THE PUFFBALLS OF NEW ZEALAND

Mycological Notes 46

Jerry Cooper, Christchurch, December 2025

Introduction

Trying to make sense of our puffballs is a journey I started seriously back in 2016. I was fortunate at that time to receive some funded time to study the groups of macro-fungi that interested a colleague, the late Ross Beever (through the Ross Beever Fellowship). That project included the stinkhorns and earthstars, and I have written informal accounts for both groups. Ross was also keenly interested in our puffballs, and he collected many specimens. So, over the intervening years I have studied Ross' deposited specimens and kept an eye open for fresh puffball specimens, and as usual, sequenced everything to try and make sense of them. One of our rare puffballs, *Abstoma purpureum*, I added to the IUCN Red Data list in 2019 as Endangered because it was known from very few sand-dune sites and not seen for decades. Rather surprisingly Zac Taylor recently posted convincing photos of this rare species on iNaturalist from a park in Christchurch[1]. That find spurred me on to finish these notes.

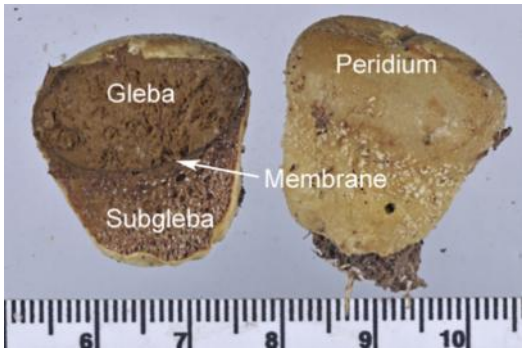


Figure 1 Terminology (*Lycoperdon glabrescens*)

As with most groups of fungi the identification of species is not always straightforward. It helps to examine a group of fruitbodies where all stages are present, from immature to fully mature. It is always useful to slice a fruitbody (carefully with a razor blade) to see the spore-bearing gleba. Make a note if the fruitbody has a sponge-like base that is sterile and usually a different colour. You should also note if there is a layer of tissue (a membrane/diaphragm) that separates the base from the gleba. Note whether the fruitbody is growing on wood, wood fragments in soil or bare soil, and whether there are rhizoids (mycelium cords) attaching the base to the substrate. The peridium (outer skin) of many puffballs will be covered in fine granules or small spikes when immature, but these get rubbed off rapidly in older fruitbodies, and they become impossible to identify. Make a note of the habitat – in bush/forest, native grassland or modified pasture, parks etc.

In common with many groups of fungi we have mis-used the names of northern hemisphere species. Our species look like these northern hemisphere species but are often not the same. On the other hand, several northern hemisphere species have been introduced and are common in pastures and parks, such as *Calvatia gigantea*, *Bovista plumbea* and *Lycoperdon pratense*. Unfortunately, each of these species has native look-alikes, often restricted to more natural habitats.

[1] Abstoma purpureum from Hornby, Christchurch, New Zealand on July 16, 2025 · iNaturalist NZ

Microscopy is essential to distinguish some species. The key microscopic features are the form of the capillitium (the spore-bearing fluffy tissue of the gleba), whether the spores are smooth, finely roughened or coarsely roughened and (critically) the presence and size of any pedicel (a fragment of the stalk that attaches the spore to the basidia).

The common puffball genera in New Zealand are *Calvatia, Lycoperdon* and *Bovista* (including *Globaria*). Typically, *Bovista/Globaria* species are relatively small and globose whereas *Lycoperdon* species are medium-sized and turbinate in shape, and *Calvatia* large to very large (> 20cm). However, these generalisations are not reliable. In *Lycoperdon* (and some *Calvatia*) the fruitbody has sterile base tissue (subgleba), sometimes elongated to form a pseudo-stem, and often with a visible sponge structure when sliced vertically. In *Bovista* these features are absent, the fruitbody often spherical, and the inner spore mass and papery covering of the endoperidium coming loose and blowing around.

The group of puffballs in New Zealand were last revised by Cunningham in 1944. He covered Australian and New Zealand species of 'gasteromycetes' including groups like the stinkhorns, earth-balls, earthstars, truffles and secotioid fungi. Many of these groups are quite unrelated to each other. Even within the family he recognised as Lycoperdaceae he included genera that we now know are not related. For the true Lycoperdaceae he covered species in *Abstoma*(1), *Mycenastrum*(1), *Disciseda*(3), *Bovista*(2), *Lycoperdon*(10) and *Calvatia*(3). So, he covered 20 species of true puffballs from New Zealand. We currently have phylogenetic data on 23 species. However, as usual, linking Cunninghams' species concepts to modern specimens is not always straightforward. In the years since 1944 many other species have been recorded from New Zealand, but most should be regarded as misidentifications.

In a recent paper (Jx et al, 2024) a revised classification of puffballs was presented. They introduced new genera such as *Globaria*, *Utraria*, *Fuscospina*, *Pseudoperdon*, *Lycoperdiscus*, *Leptocaulis* & *Sinoperdon*. Here I accept only *Globaria* (for the time being). The remaining genera I consider to be unnecessary and unhelpful divisions of a broader concept of the genus *Lycoperdon* with most of these new genera historically accepted as sub-genera within *Lycoperdon*. That arrangement is a far more practical arrangement for recognising the genera.

All the specimens cited in this revision are deposited the PDD national fungarium and more details can be found on the SCD website[2], either by searching for PDD numbers or my JAC personal accession numbers. The associated sequences will eventually be deposited in GenBank.

The JAC numbers are not necessarily specimens I have collected, and the number is used to track the associated morphological and sequence data I have added. Every specimen with a JAC number will also have PDD number. All photos were published under a Creative Commons license and the contributors acknowledged at the end of this treatment.

Recently I have been maintaining a web page with phylogenetic trees for all the New Zealand basidiomycetes. The most current phylogenetic tree for the Lycoperdaceae may be found there, and it will change as more New Zealand species get sequence data, and more relevant papers are published.

https://www.funnz.org.nz/phyloforest

[2] SCD Home

Before we dive into the species details it will be useful to describe some of the technical terminology used for describing puffballs.

Glossary

Shapes – Pyriform – shaped like a pear. Turbinate – shaped like a spinning top (ice-cream cone with a restricted waist).

Exoperidium – Most puffballs will have a skin composed of two distinct layers. This becomes more obvious as the fruitbody matures and sometimes the outer layer – the expoperidium - will break away leaving the endoperidium exposed.

Endoperdium – the inner layer of the peridium, perhaps most obvious in species like *Bovista plumbea* where the endoperidium can be seen as a smooth lead-grey surface after the exoperidium has broken away.

Gleba – the inner tissue of the puffball.

Rhizoids – the thick rope-like aggregations of hyphae attaching the puffball to the substrate and more common with wood association (lignicolous) species.

Mycosclereids – are thick-walled globose/ellipsoid terminal elements associated with the peridium hyphae. The give the peridium a minutely pubescent appearance under a lens and can be a useful diagnostic feature. I have not consistently captured information on these structures for New Zealand species and do I haven't used it as a diagnostic character.

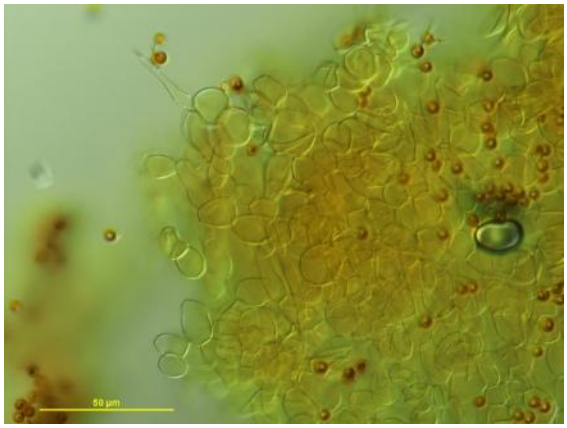


Figure 2 Mycosclereids (*Lycoperdon glabrescens*)

Capillitium –This is the cotton-wool-like gleba and the microscopic appearance is useful for confirming the genera and species. The literature commonly refers to capillitial types - Calvatia, Bovista, Lycoperdon and intermediate (Bovista/Lycoperdon). Unfortunately, these are sometimes not clear-cut and take a bit of experience to recognise. You should note if the capillitium is septate or not, branched or not, and covered in tiny pits or slits. Of more utility is the distinction between thick, thin-walled and brown/hyaline capillitial threads, or mixtures thereof. These should always be sampled from the centre of a mature fruitbody.

> **Bovista-type** capillitium –is composed of short section of sclerified hyphae, mostly aseptate, loosely or densely branched, with distinct main stems, with or without pits.

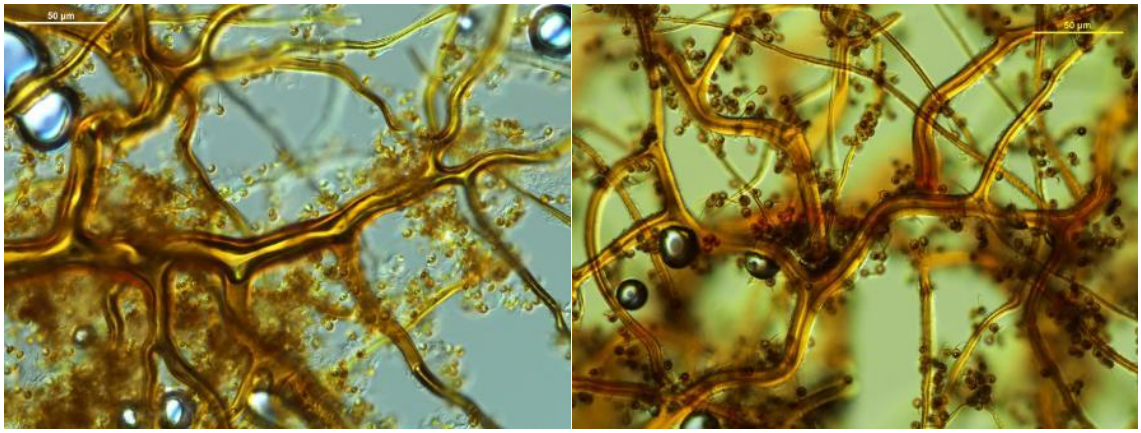


Figure 3 Bovista Type capillitium (*Bovista plumbea*)

Lycoperdon type capillitium – is composed of long sclerified hyphae, aseptate or scarcely septate, without main stems, with circular to elliptical pits, slit-like scars or without pits.

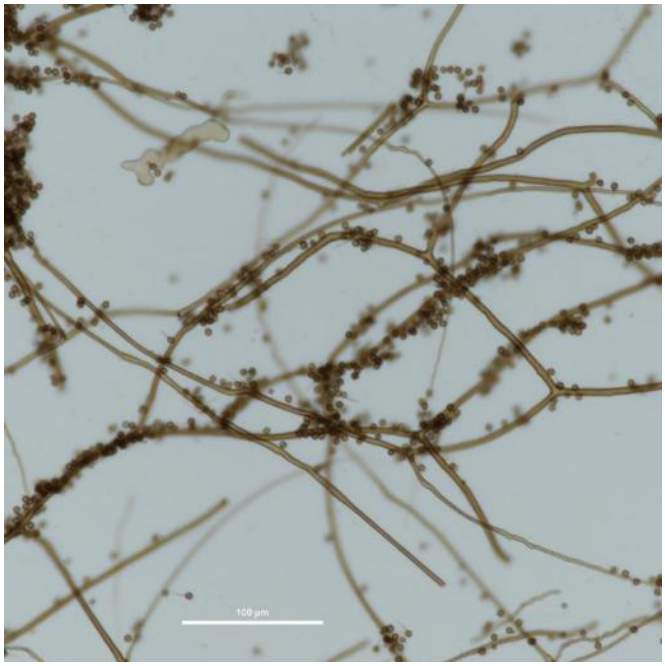


Figure 4 Lycoperdon Type capillitium (*Lycoperdon glabrescens*)

Calvatia (Handkea) type capillitium – is composed of fragile, fragmenting, regularly branched, septa common, forming 'bone-joints' and with numerous, small pores

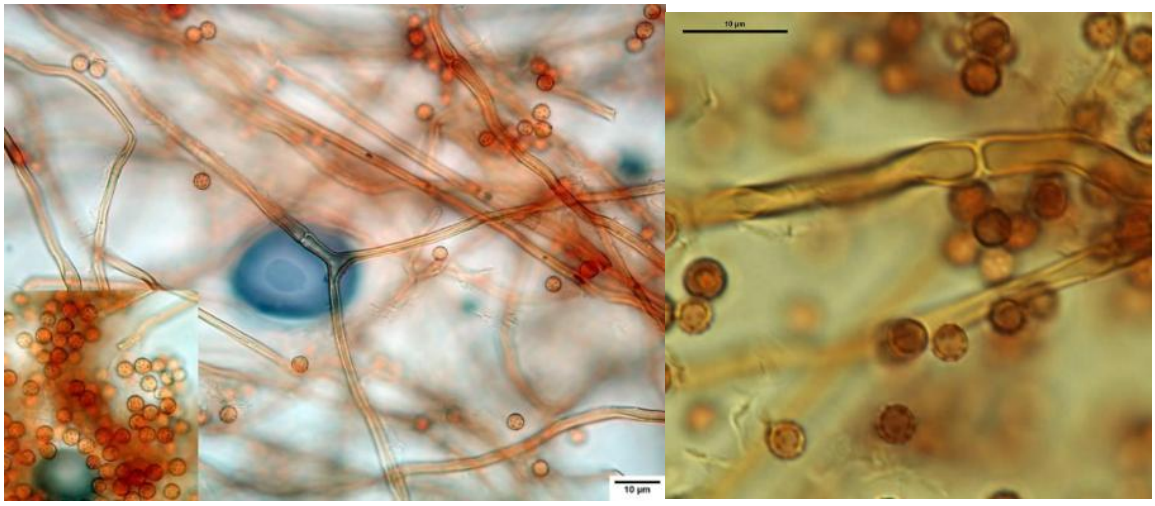


Figure 5 Calvatia Type capillitium (*Calvatia sinclairii*)

A **eucapillitium** refers to thick-walled brown hyphae (a true capillitium). Unless otherwise qualified this is what is meant by the term capillitium in the descriptions.

