grassland refugia), the kakapo (a large flightless parrot), and the weka (a rail). Even flighted species such as the kokako and saddlebacks (both wattlebirds), kea (large parrot), and the large fruit-eating kereru (pigeon) often feed on the ground.

Actual observations of birds eating fungi are rare. Medway (2000) observed a North Island robin feeding on rotting fruit bodies of the mushroom *Armillaria limonea*. Best (1984) and Forshaw (1989) reported that kakapo ate diverse fruits, shoots, leaves, mosses and fungi, and the kereru is known to feast on parasitic strawberry fungus (*Cyttaria* spp.) fruiting in *Nothofagus* trees (Clout *et al.* 1986, Peterson *et al.* 2010, Hedley 2012 p.194). In summary, this fauna included a range of species that could have fed on and been involved in dispersal of truffles, thus providing a selection pressure for evolution and subsequent retention of the truffle-like fruiting habit.

### **Truffle characteristics and bird dispersal**

A number of features of New Zealand truffles can be interpreted as adaptations to bird dispersal. Primarily these are cues that enhance the visibility of the species concerned, but odour may also play a role, as many nocturnal birds have a highly developed sense of smell (Silke *et al.* 2008). It is widely accepted that birds are highly visual animals, particularly those that are diurnal (Sillman 1973, Gervais *et al.* 1999), with well-developed colour discrimination, except perhaps for the ratites [palaeognathous species] (Sillman *et al.* 1981). Visual features are particularly well developed in the New Zealand truffle-like fungal flora, and we suggest that these reflect, at least in part, adaptation to bird dispersal. The following four features are not equally distributed amongst the species – many show more than one feature.

#### Feature 1. Epigeous habit

While comparative data is not available, the emergent to epigeous habit is common in New Zealand; certainly, many species can be found without raking (in the tradition of Northern hemisphere or Australian trufflers). We suggest that epigeous habit reflects selection by dispersal agents that use primarily visual cues rather than odour. For species in the USA and Australia, it has been suggested they have evolved in response to the dry summer climate and selection pressure of mammal mycophagy (Thiers 1984, Lebel & Syme 2012). Such an evolutionary explanation is not appropriate to much of New Zealand with its generally high, equitably distributed rainfall (we acknowledge that, prior to human arrival, some parts of the South Island had areas of semi-arid woodland), and lack of mammals. Included in the New Zealand flora are six long-stiped species of truffle *Cortinarius*, three of

*Weraroa*, and one each of *Tympanella*, *Notholepiota*, *Macrocyttidia* and *Macowanites*. The stipe reflects in part their derivation from ancestors with dehiscent mushroom fruit bodies and active spore release (Fig. 1a) (Thiers 1984, Borovička *et al.* 2011).

In the case of mushrooms it is self-evident that the stipe serves to elevate the spore-bearing tissue above the soil surface to allow aerial dispersal of spores from the gills. The reason for stipe retention by forest-dwelling truffles is less obvious, but can be interpreted as making the cap more visible and perhaps protecting the spore mass from rotting in saturated soil or woody debris. Amongst epigeous truffles without a stipe can be included *Gallacea eburnea* (Fig.1 b) and *Hysterangium rugisporum*. In most New Zealand forests except for those dominated by *Nothofagus*, the litter layers and duff are relatively poorly developed, thus even astipitate truffles are highly visible.

#### Feature 2. Colour

Many truffles are a comparatively drab shade of brown, dull pink or off-white (Castellano *et al.* 1989, Montecchi & Sarasini 2000). However quite a few, including many in New Zealand are shiny white or brightly coloured. It is widely accepted, that fruit-eating birds are attracted to highly coloured fruits with red and black preferred to white, over blue/purple, in turn preferred to yellow/orange and all preferred over green and brown (Willson & Whelan 1990, Gervais *et al.* 1999, Bach & Kelly 2004, Duan & Quan 2013).

