PRIMER NOTE

MITOCHONDRIAL MICROSATELLITE MARKERS FOR THE AUSTRALIAN ECTOMYCORRHIZAL FUNGUS Laccaria sp. A (Hydnangiaceae)¹

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• Premise of the study: Microsatellite loci were developed for the ectomycorrhizal fungus Laccaria sp. A to investigate the population genetic structure of this fungal symbiont across its fragmented distribution in southeastern Australia.

• Methods and Results: A partial genome sequence from an individual collection of Laccaria sp. A was obtained by 454 genome sequencing. Eight microsatellite markers were selected from 66 loci identified in the genome. The selected markers were highly polymorphic (4–19 alleles per locus, average 13 alleles) and amplified reproducibly from collections made across the distribution of this species. Five of these markers also amplified reproducibly in the sister species Laccaria sp. E (1). All eight of the selected microsatellite loci were from the mitochondrial genome.

• Conclusions: The highly polymorphic markers described here will enable population structure of Laccaria sp. A to be determined, contributing to research on mycorrhizal fungi from a novel distribution.

Key words: Hydnangiaceae; Laccaria; microsatellites; mitochondria; mycorrhizae; Nothofagus cunninghamii.

Ectomycorrhizal fungi are diverse and important components of ecosystems and form mutually beneficial associations with plants. Conservatively, there are 7750 species of ectomycorrhizal fungi, although there may be as many as 25,000 (Rinaldi et al., 2008). However, sets of microsatellite markers are only available for around 20 species, most from the Northern Hemisphere (Douhan et al., 2011). Microsatellite markers can be exploited to determine features of the biology and ecology of organisms, including turnover rates of individuals in a population and the gene flow between geographically disjunct populations. These types of information have been reported for very few ectomycorrhizal fungi.

Laccaria Berk. & Broome is a genus of ectomycorrhizal fungi with species in both hemispheres. Multigene phylogeny has recently distinguished considerable cryptic diversity among Australian Laccaria, with Laccaria sp. A the most readily identifiable species (Sheedy et al., 2013). Laccaria sp. A only associates with Nothofagus cunninghamii (Hook.) Oerst., the dominant tree in Australian cool temperate rainforests, and these species share a fragmented distribution in the states of Victoria and Tasmania. Microsatellite markers have been designed independently for three Northern Hemisphere species (e.g., Wadud et al., 2006a, 2006b; Labbé et al., 2011); however, Northern Hemisphere species are phylogenetically distant to Australian species (Sheedy et al., 2013). Sixteen markers from L. bicolor (Maire) P. D. Orton (Labbé et al., 2011) could not be amplified in Australian species (E. Sheedy, unpublished data). Here we report markers designed specifically for Laccaria sp. A.

METHODS AND RESULTS

Collections of Laccaria sp. A fruit-bodies were made from across the species distribution (west Tasmania, 96; northeast Tasmania, 44; west Victoria, 54; east Victoria, 56). Selected collections from each population were vouchered at the National Herbarium of Victoria (MEL) (Sheedy et al., 2013; Appendix 1). DNA was extracted from individual fruit-bodies as described in Sheedy et al. (2013).

DNA of Laccaria sp. A (MEL. 2359659), from Mt. Michael, Tasmania, was sequenced at the Australian Genome Research Facility (AGRF; Brisbane, Australia) on the next-generation Roche GS-FLX platform (454 Life Sciences, a Roche Company, Branford, Connecticut, USA). A total of 204,362 sequence reads, with an average length of 383 bp, was obtained from a quarter plate of sequencing. Reads were assembled by AGRF (using the software package Newbler; 454 Life Sciences, a Roche Company) into 13,234 contigs with an average length of 621 bp, totaling 8.2 Mb, and no further processing was done. The closest known genome size is of L. bicolor (65 Mb; Martin et al., 2008). Contigs were screened for di-, tri-, tetra-, penta-, and hexanucleotide repeats with a minimum repeat number of six, using the online software WebSat (Martins et al., 2009). A total of 66 microsatellite loci were identified, comprising mainly tri- and dinucleotide repeats (36 and 14, respectively). Using the online interface of Primer3 (version 0.4.0; Rozen and Skalentsky, 2000) and a product size range of 150–300 bp, primers were designed for 25 selected loci that had at least seven repeat units and included a mixture of repeat types (e.g., di- and trinucleotide repeats).