A **paracapillitium** refers to thick-walled hyaline hyphae, usually septate. Note however the capillitium needs to be sampled in the centre of mature fruitbodies as immature material will generally show hyaline hyphae towards the periphery.

A **pseudocapillitium** also refers to thin-walled hyaline hyphae. This term is usually applied to other groups (e.g. slime moulds) and if mentioned in relation to puffballs in the literature then it is referring to a paracapillitium.

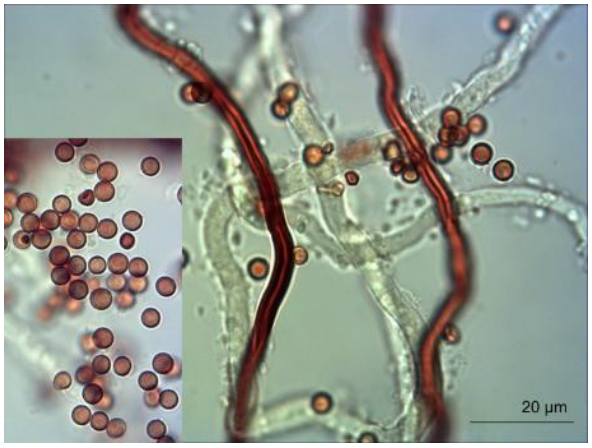


Figure 6 Hyaline thick-walled paracapillitium in *Apioperdon sp. 'Monowai'*, and true eucapillitium of thick-walled brown hyphae

Figure 7 Paracapillitium of Lycoperdon compactum

Spores – The spores of most puffballs are relatively small and spherical. The important features are the degree of any roughness. Sometimes to see the ornamentation requires a good quality microscope, x1000 oil-immersion magnification, and ideally differential phase contrast optics.

Spores with a **Pedicel** – non-deciduous spore attachment cell, usually over 7um. If deciduous or smaller then termed sub-pedicellate or a stub.

Spores **Verrucose –** For spore ornamentation where the surface is covered in short spines or warts

Spores **Asperulate** – For spore ornamentation where the surface is covered in an almost invisible roughness. This usually requires oil-immersion at x 1000 to see.

General Key

1	Fruitbodies stipitate with a woody stipe and a rounded, apical fertile part *Battarrea* & *Tulostoma*	Not treated here
1	Fruitbodies rounded, turbinate, pyriform or pestle-shaped, without a woody stipe	2
2	Spores > 8um diam. Peridium very thick, coriaceous	3
2	Spores < 8um diam. Peridium thick or not	4
3	With a very thick coriaceous endoperidium and outer surface flaking off. Capillitium with short spines, hyphae clamped, spores > 8um, in dunes or pasture	*Mycenastrum corium*
3	Spores reticulate (Scleroderma-like), capillitium spiralled. In dunes and sandy soil	*Abstoma purpureum*
4	Fruitbodies large, usually> 15 cm diam. At maturity, globose to subglobose. Capillitium of the Calvatia type.	*Calvatia*
4	Fruitbodies smaller at maturity. Capillitium of the Lycoperdon or Bovista type.	5
5	Fruitbodies tiny, conical, associated with liverworts on tree bark	*Lycoperdon sp. 'Croydon'*
5	Fruitbodies larger, not associated with liverworts, terrestrial or lignicolous	6
6	Fruitbodies terrestrial, globose, < 4cm diam., without a subgleba, in grassland or dunes	8
6	Fruitbodies other shapes, terrestrial or lignicolous, often with a subgleba, in grassland or forest/bush	7
7	Lignicolous, with basal rhizoids, subgleba white, paracapillitium present.	*Apioperdon sp. 'Monowai'*
7	Lignicolous or not, basal rhizoids present or not, subgleba (if present) not white, paracapillitium present or not	*Lycoperdon*
8	Fruitbodies forming nearly hypogeously. Central pore formed at the base but misleadingly appearing apical in detached mature fruitbodies. A thick partial endoperidium on the top surface on immature fruitbodies becomes worn away and the now top-heavy fruitbodies invert when free. Capillitium short, spiralled, rarely branched.	*Disciseda*
8	Fruitbodies not inverting after maturation	9
9	Peridium with coarse granules, and base sometimes with orange/reddish brown discolouration. Paracapillitium present, spores with no or short pedicels.	*Globaria sp. 'Craigieburn'*
9	Peridium smooth or reticulate, white to grey. Paracapillitium absent, spores with long pedicels.	*Bovista*

Mycenastrum

Mycenastrum corium

Fruitbodies 50-200mm diam., subglobose, with a thick root and basal rhizoids. Initially white and floccose then the surface becoming cracked into polygons and then flaking off to the expose the endoperidium which can be lead-grey to purplish. Eventually the very thick-walled endoperidium splits in a stellate manner to expose the brown gleba, which can become detached and lost. Old, empty fruitbodies can survive for months. There is no subgleba. The capillitium has very distinct short spikes and spores reticulate, 8-10um diam.

Figure 8 *M. corium*; fruitbodies JAC15916; capillitium PDD 31391

Abstoma

Abstoma purpureum

Fruitbodies terrestrial, semi-hypogeous, to 45mm diam., peridium smooth/polished, lilac to purplish-black, opening by a central irregular tear. Capillitium sinuous, smooth. Spores 13.2 um diam., σ=0.8 and conspicuously reticulate (*Scleroderma*-like).

The species was described from New Zealand sand-dunes and with a sand-encrusted exoperidium. There have been very few collections, and all were in the mid-20th century. A recent collection from an urban park (possibly originally inland dunes) is relatively mature and lacks the exoperidium. GenBank has a sequence labelled *A. purpureum* (GQ981488 = KM162954) which was from San Francisco (incorrectly as UK in some literature). ITS sequence data from the recent New Zealand collection indicates they are closely related, but the USA specimen is probably not *Abstoma purpureum*. However, a sequence of a specimen from Australia and identified as *A. reticulatum* (described from Australia) is the same. I've long suspected *A. reticulatum* and *A. purpureum* represent colour variants of the same species, for which the name *A. purpureum* is correct. In New Zealand the species may be indigenous or introduced from Australia. The IUCN status of this species requires re-evaluation if synonymy with *A. reticulatum* is confirmed.

Figure 9 *A. purpureum*; fruitbodies; capillitium & spores JAC18789

Disciseda

The three New Zealand species of *Disciseda* recorded by Cunningham remain uncharacterised in a modern sense. They are known from just seven specimens from 5 widely scattered sites, with the last collected in 1951. *D. cervina* was originally described from South America, *D. candida* from the USA and *D. verrucosa* from New Zealand. Of these it seems likely that only *D. verrucosa* is correctly applied (and incorrectly applied in Europe). The peculiar nature of the growth of species was outlined in the key. What looks like an apical pore in free, mature fruitbodies is a hole in the base and fruitbodies become inverted at maturity. The presence of the thick hemispherical remnant of an exoperidium may be adequate to recognise the genus but I think really you need to find the semi-buried immature fruitbodies to be certain of a correct generic identification. I can't say anything more about our species without modern collections.

1	Spores nearly smooth	*D. candida/cervina*
1	Spores verrucose	*D. verrucosa*

Calvatia

The three New Zealand species can be difficult to separate. *C. gigantea*, as the name suggests, grows to be the largest and frequently well over 15cm diam., and usually smooth, white and spherical with only a shallow attenuated base. *Calvatia sinclairii* and *C. lilacina* can both be relatively large although usually less than 20cm. They often have a more sculptured peridium than *C. gigantea* and are more turbinate in shape, (and *Lycoperdon excipuliforme* can be similar). The purple colouration of the gleba of *C. lilacina* only develops with considerable age and is not reliable. *C. gigantea* is clearly an introduction by Europeans but I can't decide if the other two species are native or not. They are both often associated with modified habitats and may represent old introductions from Australia, or they may be native. This raises a question about the many Māori names for puffballs and it isn't clear to me what species they refer to. I think they either refer to *C. sinclairii* (and that species is native) or they refer to several species of smaller native *Lycoperdon*. Other Latin names have been used incorrectly in New Zealand in my opinion. For example, *Lycoperdon utriforme, C. craniformis*, *C. candida*, *C. rubroflava*, and *C. cyathiformis* all probably refer to *C. liliacina* or *C. sinclairii*. There a few iNaturalist observations that look remarkably like the North American *C. sculpta* but we have no specimens in the national collection and its presence remains unconfirmed.

1	Mature fruitbodies globose to subglobose, surface smooth, > 150mm diam., without a subgleba	*C. gigantea*
1	Mature fruitbodies subglobose, turbinate or pyriform, surface granular or with flaky patches, sometimes forming, brain-like folds or polygonal plates, <150mm diam., with a distinct subgleba	2
2	Mature olivaceous becoming purple (after weeks). Spores > 5um diam.	*C. lilacina*
	Mature gleba remaining olivaceous. Spores < 5um diam.	*C. sinclairii*

Calvatia gigantea

Fruitbodies to 400mm diam., spherical, smooth, white, abruptly rooting and with rhizoids. Strong fungus odour in mature specimens. Without a well formed subgleba or membrane. The gleba transitions from white to olivaceous and finally reddish-brown. Spores with pedicel (to 2.5um) and

smooth and capillitium without pores but with sparse granular encrustation. Spores globose to subglobose, length μ=4.6 μm, σ=0.37; width μ=4.0 μm, σ=0.61; Q μ=1.2.

Always in urban areas, modified pasture etc.

Figure 10 *C. gigantea*; fruitbodies; capillitium & spores - JAC14350

Calvatia lilacina

Fruitbodies to 150mm diam, turbinate, cream to tan, surface often reticulate, not smooth. The common brain-like deformation of the peridium is environmentally induced by rapid drying and is not diagnostic for a species. The sterile base is separated from the gleba by a membrane. The mature gleba in this species is purple, but this colouration can take several weeks or even months to become dominant. The northern hemisphere *C. cyathiformis* has a gleba of similar colour.

Microscopically this has a Calvatia-type capillitium with numerous bone-joint-like septa. Spores globose, densely spiny, μ=5.7 μm diam., σ=0.4.

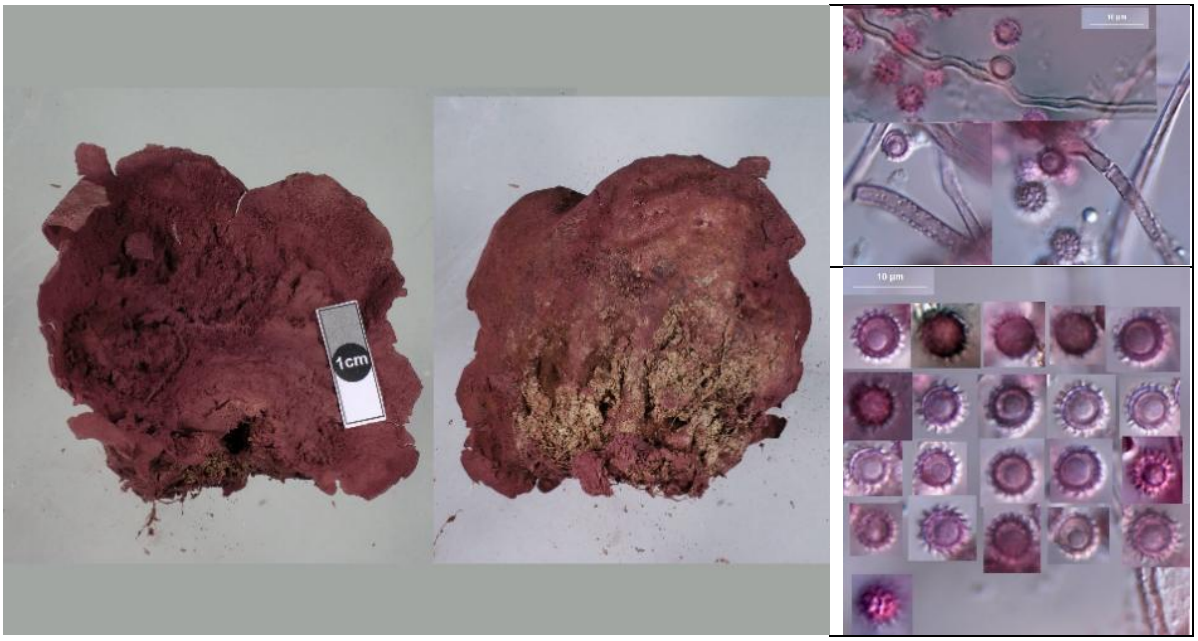


Figure 11 *C. lilacina*; fruitbodies; capillitium; spores - JAC12797

JAC17487 Figure 12 *C. lilacina*; fruitbodies - JAC16600(x2), JAC17487, JAC14762

Calvatia sinclairii

Fruitbodies to 150mm diam., turbinate, and usually with a more distinct transition to a pseudo-stipe than *C. lilacina*. cream to reddish ochraceous and brown, surface initially with granular covering, becoming smooth/polished, often becoming creviced and/or with the peridium flaking. Gleba brown to olive. With sterile base and membrane. Capillitium without pores, sometime encrusted, with bone-joints. Spores μ=3.5 μm diam., σ=0.2, echinulate, without a pedicel.