While white is generally considered to rank in the mid-range of colour preferences amongst fruit-eating birds, it is not unlikely that New Zealand birds found the fruiting bodies of *Richoniella pumila* (Fig. 1c), *Notholepiota areolata* (Fig. 1d), and species of *Gallacea*, *Hysterangium* and *Protuberata* on the forest floor. Moa certainly picked up considerable quantities (in the larger species up to 5.6 kg) of small white stones which they used as gizzard stones (Hayward 1978, Worthy & Holdaway 2002). Of course other birds could also be attracted to white - especially as a contrast on the forest floor in poor light. Also, one should perhaps not ignore lizards in the dispersal of white-coloured species, as lizards have been implicated in dispersal of white fruits and fungi in Australia and New Zealand (Lord & Marshall 2001, Cooper & Vernes 2011).

In contrast to these white truffles, many New Zealand species are brightly coloured, some spectacularly so. This feature can be interpreted as an adaptation for bird dispersal, especially the non-ratites with their well-developed colour discrimination. Coloured species include the bright red to scarlet stipitate basidiomycetes *Leratiomyces erythrocephalus* (Fig. 1e), *Russula kermesina* (Fig. 1f) and the ascomycete *Paurocotylis pila* (Fig. 1g). The colours of *Leratiomyces erythrocephalus* and





Fig. 1. a: *Cortinarius porphyroideus*, a typical epigeous, stipitate truffle, common in *Nothofagus* forest; b: *Gallacea eburnea* epigeous, astipitate truffle, on the forest floor amongst moss and litter in *Leptospermum* forest; c: *Richoniella pumila*, a white truffle of podocarp – broadleaf forest; d: *Notholepiota areolata*, an epigeous, stipitate, white truffle common in *Leptospermum* forest; e: *Leriomyces erythrocephalus* (red cap with yellowish stipe) with fruits of the monocot *Ripogonum scandens* (Smilacaceae) to left and the conifer *Prumnopitys ferruginea* (Podocarpaceae) to right. The fruits were collected from the forest floor in the vicinity of the fungus; f: *Russula kermesina*, a red-capped stipitate truffle found in *Nothofagus* forest; g: *Paurocotylis pila* on soil surface amongst litter and fruits in podocarp – broadleaf forest; h: *Gallacea scleroderma*, the purple fruiting bodies can swell to 10 cm across. Found in *Nothofagus* forest. [Scale bars = 10mm]





Fig. 2. i: *Cortinarius peraurantiacus* fruit bodies (4) amongst fruits of the dicot *Passiflora tetrandra* (Passifloraceae) collected from the nearby forest floor; j: *Stephanospora flava*, a bright orange to yellow truffle common in podocarp – broadleaf forest; k: *Phallobata alba* showing extensive sterile lobes of the fruiting body that protrude above the soil surface, which may serve to make it more visible; l: *Claustula fischeri*, showing the way the peridium splits to reveal the conspicuous white receptacle; m: *Rossbeevera pachydermis*, showing the colour change from white in immature and hypogean fruit bodies to blueish green in mature and emergent fruit bodies; n: *Gallacea eburnea*, showing development of schizogenous cavities in the gleba which serve to enlarge the fruit body; o: *Octaviania tasmanica*, a handful of large fruiting bodies. Initially white, the fruiting bodies rapidly bruise reddish, blue, and green, then darken to dull brownish blue to dark brown; p: *Labyrinthomyces varius*, a hypogeous ascomycete which has a distinct, sweet, slightly acetylenic odour. [Scale bars = 10mm]

*Paurocotylis pila* are virtually indistinguishable, at least to the human eye, and these species cannot be readily distinguished in the field until the presence of the stipe is checked. Purple to violet colours are represented in the stipeless *Gallacea scleroderma* (Fig. 1h) and the stipitate *Cortinarius porphyroideus* (Fig. 1a), their hues likewise virtually indistinguishable to the human eye. Orange to yellow species include *Cortinarius peraurantiacus* (Fig. 2i) and *Stephanospora flava* (Fig. 2j).

The bright colours of truffles in contrast with soil, leaf litter, woody debris or mossy banks would serve to attract ground-feeding birds. Fruit colour choice has been shown to be influenced by contrasting backgrounds and UV reflectance in birds and lizards (Lord & Marshall 2001, Bach & Kelly 2004, Rajchard 2009, Duan & Quan 2013). Indeed these fungi may have evolved to mimic fallen fruit on the forest floor. The red species, for example, resemble podocarp and supplejack fruits (Fig. 1e,g), the orange species fruits of passionfruit (Fig. 2i), and the purple species fruits of the common lauraceous trees belonging to *Beilschmiedia*.