Seven collections of Laccaria sp. A were used to test whether the 25 microsatellite markers amplified reproducibly (Appendix 1; Set 1). Reactions were in a volume of 25 μL containing 2.5 μL of 10x buffer, 62.5 mM of MgCl₂, 2.5 mM

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of each dNTP, 10 pmol of each primer, 0.5 unit of Taq DNA polymerase (Scientifics, Cheltenham, Victoria, Australia), and 1 µL of DNA template, diluted 1:200 or 1:100 as required. The cycle conditions were a 3-min denaturation at 94°C, 10 touchdown cycles at 94°C (30 s), 62°C (30 s) (–1°C/cycle), 72°C (30 s); 25 cycles at 94°C (30 s), 52°C (30 s), 72°C (30 s); and a final extension at 72°C (10 min). Of the 25 loci, 12 were selected (based on amplification success, lack of nonspecific binding and presence of polymorphism) for further testing on a second set of 23 collections (Appendix 1: Set 2). Amplifications of selected loci used a lower concentration of dNTPs so that PCR products could be directly sequenced as purification methods resulted in substantial product loss and poor sequence quality. The following reactions were then setup: 25 µL containing 2.5 µL of 10× buffer, 62.5 mM of MgCl₂, 0.2 mg/mL of bovine serum albumin (BSA; New England Biolabs, Ipswich, Massachusetts, USA), 1.25 mM of each dNTP, 10 pmol of each primer, 0.5 unit of Taq DNA polymerase (Scientifics), and 1 µL of DNA template, diluted 1:200 or 1:100 as required. Thermocycling conditions were as described above, but with an annealing time of 1 min and an initial annealing temperature of 60°C.

Amplification products were sequenced to confirm the presence of the targeted microsatellites. Eight primer pairs consistently produced polymorphic bands (Table 1). These primers were subsequently synthesized with a fluorescent tag (VIC, NED, PET, or FAM; Applied Biosystems, Foster City, California, USA) attached to the 5′ end of the forward primer and a GTTTCTT ‘pigtail’ appended to the 5′ end of the reverse primers. Microsatellite alleles were separated by capillary electrophoresis using an ABI 3730 DNA Analyzer (Applied Biosystems) at AGRF. Alleles were scored based on size (position of peaks) using Geneious version 5.6.4 (Drummond et al., 2012). From the 29 test collections, 27 haplotypes were detected, with duplicates being of fruit-bodies from the same fairy-ring, indicating a high level of resolution (Appendix 1). The number of alleles and unbiased haploid diversity were determined using GenAlEx (version 6.5; Peakall and Smouse, 2012). For 120 collections, the number of alleles per locus was 4–19 and the unbiased haploid diversity was 0.345–0.905 (Table 2).

All eight loci produced single alleles with a range of sizes. A BLAST search of the contigs containing the loci and the L. bicolor nuclear and mitochondrial genomes (genome version 1.0, MycorWeb; http://mycor.nancy.inra.fr/IMG/ LaccariaGenome/blast.html) revealed the eight loci were mitochondrial. Of the original 66 loci, 27 were in the mitochondrial genome, 23 did not match nuclear or mitochondrial genomes (most likely due to the high level of sequence divergence between species), and 16 matched to sequences in the nuclear genome.

The eight primer pairs that amplified polymorphic microsatellites in Laccaria sp. A were also trialed on 18 other Australian species of Hydnangiaceae (Sheedy et al., 2013) under the amplification and capillary separation conditions listed above. Five loci (ESLA06, ESLA19, ESLA41, ESLA24, and ESLA39) amplified in other species of Australian Hydnangiaceae (Appendix 2), and the species with the most consistent amplification was Laccaria sp. E (1), the sister species of Laccaria sp. A (Sheedy et al., 2013).

