Mycological Notes 41: The Phallales (Stinkhorns) in New Zealand.

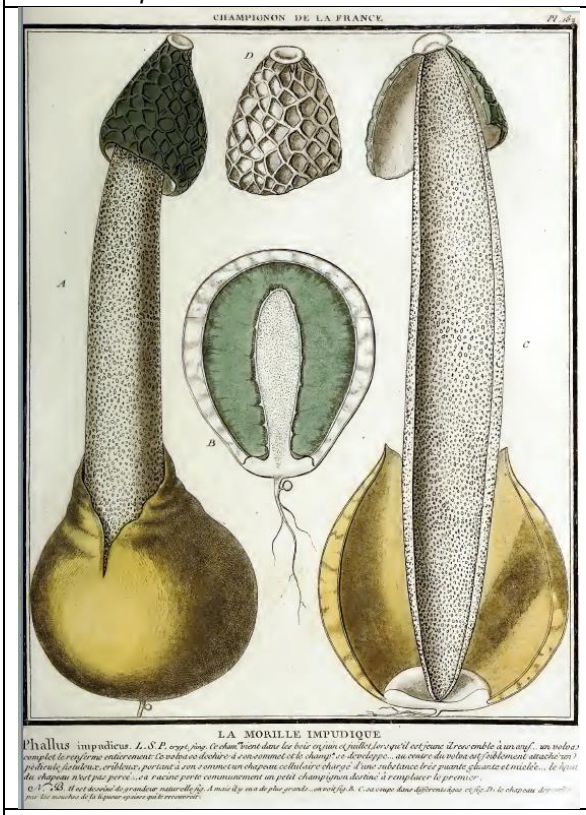
Jerry Cooper, November 12th, 2020

with contributions from Peter Buchanan

Introduction

The fungal order Phallales contains the stinkhorns and the archetypal stinkhorn is *Phallus impudicus*. The Latin scientific name *Phallus impudicus* does not need a common name to grasp its unusual appearance.

Phallus impudicus



by Jean Baptiste François Pierre Bulliard, Champignons de France, 1757

This is the classic stinkhorn fungus and like most stinkhorns the fruitbody starts as an egg-like structure in the soil litter layer connected to a buried microscopic network of branched filaments or hyphae. The egg is filled with jelly from which a shaft or tendrils rapidly emerge when ripe. They are covered in a dark slime containing spores (gleba) and often said to smell like rotting meat. Most stinkhorns are fungi you can smell long before you see them. The slime contains the spores of the fungus and the smell attracts flies and other insects that conveniently carry the spores away to new locations to spread the fungus. *Phallus impudicus* is a northern hemisphere species and is boring compared with many of our spectacular indigenous species in New Zealand.

These notes cover the New Zealand representatives of the Phallales, including some truffle-like forms. These simple forms are very similar to species in other fungal orders and not easily distinguished.

In common with many fungal groups modern phylogenetic trees derived from sequence data has revealed some surprising relationships between groups of fungi. The stinkhorns turn out to be related to the puffball-like Earthstars (in the order Geastrales), coral-like fungi in genera like *Ramaria* (in the order Gomphales), and many truffle-like species in the Hysterangiales.

Phylogenetic trees derived from sequence data can be dated so we can estimate when ancestral forms arose. The technique is subject to significant uncertainty because of the lack of recognisable and reliably dated fungal fossils used to calibrate such trees. Estimates of emergence dates for this group of fungi vary (e.g. Hosaka et al 2008). Despite the general variance the related Gomphales, Phallales, Geastrales and Hysterangiales (subclass Phallomycetidae) appear to be very old with evolutionary roots dating back to around 160 mya in the Jurassic era (Sheedy et al, 2016; Varga et al, 2019, He et al 2019). By contrast most of the familiar mushrooms and puffballs evolved on more recent timescales alongside flowering plants (~120 mya) and the diversification of mammals (66 mya). Certainly, these fungi arose well before the existence of New Zealand as a separate land mass around 80 mya, and its submergence and re-emergence 23 mya. The global distribution and diversity of modern forms in the Phallomycetidae results from ancient rafting on continents that slowly drifted due to plate tectonics (vicariance) and occasional long-distance dispersal events between separated land masses. The origin of the majority, if not all, modern forms in New Zealand will be a consequence of dispersal from nearby continents.

The ectomycorrhizal mode of nutrition, where fungi have a symbiotic relationship with plants via the exchange of nutrients between roots and hyphae, has arisen independently many times in the fungi. In the subclass Phallomycetidae most truffle-like species in the Hysterangiales are mycorrhizal whereas true Stinkhorns and Earthstars are saprophytes. However, the basal (older) groups in the Phallales containing the enigmatic *Claustula* and *Phallobata* remain untested for mycorrhizal nutrition. That is done by examining the fractions of stable isotopes which shift according food sources and trophic level (https://en.wikipedia.org/wiki/Trophic_level).