On the other hand, it should be pointed out that many epigeal mushrooms are also highly coloured (Velíšek & Cejpek 2011), for reasons not generally apparent, but thought to potentially protect from UV damage and bacterial attack, warn of toxicity, or play a role as attractants for dispersal agents.

#### Feature 3. Developmental visual flags

Some New Zealand species show particular developmental features which can be interpreted as 'flags' to make the fruiting body more visible to a dispersal agent relying on vision. In the case of *Phallobata alba*, an endemic monotypic saprophyte often on buried wood, the fruiting body develops distinctive sterile lobes extending up from the fertile portion of the fruit body. These lobes may be all that is visible above the ground (Fig. 2k). In the monotypic *Claustula fischeri* (Claustulaceae), the fruiting body is initially a dull reddish brown but on maturing splits partially open to reveal a brilliant white 'egg' or receptacle containing the spores (Fig. 2l). In this instance the receptacle inflates, and the spores remain smeared around the inner surface. In contrast, in *Rossbeevera pachydermis* (Fig. 2m) the fruiting body, which is initially white and typically hypogeous to barely emergent, on maturing turns patchily blueish green, expands significantly, and becomes epigeal. Over-mature specimens are often almost completely deep blueish green.

A somewhat less spectacular form of 'inflation' of the fruiting body as it matures involves its expansion in a balloon-like manner. This feature can be interpreted as serving to make the fruiting structure more conspicuous, in a resource-effective manner. Perhaps the most spectacular examples are *Gallacea*

*scleroderma* (Fig. 1h) and *G. eburnea* (Fig. 2n), which can expand to 10 cm in diameter, a bite-sized helping even for a moa! Other examples include *Paurocotylis pila* (Fig. 1g) and *Octaviania tasmanica* (Fig. 2o).

#### Feature 4. Presence of distinctive odours

The characters of truffles considered thus far have been visual. For small mammal dispersal, it is generally accepted that odour plays an important role in advertising the fungus's presence, particularly for nocturnal mammals (Fogel & Trappe 1978, Claridge & May 1994). A number of truffle species found in New Zealand produce distinctive odours that even humans can detect. These include *Labyrinthomyces varius* (Fig. 2p), a hypogeous ascomycete, also found in Australia and Indonesia, that has a distinct sweet, slightly acetylenic odour. Plausible candidates for their dispersal in New Zealand are kiwis with their ability to probe deeply into the litter and soil in search of food. Kiwis are furthermore unique amongst modern birds in that their external nares are at the tip of the beak, and it is apparent that they rely heavily on smell for feeding. The extinct adzebill is now known to have been a top predator and therefore unlikely to have eaten fungi. However, many of the extinct species of snipe had a similar beak structure to kiwis and may well have been important fungivores (Holdaway 1989, Worthy & Holdaway 2002). The flightless kakapo has also been found to have large olfactory lobes and to be reliant on smell for social communication (Gsell 2012), which supports evidence that some moa species had relatively large olfactory lobes, and therefore probably a good sense of smell (Worthy & Holdaway 2002). Another noticeably sweet smelling species is *Cortinarius peraurantiacus*, which usually fruits partially buried in mosses and under litter (Fig. 2i), making it fairly easily detected by birds or perhaps even by short-tailed bats, which are known to feed on fallen fruits and to be attracted to nectar of ground flowers.

#### **Fruiting patterns**

As well as these four features, the fruiting pattern of truffles needs to be considered. In the Pacific Northwest of the USA and Eastern Australia, truffle fruiting fluctuates, but some are available in all seasons, providing an ongoing food resource for small mammals (Hunt & Trappe 1987, Vernes & Dunn 2009, Vernes 2010, Danks et al. 2013). Fruiting data are sparse for the New Zealand macrofungal flora, but certainly some of the truffles show long fruiting seasons. For example, both *Hysterangium neotunicatum* and *Gallacea scleroderma* have been found fruiting in all seasons (Castellano & Beever 1994, <http://nzfungi2.landcareresearch.co.nz>). As such, these fungi would provide a source of food when true fruits are sparse.