CONCLUSIONS

The eight mitochondrial microsatellite markers reported here are highly polymorphic, making them useful for differentiating between genetic individuals as well as for investigating the population genetic structure of Laccaria sp. A. Mitochondrial markers were not deliberately sought; the markers were selected because

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**Table 1. Characteristics of microsatellite loci in Laccaria sp. A, derived from partial sequencing of the genome of collection MEL 2359659. Annealing temperature for all loci was a ‘touchdown’ of 60–50°C.**

| Locus    | Primer sequences (5′−3′) | Repeat motif       | Allele size (bp) | Fluorescent label | GenBank accession no. |
|----------|--------------------------|---------------------|------------------|-------------------|-----------------------|
| ESLA06†  | F: GGACAATGGCCACACTCAT  | (TTA)₁ sevent      | 240              | FAM               | KF736239              |
|          | R: CGCTTTAATGGACGGCTCTGA|                     |                  |                   |                       |
| ESLA12*  | F: AATAAAAACTAGACACCCTAGG| (AATGAT)₉           | 151              | VIC               | KF736240              |
|          | R: AAAGCAATAATTGACGGCAAAT |                  |                  |                   |                       |
| ESLA19*  | F: AGCAAGACGCAAAAAAGAAG | (ACAATA)₁₉         | 230              | VIC               | KF736241              |
|          | R: AGTACCTCCGACCTACCTAGG|                     |                  |                   |                       |
| ESLA24*  | F: GCTGGAACCTTGGATACCAAC | (TTA)₂₃ (TATC)₁₅ (ATTC)₅ | 224           | FAM               | KF736242              |
|          | R: GCATACGGCTTTGCTGCTTT |                  |                  |                   |                       |
| ESLA38*  | F: TTCTACCTAGTGCTCTTTGCAAT | (AATGAG)₁₇ (TATGAG)₂₃ (ATA)₉ | 348       | VIC               | KF736243              |
|          | R: CCCCCCTATTGTTGCTAATAAC |                  |                  |                   |                       |
| ESLA39*  | F: TGCCGCTTTACACATTGAGACT | (TAT)₁₀            | 182              |                   | KF736244              |
|          | R: AGCCAACAAAAAGGATGAA |                     |                  |                   |                       |
| ESLA41*  | F: CCCTGCTCCTTTTACCC | (ACAATA)₁₁        | 167              | KF736245           |
|          | R: AACAATGTAAGAAAAACAGAACAA |                  |                  |                   |                       |
| ESLA66*  | F: TTCCGAGAGAAAAACAAATAGC | (TATC)₁₅             | 282              | PET               | KF736246              |
|          | R: TGGTTGCTTTATCCTGCTTG |                     |                  |                   |                       |
| ESLA31†  | F: GGATGACAGCAAAGTACGAG | (AC)₄             | 288              |                   |                       |
|          | R: AGGGCCCAGATACTCAATT |                     |                  |                   |                       |
| ESLA45   | F: TTTTAGAGATGCGTGA | (TAT)₁₀            | 182              |                   |                       |
|          | R: AAACATCTTGGATATCTCTGCA |                  |                  |                   |                       |
| ESLA50†  | F: CATCAATCTACCTTGGCTTT | (TCC)₁₀          | 226              |                   |                       |
|          | R: GAGTGGGCAATCTCGACAT |                     |                  |                   |                       |
| ESLA54*  | F: TGCAATGACAAAAATCGTG | (AC)₄             | 156              |                   |                       |
|          | R: ACTCAGATACCCGGATTGC |                     |                  |                   |                       |
| ESLA56†  | F: CAGGGCCCTGTTCTGCTTG | (TCT)₆            | 152              |                   |                       |
|          | R: AACAGGAGAAGGCTTTCC |                     |                  |                   |                       |
| ESLA58†  | F: GGAACGTCCAGGAAAAACA | (GA)₇            | 153              |                   |                       |
|          | R: TTGGATACCTCCCTCTCAT |                     |                  |                   |                       |
| ESLA61   | F: AATCTTTGAGTGTAGGGATCTTCT | (TAATA)₃₉ (ATTAAT)₆ | 234        |                   |                       |
|          | R: TTAACCTCTGATCGACGGA CACT |                  |                  |                   |                       |
| ESLA64   | F: TTGATTTTTGGAATTTGCAAATAGCA | (TAA)₁₁             | 213              |                   |                       |
|          | R: TTGTTAAGCAGTGAAGATTGCAA |                  |                  |                   |                       |

*Fluorescent labels are from Applied Biosystems.
†These loci were used to examine population characters of Laccaria sp. A (Table 2). The remaining loci were not used due to inconsistent amplification (loci ESLA54, ESLA61, ESLA64) or lack of variation (all other loci).
‡Locus is nuclear; all other loci are mitochondrial, unless otherwise marked.
§Genomic origin of locus is unknown.
they were polymorphic and amplified consistently. The reason for the preponderance of mitochondrial markers is unknown. Due to the uniparental inheritance of the mitochondria and the presence of single alleles at each locus, the alleles are straightforward to score. These markers will significantly contribute to research on ectomycorrhizal fungi, as they allow investigation of fungal populations from a species (and close relatives) from the Southern Hemisphere, from a previously unstudied host tree (*N. cunninghamii*) and ecosystem (cool temperate rainforest).

