Inocybe tauensis, a new species from the Samoan Archipelago with biogeographic evidence for a Paleotropical origin

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ABSTRACT

Inocybe tauensis is described as a new species from the island of *Ta'u*, American Samoa. The species occurs in native littoral forest and is associated with the ectomycorrhizal tree *Pisonia grandis*. Based on an analysis of nLSU, RPB1, and RPB2 sequence data, *I. tauensis* appears to be derived from ancestors with a Paleotropical biogeographical distribution. Alternative explanations for the unexpected presence of an *Inocybe* species in the Samoan Archipelago are discussed.

Introduction

Inocybe (Fr.) Fr. is a large, complex genus for which well over 1600 names have been proposed to date (Index Fungorum, www.indexfungorum.org). Much work will be required to satisfactorily sort out the systematics and nomenclature of the genus, and undescribed species of *Inocybe* undoubtedly remain to be found. Members of the genus are widespread and typically associate with trees that form ectomycorrhizal symbioses with them. The bulk of the species placed in *Inocybe* occur in North Temperate parts of the world, but many *Inocybe* species also occur in South Temperate regions and a relatively small but growing number of taxa are known from Australasia and tropical regions of the world (Pegler 1969, 1977, 1986; Horak 1977, 1979a, b, 1980, 1981; Singer *et al.* 1983; Matheny *et al.* 2003; Matheny & Bougher 2005). Thus far, no species of *Inocybe* has been reported from Polynesia.

An unknown species of *Inocybe* was recently discovered in native littoral forest within the National Park of American Samoa on the remote Pacific island of *Ta'u*. Because very few known ectomycorrhizal host plants are present in the Samoan islands (Whistler 1992), the discovery of an *Inocybe* species on the island was completely unexpected. No name was found that can be applied to the material collected on *Ta'u*. The objectives of this paper are to propose a new species of *Inocybe* from Polynesia and to use molecular data to provide some insight into its origin.

Materials and methods

A description from fresh material and colour digital photographs of the specimens using a grey card as a background were done in the field. Microscopic study of dried specimens

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was carried out using a light microscope after rehydrating sections in 10 % NH₄OH. The microscopic measurements were done using oil immersion at 1000× and line drawings of the microscopic characters were made with the aid of a drawing tube. Spore measurements are reported as an average with ranges while measurements of the other cells are given as ranges. Colour notations were taken from the digital photographs using the Munsell Soil Color Charts (Munsell Color 2000). The specimens examined and the holotype have been accessioned into the Intermountain Herbarium (UTC) at Utah State University.

Standard protocols (White *et al.* 1990; Kropp *et al.* 1996) were used to extract DNA from dried herbarium material of *Inocybe tauensis* (UTC251538) and to amplify target sequences. Amplified PCR products were obtained for the nuclear large ribosomal subunit (nLSU) between primers LROR and LR5 (Moncalvo *et al.* 2000) and for RPB1 (largest subunit RNA Polymerase II) and RPB2 (second largest subunit RNA Polymerase II) using primer sets A-for-Ino with C-rev-Ino and bRPB2-6F with bRPB2-7.1R respectively (Matheny 2005). Direct sequencing of the PCR products was done using primers LROR and LR5 for the nLSU, primers A-for-Ino and C-rev-Ino for RPB1, and primers bRPB2-6F and bRPB2-7.1R for RPB2. The sequences for *I. tauensis* were deposited in Genbank (Table 1).

Taxon sampling was based on the global historical biogeographical analysis of the Inocybaceae recently published by Matheny *et al.* (2009) and emphasized several of their most clear-cut clades to facilitate placing our taxon in a broad geographical context. Nuclear LSU, RPB1, and RPB2 sequences from *I. tauensis* and 35 other species of *Inocybe* representing the South Temperate, North Temperate, Neotropical, and Paleotropical clades recovered by these workers were used in our analysis (Table 1). Sampling was restricted, with two exceptions for geographical completeness, to taxa for which all three genes were available on Genbank. The nLSU, RPB1, and RPB2 sequences were concatenated and aligned using Clustal X (Thompson *et al.* 1997) and final adjustments were made to the alignment by hand.