## Conclusions

In summary, some distinctive features of the New Zealand truffles are consistent with them being adapted to bird dispersal. To prove the case that this situation reflects co-evolution will be a significant challenge, as even for mammals the case is far from proven. The difficulties in satisfactorily explaining, for example, the evolution of fruit colour in relation to dispersal agents (Willson & Whelan 1990, Schaefer et al. 2007, Lomascolo & Schaefer 2010) serve as a caution.

Further work on colour and dispersal of related mushrooms, boletes, brackets and cup fungi, in the same habitats, also needs to be undertaken. Were the ancestors of New Zealand truffles mushrooms or truffles? This might lead us to some insights into the evolutionary pressures, including mycophagy, aridification or saturation, which may have led to evolution of a diverse truffle flora.

We need observations on the remnant bird fauna; their behaviour and preferences, including field observations of feeding on fungi would be invaluable. Spore analysis of droppings, as has been done with small mammals, would clearly be a starting point, with subsequent checking of the viability of spores

after passage through the bird digestive tract, and perhaps even gut retention times (Claridge *et al.* 1992, Colgan & Claridge 2002, Danks 2012, Vernes 2010). Feeding trials with captive species, which could establish whether they respond to the features outlined, are feasible. Finally the nutritional value of New Zealand truffles to potential avian or lizard dispersal agents needs to be determined.

Nevertheless, the extinction of many of the major players of pre-human New Zealand bird fauna means that some of the picture will perforce remain conjecture. Are the truffles of New Zealand anachronisms of an age when the country was a land of birds, in the same manner (as has been suggested) that large indehiscent fruits of Central America evolved in response to a now extinct megafauna of large mammals (Janzen & Martin 1982)?

## Acknowledgements.

Many thanks to all the people who provided commentary, suggestions, and discussion over the years to develop this hypothesis: Jim Trappe, Mike Castellano, Andrew Claridge, Mick Clout, Bill Lee, Ian Atkinson, Peter Johnson, Jamie Wood, and to the reviewers of the manuscript.