In old frutboidies the gleba is lost, leaving a sterile cup-like base, like the northern hemisphere *L. utriforme*. It's possible *C. sinclairii* is native to New Zealand and is probably closely related to (or the same as) *Lycoperdon retis* described from Australia, Victoria. Current sequence data suggests there is a closely related Australian species but not identified as *L. retis*.

Changing environmental conditions during the growth of *C. lilacina* and *C. sinclairii* can deform them so they display a brain-like surface or break up into polygonal plates. These forms have been identified as various species, including *C. craniformis*, Specimens identified as *C. rubro-flava* may also represent another variation. Specimens with a polygonal pattern consisting of low pyramidal scales require sequencing to compare with *C. sculpta* and may represent an unsampled species.

My recent adoption of the name *Calvatia sinclairii* requires some explanation. *L. sinclairii* was described in 1887 from New Zealand and so provides the earliest name for the New Zealand taxon if it considered distinct. Cunningham included *L. sinclairii* under his concept of *C. caelata*, which is a macroscopically similar northern hemisphere species currently treated as *L. utriforme* in subgenus *Bovistella*. PDD fungarium specimens I have examined under the name *C. caelata* (and *C. bovista* –

another synonym), and *L. utriforme* are either *C. sinclairii*, or they are *L. excipuliforme*, but I have not examined all the collections under these names. There are several digitised New Zealand specimens in the Kew fungarium also currently identified as *L. utriforme* by Demoulin, but without further information on the original identification. Coetzee & Van Wyk (2012) apparently located the type specimen of *L. sinclairii* and they too concluded that it represents *L. utriforme*. So, is *L. utriforme* present in New Zealand or not? I think all this material requires re-assessment, and especially the type of *L. sinclairii*. We know from early accounts by Elsie Wakefiled at Kew that the type consists of just the sterile base which is typical of old *C. sinclairii* as well as old *L. utriforme*. Specimen locality data for the type of *L. sinclairii* (in Berkeley's collection) has not been digitised or the type-status not annotated (potentially K(M) 837419 is the type). We do know from later treatments it was collected in 1861 by Andrew Sinclair and Julias von Haast. This was shortly before Sinclair drowned crossing the Rangitata river and he is buried at Mesopotamia Station. The specimen apparently came from the Nelson/Marlborough region and probably the vicinity of Mount Tarndale where several botanical specimens were collected at the same time in alpine/semi-alpine habitats. Sinclair & Von Haast were collecting specimens for Hooker's Handbook of the New Zealand Flora and they wouldn't have been collecting introduced species in paddocks. *L. utrifome,* is a northern hemisphere species, and if present would have been in paddocks. Whilst there were some very early introductions of northern species, I believe *L. sinclairii* represents a native species or very old introduction from Australia. In addition, given that we have no modern sequence confirmed specimens of *L. utriforme* in New Zealand, I believe identifications of early specimens of *L. utriforme* in New Zealand (including as *C. caelata* & *C. bovista*) are all based on superficial macro-morphological similarity and are likely to represent *C. sinclairii*. Therefore, I reject Coetzee & Van Wyk's assertion, for which there was no elaboration. It would be very useful to obtain a sequence from the type specimen of *L. sinclairii* at Kew, or at least more details of the capillitium to confirm the presence of slit-like pores, characteristic of *L. utriforme*, and absence of bone-joints, present in *L. sinclairii*. From Wakefield's description it seems doubtful any capillitium remains in the type. All this does not discount the possibility that *L. utriforme* is present in New Zealand as a recent introduction, but we need sequenced specimens to confirm that. Available sequence data indicate it has been introduced to Argentina.

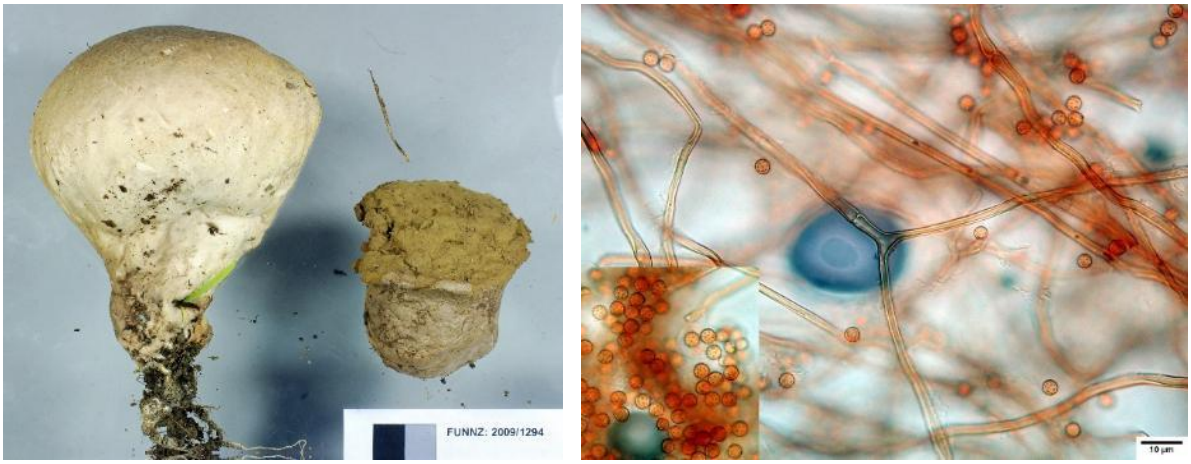


Figure 13 *C. sinclairii*; fruitbodies, capillitium & spores - JAC1085

Figure 14 *C. sinclairii*; fruitbody - JAC9627

Figure 15 *C.sinclairii;* fruitbodies, gleba & capillitium - JAC15462



Figure 16 – *C. sinclairii*; fruitbodies - JAC15775, JAC17082, JAC16565

'Lycoperdon' sp. 'Croydon

Fruitbodies small, 8-10mm high x 5-7mm diam. with a very short, small cylindrical base and rhizoids attached to parasite of?) the *Metzgeria furcata* liverwort. The egg-shaped fruitbodies are apically and irregularly dehiscent with a floury-granulose surface covering. The peridium has three layers. The capillitium is of the Calvatia-type, brown, with pits, with swollen thick-walled septa, unbranched and connected to the walls of the peridium. No subgleba or membrane is present. Spores globose, 3.5–4.3µm diam. (µ=3.9, σ=0.2), minutely verrucose, with a short pedicel.

This is an unmistakeable tiny species that appears to be parasitic on liverworts on the bark of trees. In morphology and habitat, it resembles species like *Bryoperdon acuminatum* from Europe, *Bovista ochrotricha* described from Sri Lanka, and *Lycoperdon fusiforme* from Tibet. These latter two species lack phylogenetic data. The New Zealand species is unrelated to *Bryoperdon* and appears on a long branch within the *Calvatia* clade. More phylogenetic data is needed but morphologically at least this does not resemble a *Calvatia* (and if a new genus is required then *Marchantioperdon* would be appropriate).

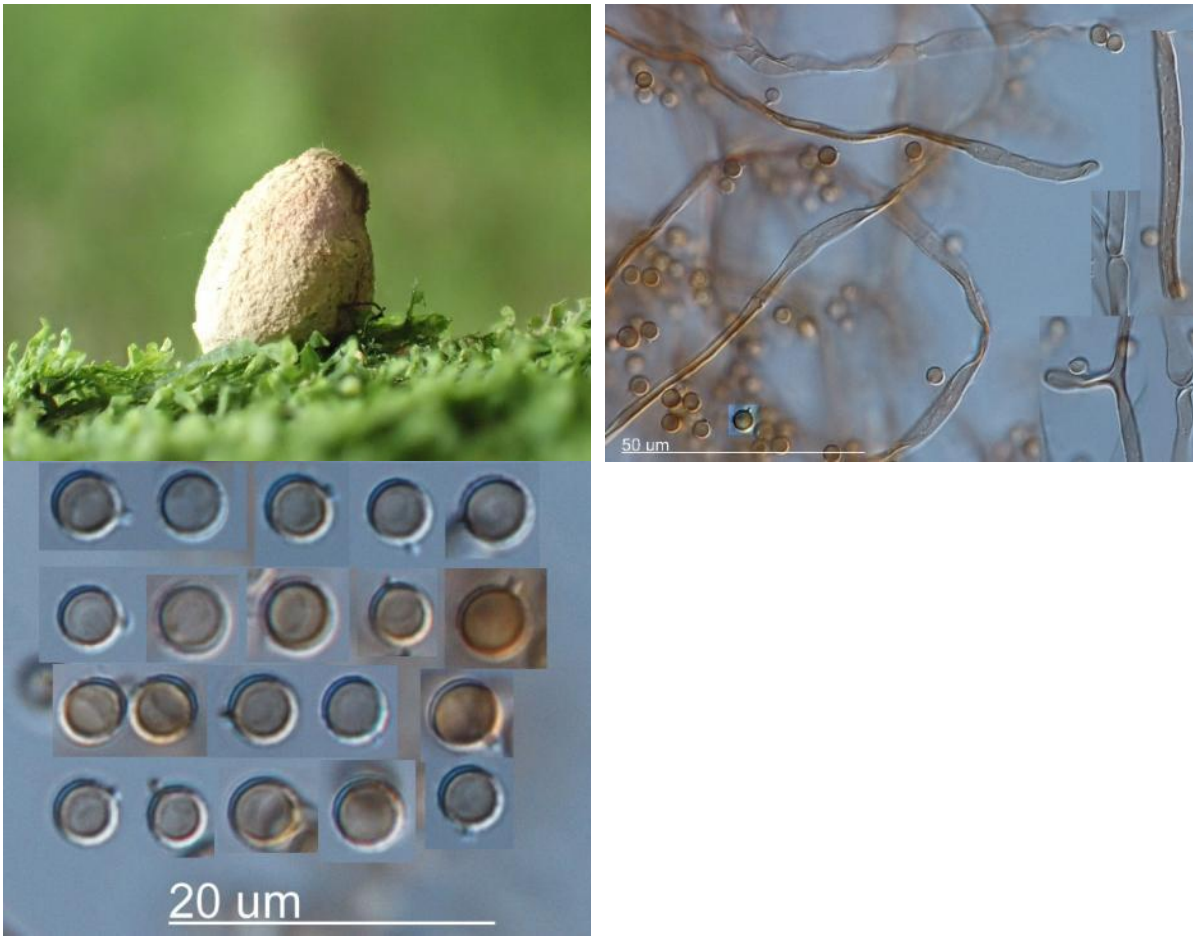


Figure 17 - *Lycoperdon sp. 'croydon'*; fruitbodies, spores & capillitium - JAC14312

Globaria

Globaria is the new generic name for a group of species related to *Bovista aestivalis*. *Bovista* and *Globaria* are difficult to distinguish macroscopically. Both are small, spherical and lack a sterile base. *Globaria* species seem to be associated with yellow/orange/reddish colours to the base of the mature fruitbody. Microscopically the capillitium in *Globaria* is of the intermediate type to Lycoperdon type, and in *Bovista* it has the Bovista type. In *B. aestivalis* and some other species the gleba is called heteromorphous because the form of the capillitium differs from the top of the gleba to the bottom, but the character is not diagnostic for the genus. The spores of *Bovista aestivalis* are finely asperulate but we do not have that species in New Zealand.

Cunningham described *Lycoperdon gunnii* from Tasmania with a single New Zealand collection. Kreisel later transferred the species to *Bovista*, noting a Lycoperdon-type capillitium, and it is possible the species belongs in *Globaria*. However, it has spores with long pedicels and perhaps better placed in *Lycoperdon* 'subgenus' Sinoperdon.

Globaria sp. 'Craigieburn'

Fruitbodies to 30mm, initially white, with fugacious spines, becoming papery and smooth, with reddish brown colours to the base of the fruitbodies, and endoperidium staining yellow. Gleba reddish brown and no sterile base. Capillitium of the intermediate type, not heteromorphous, with pits and with pseudocapillitium hyphae. Spores globose, smooth, 4.5um diam., without pedicel but small hyaline stub.

In his monograph of Australasian species Cunningham covered several species in this group: *B. pusilla*, *B. coprophila* and *B. apedicellata*. The latter two species were not recorded from New Zealand. *B. apedicellata* was a replacement name for Lloyd's *Bovistella pusilla*. In 1967 Kreisel revised species of *Bovista* and synonymised *B. apedicellata* with *B. coprophila*. In examining Cunningham's specimen under the name *B. apedicellata* he decided there were two species present, and he newly described one of them as *B. cunninghamii*. He distinguished the two species by *B. coprophila (apedicellata*) having a conspicuously heteromorphous capillitium, without pits, and with finely asperulate spores, whereas *B. cunninghami* was described without a heteromorphous capillitium, and with small pits, and with smooth spores. However, later examination of the type using SEM reveals the spores are finely asperulate.

Kreisel did not examine the type of another similar species *Lycoperdon reticulatum*, described with smooth spores from New Zealand. Kreisel accepted Cunningham's synonymy of *L. reticulatum* with B. pusilla, for which Cunningham listed New Zealand specimens. No modern specimens have been found corresponding to *B. pusilla* in the true sense and I think it quite likely that *L. reticulatum* provides the basis of a name for *B. sp. 'Craigieburn'* and perhaps also an earlier name for *B. cunninghami* in Kreisel's sense, and *B. pusilla* in Cunningham's sense (for New Zealand specimens). However, a phylogenetically anomalous specimen (JAC14811) also needs to be considered for these names. More modern collections and type studies are needed.