The aligned data set was 3421 bases in length and was analyzed using MrBayes 3.1 (Ronquist & Huelsenbeck 2003). Tree searches were performed using a time reversible model of evolution (Rodriguez *et al.* 1990; Maddison 1994) and a discrete gamma distribution with six substitution types and some invariant sites (GTR + G + I) was assumed. Posterior probabilities were approximated by sampling every 100 trees simulated using the Markov Chain Monte Carlo Method (MCMC). The initial runs were conducted with eight active MCMC chains, heated at 0.2, and started with a randomly chosen neighbor-joining tree. The first MCMC run was iterated for 1 000 000 generations and three subsequent MCMC simulations were done using 1 000 000 generations, sampling every one hundredth tree. A majority consensus tree was calculated from the last 7000 sampled trees from a 10 000 tree data set using all runs to recover the posterior probabilities of the internal nodes using the sumt command in MrBayes. The resulting statistics showing the convergence of two independent MCMC chains as described in Ronquist & Huelsenbeck (2003) with a standard deviation between the two independent chains less than 0.001. The potential scale reduction factors for all convergence statistics approached 1.001 for all parameters. Posterior probability support measures for nodes with

Table 1 – Species,[a] geographical origin, and Genbank accession numbers for the sequence data used to generate the phylogram in Fig 1.

Taxon	Location	RPB1	RPB2	nLSU
Inocybe actinospora nom. prov.	Argentina	AY351790	AY337361	AY380363
I. agglutinata	USA	AF389534	AY509113	AY038312
I. albodisca	USA	EU307820	EU307821	EU307819
I. armeniaca	USA	AY351793	AY337363	AY380367
I. ayangannae	Guyana	AY239028	AY337364	AY239018
I. cf. murrayana	Australia	EU555459	EU555460	EU555461
I. conspicuospora	Zambia	–	EU555470	EU555471
I. densifolia nom. prov.	Zambia	EU555472	EU555473	EU555474
I. eriocaulis nom. prov.	Australia	EU569841	EU569842	EU569843
I. fibrillosibrunnea	Australia	EU307849	EU307850	EU307848
I. fulvilubrica nom. prov.	Australia	EU569848	EU569849	EU569850
I. fuscodisca	USA	AY351802	AY337376	AY380376
I. griseolilacina	USA	EU307829	EU307830	EU307828
I. marginata nom. prov.	Guyana	AY509116	AY509114	AY509115
I. nothopedes nom. prov.	Australia	AY351815	AY337391	AY380388
I. persicinipes nom. prov.	Australia	EU600835	EU600836	EU600837
I. praecox	USA	AF389533	AY337360	AY038311
I. pseudocystis nom. prov.	Australia	AY351809	AY337393	AY380389
I. pudica	USA	AF389545	AY337394	AY038323
I. pusio	USA	AY351810	AY337396	AY388643
I. queletii	USA	AY351811	AY337397	AY380390
I. rimosa s. l.	USA	EU600848	EU600849	EU600850
I. rimosa s. l.	USA	EU307857	EU307858	EF561633
I. serotina	Canada	AY351812	AY337398	AY380391
I. aff. serrata	Australia	EU600857	EU600858	EU600859
I. cf. serrata	Australia	AY351816	AY337399	AY380392
I. spuria	USA	EU600866	EU600867	EU600868
I. subochracea	USA	AY351822	AY337405	AY380397
I. tahquamenonensis	USA	AY351824	AY337407	AY380399
Inocybe tauensis	Samoa	GU977212	GU977213	GU977211
I. torresia nom. prov.	Australia	EU600872	EU600873	EU600874
I. tubarioides	USA	EU307856	EU307855	AY732211
I. violaceocaulis	Australia	AY351828	AY337410	AY380404
Inocybe sp. BK8-Feb-99-1	Argentina	AF389548	–	AY038326
Inocybe sp. BK2006986	Utah	EU600888	EU600889	EU600890
Inocybe sp. PBM2181	Australia	EU307852	EU307853	EU307851

a Provisional names and locations except for that of *I. tauensis* are from Matheny *et al.* (2009).

less than a 90 % posterior probability support are not shown. TreeView (Page 1996) was used to visualize the consensus tree from the simulation. The tree was rooted with the Pseudosperma clade of Matheny *et al.* (2009).

Species description

Inocybe tauensis Kropp & Albee-Scott *sp. nov.* (Figs 2, 3).
Etymology: *tauensis* – relating to the island of *Ta'u*.