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**TABLE 2. Characteristics of eight polymorphic microsatellite markers in collections from four populations of Laccaria sp.**

| Locus | WV (n = 19) | EV (n = 25) | WT (n = 50) | NET (n = 26) | All (n = 120) |
|-------|------------|------------|------------|-------------|--------------|
|       | A          | h          | A          | h           | A            | h            | A          | h          |
| ESLA06 | 2          | 0.491      | 2          | 0.280       | 3            | 0.117        | 3          | 0.394      | 4          | 0.345       |
| ESLA12 | 3          | 0.205      | 7          | 0.833       | 11           | 0.771        | 7          | 0.809      | 12         | 0.752       |
| ESLA19 | 6          | 0.836      | 5          | 0.513       | 9            | 0.811        | 10         | 0.877      | 11         | 0.840       |
| ESLA24 | 8          | 0.766      | 6          | 0.710       | 13           | 0.896        | 8          | 0.828      | 15         | 0.855       |
| ESLA38 | 8          | 0.766      | 7          | 0.540       | 13           | 0.887        | 9          | 0.837      | 15         | 0.834       |
| ESLA39 | 5          | 0.532      | 3          | 0.227       | 7            | 0.733        | 5          | 0.649      | 10         | 0.735       |
| ESLA41 | 10         | 0.912      | 7          | 0.637       | 14           | 0.927        | 11         | 0.902      | 19         | 0.905       |
| ESLA66 | 5          | 0.620      | 5          | 0.363       | 15           | 0.914        | 11         | 0.892      | 18         | 0.842       |

*Note: A = number of alleles; h = unbiased haploid diversity; n = sample size.

+ Population: WV = west Victoria; EV = east Victoria; WT = west Tasmania; NET = northeast Tasmania.*
**APPENDIX 1.** Collections of *Laccaria* sp. A used to assess amplification and allelic variation of microsatellite loci.

| Collection | Vouchera | Latitude | Longitude | Site | Population | Setb | Hap.c |
|------------|----------|----------|-----------|------|------------|------|-------|
| ES087_7.14.1 | 2360498 | −41.47213 | 145.46077 | Philosopher Falls | West Tasmania | 1 | 1 |
| ES198_A4 | 2359650 | −37.48794 | 145.83394 | The Beeches | East Victoria | 1 | 2 |
| ES210_A11 | 2359652 | −38.42517 | 146.37214 | Tarra-Bulga | East Victoria | 1 | 3 |
| ES232_A18 | 2359653 | −38.69858 | 143.47771 | Aire River Crossing | West Victoria | 1 | 4 |
| ES270_A46 | 2359660 | −41.82715 | 145.50443 | Mt. Read | West Tasmania | 1 | 5 |
| ES291_A57 | 2359661 | −42.69452 | 146.46721 | Mt. Michael | Northeast Tasmania | 1 | 6 |
| ES295_A66* | 2359659 | −41.18582 | 148.01033 | Mt. Michael | Northeast Tasmania | 1 | 7 |
| ES011_4.1.1 | 2359645 | −41.47582 | 145.46074 | Philosopher Falls | West Tasmania | 1 | 8 |
| ES199_A5 | 2359651 | −37.48841 | 145.83418 | The Beeches | East Victoria | 1 | 9 |
| ES261_A37 | 2359656 | −41.62717 | 146.01830 | Franklin River | West Tasmania | 1 | 10 |
| ES263_A39 | 2359652 | −41.36459 | 147.85489 | Rattler Ranges | Northeast Tasmania | 1 | 11 |
| ES267_A43 | 2359655 | −41.50199 | 147.85458 | Rattler Ranges | Northeast Tasmania | 1 | 12 |
| ES269_A59 | 2359658 | −41.25240 | 147.45370 | Diddleum Plains | Northeast Tasmania | 1 | 13 |
| ES272_A47 | 2359660 | −41.82732 | 145.50516 | Mt. Read | West Tasmania | 1 | 14 |
| ES274_A44 | 2359651 | −37.48841 | 146.01830 | Franklin River | West Tasmania | 1 | 15 |
| ES276_A49 | 2359653 | −41.62717 | 145.83418 | The Beeches | East Victoria | 1 | 16 |
| ES278_A50 | 2359654 | −41.82732 | 145.50516 | Mt. Read | West Tasmania | 1 | 17 |
| ES280_A51 | 2359655 | −41.50199 | 147.85458 | Rattler Ranges | Northeast Tasmania | 1 | 18 |
| ES282_A52 | 2359656 | −41.36459 | 147.85489 | Franklin River | West Tasmania | 1 | 19 |
| ES284_A53 | 2359657 | −41.82732 | 145.50516 | Mt. Read | West Tasmania | 1 | 20 |
| ES286_A54 | 2359658 | −41.50199 | 147.85458 | Franklin River | West Tasmania | 1 | 21 |
| ES288_A55 | 2359659 | −41.82732 | 145.50516 | Mt. Read | West Tasmania | 1 | 22 |
| ES290_A56 | 2359660 | −41.50199 | 147.85458 | Franklin River | West Tasmania | 1 | 23 |
| ES292_A57 | 2359661 | −41.82732 | 145.50516 | Mt. Read | West Tasmania | 1 | 24 |
| ES294_A58 | 2359662 | −41.50199 | 147.85458 | Franklin River | West Tasmania | 1 | 25 |
| ES296_A59 | 2359663 | −41.82732 | 145.50516 | Mt. Read | West Tasmania | 1 | 26 |
| ES298_A60 | 2359664 | −41.50199 | 147.85458 | Franklin River | West Tasmania | 1 | 27 |