The spectacular forms we see today in the stinkhorns are testament to the power of evolutionary adaptation over staggeringly long timescales. We have little idea what early forms looked like back in the Jurassic era. Perhaps some were simpler in form than the elaborate common species today, and indeed some less common simpler forms exist today as truffle-like balls. Some such as *Protubera* are very much like stinkhorns that have not progressed beyond the egg-stage, buried in the litter layer, and decaying to release spores. These truffle-like fungi often have a powerful odour. Sometimes they are perfumed and sometimes nasty smelling, like the more familiar stinkhorns. Clearly the smell is intended to attract dispersers and the stinkhorns are well known for attracting flies. The truffle-like species are differently adapted. In many parts of the world these smelly truffle-like fungi are now dispersed by mammals, but what is dispersing these fungi here in New Zealand where we do not have native land mammals (except bats)? That is the subject of ongoing research in Manaaki Whenua. Perhaps the Moa and other extinct ground dwelling birds played the role of mammals. If that is correct these fungi might in serious trouble because they can no longer disperse, or perhaps possums and rats are filling the gap – until we eradicate them.

An overview of the New Zealand families, genera and species within the Phallales

Order Phallales

Family Clathraceae

Ileodicytyon cibarium

Anthurus archeri

Asero rubra

Clathrus chrysomycelinus (identity uncertain)

Pseudocolus garciae (identity uncertain)

Pseudocolus fusiformis (presence uncertain)

Family Claustulaceae

Claustula fischeri

Family Lysuraceae

Lysurus cruciatus

Family Phallaceae

Mutinus sp. 'Golden'

Mutinus ravenelii

Phallus impudicus (presence uncertain)

Family Protophallaceae

Protubera parvispora (Other NZ species belong in the Hysterangiales)

Family Trappeaceae (perhaps Hysterangiales)

Phallobata alba

The family Clathraceae

Ileodictyon cibarium

This is the White Basket Fungus, *Ileodictyon cibarium*, with many Māori names like kōpurawhetū, matakupenga, tūtaewhatitiri, and whareatua.

Ileodictyon cibarium	
	
Sunita Singh iNat 1011384	Peter de Lange iNat 3721501

The wrinkled geodesic lattice expands from the egg leaving the ruptured wall of the egg at its base. The slime with spores covers the inside of the wrinkled arms. The eggs are around 4-5cm in diameter and the fully expanded fruitbodies reaching 20cm.

This is an iconic New Zealand fungus and was given the western scientific name after collections made in Akaroa in the 1830s were sent to Europe. The collector was Etienne Raoul https://en.wikipedia.org/wiki/%C3%89tienne_Raoul , the surgeon on the French ship L'Aube. Of course, Māori were already aware of this fungus and reportedly used the outer part of the enclosed egg as food. It has over 35 Māori names, suggesting that it was both well-known and named differently depending on iwi and geographic region. *Ileodictyon cibarium* is present in both New Zealand and Australia according to sequence data.

The related *Ileodictyon gracile* was originally described from Western Australia and is a smaller species with thinner arms and no wrinkles. For many years it was suspected that *I. gracile*, or another species, is present in sand dunes in New Zealand. The odour of this variant seems to have less pungency. However, sequence data indicate these sand-dune versions are also *Ileodictyon cibarium*. It is worth noting a problem with some commonly referenced sequences in the literature Trierveiler-Perira et al, 2014 contains some mislabelled and perhaps misidentified material. In that paper the collections OSC 122734 & OSC107652 of '*I. cibarium*' are listed for New Zealand. Neither collection seems to represent the true *I. cibarium* from New Zealand. One of the specimens is documented as being collected from Western Australia, not New Zealand (e.g. OSC 107652 https://mycoportal.org/portal/collections/individual/index.php?occid=3874619&clid=0).

The following table contains my interpretation of the relevant collections used in that paper.

Table 1. Proposed re-assignments of sequences in Trierveiler-Perira et al, 2014

Original name	Coll ID	Verbatim Origin Country	Proposed name	True Origin
Ileodictyon cibarium	OSC 107652	New Zealand	Ileodictyon gracile	Western Australia
Ileodictyon cibarium	OSC 122734	New Zealand	Ileodictyon sp.	Australia?
Ileodictyon gracile	MEL 2024221	Australia	Ileodictyon sp.	Victoria: Australia
Ileodictyon gracile	MEL 2037639	Australia	Ileodictyon cibarium	Victoria: Australia
Ileodictyon gracile	MEL 2054561	Australia	Ileodictyon sp.	Victoria: Australia

The Australian name *Protubera canescens* for a truffle-like species represents the unexpanded (permanently?) egg stage of one or more of the Australian species of *Ileodictyon*.

