



The Maluridae: Inferring Avian Biology and Evolutionary History from DNA Sequences

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1 **The Maluridae: inferring avian biology and evolutionary history from DNA sequences**

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10
11 **Abstract.** The Australo-Papuan fairy-wrens, emu-wrens and grasswrens comprise the passerine
12 family Maluridae. They have long been known for their spectacular plumages, remarkable
13 behavioural ecology, and intriguing biogeography. The family has provided an ideal model with
14 which to explore how phylogenetic and phylogeographic analyses of DNA sequence data can inform
15 understanding of evolutionary history and present-day biology. We review what has been learned of
16 the phylogeny of the group and the phylogeographic history of individual species. We conclude that
17 there is now a strong framework within which to pursue the remaining species-level taxonomic issues,
18 and to extend ecological and behavioural studies into a new era of more detailed genetic questions
19 such as the role of gene-environment interactions in adaptation. We highlight some remaining
20 examples of such questions and discuss how they might be addressed.

21 **Introduction**

22 The life history, systematics and biogeography of Australo-Papuan fairy-wrens, emu-wrens
23 and grasswrens (Passeriformes: Maluridae) are a rich source of challenging evolutionary questions.
24 Field, population-based studies that are reviewed in this suite of papers have illuminated these
25 questions and such work will continue to do so. Complementing field studies has been a growing
26 contribution from the fields of molecular systematics, phylogeography and population genetics all of
27 which have undergone revolutions since the advent of DNA sequencing in the 1980s. Systematics is
28 the study of how species are related to each other phylogenetically and how taxonomy can best
29 express hypotheses of phylogenetic relationships. Similarly, looking within species, phylogeography
30 is the DNA sequence-based study of the evolutionary forces that explain how genetic diversity within
31 species is organized in space and time (Awise *et al.* 1987; Edwards *et al.* 2012). It has revolutionized

32 understanding of evolutionary history within species. The Maluridae is almost unique in the
33 foundation that molecular data have helped build for understanding of evolutionary history and
34 ecological diversity within and among its species. Indeed, malurids are now a leading model for the
35 integration of evolutionary and ecological data. Here we review how phylogenetic and
36 phylogeographic analyses of DNA sequence data from the Maluridae have sharpened understanding
37 of their relationships to other groups of birds as well as within and among its own member species.
38 We provide a framework against which the spectacular behavioural ecology, reproductive biology,
39 feeding ecology, behaviour, and morphology of malurids can be articulated in the accompanying
40 papers.

41 After reviewing how the Maluridae are related to other passerine birds, we discuss how
42 phylogenetic studies have informed understanding of the family's genera, species, populations and
43 individuals. We will touch on questions of molecular systematics and historical biogeography,
44 phylogeography, hybrid zones, population genetics, parentage and individual kinship.

45 **Who are the Maluridae and Where Do They Fit Among Passerines?**

46 The defining and distinguishing traits of the Maluridae (its diagnosis) and the genera and
47 species that belong in it and those that do not (its circumscription) are not controversial.
48 Morphological diagnoses of the Maluridae are in Schodde (1982), Sibley and Ahlquist (1985),
49 Schodde and Mason (1999), Rowley (2001), and Rowley and Russell (1997, 2007). Diagnostic
50 morphological traits include the interscapular gap of feathers and osteological characters of the
51 humerus and palate. It has never been controversial that the Maluridae comprises the grasswrens
52 *Amytornis* spp and the emu-wrens *Stipiturus* spp, both exclusively Australian, and the “true” fairy-
53 wrens *Malurus*, *Sipodotus*, *Clytomyias* and *Chenoramphus* of Australia and New Guinea. Initial DNA
54 sequence-based analyses of relationships across passerines therefore only used *Malurus* to represent
55 the Maluridae (e.g., Barker *et al.* 2002, 2004; Ericson *et al.* 2002). These studies were not designed to
56 provide independent, molecular tests of which genera belong in a natural group to be called the
57 Maluridae. The point here is that analyses aiming to evaluate generic boundaries suggested by
58 morphology do often surprise us. They can necessitate re-thinking of the membership of some higher
59 groupings of birds. A spectacular, albeit non-malurid, example is Macgregor's Bird-of-Paradise
60 *Macgregoria pulchra*, which is now known to be a honeyeater (Meliphagidae) (Cracraft and Feinstein
61 2000). Appropriately designed molecular studies of the Maluridae have now been done and
62 unequivocally support the morphology-based diagnosis and circumscription of the Maluridae
63 (Gardner *et al.* 2010; Driskell *et al.* 2011; Lee *et al.* 2012). Gardner *et al.* (2010) drew together the
64 findings of all previous molecular studies and, with further data, affirmed that the Maluridae along
65 with the Meliphagidae (honeyeaters) and the Acanthizidae (thornbills and their relatives) together
66 make up one of the largest and indeed oldest radiations of Australo-Papuan birds, the superfamily

67 Meliphagoidea. Among passerines, the Meliphagoidea in turn appears to have evolved from one of
68 the earliest, major branches of the oscine tree in the Australia-New Guinea-New Zealand region.