a Herbarium voucher numbers for the National Herbarium of Victoria (MEL).
b Set identifies collections used in the first and second sets of microsatellite amplification testing.
c Hap. identifies unique haplotypes in these collections.

*Collection ES295_A66 was included in both sets as a positive control.*

**APPENDIX 2.** Cross-amplification of five microsatellite loci, designed from *Laccaria* sp. A, in species of Australian Hydnangiaceae.

| Speciesb | alb | ESLA06 | ESLA19 | ESLA24 | ESLA39 | ESLA41 |
|----------|----|--------|--------|--------|--------|--------|
| L. sp. E (1) | 5 | + | + | + | + | + |
| L. sp. E (2) | 1 | — | — | — | — | — |
| L. canaliculata (1) | 3 | + | +/− | — | +/− | +/− |
| L. canaliculata (2) | 1 | + | — | — | + | + |
| L. canaliculata (3) | 1 | — | — | — | — | — |
| L. canaliculata (4) | 1 | — | — | — | — | — |
| L. lateritia (1) | 3 | — | — | — | — | — |
| L. lateritia (2) | 1 | + | — | — | — | — |
| L. sp. B (1) | 4 | +/− | — | — | + | +/− |
| L. sp. B (2) | 2 | + | — | — | — | — |
| L. sp. B (3) | 3 | +/− | — | — | — | — |
| L. sp. B (4) | 1 | — | — | — | — | — |
| L. sp. D | 2 | +/− | — | — | +/− | +/− |
| L. masoniae (1) | 3 | — | — | — | +/− | +/− |
| L. masoniae (2) | 1 | — | — | — | — | — |
| Hydnangiunm carneum (1) | 4 | — | — | — | — | — |
| H. carneum (2) | 1 | — | — | — | — | — |
| H. sublamellatum | 1 | + | — | — | — | — |

Note: + = locus amplified in every collection tested; +/− = locus amplified in at least one but not all collections tested, for example, one or two of three collections amplified; — = locus did not amplify; n = sample size.

*Of the eight loci tested, three (ESLA12, ESLA38, ESLA66) did not amplify in any species other than *Laccaria* sp. A; these loci are not included in this table.

Species are as delimited in Sheedy et al. (2013) from a multigene (ITS, rpb2, and tef-1α) phylogeny, with cryptic phylogenetic species within morphological species indicated by numbers in parentheses. Described morphological species are *L. lateritia* Malençon, *L. canaliculata* (Sacc.) Massee, *L. masoniae* G. Stev., *Hydnangiunm carneum* Wallr., and *H. sublamellatum* Bougher, Tommerup & Malajczuk.

*Voucher information for all collections is provided in Sheedy et al. (2013).*

*Only one allele size was obtained for two loci sequenced in the same run with the same fluorescent tag; therefore, the locus from which this allele was amplified cannot be identified.*

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