Anthurus archeri

Commonly known as the Devil's Fingers. This species was originally described from Tasmania. The name *Clathrus archeri* is used in the literature but the phylogenetic data do not support the inclusion of this species in the genus *Clathrus* and the name *Anthurus archeri* is available. The species is more closely related to *Aseroe rubra* than real *Clathrus* species, and both have spread around the globe on wood chips. In New Zealand it is found in modified habitats and is probably an introduction from Australia. It can be confused with *Aseroe rubra* from which it differs in the much larger stature and the presence of the gleba along the arms. *Aseroe rubra* is smaller and the gleba restricted to the central area. Both species eventually develop a throat at the centre, and both possess a variable pseudostipe at maturity, although it is usually more pronounced in *Aseroe rubra*. *Anthurus archeri* generally has thick arms that are not fused at the base, but sometimes fused at the tips before maturity (and then looking clathrate), whereas *Aseroe rubra* has thinner bifid arms that are never

fused at the tips. However, some of these differences are variable and should not be used to distinguish them. The distinction is also confused by a variant of *Anthurus archeri* present in the Auckland region which has consistently bifid arms but is large and has a gleba spread along the arms. The phylogenetic data indicate it is indeed marginally different to strict *Anthurus archeri* but not enough to consider it a separate species. It is however phylogenetically quite different to true *Aseroe rubra*.

Anthurus archeri

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Anthurus archeri has eggs to 4cm in diameter and an expanded fruitbody reaching 15 cm.

Anthrus archeri and *Aseroe rubra* side by side

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The Auckland variant of *Anthurus archeri*.	

	
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Aseroe rubra

This is the anemone stinkhorn which as the common name suggests, just sticks produces a few bifid (split-paired) tentacles. The species was originally described from New South Wales but unlike *Anthurus archeri* it is often found deep into native bush and may be indigenous in New Zealand, and is much more common than *Anthurus archeri*, at least south of Auckland. The gleba is restricted to the area central throat and not spread along the arms like *Anthurus archeri*. The species is always much smaller than the various forms of *Anthurus archeri*, ranging 3 -5 cm, and can be rather variable in colour.

Aseroe rubra	
	
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(c) Julie Vause, CC BY-NC. iNat 26432589	(c) emma_curtin, CC BY-NC. iNat 28587193

Clathrus chrysomycelinus

The Golden Basket Fungus was originally described from Brazil and is also known from the Caribbean, and with recent iNaturalist records from across South and Central America, but perhaps these are not all the same species. The use of the name in New Zealand is probably incorrect and it is likely ours is an undescribed and rare endemic species. Our version does not seem to possess the yellow mycelium attached to the egg stage that gives the fungus its scientific name. A confirmed distribution confined to Brazil, the Caribbean and New Zealand would also be very strange, as would an introduction just to New Zealand from Brazil. Typical iNaturalist records of *C. chrysomycelinus* from Brazil show broader arms. The New Zealand species reaches around 10cm in diameter and so is generally smaller than *Ileodictyon cibarium* and has the gleba restricted to the orange junctions on the lattice. It is known only from two locations in the North Island of New Zealand.

Clathrus chrysomycelinus auct NZ	*Clathrus chrysomycelinus* (Brazil)
	
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Pseudocolus garciae

The genus *Pseudocolus* is often placed in the family phallaceae but it does not belong there and is part of the clathraceae family. The name *P. fusiformis* has been used in the past in a rather broad sense for what are probably different species in different biogeographic regions. *P. fusiformis* was

originally described from the island of Réunion in the Indian Ocean. Presumed later synonyms have included *P. javanicus* described from Java, *P. rothae* described from Australia, and *P. schellenbergiae* described from the USA (and probably introduced there). In the original sense it is a red species, but the broad use around the world includes versions that are orange through to white in New Zealand. The more common New Zealand version is pure white, has different sequences to material labelled *P. fusiformis*, and it has recently been referred to *P. garciae* described from Brazil (like *Clathrus chrysomycelinus*). This is a small species, reaching about 4cm high when mature. There are currently no deposited sequences of *P. garciae* allowing me to verify that relationship and it would not surprise me to find the New Zealand species is an undescribed endemic. However, using the name *P. garciae* does at least distinguish this as a different, white species and not the same as *P. fusiformis*.

Pseudocolus garciae	
	
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Pseudocolus fusiformis

In addition to the relatively common white species we do have a reddish/orange version in New Zealand that must be more closely related to the real *P. fusiformis/javanicus*. We have no collections or sequences of this red form in New Zealand. Like *P. garciae* this is also a small species to 6 cm long. It can look superficially rather like an immature *Anthurus archeri* before the fingers have separated, but that is a very much larger and more robust species.

Pseudocolus fusiformis

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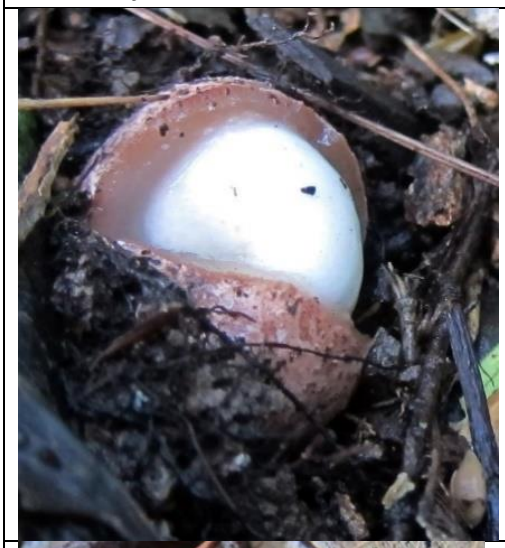
Familiy Claustulaceae

This small family contains the genera *Claustula*, *Gellopellis* and a couple of others in need of verification (in my opinion). In addition, the genera *Gellopellis* and *Claustula* may turn out to be synonyms, with *Claustula* having priority.