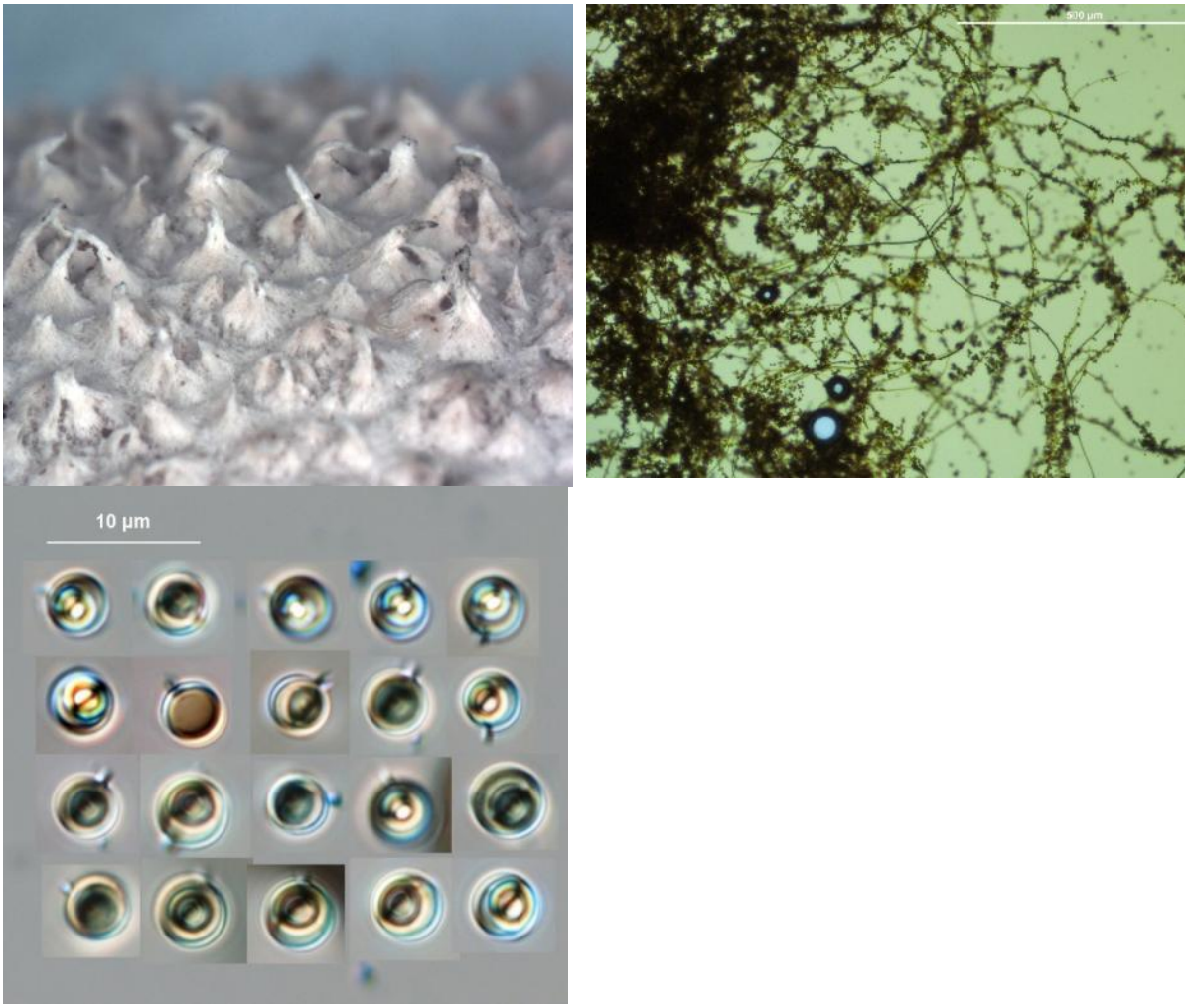


Figure 18 *G. sp. 'Craigieburn'*; fruitbodies, peridium, capillitium & spores - JAC14397

Apioperdon

This is another relatively new genus introduced for the northern hemisphere *Lycoperdon pyrifome* (the stump puffball or pear-shaped puffball) and is not phylogenetically within the *Lycoperdon* clade. *L. pyriforme* grows on rotting wood and is associated with prominent rhizoids and has a white subgleba. *L. pyriforme* is not present in New Zealand. We do have a closely related species in the genus which has much coarser and darker granules covering the immature peridium, a different shape, but does share the presence of a white subgleba and rhizoids.

Apioperdon sp. 'Monowai'

Fruitbodies to 60mm, subglobose (not pyriform) with a tapering root and copious rhizoids, on very decayed wood or woody debris in soil. Peridium initially covered with small brown fugacious stellate warts. Gleba brown, with a pale sterile base and no membrane. Capillitium of the Lycoperdon type, with no pits, and with an abundant paracapillitium. Spores 3.8-4.2um diam., dark brown, smooth to minutely asperulate, without a pedicel.

This is Cunningham's concept of *L. pyriforme* in New Zealand and it can easily be confused with *L. sp. 'Okuti'*. The latter has a distinct tap root and no rhizoids, and *L. sp. 'nigroperlatum'* has rhizoids and a different shape and a brown subgleba.

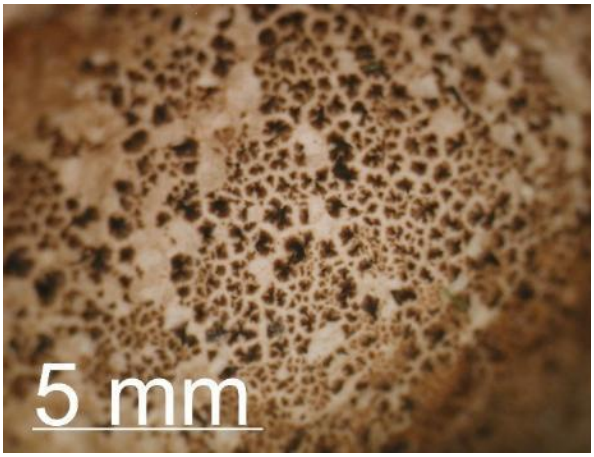
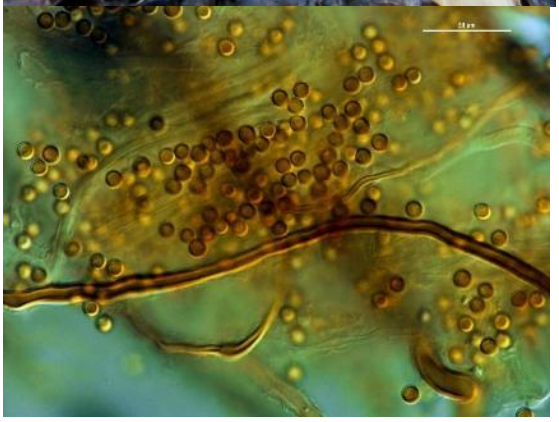
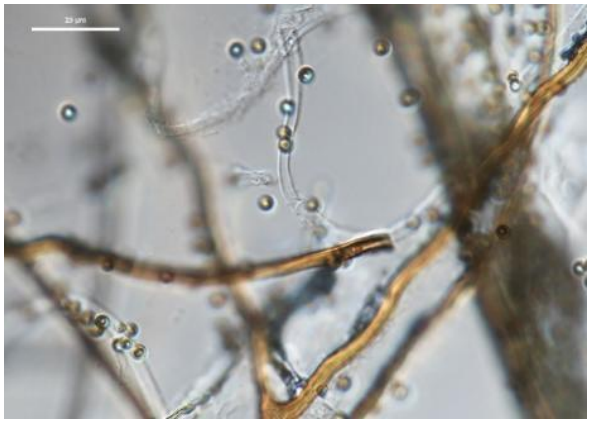


Figure 19 *L. sp. nigroperlatum*; fruitbodies, expoperidium, gleba & spores - JAC12641





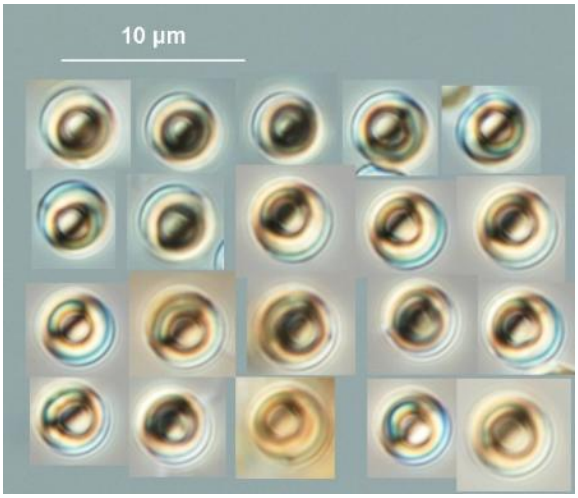


Figure 20 *L. sp. 'nigroperlatum'*; fruitbodies, capillitium & spores - JAC14189

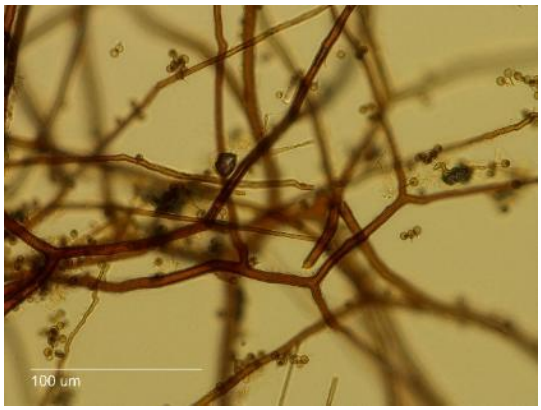
Bovista

Bovista in the true sense is characterised by a capillitium of the Bovista type. By far the most common species in New Zealand is the introduced *B. plumbea* associated with pasture and lawns. If a species is *Bovista*-like but in native grass/herb fields then it is probably *B. brunnea* or *Globaria sp. 'Cragieburn'*. These two species do also occur in modified grassland and lawns but neither have the lead-grey endoperidium of mature *B. plumbea*.

Bovista brunnea

Fruitbodies to 25mm diam., subglobose, white, smooth but maturing with mosaic depressions. Capillitium of the Bovista type with long tapering terminals, with pits, no hyaline hyphae. Spores globose, 4.8um diam., weakly verrucose, with distinct brown pedicel.

The name has been misapplied in Australia to a species in the *L. glabrescens* group, and probably also misapplied in South America. In New Zealand if another species turns up in *Bovista* sensu stricto then the name *B. gunnii* is a possibility. It is said to have a capillitium of Lycoperdon type and may conceivably represent a true *Lycoperdon* in the Sinoperdon group.



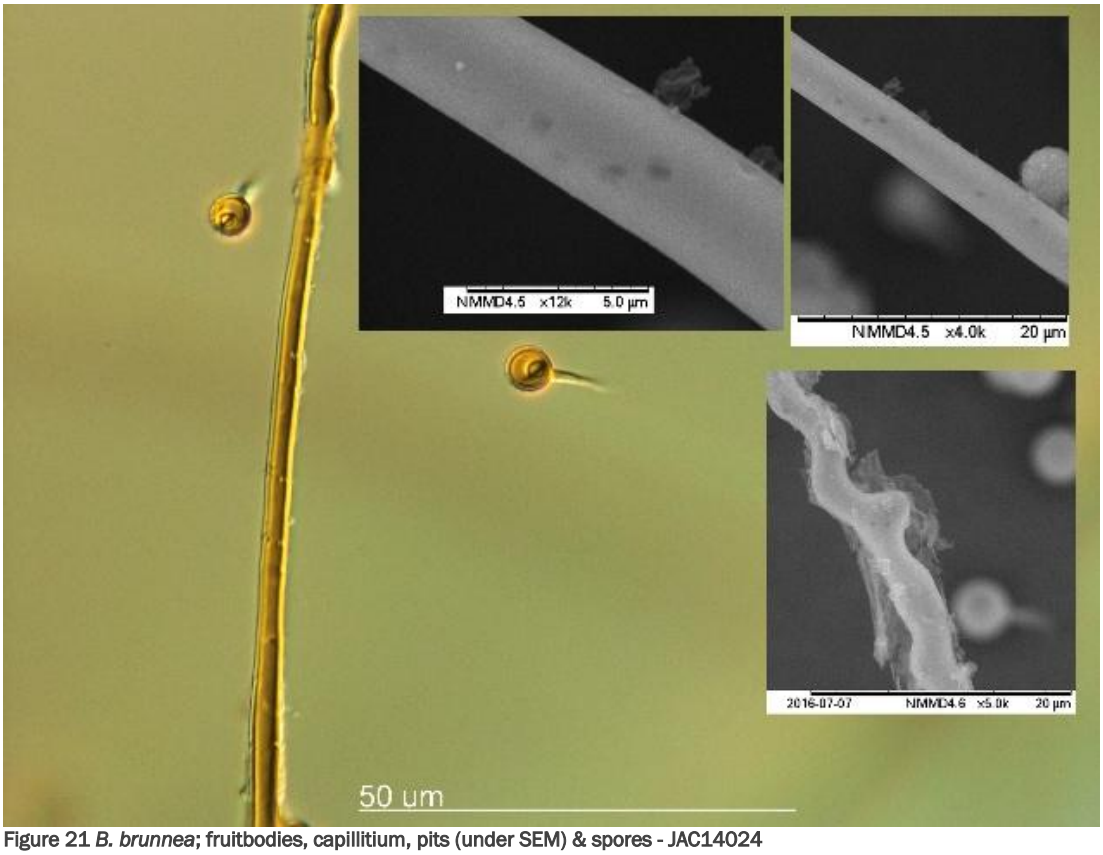


Figure 21 *B. brunnea*; fruitbodies, capillitium, pits (under SEM) & spores - JAC14024

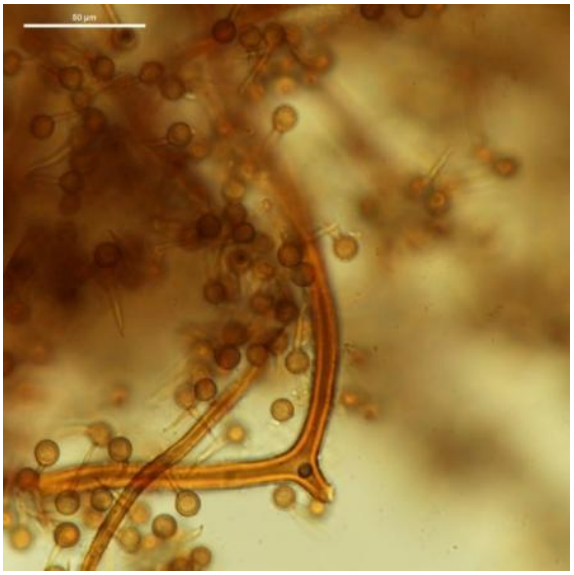


Figure 22 *B. brunnea*; capillitium & spores - PDD 91327

Bovista plumbea

Syn. *B. purpurea*

Fruitbodies to 30mm diam., globose, white, flaking off at maturity to reveal a lead-grey shiny endoperidium. Gleba yellow/brown/olive, no sterile base. Capillitium of the Bovista type. Spores smooth to asperulate, with long brown pedicel.