## References

- Abell S.A.; Gadek P.A.; Pearce C.A.; Congdon B.C. 2006: Seasonal resource availability and use by an endangered tropical mycophagous marsupial. *Biological Conservation*. 132(4): 533–540.
- Alsheikh A.M.; Trappe J.M. 1983: Taxonomy of *Phaeangium lefebvrei*, a desert truffle eaten by birds. *Canadian Journal of Botany*. 61: 1919–1925.
- Atkinson I.A.E.; Greenwood R.M. 1989: Relationships between moas and plants. *New Zealand Journal of Ecology*. 12 (supplement): 67–96.
- Bach C.E.; Kelly D. 2004: Effects of forest edges, fruit display size, and fruit colour on bird seed dispersal in a New Zealand mistletoe, *Alepis flavida*. *New Zealand Journal of Ecology*. 28(1): 93–103.
- Best H.A. 1984: The foods of kakapo on Stewart Island as determined from their feeding sign. *New Zealand Journal of Ecology*. 7: 71–83.
- Blaschke H.; Bäumler W. 1989: Mycophagy and spore dispersal by small mammals in Bavarian forests. *Forest Ecology and Management*. 26: 237–245.
- Borovička J.; Noordeloos M.E.; Gryndler M.; Oborník M. 2011: Molecular phylogeny of *Psilocybe cyanescens* complex in Europe, with reference to the position of the secotioid *Psilocybe weraroa*. *Mycological Progress*. 10(2): 149–155.
- Boudier E. 1876: Du parasitisme probable de quelques espèces du genre *Elaphomyces* et de la recherche de ces Tubéracées. *Bulletin de la Société botanique de France* 23: 115–119.
- Carron P.L.; Happold D.C.D.; Bubela T.M. 1990: Diet of two sympatric Australian subalpine rodents, *Mastacomys fucus* and *Rattus fuscipes*. *Australian Wildlife Research*. 17: 479–8.
- Castellano M.A.; Beever R.E. 1994: Truffle-like basidiomycotina of New Zealand: *Gallacea*, *Hysterangium*, *Phallobata*, and *Protuberata*. *New Zealand Journal of Botany*. 32: 305–328.
- Castellano M.A.; Trappe J.M.; Maser Z.; Maser C. 1989: *Key to Spores of the Genera of Hypogeous Fungi of North Temperate Forests with special reference to animal mycophagy*. Illustrated by J. Atzet, W. Madar, & G. Bracher. Mad River Press, Eureka.
- Cazares E.; Trappe J.M. 1994: Spore dispersal of ectomycorrhizal fungi on a glacier forefront by mammal mycophagy. *Mycologia* 86: 507–510.
- Claridge A.W.; Cork S.J. 1994: Nutritional value of hypogeous fungal sporocarps for the long-nosed potoroo (*Potorous tridactylus*), a forest-dwelling mycophagous marsupial. *Australian Journal of Zoology* 42: 701–710.
- Claridge A.W.; May T.W. 1994: Mycophagy among Australian mammals. *Australian Journal of Ecology* 19(1): 251–275.
- Claridge A.W.; Tanton M.T.; Seebeck J.H.; Cork S.J.; Cunningham R.B. 1992: Establishment of ectomycorrhizae on the roots of two species of *Eucalyptus* from spores contained in the faeces of the long-nosed potoroo (*Potorous tridactylus*). *Australian Journal of Ecology*. 17: 207–217.
- Clout M.N.; Hay J.R. 1989: The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology*. 12 (supplement): 27–33.
- Colgan W III.; Claridge A.W. 2002: Mycorrhizal effectiveness of *Rhizopogon* spores recovered from faecal pellets of small forest-dwelling mammals. *Mycological Research*. 106(3): 314–320.
- Cooper T.; Vernes K. 2011: Mycophagy in the larger bodied skinks of the genera *Tiliqua* and *Egernia*: are there implications for ecosystem health? *Australian Zoologist*. 35(3): 681–684.
- Danks M.A. 2011: *The swamp wallaby Wallabia bicolor: a generalist browser as a key mycophagist*. PhD thesis, University of New England, New South Wales, Australia. 262 pp.
- Danks M.A. 2012: Gut-retention time in mycophagous mammals: a review and a study of truffle-like fungal spore retention in the swamp wallaby. *Fungal Ecology*. 5(2): 200–210.