69 Fundamentals of relationships among the three major groups of the Maluridae are again
70 unremarkable. Phylogenetic analyses consistently and unambiguously recover the grasswrens, emu-
71 wrens and fairy-wrens as three natural groups, or clades, within the Maluridae. The grasswrens are
72 clearly more divergent from the other two groups than the latter are to each other (Fig. 1). Therefore,
73 the three clades are classified into two subfamilies, the Amytornithinae (grasswrens) and the
74 Malurinae (emu-wrens and fairy-wrens). Within the Malurinae, the emu-wrens and fairy-wrens are
75 formally recognized as the tribes Stipiturini and the Malurini, respectively (Driskell *et al.* 2011).

76 Figure 1

77 Relationships within genera have been more controversial and confusing. The debate has
78 hinged on how four species endemic to New Guinea are related to Australian *Malurus*. The four are
79 Orange-crowned Wren *Clytomyias insignis*, Wallace's Wren *Sipodotus wallacii*, Emperor Fairy-wren
80 *Malurus cyanocephalus*, and Broad-billed Fairy-wren *Chenoramphus grayi*. *Clytomyias* had long
81 been retained for the Orange-crowned Wren if only because of uncertainty in its relationship to
82 *Malurus* and *Stipiturus* (*cf* Schodde 1992; Christidis and Schodde 1997). Alternative hypotheses
83 placed *Chenoramphus* either in *Malurus* or with *Clytomyias* and *Sipodotus* in the sister group to
84 *Malurus* (Schodde 1992; Christidis and Schodde 1997; Rowley and Russell 1997, 2007; Driskell *et al.*
85 2011; Lee *et al.* 2012; Fig. 1a, b). *M. cyanocephalus* had been placed in monotypic *Todopsis*. DNA
86 studies (Driskell *et al.* 2011; Lee *et al.* 2012) agree that *M. cyanocephalus*, is the sister to all other
87 species conventionally placed in *Malurus*. They also agree that *Malurus* so construed is sister to a
88 group that includes *Clytomyias* and *Chenoramphus* (Fig. 1a, b). *Sipodotus* has appears closest to
89 *Clytomyias* (Driskell *et al.* 2011; Fig. 1b). Fortunately, therefore, genus-level stability has emerged.
90 Consensus sees the biological merit of expanding *Malurus* to include *M. cyanocephalus* but to
91 continue recognizing *Clytomyias*, *Sipodotus* and *Chenoramphus*

92

93 **A closer look at *Malurus***

94 *Malurus* comprises nine Australian species: *M. elegans*, *M. pulcherrimus*, *M. lamberti*, *M.*
95 *amabilis*, *M. cyaneus*, *M. splendens*, *M. leucopterus*, *M. coronatus*, *M. melanocephalus*), and two
96 New Guinean ones (*M. alboscapulatus*, *M. cyanocephalus*). Not only is *M. cyanocephalus* sister to
97 other *Malurus* as noted, but Australian *M. leucopterus* is sister to *M. alboscapulatus* and *M.*
98 *melanocephalus* (Driskell *et al.* 2011; Lee *et al.* 2012). This scenario rejects a simple hypothesis of
99 one episode of vicariance between Australia and New Guinea explaining the biogeographical history

100 of the group. A more complex history of connections and breaks between the two land masses is
101 suggested. The phylogeny implies multiple evolutionary gains and losses of traits such as fine, narrow
102 bills of Australian species *versus* broader bills of New Guinean species (Schodde 1982). Driskell *et*
103 *al.* (2011) argue that the Malurini originated in New Guinea not Australia; Lee *et al.* (2012) urged
104 more quantitative analyses to test this.

105 Within *Malurus* several groupings have consistently been recovered in molecular studies and
106 we discuss them sequentially.

107 *Chestnut-shouldered fairy-wrens (CSFW)*

108 CSFW comprises the Red-winged Fairy-wren *M. elegans* of south-western Australia, the
109 Blue-breasted Fairy-wren *M. pulcherrimus* of drier south-western Australia and Eyre Peninsula, South
110 Australia, the Lovely Fairy-wren *M. amabilis* of Cape York Peninsula, and the Variegated Fairy-wren
111 *M. lamberti* having a vast range across inland, tropical northern and subtropical eastern Australia.
112 CSFW has long been recognized as a natural group (Ford 1966; Harrison 1972; Schodde 1982;
113 Rowley and Russell 1997, 2007). Molecular data affirm the CSFW's monophyly (Christidis and
114 Schodde 1997; Driskell *et al.* 2011; Lee *et al.* 2012; McLean *et al.* 2012). Recognition of *M. amabilis*
115 as a species distinct from *M. lamberti* (which was argued as late as Schodde 1982 and questioned by
116 Cracraft 1986) poses questions that phylogenetic perspectives could inform. How and why have some
117 *Malurus* species and not others evolved blue-backed females? How has *M. lamberti* evolved its high
118 diversity of climatic environments and habitats, notwithstanding that all populations favour shrubby
119 undergrowth? What are the dynamics at zones where two of its component forms meet? We now
120 examine the CSFW and these questions more closely.