Claustula fischeri

The only species in this genus and is one of the oddest members of the order. Back in 1923 Kathleen Curtis (later Lady Rigg), a founding member Cawthron Institute (https://en.wikipedia.org/wiki/Kathleen_Curtis), was foraying in the hills around Nelson and came across an unusual fungus which she recognised as related to stinkhorns. She called the fungus *Claustula fischeri* in honour of the Swiss Mycologist Eduard Fisher (https://en.wikipedia.org/wiki/Eduard_Fischer_(mycologist)) and it has become known as Fischer's Egg.

Claustula fischeri	
	
	
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This peculiar fungus forms the usual egg-like fruitbody about 4-5 cm in diameter growing in the surface litter and has a gelatinous (and lubricating) inner skin. When mature the outer skin ruptures and an inner egg emerges and sometimes pops-out onto the surrounding soil, lubricated by the jelly. Initially this inner egg remains attached by a thin cord. The inner egg contains the maturing spores which are eventually dispersed, but dispersed by what?

This is a very rare fungus and the sole New Zealand survivor of an ancient lineage restricted to Australasia and South America (a Gondwana distribution). The species has been sporadically recorded over the decades in the original Nelson locality. The latest sightings have been by Wayne Hennesy in a protected area near other known locations.

Apart from the Nelson region, in the north-west, the fungus is also known from the Otago region, in the south-east. Along with many other organisms *Claustula fischeri* shows this disjunct distribution in New Zealand for which various hypotheses have been put forward. These include loss of populations in the middle of South Island due to glaciation. More interesting (and contentious) is the hypothesis these disjunct North/South populations are a consequence of the 480 km slippage of the alpine fault over the last 25 million years. Movement of the fault may have slowly rafted populations in opposite directions during the relatively recent formation of the alps and modern New Zealand.

In the mid-1990s *Claustula fischeri* was also discovered at several locations in Tasmania. Despite the increase in known sites the fungus is still considered to be very rare and under threat. Indeed, at least one location in the Nelson area was potentially threatened by the development of a mountain bike track, but amicable negotiations re-routed the proposed track.

The threats to *Claustula fischeri* are recognised and it is listed on the IUCN red-list as Endangered.

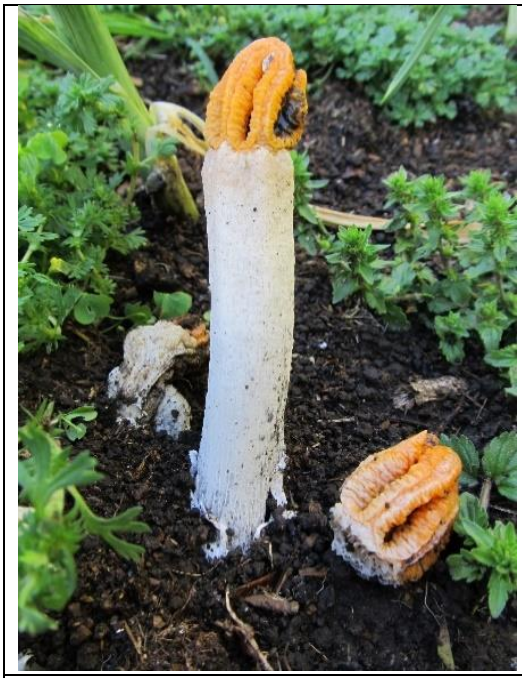
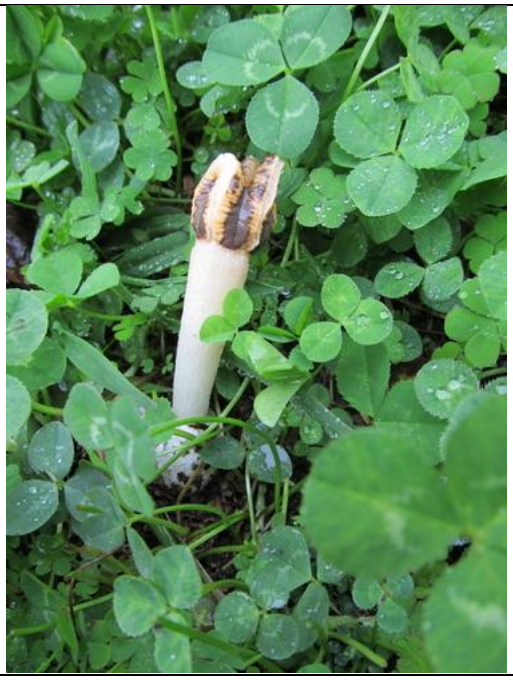
Recent increased awareness of these rare and threatened species, especially by the iNaturalist community of Citizen Scientists, has allowed us to study them in more detail. Molecular sequencing of recent Australian and New Zealand collections of *Claustula fischeri* allows us to look in more detail at the evolutionary relationships. The data indicate the Australian and New Zealand species are different but closely related, and indeed there are recorded differences in colour and form. If we have different species in New Zealand and Australia, then the conservation of remaining populations and understanding their ecology becomes even more critical.