- Danks M.A.; Lebel T.; Vernes K.; Andrew N. 2013: Truffle-like fungi sporocarps in a eucalypt- dominated landscape: patterns in diversity and community structure. *Fungal Diversity* 58(1): 143–157.
- Duan Q.; Quan R.-C. 2013: The effect of color on fruit selection in six tropical Asian birds. *The Condor* 115(3): 623–629.
- Duncan R.P.; Blackburn T.M. 2004: Extinction and endemism in the New Zealand avifauna. *Global Ecology and Biogeography*. 13(6): 509–517.
- Fogel R.; Trappe J.M. 1978: Fungus consumption (mycophagy) by small mammals. *Northwest Science* 52: 1–30.
- Forshaw J.M. 1989: *Parrots of the World*, 3rd ed. Willoughby: Lansdowne Editions, Willoughby, Australia.
- Frank J.L.; Barry S.; Southworth D. 2006: Mammal Mycophagy and Dispersal of Mycorrhizal Inoculum in Oregon White Oak Woodlands. *Northwest Science* 80(4): 264–273.
- Gervais J.A.; Noon B.R.; Willson M.F. 1999. Avian selection of the color-dimorphic fruits of salmonberry, *Rubus spectabilis*: a field experiment. *Oikos* 84(1): 77v86.
- Gill B.J.; Bell B.D.; Chambers G.K.; Medway D.G.; Palma R.L.; Scofield R.L.; Tennyson A.J.D.; Worthy T.H. 2010: *Checklist of the Birds of New Zealand, Norfolk and Macquarie Islands, and the Ross Dependency, Antarctica*. 4th ed. Pp 501. Wellington, Te Papa Press in association with the Ornithological Society of New Zealand.
- Gsell A.C. 2012: *The ecology and anatomy of scent in the critically endangered kakapo (Strigops habroptilus)*. PhD thesis, Zoology, Massey University, New Zealand. 176 pp.
- Hammond P.M.; Lawrence J.F. 1989: Mycophagy in insects: a summary. In: N. Wilding, N. M. Collins, P. M. Hammond and J. F. Weber [eds.], *Insect-Fungus Interactions*. 14th Symp. Royal Entomol. Soc. London. Academic Press, London, pp. 275–324.
- Hayward B.W. 1978: Moas - New Zealand's first rock hounds. Evidence from Kawerua. *Tane* 24: 159–172.
- Hedley A. 2012: *High Country Legacy: four generations of Aspinalls at Mt Aspiring Station*. Pp 256. Harper Collins Publishers.
- Holdaway R.N. 1989: New Zealand's pre-human avifauna and its vulnerability. *New Zealand Journal of Ecology* 12: 11–25.
- Houston T.F.; Bougher N.L. 2010: Records of hypogeous mycorrhizal fungi in the diet of some Western Australian bolboceratine beetles (Coleoptera: Geotrupidae, Bolboceratinae). *Australian Journal of Entomology* 49(1): 49–55.
- Howe H.F. 1986: Seed dispersal by fruit-eating birds and mammals. In: *Seed dispersal* (ed D.R. Murray). Academic Press, North Ryde, Australia, pp 123–190.
- Hunt G.A.; Trappe J.M. 1987: Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand. *Canadian Journal of Botany* 65: 438–445.
- Janzen D.H.; Martin P.S. 1982: Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215: 19–27.
- Kendrick B. 2000: *The Fifth Kingdom*. Focus Publishing/R. Pullins Company Incorporated, USA.
- Kotter M.M.; Farentinos R.C. 1984: Formation of ponderosa pine ectomycorrhizae after inoculation with feces of tassel-eared squirrels. *Mycologia* 76: 758–760.
- Lamont B.B.; Ralph C.S.; Christensen P.E.S. 1985: Mycophagous marsupials as dispersal agents for ectomycorrhizal fungi on *Eucalyptus calophylla* and *Gastrolobium bilobum*. *New Phytologist* 101: 651–656.
- Lawrence J.F.; Milner R.J. 1996: Associations between arthropods and fungi. In: *Fungi of Australia 1B* (ed. AE Orchard). Australian Biological Resources Study, Canberra, Australia, pp. 137–202.
- Lebel T. 2013: Two new species of sequestrate *Agaricus* (section *Minores*) from Australia. *Mycological Progress*. 12: 699–707.
- Lebel T.; Syme A. 2012: Sequestrate species of *Agaricus* and *Macrolepiota* from Australia: new species and combinations and their position in a calibrated phylogeny. *Mycologia* 104(2): 496–520.
- Lee W.G.; Wood J.R.; Rogers G.M. 2010: Legacy of avian-dominated plant – herbivore systems in New Zealand. *New Zealand Journal of Ecology* 34(1): 28–47.
- Levey D.J.; Silva W.R.; Galetti M. 2002: *Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation*. CABI Publishing, Wallingford, UK.
- Lomascolo S.B.; Schaefer H.M. 2010: Signal convergence in fruits: a result of selection by frugivores? *Journal Evolutionary Biology* 23: 614–624.
- Lord J.M.; Marshall J. 2001: Correlations between growth form, habitat, and fruit colour in the New Zealand flora, with reference to frugivory by lizards. *New Zealand Journal of Botany* 39: 567–576.
- Malajczuk N.; Trappe J.M.; Molina R. 1987: Interrelationships among some ectomycorrhizal trees, hypogeous fungi and small mammals: Western Australian and northwestern American parallels. *Australian Journal of Ecology* 12: 53–55.
- Maser C.; Trappe J.M.; Nussbaum R.A. 1978: Fungal – small mammal inter-relationships with emphasis on Oregon coniferous forests. *Ecology* 59: 799–809.
- Matias L.; Zamora R.; Mendoza I.; Hodar J.A. 2010: Seed dispersal patterns by large frugivorous mammals in a degraded mosaic landscape. *Restoration Ecology* 18(5): 619–627.
- Medway D.G. 2000: Mycophagy by North Island robin. *Australasian Mycologist* 19(3): 102.
- Montecchi A.; Sarasini M. 2000. *Funghi Ipogei D'Europa*. Associazione Micologica Bresadola, Italy.
- Nunez M.A.; Hayward J.; Horton T.R.; Amico G.C.; Dimarco R.D. 2013: Exotic Mammals Disperse Exotic Fungi That Promote Invasion by Exotic Trees. *PLoS ONE* 8(6): e66832. doi:10.1371/journal.pone.0066832.
- Orlovich D.A.; Cairney J.W.G. 2004: Ectomycorrhizal fungi in New Zealand: current perspectives and future directions. *New Zealand Journal of Botany* 42(5): 721–738.
- Peterson K.R.; Pfister D.H.; Bell C.D. 2010: Cophylogeny and biogeography of the fungal parasite *Cyttaria* and its host *Nothofagus*, southern beech. *Mycologia* 102 (6): 1417–1425.
- Pirozynski K.A.; Malloch D.W. 1988: Seeds, spores and stomachs: coevolution in seed dispersal mutualisms. In: KA Pirozynski & DL Hawksworth, eds. *Coevolution of fungi with plants and animals*. Academic Press, New York, USA, pp. 227–246.
- Pyare S.; Longland W.S. 2001: Patterns and consequences of ectomycorrhizal fungi consumption by small mammals in Sierra Nevada old-growth forests. *Journal of Mammalogy* 82: 681–689.
- Rajchard J. 2009: Ultraviolet (UV) light perception by birds: a review. *Veterinari Medicina* 54(8): 351–359
- Schaefer H.M.; Schaefer V.; Vorobyev M. 2007: Are fruit colors adapted to consumer vision and birds equally efficient in detecting colorful signals? *The American Society of Naturalists* 169(1): 159–169.
- Schickmann S.; Urban A.; Kräutler K.; Nopp-Mayr U.; Hackländer K. 2012: The interrelationship of mycophagous small mammals and ectomycorrhizal fungi in primeval, disturbed and managed Central European mountainous forests. *Oecologia* 170(2): 395–409.
- Segedin B.P.; Pennycook S.R. 2001: A nomenclatural checklist of agarics, boletes, and related secotioid and gasteromycetous fungi recorded from New Zealand. *New Zealand Journal of Botany* 39(2): 285–348.
- Silke S.; Steiger A.E.; Fidler M.V.; Kempnaers B. 2008: Avian olfactory receptor gene repertoires: evidence for a well-developed sense of smell in birds? *Proceedings of the Royal Society B* 275(1649): 2309–2317.
- Sillman A.J. 1973: Avian vision. In: Farner DS, King JR, Parkes KD, eds. *Avian Biology, vol III*. Academic Press, New York, pp 349–387.
- Sillman A.J.; Bolnick D.A.; Haynes L.W.; Walter A.E.; Loew E.R. 1981: Microspectrophotometry of the photoreceptors of palaeognathous birds – the emu and the tinamou. *Journal Comparative Physiology* 144: 271–276.