121

122 *Variegated Fairy-wren M. lamberti*

123 This species is the most widespread, climatically diverse and phenotypically variable malurid
124 (Fig. 2). *M. l. lamberti* of wetter central eastern Australia inhabits tall, rank grass and shrubby
125 understoreys. *M. l. assimilis* has a vast range across inland Australia in open shrublands and
126 grasslands. *M. l. rogersi* occurs in rocky *Triodia*-clad hills in the Kimberley of north-western
127 Australia. *M. l. dulcis* inhabits sandstone escarpments in the Top End of the Northern Territory. A
128 fifth, *M. l. assimilis*-like form, *M. l. bernieri*, is recognized and inhabits Bernier and Dorre Islands off
129 the Western Australian coast.

130 Molecular data have built a framework for understanding the evolution of this species'
131 extraordinary diversity. McLean *et al.* (2012) showed it to be the result of a recent, explosive radiation
132 such that mtDNA diversity does not yet closely match the geographically structured phenotypic

133 diversity. The genomic basis of its climatic flexibility could be a rewarding study potentially
134 illuminating how ecologically less flexible species might be managed under climate change.

135 Figure 2

136 McLean *et al.* (2012) found that for mtDNA *M. l. lamberti* was sister to a clade comprising all
137 other subspecies of *M. lamberti* and *M. amabilis*. Pursuing this with data from the nuclear genome,
138 however, they found that when up to four individuals per taxon per locus were used in analyses, the
139 monophyly of all *M. lamberti* was recovered. The best defended hypothesis at present, therefore,
140 combines Schodde's (1982) compelling morphological arguments with McLean *et al.*'s molecular
141 analyses to recognize as sister species *M. amabilis* and *M. lamberti* (including *M. l. dulcis*, *M. l.*
142 *assimilis* and *M. l. rogersi*). These studies caution that sampling multiple individuals per species as
143 well as multiple genetic loci can yield a clearer, albeit often complex, picture of evolutionary history.
144 The discordance here probably reflects different rates of evolution in the DNA of the mitochondria
145 and nucleus. That is, genetic diversity in the nuclear genome of a common ancestor can be shared
146 between diverging species for significantly longer than diversity in the mitochondrial genome.

147 *Origin and variation of the blue-backed phenotype across northern Australia*

148 *M. l. rogersi*, *M. l. dulcis* and *M. amabilis* share the unusual trait of blue-backed females and
149 replace each other geographically across northern Australia. In the strongly sexually dimorphic
150 species of *Malurus* in which alternate plumaged (breeding) males are colourful and female and basic
151 (eclipse) male plumages are not, the blue dorsal plumage in females is clearly exceptional. Also,
152 female *M. l. dulcis* and *M. amabilis* have white lores. An enduring puzzle, therefore, is the evolution
153 and underlying biology of blue dorsal plumage in females of three tropical Australian taxa that are not
154 each other's closest relatives.

155 Molecular data (Odeen *et al.* 2011; McLean *et al.* 2012; Lee *et al.* 2012) suggest answers to
156 the problem and directions for closer study. Within the *M. lamberti* complex, *M. l. dulcis* and *M. l.*
157 *rogersi* are apparently relatively recently evolved members of the group: their alleles are not
158 reciprocally monophyletic with respect to each other or to other populations of *lamberti* (McLean *et*
159 *al.* 2012); *M. amabilis* is sister to the whole *M. lamberti* group. Two hypotheses are suggested. First,
160 blue dorsal plumage in females arose at least twice, once and probably earliest in *M. amabilis* and
161 later in *M. l. rogersi* and *M. l. dulcis*. Conceivably, some facet of tropical light spectra in the birds'
162 environments (Endler 1993) provides selective pressure for this. Alternatively, blue dorsal plumage in
163 females may have been lost independently in most lineages of *Malurus*. The latter hypothesis is
164 suggested because female plumages in *M. cyanocephalus*, which is sister to all other *Malurus*, and *C.*
165 *grayi*, which is part of the sister group to *Malurus*, do involve blue on the head or dorsum. Homology
166 or otherwise of the blue in females of all of these species (and white lores in *M. l. dulcis* and *M.*

167 *amabilis*) should be tested to determine which evolutionary force(s) drove the loss, or gain, of blue
168 dorsal female plumage in Australian species. Relevant here is the *SWS1* opsin gene, which encodes a
169 visual pigment sensitive to the ultraviolet-violet region of the visible spectrum and which fall into at
170 least two discrete classes - violet sensitive and ultra-violet sensitive; only CSFW, *M. cyaneus* and *M.*
171 *splendens* have the latter pigments (see Odeen *et al.* 2011). Certainly, a challenging study awaits to
172 integrate phylogenetic relationships, light spectra in different environments across all *Malurus*, the
173 *SWS1* gene, and the birds' biology.