Pileus 17–35 mm latus, conicus vel late conicus demum paene applanatus, saepe umbonatus, grosse fibrillosus vel plus minusve squamulosus, ochraceous vel melleus; centro laevi et brunneo. Lamellae pallidae brunnae, simpliciter adnatae. Stipes 25–35 mm longus, 4–5 mm crassus, solidus, aequalis vel basi plus minusve inflata vel bulbo parvo, ex apice ad medium leviter pruinosus, pallide bubalinus, dimidio superiore dilute incarnato. Sporae 4.5–5.3–6.0 × 6.5–7.5–9.0 μm, subglobosae vel ellipsoidae; nodulis 11–22. Basidia 8–10 × 15–27 μm, clavata. Pleurocystidia 14–19 × 42–60 μm, anguste fusiformia. Cheilocystidia 9–17 × 42–60 μm, anguste fusiformia. Holotypus hic designatus BK

17-May-99-2009-2 (UTC25136) *in Herbario Intermontanis* (UTC) *conservatus*.

Pileus — 17—35 mm wide, conic to broadly conic when young, becoming nearly plane, occasionally with raised margins, often umbonate; surface slightly tacky, coarsely radially fibrillose to somewhat lacerate-scaly, having some pallid veil remnants at the margin; colour ochraceous, brownish yellow to pale brown (10YR 6/6-7/4) becoming lighter toward the margin; disk smooth, brown to dark brown (7.5YR 4/6-4/4), lacking a velipellis; cortina not observed; context pallid; odour lightly spermatic. Lamellae — close, narrowly attached, up to 4—5 mm broad; colour buff to very pale brown (10YR 9/2), margins not fimbriate. Stipe — 25—35 × 4—5 mm, solid, cylindrical, equal to a slightly enlarged or small bulbous base, bulb when present not marginate; surface finely pruinose over the upper half but this is hard to see without magnification; colour light buff to very pale brown (10YR 8/2) with faint incarnate hues in the upper half of the stipe; context concolorous with surface except white at base. Basidiospores — 6.5—7.5—9.0 × 4.5—5.3—6.0 µm, subglobose to ellipsoid, nodulose with 11—22 nodules. Basidia — 15—27 × 8—10 µm, clavate with four sterigmata. Pleurocystidia — 42—60 × 14—19 µm, narrowly fusiform with apical incrustations, cell walls up to 2 µm thick, pale yellowish in NH_4OH, many lacking a basal pedicel. Cheilocystidia — 42—60 × 9—17 µm, narrowly fusiform with apical incrustations, cell walls up to 2 µm thick, many lacking a basal pedicel, paracystidia not observed. Lamellar trama — consisting of interwoven to subparallel hyphae 3—7 µm wide. Pileipellis — a cutis of light brownish and slightly incrusted hyphae 5—14 µm wide. Stipitipellis — near the stipe apex abundant metuloids similar to those in the hymenium and clavate paracystidia are present; a light covering of hyphae with numerous metuloids and paracystidia is present midway toward the base, the metuloids having thinner cell walls than those in the hymenium; at the stipe base a light covering of hyphae is present with very few cystidioid cells. Clamps — present.

Habitat and distribution: Scattered along an unpaved road in a mixed littoral forest growing on coral rubble. Thus far, known only from within the National Park of American Samoa on the island of Ta'u, American Samoa. Appearing mid-May.

Specimens examined: AMERICAN SAMOA. National Park of American Samoa, *Ta'u* unit, May 17, 2009, leg. B. R. Kropp, BK17-May-2009-2 (HOLOTYPE, UTC251536); National Park of American Samoa, *Ta'u* unit, May 17, 2009, leg. B. R. Kropp, BK17-May-2009-9 (UTC251537); National Park of American Samoa, *Ta'u* unit, May 17, 2009, leg. B. R. Kropp, BK17-May-2009-9 (UTC251538).

Results

The Bayesian analysis done using the data set in Table 1 gave results that are consistent with the findings of Matheny *et al.* (2009). Although we made no attempt to assess divergence dates and did not sample all of the clades that these authors recovered, the taxa that we sampled clustered with good posterior probability support into clades that correspond well to the geographical groupings employed by these authors (Fig 1).

The newly described species, *Inocybe tauensis* from American Samoa was clustered within a strongly supported basal lineage that includes several Paleotropical representatives from Africa and one undescribed taxon *Inocybe torresia* nom. prov. from Australia (PAL, see Fig 1). The collection of "*I. torresia*" is from the Paleotropical northern part of Western Australia (P.B. Matheny, pers. comm.). The South Temperate taxa sampled for our study were primarily Australian and were distributed among two well-supported clades (STa, STb, Fig 1). Our analysis found that a single un-named taxon from South Temperate South America clustered among the Australian taxa in clade STb while an un-named Neotropical species (*Inocybe marginata* nom. prov.) clustered with the South Temperate species in clade STa (Fig 1); both of these results are consistent with the findings of Matheny *et al.* (2009). The North Temperate species clustered together in a well-supported clade (NT) made up primarily of North American representatives, although as also reported by Matheny *et al.* (2009), the South Temperate species *Inocybe violaceocaulis* also occurred in this clade. Neotropical species were associated with different clades although one of them formed a moderately well-supported clade (NT/Neo) with two North Temperate taxa.