Family Lysuraceae

Lysurus cruciatus

The Lizard's Claw Stinkhorn was originally described from French Guiana. This is another species with many synonyms and relatively few gene sequences, and no NZ material has yet been sequenced or even preserved in the national collection. Consequently, I cannot confirm the New Zealand version is the same as that reported widely overseas, although our version appears in gardens and is probably introduced. The New Zealand material is around 10cm long when mature. *Lysurus mokusin* is reported from Australia and has a reddish fluted stem. *Lysurus gardneri* is reported to have narrow sterile bases to the arms and is not confirmed as present in New Zealand.

Lysurus cruciatus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The Family Phallaceae

The family contains the traditional stinkhorn genera *Phallus* and *Mutinus*. Several species have been recorded in New Zealand, but I am not convinced the names have been applied correctly.

Mutinus

A common species of *Mutinus* in New Zealand has been called *M. bambusinus* or *M. borneensis.* These names have both been used incorrectly for what is really an undescribed indigenous species I am calling *Mutinus sp. 'Golden'*. Some other names have also probably been used incorrectly for other *Mutinus* species in New Zealand. *Mutinus elegans* is a bright orange species with a pointed apex and probably not present. *Mutinus caninus* has predominantly orange colours and not pointed, and probably not present. New Zealand records of these last two are probably a reddish coloured 'dogs stinkhorn' and are currently best referred to *Mutinus ravenelii*, originally described from South Carolina. Unfortunately, there are no reference sequences available for verification.

Mutinus sp. 'Golden'

This slender species, reaching around 12cm in length, seems to be quite common in New Zealand and Australia and is also present in New Caledonia. As stated above it has been misidentified under several inappropriate names and needs describing as a new species.

Mutinus sp. 'Golden'

Mutinus ravenelii

This red species, similar in size to *M. sp. 'Golden'*, has been recorded a few times in New Zealand. Sequence-level equivalence with the species originally described from the USA requires confirmation. It has been misidentified as *M. caninus*.

Mutinus ravenelii

PDD 100676/ PDD 82735

Phallus

A couple of *Phallus* names have been used in New Zealand, *P. impudicus* and *P. impudicus* var. *togatus*. I am not convinced that either name has been correctly. They probably refer to different introduced *Phallus* species from the Pacific Islans. Further collections and research are necessary.

Phallus sp.

PDD 71080 as *P. impudicus*

Family Protophallaceae

The family Protophallaceae is represented by the truffle-like genus *Protubera* in New Zealand. Three endemic species have been described in the genus; *Protubera hautensis*, *P. nothofagi* and *P. parvispora*. Only the last of these three is a true *Protubera*. Sequence data show the first two species belong in the order Hysterangiales. *P. hautensis* represents an undescribed genus near *Phallogaster* and *P. nothofagi* is a *Gallacea*-related species.

Protubera parvispora

In general, the genus is characterised by a very thick gelatinous outer layer covered in a white skin. The gelatinous layer has white inclusions running through it (sutures). It can look like the egg stage of *Ileodicyton cibarium*, and indeed the Australian *P. canescens* has been shown to be an *Ileodictyon*. However, in *Ileodictyon cibarium* eggs the white inclusions in the gelatinous layer are dominant, and a careful peeling of the skin reveals the latent lattice structure. In addition, in *P. parvispora* the fruitbodies are convoluted/cerebriform and not smooth eggs, and the surface bruises brown.

Protubera parvispora	*Ileodictyon cibarium* eggs for comparison
	
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Family Trappeaceae

In New Zealand the family is represented by the genus *Phallobata* with a single species known only from New Zealand. The family has been accepted as basal within the Phallales (Hosaka et al, 2006), but in my analysis it appears within the Hysterangiales and so not included in my final phylogenetic analysis. Nevertheless, it is treated here pending verification of placement.

Phallobata alba

This is an enigmatic species, growing irregularly to around 6 cm long, is known from just a few localities around the country. In many ways it has a parallel with *Claustula fisheri* in its peculiarity and rarity.