174 *Intergradation between M. l. lamberti and M. l. assimilis in subtropical Australia.*

175 Hybridization and introgression are common in birds and provide important windows into
176 species interactions and speciation dynamics (Rheindt and Edwards 2011). Putative hybridization and
177 zones of intergradation have been inferred between *M. l. dulcis* and *M. l. assimilis* (Harrison 1972),
178 and *M. l. rogersi* and *M. l. assimilis* (Ford and Johnstone 1991) (reviewed in Schodde 1982). Mack's
179 (1934) remark that "some examples of [*M. l.*] *lamberti* from the northern part of its range provide
180 evidence of intergradation [with *M. l. assimilis*]", has long been the only basis that a zone of
181 intergradation exists in south-east Queensland between *M. l. lamberti* and *M. l. assimilis* (Parker in
182 Schodde 1975; Schodde 1982; Fig. 3). McLean *et al.* (2012) recovered *M. l. lamberti* as being highly
183 divergent molecularly from *M. l. assimilis* (4.3% divergence in mtDNA, or over 4 sites per 100 in this
184 molecule, which is substantial), but noted that the Great Dividing Range essentially separates the two
185 subspecies. Some work has explicitly assessed the Great Dividing Range's role as a barrier promoting
186 vicariance (*cf* Pavlova *et al.* 2010, accepted). Closer study of this zone with new specimens revealed
187 discordant patterns in mtDNA diversity, which was structured geographically (Fig. 3: right) and ;
188 microsatellite loci, which were not. This implies that gene flow may still be substantial. Conflicting
189 results between mtDNA and microsatellites are not uncommon (Caparroz *et al.* 2009; Rollins *et al.*
190 2012) and have often been explained through male-biased dispersal (Zink and Barrowclough, 2008).
191 Sex-biased dispersal has not been studied in this species but is an unlikely explanation of these
192 findings. In *M. cyaneus*, for example, males show natal philopatry whereas females are more likely to
193 disperse (Double *et al.* 2005) and indeed female-biased dispersal is common in most species of birds
194 (Greenwood, 1980). The conflict between mtDNA and nuclear loci here may result from differences
195 in their population genetics and sensitivity to demographic changes, as well as challenges of
196 deciphering evolutionary history from microsatellites. Evolution of microsatellites by their expansion
197 and contraction is erratic and difficult to model (Zink and Barrowclough, 2008; Brito and Edwards
198 2009). Nuclear markers that more closely resemble the type of data used for mtDNA, such as
199 sequence-based nuclear markers (Brito and Edwards 2009), may provide more insight into the history
200 of intergradation in this group.

201

202

Figure 3.

203

204 *Additional complexities of chestnut-shouldered fairy-wrens*

205 Understanding how three species of CSFW have come to occur in south-western Australia has
206 been a challenge to address at least in part through understanding how the species are related to each
207 other. Yet the relationships among CSFW have proven difficult to resolve. This difficulty illustrates
208 well the challenges that arise in reliably determining relationships among a close-knit group of species
209 that have undergone rapid evolution (Fig.6 of McLean et al. 2012; Edwards *et al.* 2009; Lee *et al.*
210 2012). Fig. 4 shows alternative hypotheses. Christidis and Schodde (1997) and Lee *et al.* (2012)
211 recovered *M. elegans* and *M. pulcherrimus* as sister species, the four CSFW thus being two simple
212 sister species pairs. Conversely, Driskell *et al.* 2011 and McLean *et al.* (2012) found *M. pulcherrimus*
213 to be sister to *M. l. lamberti/M. amabilis* and *M. elegans* sister to the other three. Clearly, further work
214 is needed to discriminate among these hypotheses and build correlations between the evolutionary
215 history of the birds and their habitats, for example.

216

217

Figure 4

218 *The Blue group*

219 Two primarily southern Australian species, the Superb *M. cyaneus* and Splendid Fairy-wrens
220 *M. splendens* unremarkably form a sister species pair. They replace each other vicariously in south-
221 eastern mesic (*M. cyaneus*) and mostly drier western and inland (*M. splendens*) habitats. *M. cyaneus*
222 has been extensively studied at the population level (see companion papers). Notable here are island-
223 mainland comparisons of populations in *M. cyaneus*. This work first used morphology to affirm the
224 prediction from ecological speciation theory that natural selection shapes adaptive divergence
225 (Schlotfeldt and Kleindorfer 2006). Later work with molecular data then found highly restricted gene
226 flow between the same island and mainland populations and presented concordant morphological and
227 molecular evidence of evolutionary divergence occurring between the two populations (Dudaniec *et*
228 *al.* 2011). Kleindorfer *et al.* (this issue) further examine this particular island-mainland comparison.

229

230 Kearns *et al.* (2009) examined the phylogeography of *M. splendens*, a textbook case of
231 geographical replacement of morphologically defined subspecies. They found general concordance
232 among morphology and molecules. The exception was in inland eastern Australia where decoupled
233 evolution in the two character sets had to be explained. They suggested that morphological
234 differentiation may have occurred without periods of isolation, possibly in response to differences in

234 local environmental conditions, or alternatively, mtDNA and plumage may have different rates of
235 evolution.