Discussion

The results of the Bayesian analysis (Fig 1) provide evidence that *Inocybe tauensis* has Paleotropical roots. It belongs to an old lineage that includes both African and Paleotropical Australian taxa and occupies a basal position within *Inocybe*. Matheny *et al.* (2009) concluded that the major lineages of the Inocybaceae diversified during the Cretaceous and that the younger lineages within *Inocybe* s. str. split from their Paleotropical ancestors in the late Cretaceous or early Paleogene. They also concluded that vicariance between Africa and Australia cannot be rejected as an explanation for the distribution of at least some ancestral lineages in the Inocybaceae. Thus, one possible explanation for the presence of both African and Paleotropical Australian taxa along with *I. tauensis* in a single clade (PAL) is that *I. tauensis* is derived from a Paleotropical, Australasian lineage that was in turn derived from an ancestral vicariance event between Africa and Australia.

Exactly how it made its way further east to the Samoan islands is an open question. The islands are both volcanic in origin and relatively young. For example, the island of *Tutuila* in American Samoa is only about 1.2—1.5 million years old (McDougall 1985). Thus, the islands would never have had a direct connection to a large land mass and *I. tauensis* must either have evolved in Polynesia from Paleotropical ancestors or have arrived more recently by long-distance dispersal.

One obvious means by which *I. tauensis* could have gotten to the Samoan islands is by being transported by humans on the roots of ectomycorrhizal host plants, either through an ancient Polynesian or modern introduction. There are many examples of ectomycorrhizal fungi known to have been introduced in this way into exotic environments along with their hosts. For example, *Amanita marmorata* subsp. *myrtacearum* O.K. Miller, Hemmes, and G. Wong is thought to have been introduced to the Hawaiian islands with *Eucalyptus* (Miller *et al.* 1996). Giachini *et al.* (2000) reported another example in which a number of exotic ectomycorrhizal fungi had been introduced to Brazilian pine and *Eucalyptus* plantations.
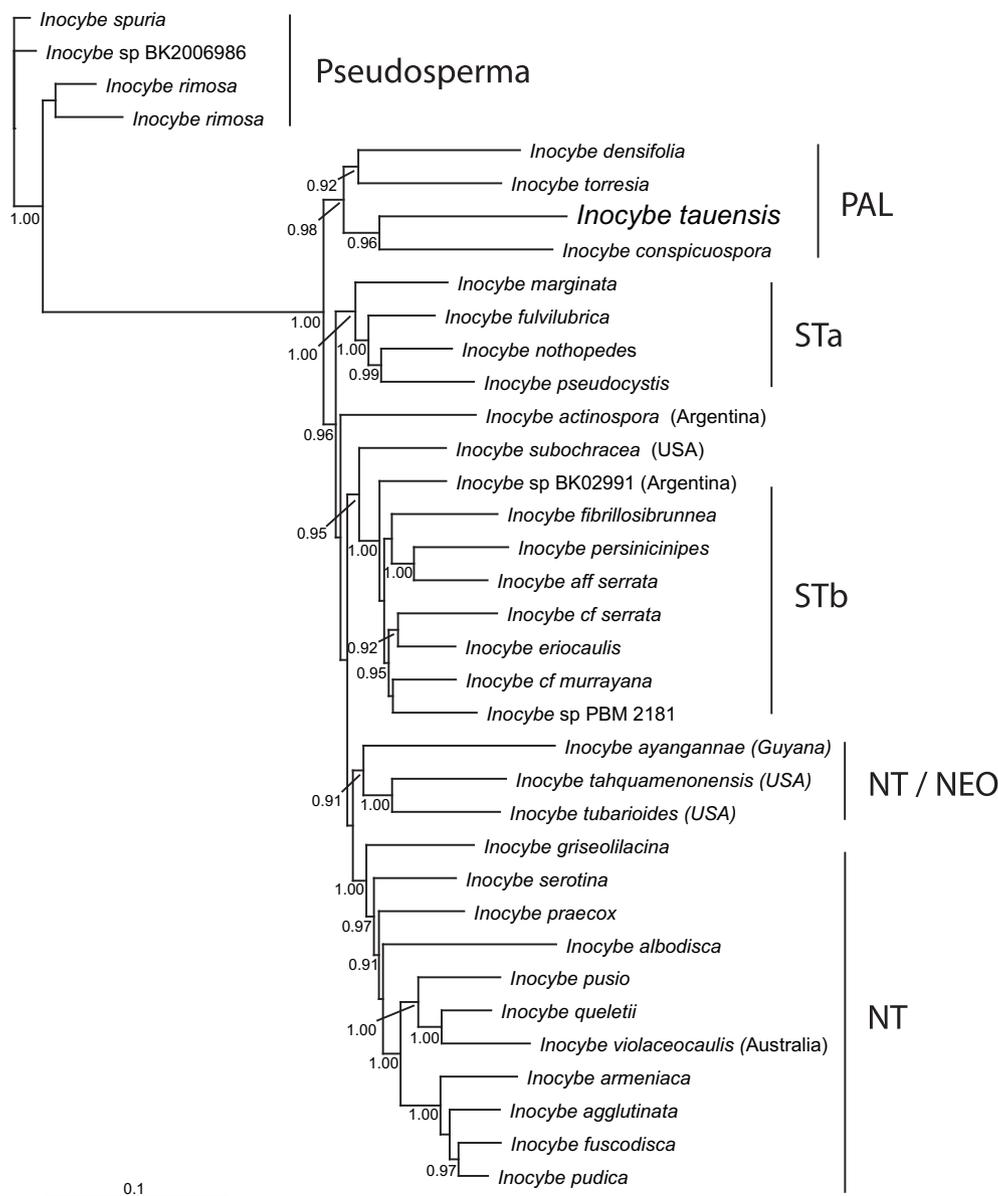
Fig 1 — Phylogram resulting from a Bayesian analysis of a data set combining nLSU, RPB1, and RPB2 sequences of *Inocybe* species from different geographical regions. Support measures are not shown for nodes with less than a 90 % posterior probability support. The phylogram has been rooted with members of the *Pseudosperma* lineage (Matheny *et al.* 2009). ST = South Temperate (clades a and b), NT = North Temperate clade, NT/NEO = North Temperate and Neotropical clade, PAL = Paleotropical clade.