Phallobata alba

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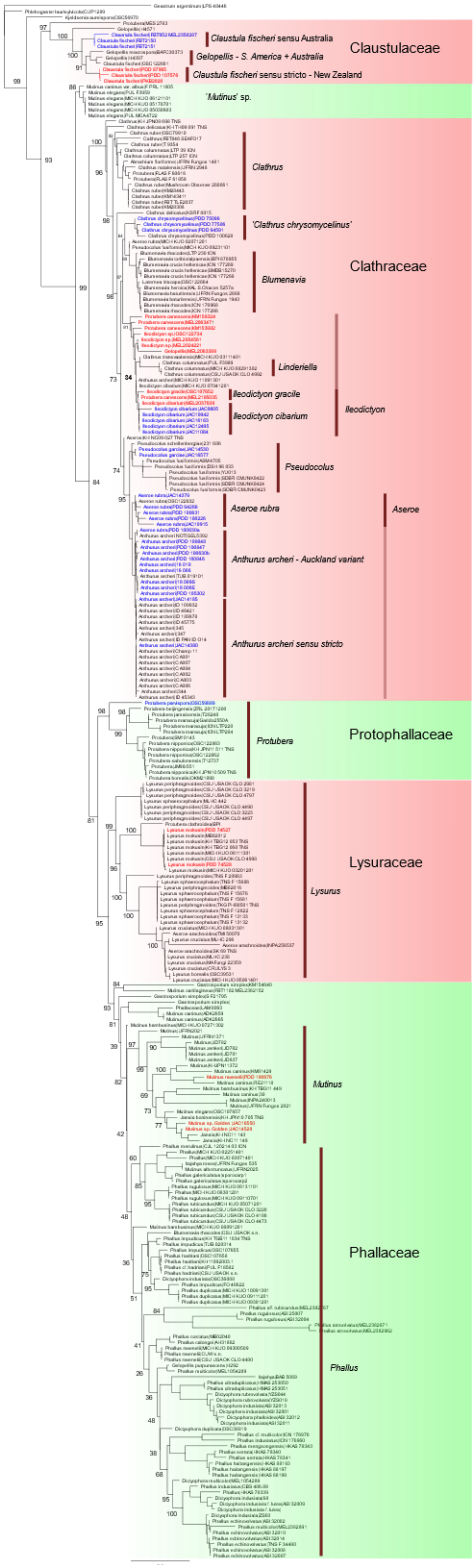
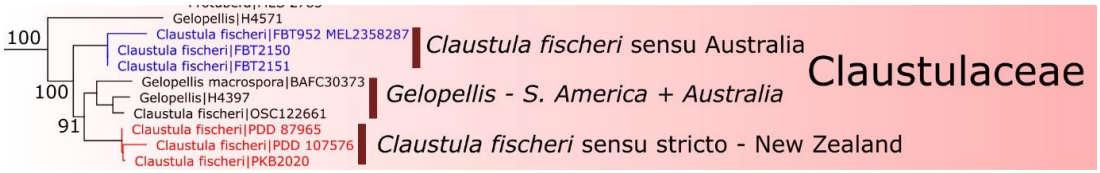
Phylogenetic Analysis

The analysis was carried out on published sequences in the relevant groups together with new sequences from New Zealand collections. The multi-gene analysis includes ITS+LSU+ATP6+SSU+RPB2+Tef. The figure shows an IQ-Tree2 Maximum Likelihood analysis of a concatenated alignment generated using Muscle.

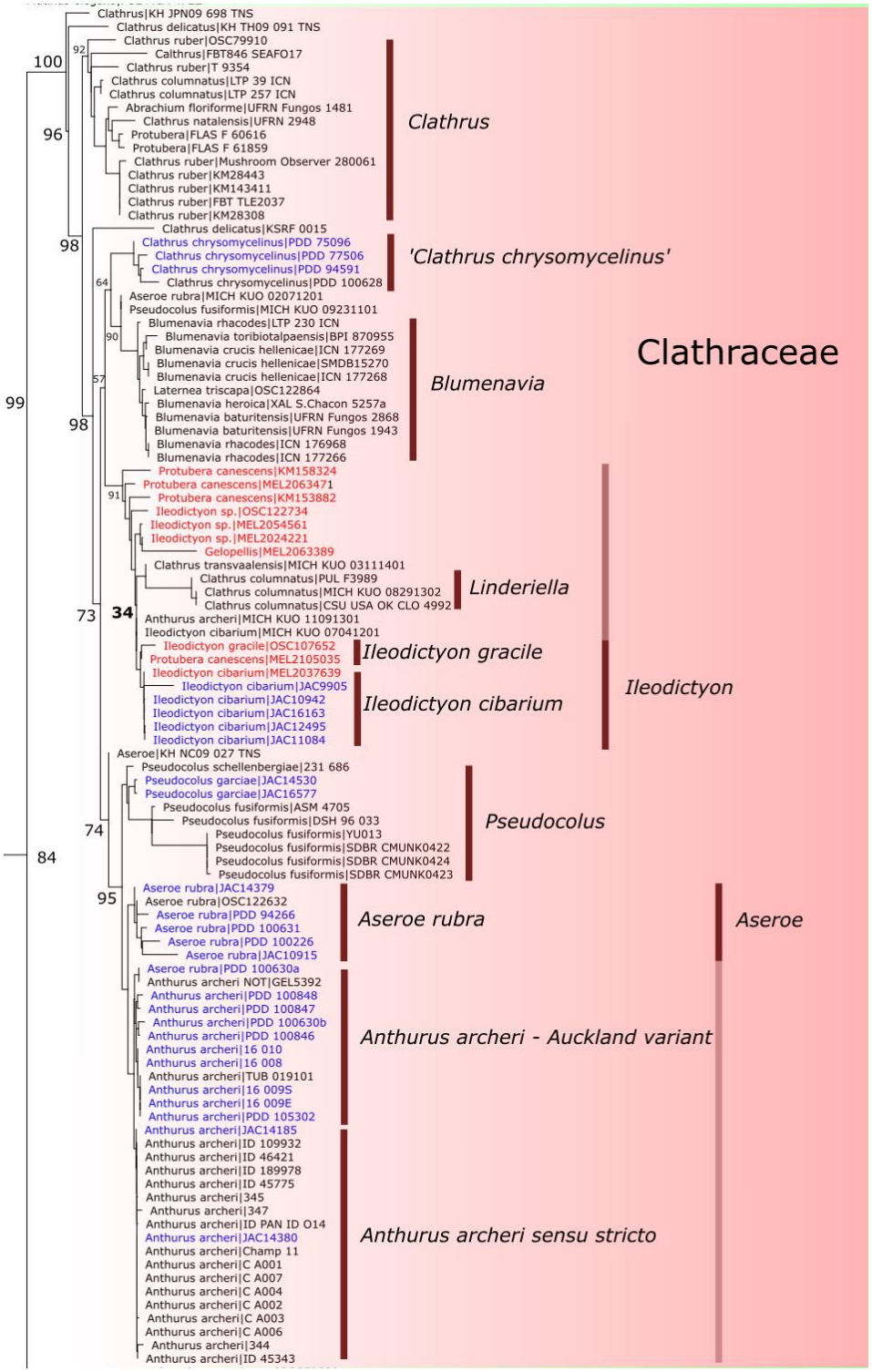
Family-level outline. Zooming in to the page should expand the following figure legibly