236 *The Bicoloured group*

237 The bicoloured group comprises the White-shouldered Fairy-wren *M. alboscapulatus* of New
238 Guinea (black-and-white males and geographically variable females), and White-winged Fairy-wren
239 *M. leucopterus* (blue-and-white or black-and-white males) and Red-backed Fairy-wren *M.*
240 *melanocephalus* (red-and-black males) of Australia. Adult male *M. leucopterus* over the species' vast
241 inland Australian range have alternate or nuptial plumage that is blue with white scapulars, secondary
242 wing-coverts and innermost secondaries. The populations isolated on Dirk Hartog and Barrow Islands
243 (*M. l. leucopterus* and *M. l. edouardi*, respectively) have blue replaced by black. Evolution of
244 differences between mainland and island populations has been addressed. Driskell *et al.* (2002) used
245 mtDNA diversity across the entire range to derive a framework of the species' history. They found
246 that the two island populations are not each other's closest relatives. Also, western mainland
247 populations (with blue-and-white males) are more closely related to, and may have had relatively
248 recent gene flow with, Dirk Hartog birds (black-and-white males) than to blue-and-white mainland
249 populations further east. Two equally parsimonious hypotheses then could explain the shift between
250 blue and black plumage: black plumage arose from blue convergently on the two islands, or black
251 arose from blue and was followed by re-evolution of blue plumage in mainland Western Australia.
252 Next, Doucet *et al.* (2004) studied a nuclear gene, *MC1R*, the melanocortin-1 receptor locus; work in
253 a Neotropical bird, the Bananaquit *Coereba flaveola*, had shown that changes at a single nucleotide
254 position in *MC1R* correlate perfectly with whether individual birds have the species' usual plumage or
255 are melanic (all black) (Theron *et al.* 2001). Its relevance to melanic plumage polymorphism in
256 various birds has since been studied (Mundy 2005; Mundy *et al.* 2004; Uy *et al.* 2009). Doucet *et al.*
257 (2004) found in *M. leucopterus* that of 34 variable sites at the *MC1R* locus, 23 did not change the
258 amino acid and 11 did. Five of the latter were perfectly associated with divergence in plumage
259 phenotypes between mainland and island birds. They also argued on the basis of nanostructure of the
260 feathers that black most likely evolved from blue. Driskell *et al.* (2010) then conducted a
261 phylogenetically broader survey of *MC1R* variation across *Malurus* generally and revisited feather
262 nanostructure. They reasoned that across *Malurus* there is no correlation between *MC1R* variation
263 and whether plumage is blue or black. They further supported the hypothesis that there have been two
264 independent transitions from blue to black in this species, and probably a third in the lineage leading
265 to *melanocephalus* and *alboscapulatus*.

266 *The Purple-crowned Fairy-wren M. coronatus*

267 The Purple-crowned Fairy-wren *M. coronatus* of tropical northern Australia is of great
268 interest given its unique biology within *Malurus*. Like other *Malurus* it is a cooperative breeder but

269 unlike them has very low levels of extra pair paternity and is essentially monogamous (Kingma *et al.*
270 2009). It is a riparian specialist, restricted to *Pandanus*-dominated vegetation along the rivers across
271 tropical savannas of northern Australia (Rowley and Russell 1997; Skroblin and Legge 2010). It lacks
272 erectile ear-coverts and scapulars that other *Malurus* use in display and no courtship displays or petal-
273 carrying have been recorded in it (Rowley and Russell 1997). It mostly lacks bright colour in its
274 plumage, both sexes being predominantly grey and blue-tailed, males having the eponymous purple-
275 crown and females having brown ear-coverts. It is also relatively large. Three phylogenetic analyses
276 have each reached different conclusions. Historical perspectives on the bird's biology are perhaps
277 most cautiously considered as unresolved, despite Kingma *et al.*'s (2009) analysis based on an
278 allozyme study Christidis and Schodde (1997). Gardner *et al.* (2010) found it to be sister to the blue
279 group (*M. cyaneus* and *M. splendens*). Driskell *et al.* (2011) found it weakly supported as sister to the
280 chestnut-shouldered group. Lee *et al.* (2012; Fig. 1) in the most exhaustive analysis found it on a
281 branch that diverged after *M. cyanocephalus* and before the rest of *Malurus*. We are left with two
282 alternatives that need further testing. One is that the data analysed to date genuinely reflect early
283 branching of the *M. coronatus* lineage. The other is that the times between speciation events involving
284 *M. coronatus* were short. By that alternative, the data still lack the power to place the species reliably
285 in a sequence of phylogenetic divergence.