At least two introduced tree species that have the ability to form ectomycorrhizae (*Casuarina equisetifolia* L. native to Australasia and Southeast Asia and *Acacia auriculiformis* A. Cunn. *ex* Benth. which is an Australasian native) have been reported on the island of *Ta'u* (Theodorou & Reddell 1991; Space & Flynn 2000; Duponnois & Plenchette 2003). However, a vegetation survey of the *Ta'u* unit of the National Park of American Samoa indicates that the forest within the park represents one of the best remaining examples of native Samoan vegetation (Whistler 1992). No introduced ectomycorrhizal trees were reported from the park unit and the littoral forest on the eastern shore of the island where *I. tauensis* was

collected is a mixed-species forest dominated by *Barringtonia asiatica* (L.) Kurtz and *Pisonia grandis* R. Br., a known ectomycorrhizal tree (Ashford & Allaway 1982; Whistler 1992). Thus, regardless of whether *I. tauensis* originally arrived on the island with an introduced host, it currently appears to be associated with a native tree. If populations of *I. tauensis* are eventually found in Australasia, especially with hosts like *C. equisetifolia* that have been introduced to the Samoan islands, it would indicate that the species was introduced with these plants.

Long-distance spore dispersal is another means by which *I. tauensis* could have traveled to the Samoan Archipelago. Certainly, some plant pathogenic fungi are known to have been

Fig 2 – Basidiomes of the Holotype for *Inocybe tauensis* (UTC25136). Scale = 1 mm.