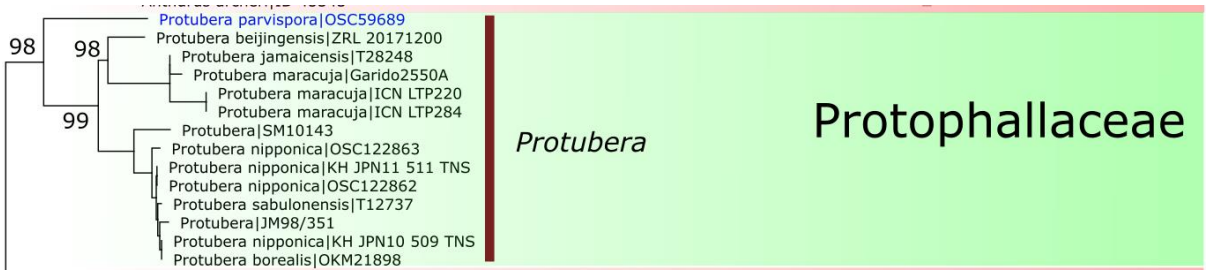
Claustulaceae



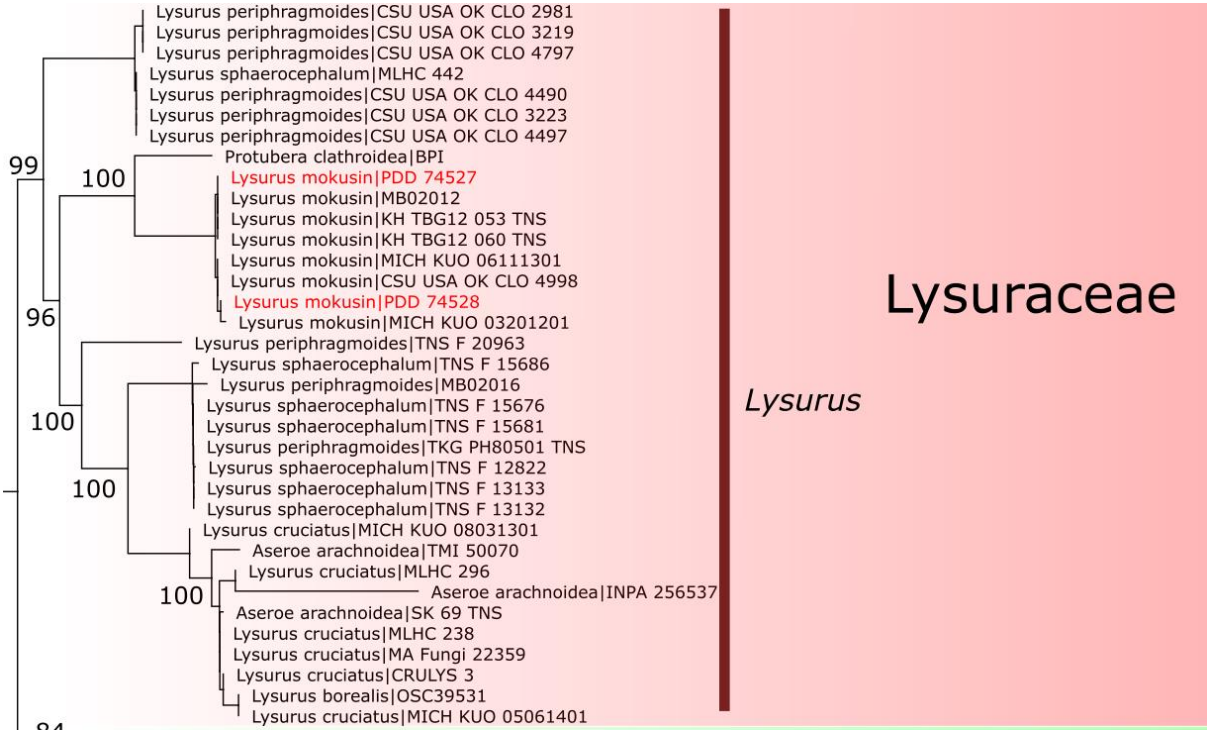
Clathraceae



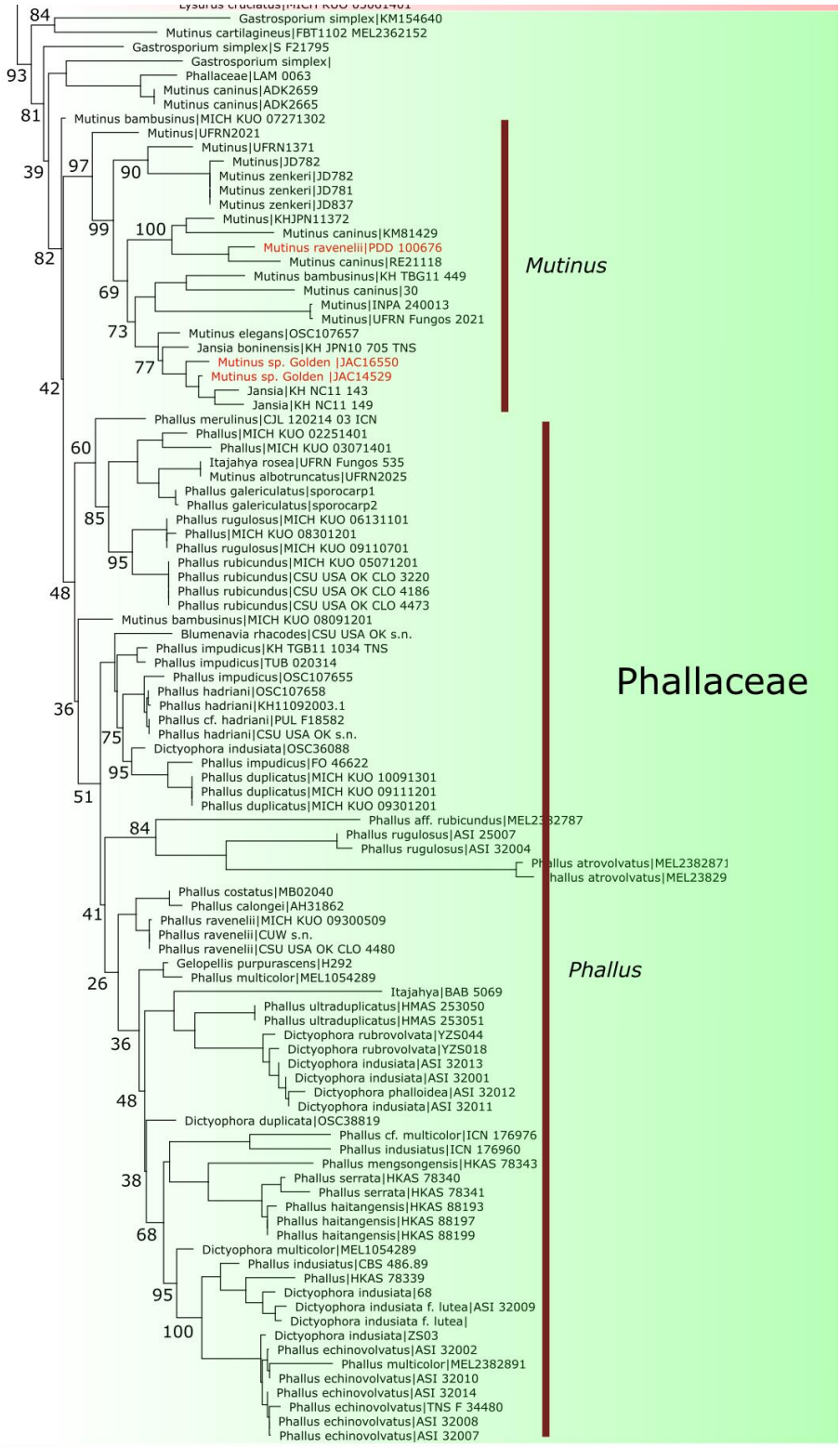
Protophallaceae



Lysuraceae



Phallaceae



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iNaturalist is gratefully acknowledged, especially those willing to make their records and photographs available under a Creative Commons license.

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