Cunningham described B. purpurea based on a New Zealand specimen, but it represents variation with *B. plumbea*.

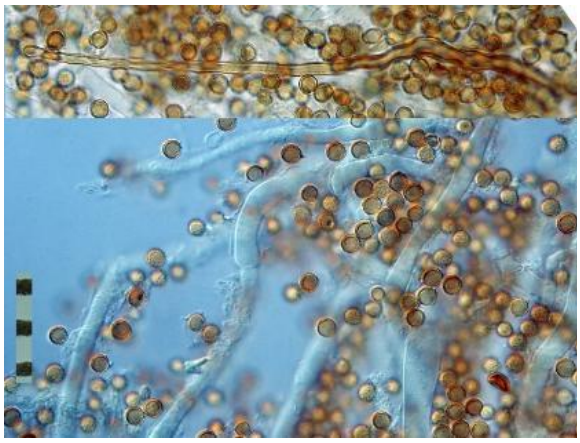


Figure 23 *B. plumbea*; fruitbodies, capillitium - JAC10565

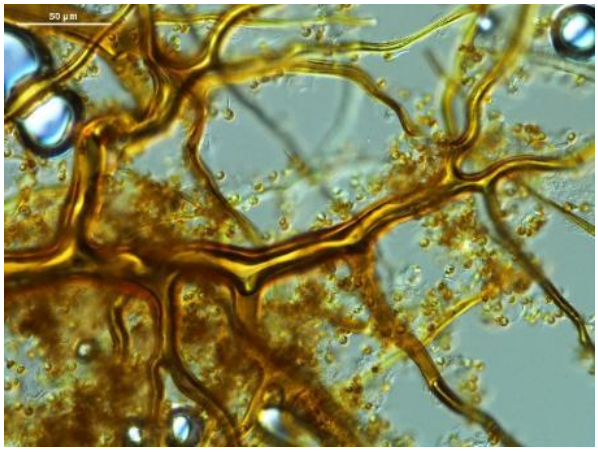


Figure 24 *B. plumbea*; immature fruitbodies, capillitium - JAC9546

Lycoperdaceae gen. nov.

Fruitbodies to 20mm diam., white, peridium covered in fine granules. Gleba olivaceous, no sterile base. Capillitium of the Bovista type but pale olivaceous and frequently septate, densely pitted. Spores 4um diam., smooth (but perhaps very weakly asperulate), pale, without a pedicel.

The single New Zealand collection of this *Bovista*-like species from a modified habitat is a bit of an oddity. From a phylogenetic perspective it seems basal to the main *Lycoperdon* group but confirmation requires the sequencing of more genes. Deposited sequences indicate related species are present in Asia and North America from modified habitats where they have been misidentified as *Bovista pusilla* and *B. dermoxantha*.

This is another candidate for *Lycoperdon reticulatum/B. cunninghamii*. The type of the former needs examining to determine if the capillitium has septa. For *B. cunninghamii* it seems unlikely that Kreisel would have missed this character.

Figure 25 *Lycoperdaceae gen. nov*. fruitbodies, capillitium & spores - JAC14811

Lycoperdon

1	Fruitbodies with a rooting stipe, no paracapillitium, spores without pedicel or subpedicellate	2 (subg. Holocotylon)
1	Fruitbodies without a rooting stipe	4
2	Fruitbodies subglobose above, with dark brown deciduous granules when immature.	*L. sp. 'Okuti'*
2	Fruitbodies pyriform above	3
3	Peridium becoming grey polished, without rhizoids, spores to 5.5um, modified habitats	*L. sp. 'Groynes'*
3	Peridium becoming brown polished, small, with rhizoids, spores to 4.5um, native habitats	*L. sp. 'Mt Lyford'*
4	Fruitbodies > 4cm diam. Eventually pestle-shaped, modified habitats	L. *excipuiforme* (subg. Utraria)
4	Fruitbodies < 4cm diam. If pestle-shaped then native habitats	5
5	Fruitbodies pyriform, with a flattened top, in modified grassland. Paracapillitium dominant.	*L. pratense* (subg. Vascellum)
5	Fruitbodies pyriform or not, with a rounded apex, native bush/forest. Paracapillitium absent or not dominant	6
6	Fruitbodies lignicolous or terrestrial with wood fragments in soil, with copious rhizoids.	7
6	Fruitbodies terrestrial, without rhizoids	8
7	Peridium with brown spines < 2mm, forming a mosaic-like pattern, deciduous, leaving white scars when removed. Eucapillitium and paracapillitium present.	*L. sp. 'nigroperlatum'* (subg. Lycoperdon)
7	Peridium with black spines> 3mm, deciduous, leaving a reticulate pattern. Only a paracapillitium present.	*L. compactum* (subg. Morganella)
8	Fruitbodies pestle shaped, to 100 mm tall, spores without long pedicels	*L. colensoi* (subg. Lycoperdon)
8	Fruitbodies turbinate to pyriform, < 5cm tall, spores with long pedicels	9 (subg. Sinoperdon)
9	Fruitbody peridium with long pale brown spines	*L. scabrum*
9	Fruitbody peridium with short warts not long spines	10
10	Without basal rhizoids, subgleba reduced, pedicels to 15um	*L. glabrescens* #1
10	With basal rhizoids, subgleba distinct, pedicels to 8um	*L. glabrescens* #2

Lycoperdon contains the majority of our species, and some are difficult to distinguish. I mentioned earlier that I have chosen not to accept the recent segregate genera within the *Lycoperdon* clade. Some of these genera aligned with accepted historical sub-divisions of the genus, and some do not. Recognition as separate genera is not helpful or necessary in my opinion.

Cunningham recognised 14 species in his concept of the genus *Lycoperdon*. For New Zealand he recorded *L. hiemale L. compactum*, *L. pyriforme*, *L. perlatum*, *L. spadiceum*, *L. polymorphum*, *L. pusillum* ,*L. glabrescens*, *L. scabrum* and *L. gunnii*.

Some of Cunningham's adopted names were originally described from Australia and disentangling the modern meaning of those names will require considerable work on Australian specimens. Since Cunningham's revision several species he recorded for Australia have also been recorded for New Zealand. Most of these records require careful re-assessment and I doubt most are correct.

Here is my interpretation of Cunningham's New Zealand species he placed in *Lycoperdon*:

L. hiemale (northern hemisphere name) = introduced subg. Vascellum *L. pratense*

L. compactum = native subg. Morganella *L. compactum*

L. pyriforme (northern hemisphere name) = native *Apioperdon sp. 'Monowai'*

L. perlatum (northern hemisphere name) = native L. subg. Lycoperdon *L. colensoi*

L. spadiceum (northern hemisphere name) = native subg. Holocotylon (1 of 3 candidates)

L. polymorphum (northern hemisphere name) = native subg. Holocotylon (1 of 3 candidates)

L. pusillum (northern hemisphere name) = native subg. Holocotylon (1 of 3 cadidates)

L. glabrescens (Australian name) = native subg. 'Sinoperdon' 1 of multiple native species

L. scabrum (Australian name) = native subg. 'Sinoperdon' *L. scabrum*

L. gunnii (Australian species) = *Bovista gunnii* status uncertain (a *Bovista* for Kreisel & Grgurinovich, but potentially Lycoperdon subg. Sinoperdon.)

For species described from New Zealand (and which we cannot ignore), and within the modern (and generally accepted) concept of *Lycoperdon*, we need to work out what Cunningham meant by *L. compactum*, *L. colensoi*, and *L. scabrum*. Fortunately, we have good modern candidates for all of them.

Lycoperdon subgenus Holocotylon

From a phylogenetic perspective this group of species sits within a clade that contains *Holocotylon bridgearum*. That species has a peculiar gleba consisting of disrupted plates rather than a fluffy capillitium. That character does not extend to other species in the clade. It isn't clear what other morphological characters separate this subgenus. For the New Zealand species then the presence of a rooting stipe seems diagnostic. Cunningham adopted three northern hemisphere names in this group: *L. spadiceum*, *L. polymorphum* and *L. pusillum*. I suspect all three concepts represent variants of a single species, *L. sp. 'Mt Lyford'*.

Lycoperdon sp. 'Okuti'

Fruitbodies terrestrial to 30mm diam., subglobose, with rooting stipe, peridium with brown granules, gleba brown, small sterile base, no membrane. Capillitium of the Lycoperdon type, without pits, spores globose/subglobose, 4-5um, smooth to very finely asperulate, without pedicel or sub-pedicellate.

The species does not convincingly match any of the descriptions by Cunningham. It is probably a native species as it occurs on the Kermadec islands as well as the mainland.

Figure 26 *L. sp. 'Okuti'*; fruitbodies, capillitium & spores - JAC13291

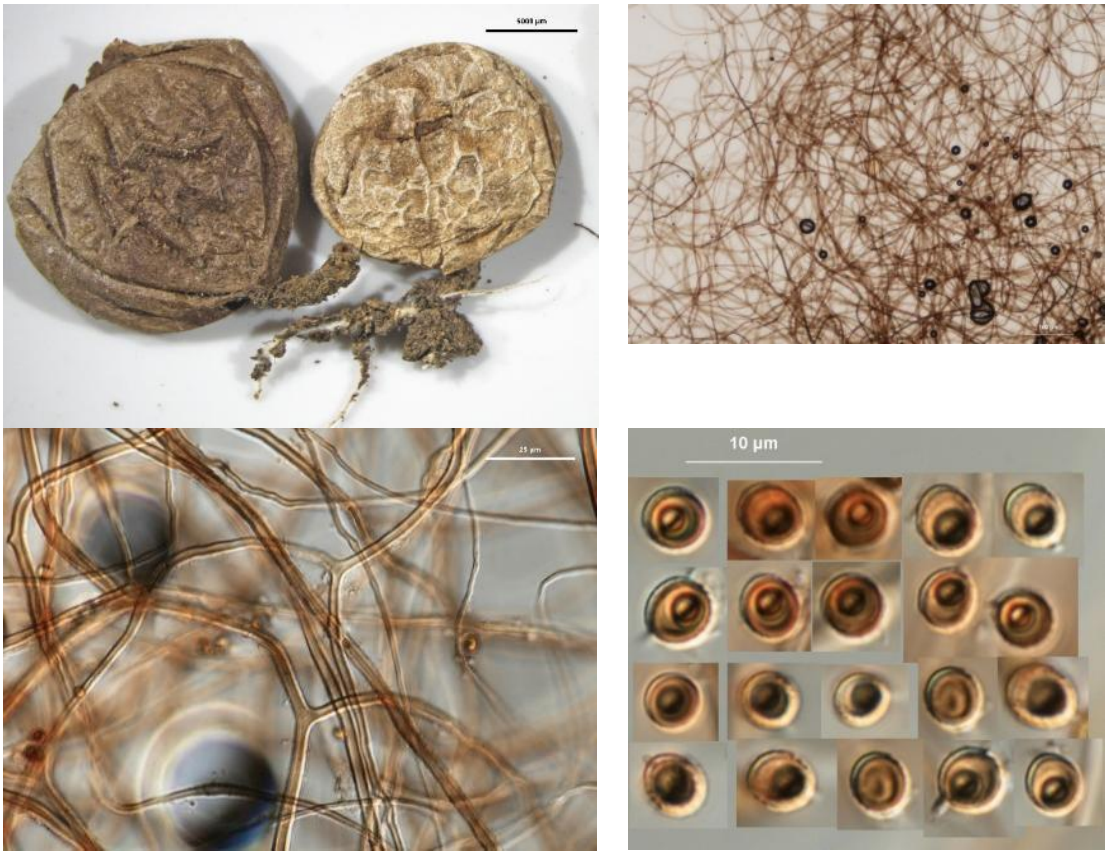


Figure 27 *L. sp. 'Okuti'*; dried fruitbodies, capillitum & spores - JAC16922

Lycoperdon sp. 'Groynes'

Fruitbodies terrestrial, to 30mm diam., with a well-developed pseudostipe extending into a rooting stipe, exoperidium initially white becoming brown, very finely pubescent or with very small granules and soon becoming polished. Gleba brown to olivaceous, subgleba present, of sterile cells < 1mm diam., no membrane. Capillitium of the Lycoperdon type, pitted. Spores globose, to 4.5-5.5um diam., pale, smooth to finely asperulate, with short sub-pedicel.