dispersed by spores over large geographical distances (Brown & Hovmøller 2002) and gene flow *via* spores of the saprotrophic species *Schizophyllum commune* Fr. can occur over long distances (James *et al.* 1999), although, overall, these events appear to be relatively rare. In the case of ectomycorrhizal fungi, there is evidence to indicate that spores are not a frequent means of long-distance dispersal. The work of Halling
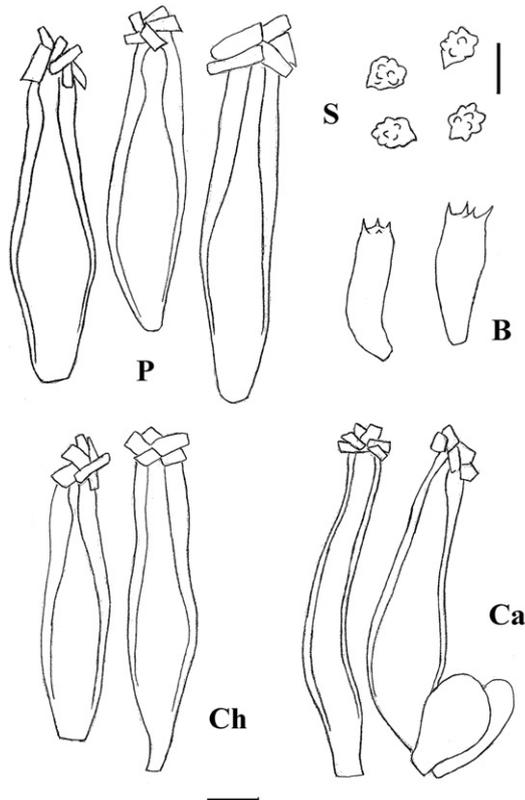

Fig 3 – Microscopic characters of *Inocybe tauensis*. B = basidia, Ca = caulocystidia with clavate paracystidia, Ch = cheilocystidia, P = pleurocystidia, S = basidiospores. Scale = 10 μm.

et al. (2008) showed that panmixis among distantly separated populations of the ectomycorrhizal fungus *Tylopilus ballouii* (Peck) Singer is unlikely and that these populations have probably been genetically isolated for long periods of time. These authors also presented two arguments against frequent long-distance dispersal by spores of ectomycorrhizal fungi. The first of these is that basidiospores of some ectomycorrhizal species may not travel long distances from their parent basidiome (Li 2005) and would be unlikely to reach distant parts of the globe. The second is that evidence exists to show that gene flow between populations of *Russula brevipes* Peck happens readily over relatively short distances of only 230–1090 m but less readily over longer distances (Bergemann & Miller 2002; Bergemann *et al.* 2006). An additional argument against frequent long-distance dispersal of ectomycorrhizal fungi *via* basidiospores is that many if not most of them have monokaryotic spores with bifactorial mating systems (Kropp 1988). Given that fact, individual spores would not only have to survive the rigours of long-distance aerial transport, they would also need to encounter both a suitable host plant and a sexually compatible mycelium after arriving in a new environment. Yet, in spite of the barriers to long-distance spore dispersal, it is not unreasonable to assume that it could have happened over time spanning millions of years.

An interesting aspect of the biology of *P. grandis*, the probable host of *I. tauensis*, is that it is widely distributed only on small, often remote, islands ranging from the Seychelles to French Polynesia (Airy Shaw 1952). Because its' seeds are sticky, it is thought to be carried over enormous expanses of water after sticking to seabirds that nest in or near the trees (Burger 2005). Thus, another possibility for the dispersal of *Pisonia*-associated fungi would be that their spores adhere to the seeds and are then transported with them by the birds. If this were to happen, then *I. tauensis* could possibly have arrived in Samoa fairly recently with birds moving from Australasia or even from islands such as the Seychelles that lie close to Africa; potentially providing an alternate explanation of why an *Inocybe* related to species from Africa occurs on an isolated island in Polynesia. More sampling is needed to determine whether *I. tauensis* occurs more widely with *P. grandis* throughout the Pacific and Indian Oceans. If it does, this would lend support to the idea that it is dispersed with *P. grandis* seed by birds.

Van Balgooy *et al.* (1996) indicate that the floras of the South Pacific islands, including the Samoan Archipelago, have Australasian connections while those of both the Hawaiian islands and the Galapagos islands have additional ties to the Americas. Species diversification would have occurred after the first plants arrived in these islands and about 30 % of Samoan angiosperms are endemic (Whistler 1992). Hemmes & Desjardin (2002) reported a number of fungi that are endemic to native forests in the Hawaiian islands and, given that there is such a high proportion of endemic Samoan plants, it would not be surprising to find a correspondingly high number of endemic fungi there as well. The mycoflora of the Samoan Archipelago is almost completely unknown but a brief survey of fungi from these islands indicates that a number of potentially undescribed species are present (B.R.K., unpubl.). In fact, plant surveys by Whistler (1992, 1994) have shown that at least two

trees from ectomycorrhizal genera besides *P. grandis*, *Intsia bijuga* (Colebr.) Kuntze and *Pisonia umbellifera* (Forst.) Seem. occur in the islands and at least two other ectomycorrhizal fungi, an unidentified *Hebeloma* species and a *Cantharellus* species, are also present (B.R.K., unpubl.).