286

287 ***Stipiturus* Emu-wrens**

288 Systematic issues concerning the three species of emu-wrens are few. They mainly concern
289 the taxonomic question of whether the Mallee Emu-wren, *S. mallee*, isolated in the Murray Mallee of
290 South Australia and Victoria should be treated as a separate species, which current usage favours, or
291 as a subspecies either of the Rufous-crowned Emu-wren *S. ruficeps* widespread in the western and
292 central arid zone, or the Southern Emu-wren *S. malachurus* of southern Australian heaths and
293 swamps. Phylogenetic analyses (Donnellan *et al.* 2009; Lee *et al.* 2012) affirm *S. mallee* and *S.*
294 *ruficeps* are more closely related to each other than either is to *S. malachurus* and that contact
295 between *S. malachurus* and *S. mallee* is secondary. We suggest that understanding the historical
296 biogeography of how *mallee* came to be isolated in its present range is now of far more interest.
297 Understanding that it is closest to *S. ruficeps* is a key step in that process. Among birds, it shares its
298 unusual distribution with several other unrelated species such as the Red-lored Whistler *Pachycephala*
299 *rufogularis*, the Black-eared Miner *Manorina melanotis* and the easternmost form of the Western
300 Whipbird *Psophodes nigrogularis* complex.

301 Donnellan *et al.* (2009) studied a 281 base pair fragment of the mitochondrial cytochrome *b*
302 gene across the range of *S. malachurus*. Several major disjunctions highlighted the need for nDNA
303 data to clarify some of the issues raised. Most notable were the separation of western and eastern

304 populations generally and, within eastern Australia, the distinct position of the Kangaroo Island and
305 Eyre Peninsula populations being separated from other eastern populations by nine substitutions.

306

307 *Amytornis* Grasswrens

308 Grasswrens, among Australia's most unique birds, are a particularly rich and, at least relative
309 to *Malurus*, untapped source of systematic and biogeographical questions. Although much of their
310 species-level taxonomic confusion has been resolved (e.g., Parker 1972; Schodde and Mason 1999;
311 Black 2004; Black *et al.* 2009; Christidis *et al.* 2010), some debate remains for populations of the
312 widespread Striated Grasswren *A. striatus* and the Thick-billed Grasswren *A. modestus*.
313 Notwithstanding such debate, the genus comprises four species (*A. housei* - Black, *A. woodwardi* -
314 White-throated, *A. dorotheae* - Carpentarian, *A. ballarae* - Kalkadoon) found disjunctly in rocky
315 *Triodia*-clad habitats across tropical northern Australia, one (*A. barbatus* - Grey) confined to the Lake
316 Eyre and Bullo drainages of inland eastern Australia, and others (*A. striatus* - Striated, *A. textilis* -
317 Western, *A. merrotsyi* - Short-tailed, *A. goyderi* - Eyrean, *A. modestus* - Thick-billed, *A. purnelli* -
318 Dusky) in a diversity of habitats, (eucalypt-porcupine grass *Triodia* or chenopod shrublands, rocky
319 *Triodia*-clad hills; desert dune shrublands) in arid and semi-arid habitats across drier inland Australia
320 (see Schodde 1982; Rowley and Russell 1997 for details).

321 Phylogenetic relationships among grasswrens are now relatively well understood (Keast
322 1958; Christidis 1999; Christidis *et al.* 2008, 2010; Lee *et al.* 2012). Changing understanding of the
323 positions of *A. goyderi* and *A. merrotsyi* are instructive as to how molecular data have discriminated
324 between morphologically based alternative hypotheses. Keast (1958) considered *A. goyderi* closely
325 related to two largely chenopod shrubland-based species, *A. textilis* and *A. modestus*, an ecologically
326 coherent arrangement. Later studies aligned it with *A. striatus* (Parker *et al.* 1978; Schodde 1982;
327 Rowley and Russell 1997). Molecular data (Christidis *et al.* 2010; Lee *et al.* 2012) favoured the
328 former hypothesis although clarified that *A. housei* and *A. ballarae* are part of the group to which *A.*
329 *gyderi* belongs. Reassessment of its morphology revealed pitfalls into which earlier morphological
330 analyses had fallen (see discussion in Schodde and Mason 1999; Christidis 1999). Similarly, *A.*
331 *merrotsyi* was long considered a subspecies of *A. striatus* partly because of its geographical proximity
332 to that group (Condon 1951; Keast 1958; Parker 1982; Schodde 1982). Molecular data (Christidis
333 1999; Christidis *et al.* 2008, 2010; Lee *et al.* 2012) and reassessment of its morphology (Schodde and
334 Mason 1999) have shown it to be not part of the *striatus* group although there is some residual
335 uncertainty about its precise placement.

336 Biogeographically, debate has centred on whether the origins of *Amytornis* were in northern
337 (Schodde 1982) or central (Keast 1961; Ford 1974, 1987) parts of the continent. Lee *et al.*'s (2012)

338 analysis favoured a central origin. Christidis et al. (2010) concluded that there may have been an early
339 division of *Amytornis* into a lignum-swamp clade and at least one lineage in *Triodia*-clad, rocky
340 escarpments.