The species does not convincingly match any of the descriptions by Cunningham. It is probably an introduced species.

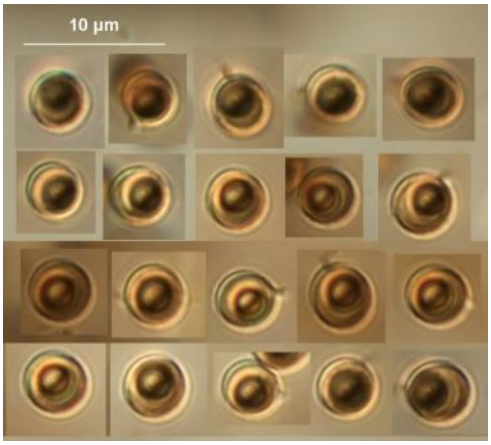
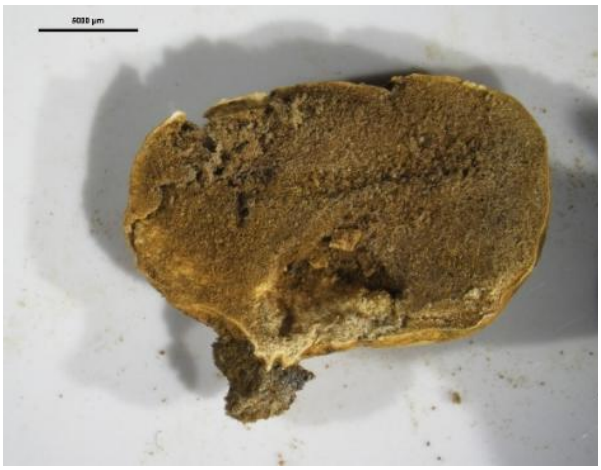


Figure 28 *L. sp. 'Groynes'*; fruitbodies, capillitium & spores - JAC17126



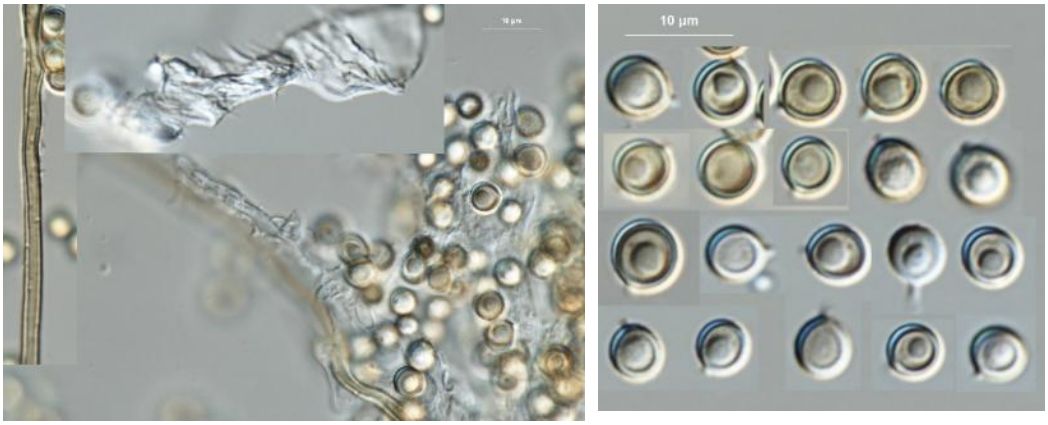


Figure 29 *L. sp. 'Groynes'*; fruitbodies, capillitium & spores - JAC16660

Lycoperdon sp. 'Mt Lyford'

Fruitbodies terrestrial, to 20mm, pyriform, with an extended tap root and copious rhizoids, peridium cream becoming reddish brown, very finely pubescent but rapidly becoming polished. Gleba olivaceous, with sterile pale subgleba, no membrane. Capillitium of the Lycoperdon type, with pits. Spores globose, 4-4.5um diam., asperulate, subpedicellate.

This is in Cunningham's group of *L. spadiceum*, L. *polymorphum* and L. *pusillum*, where it most resembles his concept of *L. spadiceum* in having fruitbodies with a sterile base. There may be an Australian name for this native species.

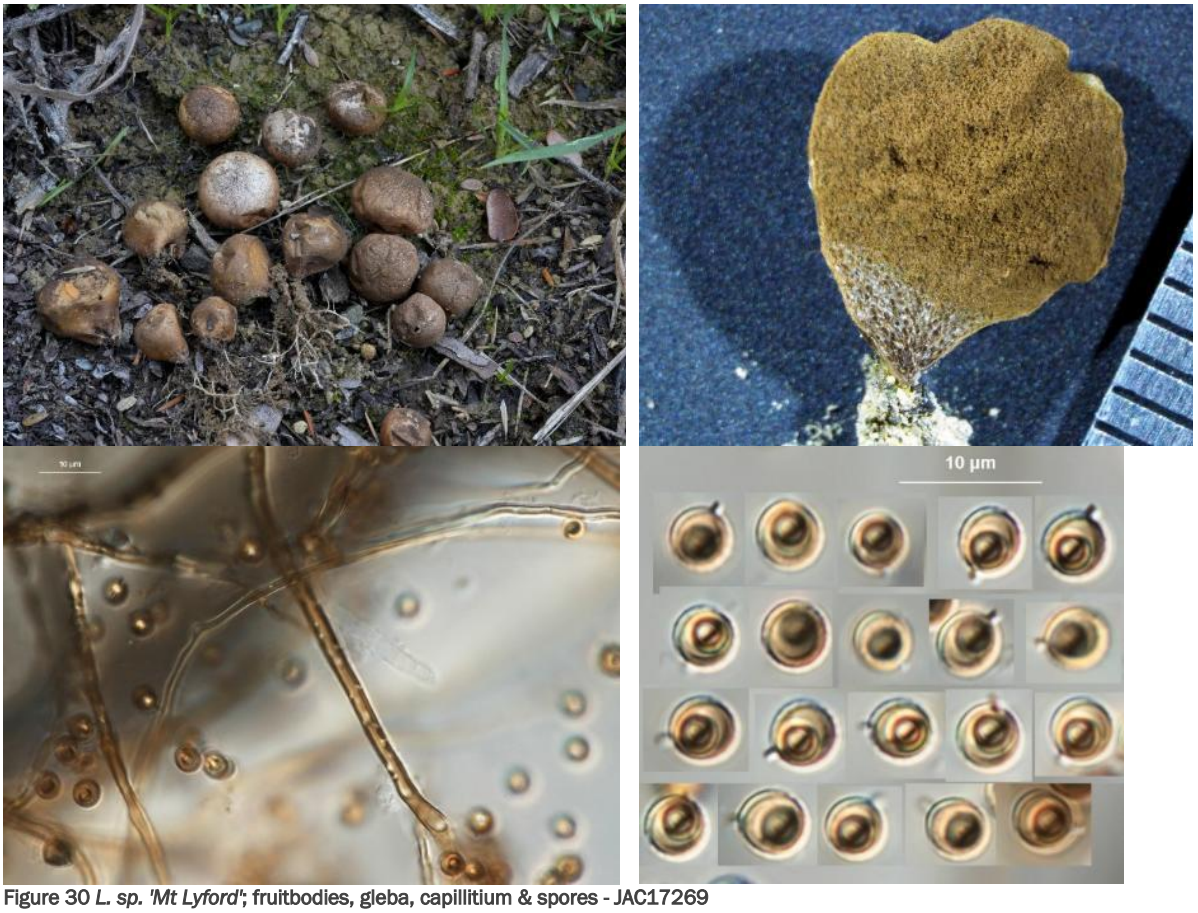


Figure 30 *L. sp. 'Mt Lyford'*; fruitbodies, gleba, capillitium & spores - JAC17269

Figure 31 *L. sp. 'Mt Lyford'*; fruitbodies - JAC17205

Lycoperdon subgenus Utraria

Lycoperdon excipuliforme

Fruitbodies relatively large, 40-70 mm diam., by 100-150mm high, subglobose becoming pyriform and finally pestle-shaped. Peridium initially white and covered with small white spines, eventually becoming brown. The upper exoperidium disintegrating with age to leave the just the base. Gleba brown, subgleba sterile, of cells < 1mm diam. Capillitium of the Lycoperdon type, with slit-like pores, no paracapillitium. Spores verrucose, globose, without pedicel but usually with long fragments of the sterigma present and obvious in slides.

This is a relatively large introduced species in modified grassland habitats and commonly known in the northern hemisphere as the 'pestle-shaped puffball'. It seems to have a northern distribution in New Zealand and isn't a species I have yet seen (in New Zealand) and so the microscopy is limited. Along with *L. utrifome* it has slit-like pores on the capillitium, but that species has smooth (or nearly smooth) subglobose spores. Both *L. excipuliforme* and *L. utriforme* have been frequently misidentified in New Zealand. Large pestle-shaped fruitbodies (or remnant cups) in native habitats are more likely to represent the unrelated *L. colensoi* or smaller forms of *Calvatia lilacina* or *C. sinclairii*. These all have a membrane separating the subgleba, and do not have a capillitium with slit-like pits.

Figure 32 *L. pratense*; fruitbody, gleba & spores - PDD 81200

Figure 33 *L. excipuliforme*; fruitbodies & spores - PDD 117436

Lycoperdon subgenus Vascellum

The subgenus is recognisable, microscopically at least, because it has a gleba dominated by a paracapillitium.

Lycoperdon pratense

Fruitbodies 10 – 40mm, turbinate with a flattened top, peridium initially white becoming brown, covered in granules. The olivaceous gleba separated from the brown subgleba by a distinct membrane. Capillitium almost entire a paracapillitium. Spores globose, 4um diam., verrucose, without pedicel.

This introduced species is extremely common in modified grassland. When old you can frequently find the bases with a deflated upper part where the gleba has been lost down to the separating membrane. The similar *L. glabrescens* (group) does not have the flat top, or a membrane separating the gleba, and microscopically is quite different. That species occurs in both modified and native habitats but rarely modified grassland.

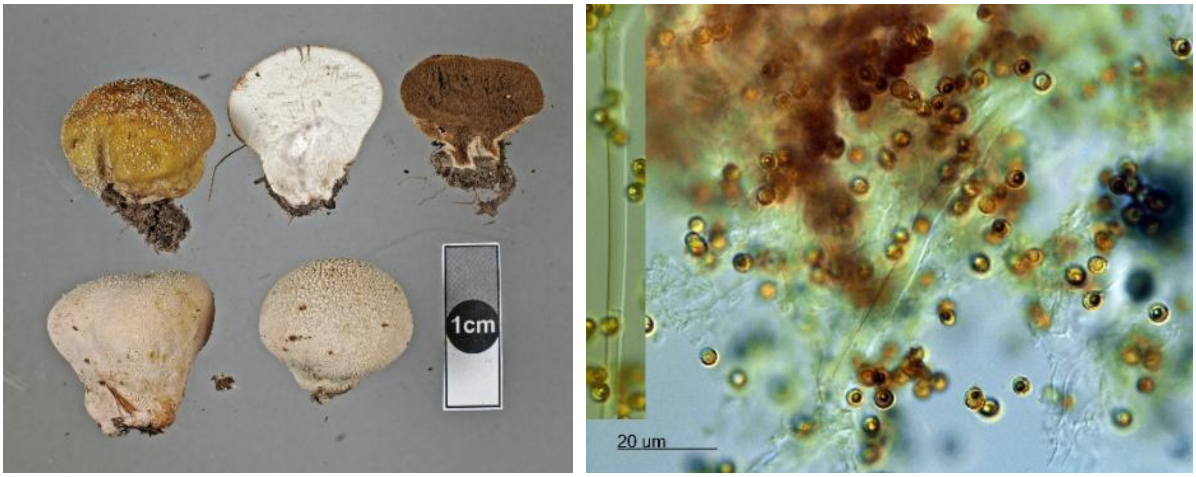


Figure 34 *L. pratense*; fruitbodies, capillitium & spores - JAC13139

Figure 35 *L. pratense*; fruitbodies - JAC17493

Lycoperdon subgenus Lycoperdon

This subgenus contains the generic type species *Lycoperdon perlatum*. Our two species are somewhat similar in appearance, but both are native.

Lycoperdon colensoi

Fruitbodies terrestrial, to 50mm diam., and 100mm tall, pestle-shaped, pale brown to grey, initially with prominent warts. Gleba becoming olivaceous, separated from the white subgleba by a weak membrane, subgleba cells sometimes > 1mm. Capillitium of the Lycoperdon type, with pits. Parcapillitiium present in the upper parts of the gleba. Spores 3.8um diam., verrucose, without pedicels, sometimes sterigmal fragments visible in slides.

This is a native species growing on the ground in native bush and forest. Macroscopically it can easily be misidentified as *L. excipulforme*. Generally, the two species occur in different habitats. Other key differences are the presence of the weak diaphragm, large sterile subgleba cells, and microscopically the presence of a paracapillitium in the upper parts of the gleba. Cunningham lumped this species under his concept of *L. perlatum*.