It is not yet known whether *I. tauensis* is endemic to the Samoan islands but it is derived from a lineage that is much older than the islands. If it is endemic, it could potentially have evolved from a Paleotropical ancestor after a long-distance dispersal event and then survived through time by hopping between islands that have long since disappeared. If this is the case, evidence of an adaptive radiation might eventually be found if further work shows that additional related species of *Inocybe* exist in the Samoan Archipelago.

Our proposal that this species has Paleotropical, Australasian roots is consistent with the conclusion of most phytogeographers that Polynesian plant communities have Australasian origins (Van Balgooy et al. 1996). The overall structure of our phylogeographical analysis (Fig 1) is consistent with the findings of Matheny et al. (2009) and several major clades recovered by these authors were also recovered in our analysis and the data indicate with good support that *I. tauensis* has a Paleotropical origin. Although, the question of when and how it arrived in the Samoan islands remains to be resolved.

R E F E R E N C E S

Airy Shaw HK, 1952. On the distribution of *Pisonia grandis* R. Br. (*Nyctaginaceae*), with special reference to Malaysia. *Kew Bulletin* 7: 87–97.

Ashford AE, Allaway WG, 1982. A sheathing mycorrhiza on *Pisonia grandis* R. BR. (*Nyctaginaceae*) with development of transfer cells rather than a Hartig net. *New Phytologist* 90: 511–519.

Bergemann SA, Miller SL, 2002. Size, distribution, and persistence of genets in local populations of the late stage ectomycorrhizal basidiomycete, *Russula brevipes*. *New Phytologist* 156: 313–320.

Bergemann SA, Douhan GW, Garboletto M, Miller SL, 2006. No evidence of population structure across three isolated subpopulations of *Russula brevipes* in an oak/pine woodland. *New Phytologist* 170: 177–184.

Brown JKM, Hovmøller MS, 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science* 297: 537–541.

Burger AE, 2005. Dispersal and germination of seeds of *Pisonia grandis*, an Indo-Pacific tropical tree associated with insular seabird colonies. *Journal of Tropical Ecology* 213: 263–271.

Duponnois R, Plenchette C, 2003. A mycorrhiza helper bacterium enhances ectomycorrhizal and endomycorrhizal symbioses of Australian *Acacia* species. *Mycorrhiza* 13: 85–91.

Giachini AJ, Oliveira VL, Castellano MA, Trappe JM, 2000. Ectomycorrhizal fungi in *Eucalyptus* and *Pinus* plantations in Southern Brazil. *Mycologia* 92: 1166–1177.

Halling R, Osmundson TW, Neves M-A, 2008. Pacific boletes: implications for biogeographic relationships. *Mycological Research* 112: 437–447.

Hemmes DE, Desjardin DE, 2002. *Mushrooms of Hawaii*. Ten Speed Press, Berkeley, 212 pp..

Horak E, 1977. Fungi Agaricini Novaezelandiae. VI. *Inocybe* (Fr.) Fr. and *Astrosporina* Schroeter. *New Zealand Journal of Botany* 15: 713–747.

Horak E, 1979a. *Astrosporina* (Agaricales) in Indomalaya and Australasia. *Persoonia* 10: 157–205.

Horak E, 1979b. *Fungi, Basidiomycetes Agaricales y Gasteromycetes secotioides*. In: *Flora Criptogámica de Tierra del Fuego, Orden Agaricales*, **Tomo XI, Fasciculo 6**. Fundación para la Educación, la Ciencia y la Cultura, Buenos Aires, 525 pp..

Horak E, 1980. *Inocybe* (Agaricales) in Indomalaya and Australasia. *Persoonia* 11: 1–37.

Horak E, 1981. On Himalayan species of *Astrosprina* and *Inocybe* (Agaricales). *Persoonia* 11: 303–310.

James TY, Porter D, Hamrick J, Vilgalys R, 1999. Evidence for limited intercontinental gene flow in the cosmopolitan mushroom *Schizophyllum commune*. *Evolution* 53: 1665–1677.

Kropp BR, 1988. Ectomycorrhizal genetics: what we know. In: Lalonde M, Piché Y (eds), *Canadian Workshop on Mycorrhizae in Forestry*. Université Laval, Ste-Foy, Québec, pp. 131–133.