341 Within *Amytornis*, there are clear disparities between patterns of morphological and
342 molecular divergence and Christidis *et al.* (2010) presented a detailed analysis. For example, the 2.6%
343 mtDNA divergence between phenotypically distinct *A. woodwardi* and *A. dorotheae* closely matches
344 the 2.1% between weakly differentiated subspecies of *A. merrotsyi* (*cf* Christidis *et al.* 2008, 2010).
345 This warrants closer study because members of both pairs are clearly isolated genetically and
346 geographically from each other.

347 Remaining areas of most interest to species-level taxonomy in *Amytornis* concern *A. textilis*
348 and *A. modestus* (Black 2011a, b; Black *et al.* 2010) and the *A. striatus* group. *A. striatus* is
349 extraordinarily widespread and has been difficult to sample well across its vast range. Questions
350 needing resolution concern the relationships and structure of genetic diversity among the four main
351 populations that currently comprise it: the Pilbara form *A. s. whitei*, its widespread western sand plain
352 and eastern mallee populations often regarded together as the nominotypical subspecies *A. s. striatus*
353 and the western Queensland isolate *A. s. rowleyi*. Austin *et al.* (in review) have studied mtDNA
354 diversity in nearly all extinct and extant populations of *A. modestus* and *A. textilis*. They found
355 evidence of past gene flow between the extant *A. t. myall* of eastern Australia and one or more of the
356 now extinct south-western populations of *A. textilis*. This means that the extant population harbours a
357 “ghost” lineage of genetic diversity more typical of a now extinct form.

358

359 **Time frames and detailed studies of biogeography of malurids**

360 Molecular data often may provide the only quantitative, if imperfect, window into the time
361 frame of a particular radiation. Notably, molecular data have affirmed suggestions of earlier authors
362 (e.g., Ford 1974; Schodde 1982) that the Australian radiations of *Malurus* (McLean *et al.* 2012),
363 *Stipiturus* (Donnellan *et al.* 2009) and *Amytornis* (Christidis *et al.* 2010) coincide, given indicated
364 error margins, with the Miocene aridification of the continent. This pattern is increasingly clear from
365 molecular studies of Australian vertebrates (Byrne *et al.* 2008; Toon *et al.* 2012). Here, we review
366 biogeographic patterns in two clades, the four CSFW species and the red-backed fairy wren *M.*
367 *melanocephalus*, and show how molecular data provide insight into the role of later, Pleistocene
368 diversification patterns. Such analyses are particularly relevant given the controversies about the role
369 of the Pleistocene in having shaped present-day diversity in different continents (Klicka and Zink
370 1999; Johnson and Cicero 2004; Hewitt 2004; Byrne *et al.* 2008; D’Horta *et al.* 2011).

371

372 *Biogeographic reconstruction of the CSFWs*

373 Elsewhere, we will present a detailed biogeographical reconstruction of the chestnut-
374 shouldered fairy-wrens (CSFW) but we here present a summary (Fig. 5) of the findings, which were
375 based on a subset of anonymous loci and introns used by Lee *et al.* (2012). Reconstruction of
376 ancestral distributions suggests that dispersal and vicariance have both been vital in shaping the
377 current distribution pattern in CSFWs (15 dispersal events, 6 vicariant events and 1 extinction event).
378 Given a phylogeny in which *M. elegans* is sister to other CSFW, the analysis suggests that CSFWs
379 originated in south-western Australian forests, followed by an early dispersal event to Eyre Peninsula.
380 A vicariant event would have given rise to *M. elegans* and the ancestor of other CSFW during a
381 period spanning the Plio-Pleistocene border, 2.5 million years ago (MYA) (highest posterior density
382 interval (HPD) 1.2 – 3.9 MYA). South-western Australia is a region characterized by extreme
383 endemism and high species diversity (Myers *et al.* 2000; Hooper and Gioia 2004; Edwards *et al.*
384 2007). A south-western endemic being sister to a suite of other species found elsewhere does not
385 necessarily mean a south-western area of origin for the endemic (Ladiges *et al.* 2011, 2012).
386 Certainly, south-western Australia is a region in which some present day species represent old
387 differentiation events.

388 The estimated time of this initial vicariance (see also McLean *et al.* 2012, their Fig. 6)
389 coincides with immense climatic change in Australia following the initiation of major oscillations
390 between aridity and pluviality (Byrne *et al.* 2008). It also coincides with the late Pliocene
391 aridification of the Nullarbor Plain between mesic south-western and south-eastern Australia. The
392 role of the Nullarbor and its fringing xeric habitats as an important barrier to dispersal for birds during
393 Pleistocene periods of aridity has been explored in other birds (Cracraft 1986; Toon *et al.* 2007)
394 including malurids (Dolman and Joseph 2012).

395

396

Figure 5

397

398 The currently fragmented distribution of *M. pulcherrimus* suggests that when sea level was
399 lowered at one or more Pleistocene glacial maxima, this species may have been more continuous
400 across southern Australia; presumably, it has maintained ecological separation from *M. elegans* by
401 habitat (Ford 1966; Schodde 1982) but the temporal dynamics of this are not well understood.
402 Similarly fragmented distributions are known in other species (e.g., Western Yellow Robins
403 *Eopsaltria griseogularis*) and divergence between such isolated populations has been argued to have
404 occurred at several times in the Pleistocene since the early-mid Pleistocene (Dolman and Joseph
405 2012).