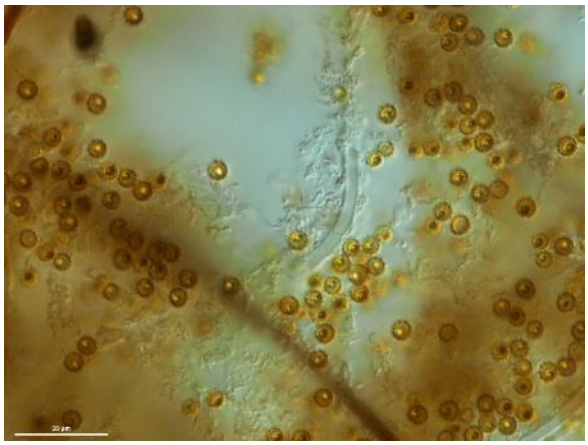
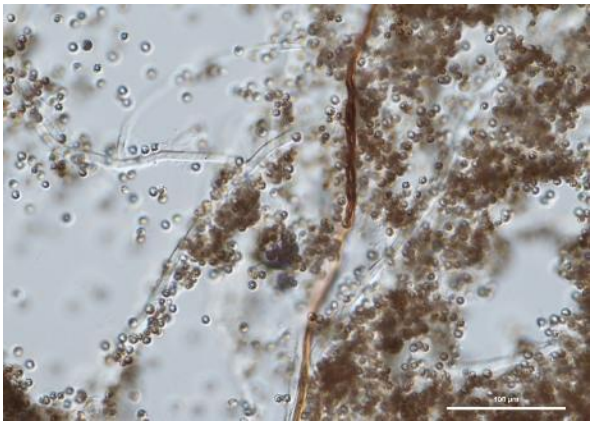


Figure 36 *L. colensoi*; capilittium & spores - JAC14605



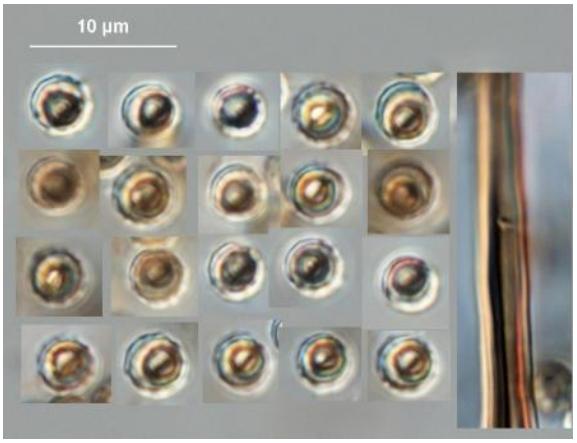


Figure 37 *L. colensoi*; fruitbodies, peridium, gleba, capillitium & spores - JAC14766

Figure 38 *L. colensoi*; fruitbodies & gleba - JAC15548, JAC13915

Lycoperdon sp. 'nigroperlatum'

Fruitbodies terrestrial/lignicolous, to 60mm diam. and 115mm tall, pestle-shaped, peridium with dark brown to black prominent pyramidal spines to 1.5mm tall, forming a mosaic-like pattern and leaving white scars when rubbed off. Gleba olivaceous brown, subgleba brown at maturity, cells > 1mm diam., weak membrane present. Stipe base with copious rhizoids. Capillitium of the Lycoperdon type, without pits. Paracapillitium present, but abundant only at the apex. Spores 3-4um diam., verrucose, without pedicels.

This is close morphologically and phylogenetically to the northern hemisphere *L. perlatum*, and Cunningham treated it under that name. It is distinguished by the reticulate pattern of nearly black spines, which are easily dislodged to leave white scars, and association with decaying wood on stumps or wood fragments in soil. The somewhat similar *L. compactum* has much larger spines. *Apioperdon sp. 'Monowai'* has a different less pestle-like shape. These all have a white mature subgleba, and a peridium that does not have white scars where granules are removed and have nearly smooth spores.

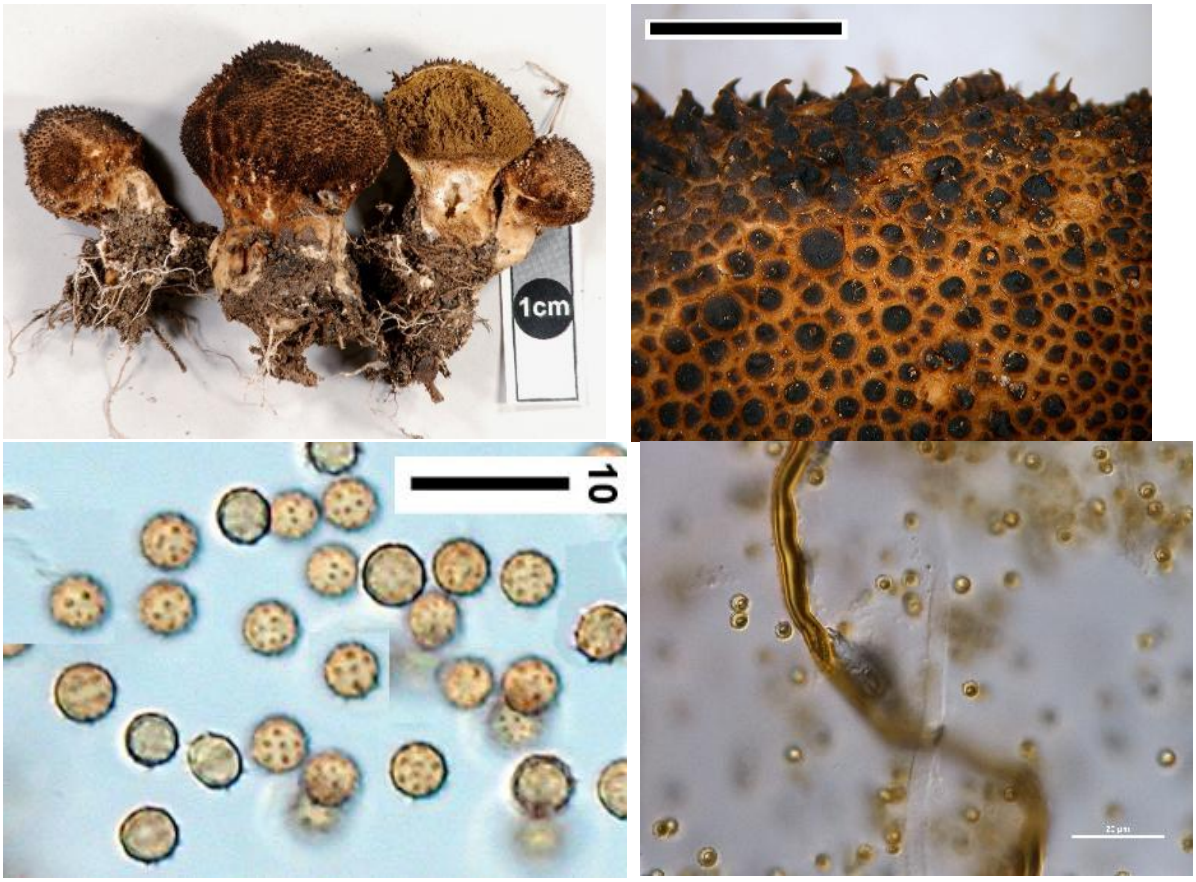


Figure 39 *L. sp. 'nigroperlatum'*; fruitbodies, peridium, capillitium & spores - JAC10420

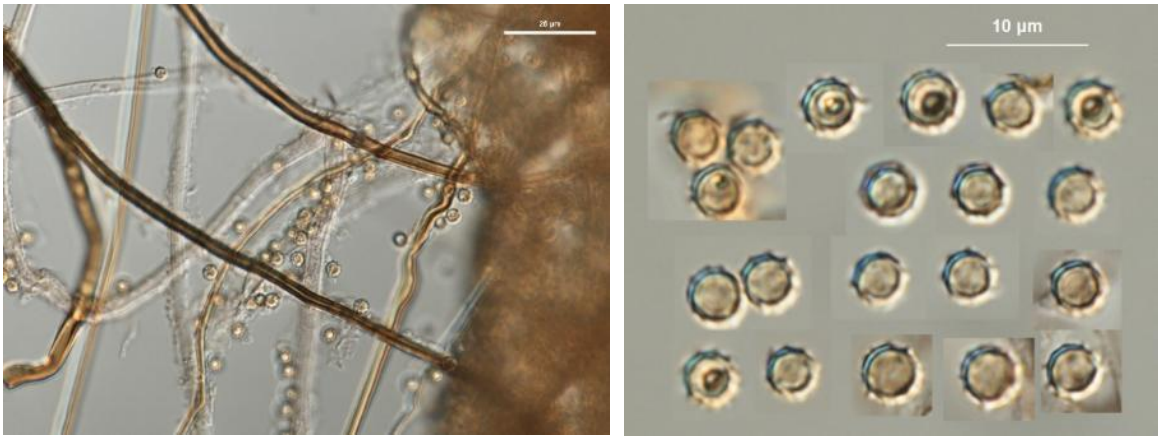


Figure 40 *L. sp. 'nigroperlatum'*; fruitbodies, gleba, capillitium & spores - JAC17492

Figure 41 *L. sp. 'nigroperlatum'*; fruitbodies, gleba, capillitium & spores - JAC15463

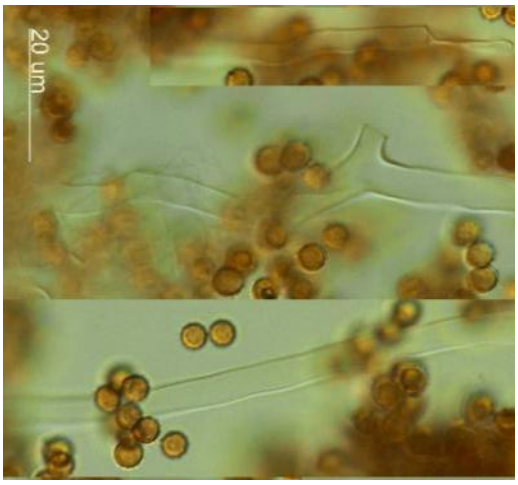

Figure 42 *L. sp. 'nigroperlatum'*; fruitbodies - JAC10893, JAC26003; JAC18506, JAC16775

Lycoperdon subgenus Morganella

Lycoperdon compactum

Fruitbodies lignicolous, to 40mm diam. Subglose to shortly pyriform, with dense black spines reaching 3-4mm and soon deciduous to leave a diagnostic reticulate pattern on the paler brown peridium. Stipe base with copious rhizoids. No eucapillitium and only a paracapillitium with associated sinuous fragments/plates. Spores globose, 4.3um diam., sparsely spiny, without a pedicel (but occasional sterigmal fragments present).

This species is lignicolous like *Apioperdon sp. 'monowai'* and *L. sp. 'nigroperlatum'*. It is easily distinguished by the relatively large deciduous black spines which are easily detached to leave a distinct reticulate pattern on the peridium.

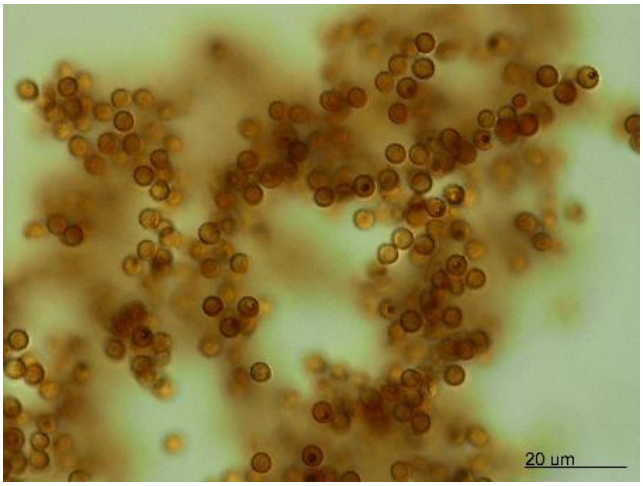


Figure 43 *L. compactum*; fruitbodies, capillitium & spores - JAC14604

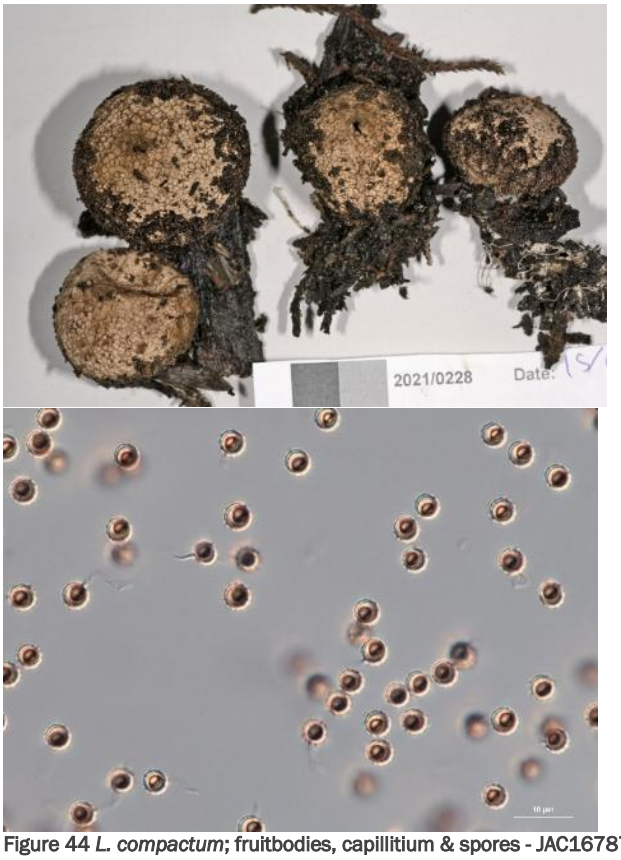


Figure 44 *L. compactum*; fruitbodies, capillitium & spores - JAC16787



Figure 45 *L. compactum*; fruitbodies - JAC14653, JAC16339

Lycoperdon subgenus Sinopoderdon (ined.)