- Thiers H.D. 1984: The secotioid syndrome. *Mycologia* 76:1–8.
- Trappe J.M.; Maser C. 1977: Ectomycorrhizal fungi: interactions of mushrooms and truffles with beasts and trees. In: Walters T, ed. *Mushrooms and man: 4th Interdisciplinary Approach to Mycology*. Linn-Benton Community College, Albany, Oregon, pp. 163–179.
- Velišek J.; Cejpek K. 2011: Pigments of Higher Fungi: A Review. *Czech J. Food Sci.* 29(2): 87–102.
- Vernes K. 2010: Ch 14. Mycophagy in a community of macropodoid species. In: Coulson G, Eldridge MDB, eds. *Macropods: The Biology of Kangaroos, Wallabies, and Rat-kangaroos*. CSIRO Publishing, Collingwood, Australia.
- Vernes K.; Dunn L. 2009: Mammal mycophagy and fungal spore dispersal across a steep environmental gradient in eastern Australia. *Austral Ecology* 34(1): 69–76.
- Vernes K.; Lebel T. 2011: Truffle consumption by New Guinea forest wallabies. *Fungal Ecology* 4: 270–276.
- Vernes K.; McGrath K. 2009: Are introduced black rats (*Rattus rattus*) a functional replacement for mycophagous native rodents in fragmented forests? *Fungal Ecology* 2(3): 145–148.
- Vernes K.; Trappe J.M. 2007: Hypogeous fungi in the diet of the red-legged pademelon *Thylogale stigmatica* from a rainforest – open forest interface in northeastern Australia. *Australian Zoologist* 34(2):203–208.
- Willson M.F.; Whelan C.J. 1990: The evolution of fruit color in fleshy-fruited plants. *The American Naturalist* 136: 790–809.
- Wilmhurst J.M.; Higham T.F.G. 2004: Using rat-gnawed seeds to independently date the arrival of Pacific rats and humans in New Zealand. *Holocene* 14: 801–806.
- Wood J.R.; Rawlence N.J.; Rogers G.M.; Austin J.J.; Worthy T.H.; Cooper A. 2008: Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes). *Quaternary Science Reviews* 27(27–28): 2593–2602.
- Worthy T.H.; Holdaway R.N. 2002: *The Lost World of the Moa: Prehistoric Life of New Zealand*. Bloomington/Christchurch: Indiana University Press/Canterbury University Press. 718 pp.