Kropp BR, Hansen D, Flint KM, Thomson SV, 1996. Artificial inoculation and colonization of Dyer's Woad (*Isatis tinctoria*) by the systemic fungus *Puccinia thlaspeos*. *Phytopathology* 86: 891–896.

Li D-W, 2005. Release and dispersal of basidiospores from *Amanita muscaria* var *alba* and their infiltration into a residence. *Mycological Research* 109: 1235–1242.

Maddison DR, 1994. Phylogenetic methods for inferring the evolutionary history and processes of change in discretely valued characters. *Annual Review of Entomology* 39: 267–292.

Matheny PB, Aime MC, Henkel TW, 2003. New species of *Inocybe* from *Dicymbe* forests of Guyana. *Mycological Research* 107: 495–505.

Matheny PB, 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). *Molecular Phylogenetics and Evolution* 35: 1–20.

Matheny PB, Bougher NL, 2005. A new violet species of *Inocybe* from urban and rural landscapes in Western Australia. *Australasian Mycologist* 24: 7–12.

Matheny PB, Aime MC, Bougher NL, Buyck B, Desjardin DE, Horak E, Kropp BR, Lodge DJ, Soytong K, Trappe JM, Hibbet DS, 2009. Out of the Paleotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family Inocybaceae. *Journal of Biogeography* 36: 577–592.

McDougall I, 1985. Age and evolution of the volcanoes of Tutuila, AS. *Pacific Science* 39: 311–320.

Miller OK, Hemmes DE, Wong GJ, 1996. *Amanita marmoratum* subsp. *myrtacearum* – a new subspecies in *Amanita* sect. *Phalloideae* from Hawaii. *Mycologia* 88: 140–145.

Moncalvo J-M, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R, 2000. Phylogenetic relationships of Agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Systematic Biology* 49: 278–305.

Munsell Color, 2000. *Munsell Soil Color Charts*. GretagMacbeth, New Windsor, NY.

Page RDM, 1996. TreeView: an application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences* 12: 357–358.

Pegler DN, 1969. Studies on African Agaricales II. *Kew Bulletin* 23: 219–249.

Pegler DN, 1977. *A Preliminary Agaric Flora of East Africa*, **Kew Bull. Add. Series VI**, Royal Botanical Gardens Kew, Her Majesty's Stationary Office, London, 615 pp..

Pegler DN, 1986. *Agaric Flora of Sri Lanka*, **Kew Bull. Add. Series XII**, Royal Botanical Gardens Kew, Her Majesty's Stationary Office, London, 519 pp..

Rodriguez F, Oliver JL, Marin A, Medina JR, 1990. The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* **142**: 485−501.

Ronquist F, Huelsenbeck JP, 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572−1574.

Singer R, Araujo I, Ivory MH, 1983. *The Ectotrophic Mycorrhizal Fungi of the Neotropical Lowlands Especially Central Amazonia* Beiheft zur Nova Hedwigia Heft 77. J. Cramer, Vaduz, 352 pp.

Space JC, Flynn T, 2000. *Observations on Invasive Plant Species in American Samoa*. USDA Forest Service, Honolulu, US Forest Service, Pacific Island Ecosystems at Risk (PIER). Online resource at: http://www.hear.org/pier/ 51 pp. (accessed 24.02.10).

Theodorou C, Reddell P, 1991. *In vitro* synthesis of ectomycorrhizas on *Casuarinaceae* with a range of mycorrhizal fungi. *New Phytologist* **118**: 279−288.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG, 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **24**: 4876−4882.

Van Balgooy MMJ, Hovenkamp PH, Van Welzen PC, 1996. Phytogeography of the Pacific − floristic and historical distribution patterns in plants. In: Keast A, Miller SE (eds), *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: patterns and processes*. SPB Academic Publishing, Amsterdam, pp. 191−213.

Whistler WA, 1992. *Botanical Inventory of the Proposed Ta'u Unit of the National Park of American Samoa*. National Park Service, Honolulu, Hawaii, Technical Report 83.

Whistler WA, 1994. *Botanical Inventory of the Proposed Tutuila and Ofu Units of the National Park of American Samoa*. National Park Service, Honolulu, Hawaii, Technical Report 87.

White TJ, Bruns T, Lee S, Taylor J, 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds), *PCR Protocols: a guide to methods and applications*. Academic Press, Inc., New York, pp. 315−322.