For New Zealand species this group within *Lycoperdon* seems to be characterised by the presence of spores with long pedicels, a reduced subgleba, and absence of an obvious paracapillitium. In this respect it resembles some species of *Bovista* but those are distinguished by the possession of a Bovista-type capillitium and the total absence of a subgleba. The peridium in the Sinoperdon group can be echinulate or not and the character is not of diagnostic value. Another anomalous character is the absence of a paracapillitum in the New Zealand representatives, which is said to be abundant in the Asian species described in this group. Grgrurinovich (1997) in her study of the species in Australia indicated a paracapillitium was "virtually absent" in Australian *L. glabrescens* but I have not seen any indications of a paracapillitium in New Zealand material.

Cunningham included three New Zealand species in this group; *L. glabrescens*, *L. scabrum* and *L. gunnii*. All three names were originally described based on Australian specimens and so may or may not apply to New Zealand species. A New Zealand version of *L. scabrum* is known with reasonable certainty from a single, immature but sequenced modern specimen. That leaves us with assigning Cunningham's concepts of *L. glabrescens* and *L. gunnii* to modern specimens. *L. glabrescens* was described with a distinct (but reduced) subgleba and verrucose spores with pedicels to 20um long. *L. gunnii* was described with a small or absent subgleba and verrucose spores with pedicels to 12um long. The absence of a subgleba led Kreisel to move *L. gunnii* to *Bovista*. I think the relatively small globose fruitbodies supports that assignment, although it is possible *L. gunni* represents another species in this Sinoperdon group.

Unfortunately, none of the taxa in this group defined by sequence data do not strictly align with Cunningham's concept of *L. glabrescens*. One species with a distinct subgleba has smooth spores with long pedicels and another with a poorly developed subgleba has asperulate spores with shorter pedicels. In addition, we have a single sequenced specimen in the group, PDD 104664, for which we have no photo of fresh material or data on the micro-features. Pending the resolution of species concepts in this group I have decided to label the two main species *L. glabrescens* #1 & #2. More sequenced specimens of the different phylogenetic taxa are needed, along with detailed comparison with authentic specimens from Australia.

Lycoperdon scabrum

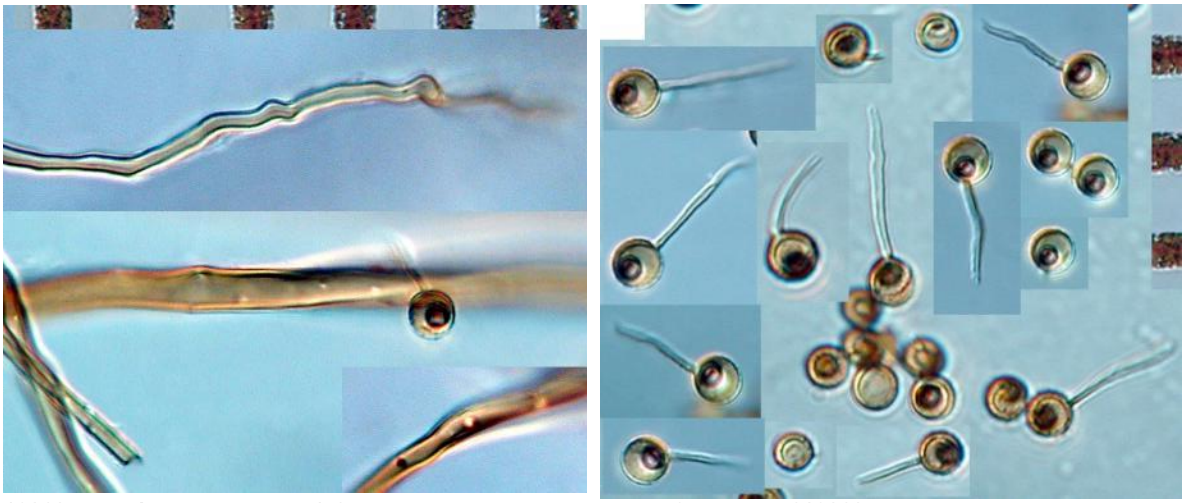
Syn. *Bovistella nigrica*

Unfortunately, we have just a single collection of this species (terrestrial, 30mm diam. With long pale spines) and it is immature. Phylogenetically it is basal to 'subgenus' Sinoperdon. It is likely this represents Cunningham's concept of *L. scabrum*, originally described from Australia. Lloyd described *Bovistella nigrica* from a New Zealand specimen and Cunningham considered it to be a darker colour form of the same species.

Figure 46 *L. scabrum*; fruitbody - JAC16114

Lycoperdon glabrescens #1

Fruitbodies to 50mm diam., 50mm tall, subglobose to turbinate/pyriform, with a pseudostipe, peridium grey-white to brown, with deciduous granules/warts, no basal rhizoids observed. Gleba brown, subgleba small. Capillitium of the Lycoperdon type, with pits. Spores brown, 5-5.5um diam., smooth, with a pedicel to 15um.



10862 Figure 47 *L. glabrescens* #1; fruitbodies, thin subgleba, capillitium & spores - JAC10862

Figure 48 *L. glabrescens* #1; fruitbodies, perdium, thin subgleba, capillitium & spores - JAC15577

Figure 49 *L. glabrescens* #1; fruitbodies & peridium - JAC17138

Figure 50 *L. glabrescens* #1; fruitbodies - JAC17139, JAC17648; JAC15678

Lycoperdon glabrescens #2

Fruitbodies terrestrial, to 60mm diam., 60mm tall, turbinate with pseudostipe, peridium grey-white to brown with deciduous granules, with basal rhizoids. Gleba olivaceous brown, with distinct subgleba, cells < 1mm, no membrane. Capillitium of the Lycoperdon type, with pits. Spores to 4.6um, asperulate, with long pedicels, to 7.5um diam., (noting that PDD 100384 is anomalous, without pedicels).

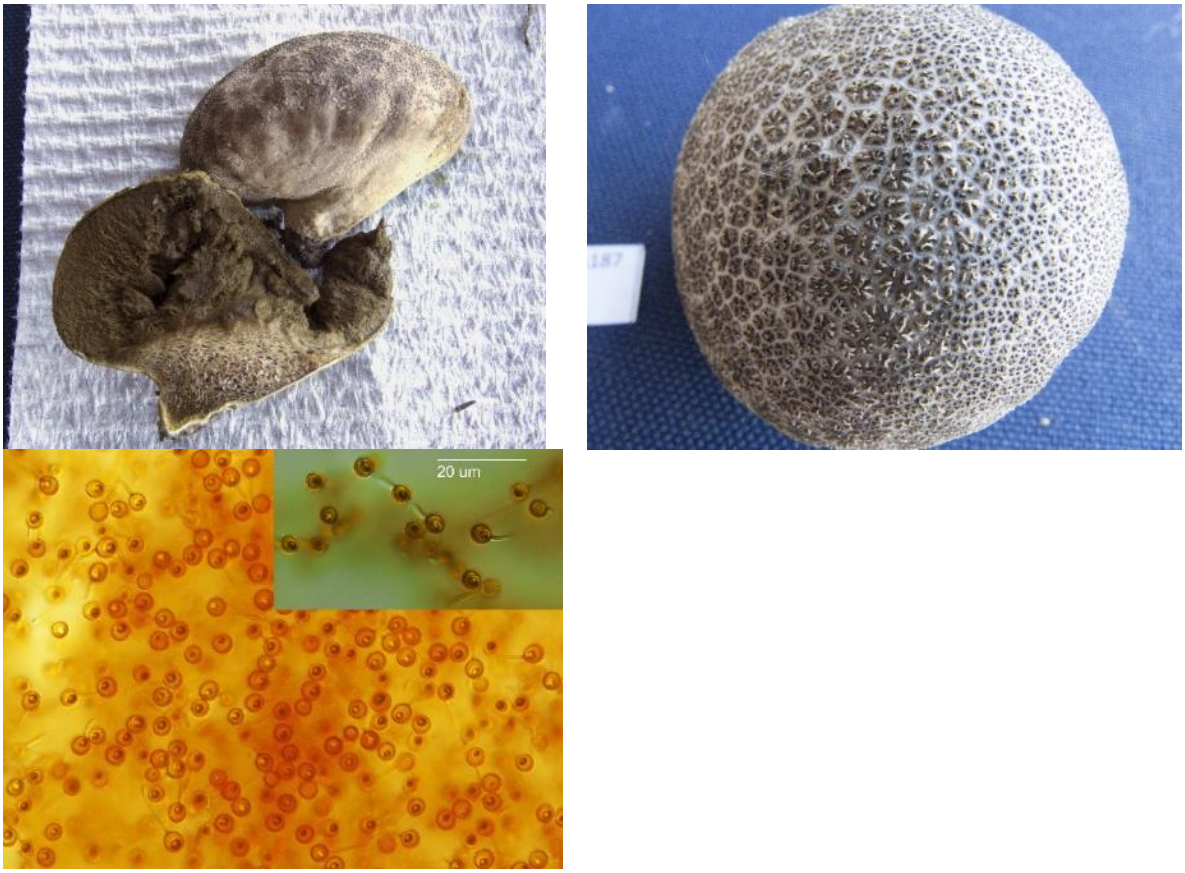


Figure 51 *L. glabrescens* #2; fruitbodies, peridium, spores - JAC14018

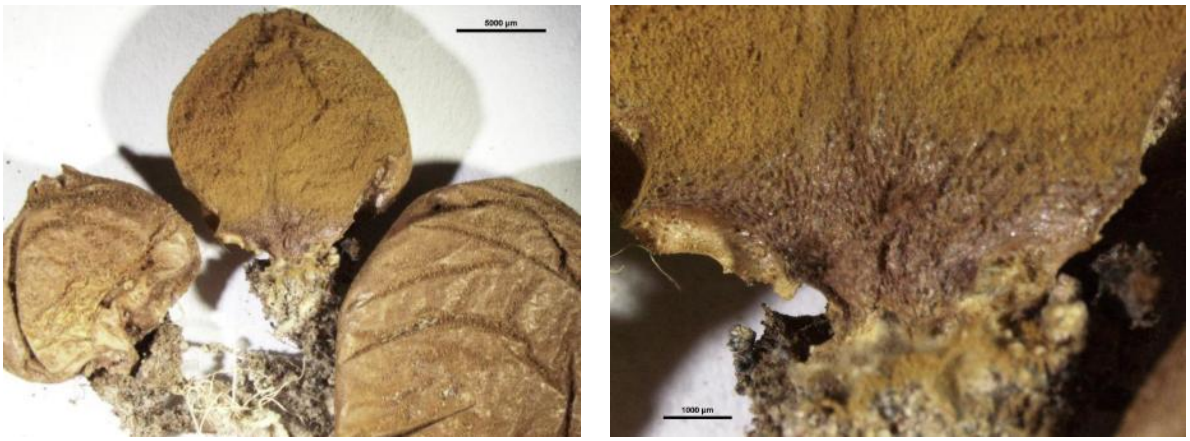


Figure 52 *L. glabrescens* #2; fruitbody (dried), capillitium & spores - PDD 100453

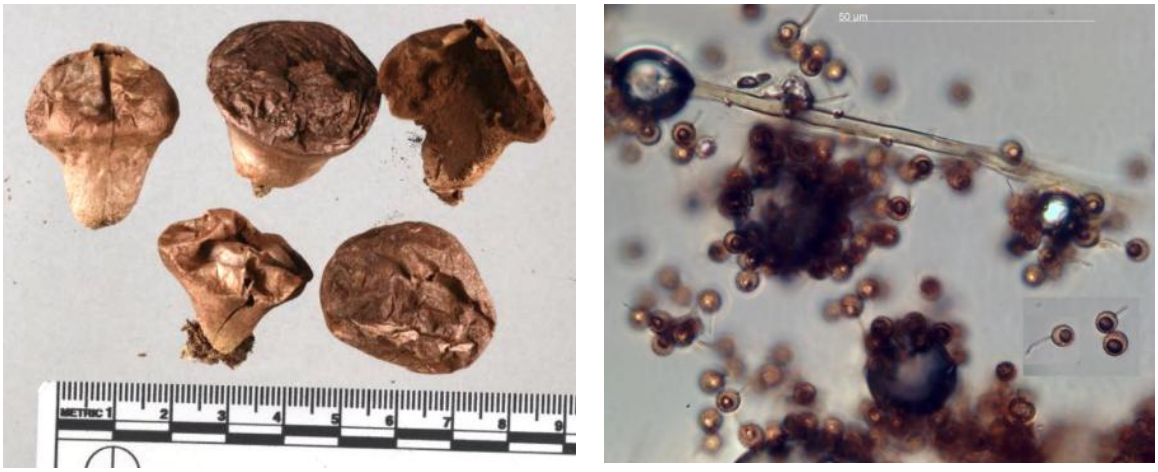


Figure 53 L. glabrescens *#2; fruitbodies (dried), capillitium & spores - PDD 89187*

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