## Plants named for our “two Lucies”.

### An occasional paper in the series “Plants named for ABS members”

Maureen Young and Ewen Cameron

Lucy Cranwell (1907–2000) (Cameron 2000, Thomson 2000), founder and patron of the Auckland Botanical Society, and her friend and botanising companion, Lucy Moore (1906–1987) (Beever 1987, Moore 1925–1987), were first called the “two Lucies” by Leonard Cockayne, and the name stuck. The first name of these two redoubtable botanists was used in the naming of the grass, *Festuca luciarum* Connor (1998). This grass, endemic to the East Coast region, honours both of the Lucies who were together on the remote Mt Maungapohatu in 1932 (Fig. 1) where Lucy Cranwell collected the type specimen (AK 200090).

In the late twenties and the thirties the two young women were actively attempting to learn the whole New Zealand flora, encompassing algae, bryophytes and vascular plants. As Lucy Moore (Morton 2000, p.356) was to write “we were jacks, or jills, of many trades”. John Morton stated in his Lucy Cranwell Lecture (Morton 1995, p.1), “These were historic years when the “two Lucies” ... were making their own first incursion into marine intertidal ecology at the Poor Knights. ...this was to be the first real insight into the zoning of our marine shores.” Their seaweed studies on northern islands, the Waitakere coast and the Hauraki Gulf, together with Lucy Moore’s wartime work on obtaining agar from local seaweeds (as it was no longer available from Japan), resulted in the naming of four species of algae for the pair – two for each. For Lucy Cranwell, two North Island marine algae, *Codium cranwelliae*

Setch. (1940) and *Gigartina cranwelliae* Chapm. (1979); for Lucy Moore, two red seaweeds, *Euptilia mooreana* Lindauer (1949) (now *Aristoptilon mooreanum*) and *Ptilonia mooreana* Leving (1955). A moss found on the exposed coastal rock platforms of Rangitoto Island, and at other northern sites, was named *Tortella mooreae* Sainsbury (1955), but is now considered to be synonymous with the Australian *T. cirrhata* Broth.

Lucy Cranwell was the inaugural curator of botany at the Auckland War Memorial Museum, 1929–1944. She was involved in the Hawaiian Bog Survey in 1938 and, after her marriage during the war to an American army captain (later major), Lucy Cranwell left New Zealand in February 1944, and carried on her interest in palynology, the study of fossilised pollen, in Tucson, Arizona. Because of this it is not only plants from New Zealand, but three from Hawaii and several fossil plant taxa, which have been named in her honour. Living taxa include three Hawaiian dicots: *Stenogyne cranwelliae* Sherff (1939) (Lamiaceae), *Peperomia cranwelliae* Yunker (1949) (Piperaceae), and *Fagara mauiensis* var. *cranwelliae* Skotts. (1944) (Rutaceae) (now included in *Zanthoxylum kauaense*); a crustose lichen known from its original gathering by Lucy in 1933 at Anawhata, west Auckland, and a few recent collections, *Buellia cranwelliae* Zahlbr. (1941); fossil taxa include a pentoxylean seed collected by Lucy in 1931 south of Auckland by the Waikato Heads, *Carnocarnites cranwelli* T.Harris; and four