406

407 The analysis also suggested a mid-Pleistocene vicariant event isolating the ancestors of *M.*
408 *amabilis* in Cape York Peninsula and *M. lamberti* in eastern Queensland. Causative biogeographic
409 barriers may have been the Black Mountain Corridor and the Burdekin Gap, across which significant
410 population differentiation has been observed in birds (Joseph *et al.* 1995; Nicholls and Austin 2005;
411 Kearns *et al.* 2011) and reptiles (Dolman and Moritz 2006; Schneider *et al.* 1998). Pertinent here is
412 that *M. amabilis* and *M. lamberti* in eastern Australia are restricted to coastal mesic zones and habitats
413 such as mangrove, grassland and wetlands, rarely penetrating more than eighty metres into rainforest
414 (Schodde 1982).

415

416 Around 400,000 years ago (0-0.306 MYA, HPD 0-0.504 MYA) as Australia became a “dusty
417 world” (Byrne *et al.* 2008), the analyses suggest that the *M. lamberti* lineage then expanded into the
418 arid interior. This is consistent with recent Pleistocene range expansions across arid Australia for
419 many species of birds and reptiles (see Table 1 of Byrne *et al.* 2008; Joseph and Omland 2009),
420 leading to evolution of more arid-adapted lineages. Further biogeographic reconstruction of CSFW,
421 especially within *M. lamberti*, is constrained by poorly resolved relationships among *M. l. rogersi*, *M.*
422 *l. dulcis* and *M. l. assimilis* (McLean *et al.* 2012).

423

424 *Red-backed Fairywren: recent subspeciation across the Carpentarian barrier*

425 The Red-backed Fairy-wren *M. melanocephalus* ranges widely across northern Australia’s
426 subtropical and tropical grasslands and savannas. Two subspecies, *M. m. melanocephalus* and *M. m.*
427 *cruentatus*, have been diagnosed by variation in the red colour of the birds’ wings, back and scapulars.
428 Broad intergradation between the two is reported in north-eastern Queensland (Schodde and Mason
429 1999; Higgins *et al.* 2001). Lee *et al.* (2008) performed multilocus phylogeographic analyses of the
430 species. The study was designed to test the biogeographic predictions of this taxonomy and sampled
431 broadly over four biogeographic areas (*sensu* Cracraft 1986): the Kimberley Plateau, the Top
432 End/Arnhem Land, Cape York and Eastern Forests. This strategy spanned the Carpentarian Gap (or
433 Barrier), a region today of dry, sparsely wooded plains south of the Gulf of Carpentaria and where the
434 Pleistocene Lake Carpentaria periodically existed up to 8500 years ago on the Australian–New
435 Guinea continental shelf (Chivas *et al.* 2001; Cook *et al.* 2012). This gap has variously influenced
436 diversification in Australian species including numerous birds (Edwards 1993; Jennings and Edwards
437 2005; de Bruyn *et al.* 2004; Kearns *et al.* 2010; Toon *et al.* 2010). Overall, the signals from mtDNA
438 and the nuclear genome similarly and strongly indicated that the major biogeographic break within
439 this species occurred not between Cape York and the Eastern Forests in north-eastern Queensland as
440 inferred from plumage variation but further west across the Carpentarian Gap.

441 This study also estimated the time of divergence between lineages on either side of the
442 Carpentarian Gap. The results illustrate the need for data sets to be comparable across studies. Early
443 suggestions that North American sister species pairs diverged well before the Pleistocene (2.4 – 0.01
444 MYA) came from mitochondrial DNA, which evolves rapidly in birds, at a rate of about 2% per MYA
445 (Lovette 2004). Although this conclusion was disputed (Cicero and Johnson 2004), mtDNA often
446 gives older divergences than sequence-based markers from the nuclear genome. It may not have been
447 surprising that estimates of divergence from nuclear genes between eastern and western lineages of *M.*
448 *melanocephalus* were very recent, around 0.3 MYA. This recent divergence also reflects, of course,
449 the divergence between forms that are very closely related, such as taxonomic subspecies. However,
450 other studies of divergence across the Carpentarian barrier, such as that between grassfinches
451 (*Poephila*), which are recognized taxonomically at the species level, also yield a very recent
452 divergence time of about 0.6 MYA (Jennings and Edwards 2005; Balakrishnan *et al.* 2010). Thus
453 nuclear genes from malurids and other birds across the Carpentarian Gap suggest divergences well
454 within the Pleistocene. Yet the estimates of divergence times from mitochondrial DNA can be deep,
455 particularly for Neotropical taxa (Weir and Schluter 2007; Miller *et al.* 2010; Weir and Price 2011;
456 Gutierrez-Pinto *et al.* 2012). Australian birds have much to contribute to the global inventory of
457 diversification times and the role of the Pleistocene, but it will be important that different studies use
458 the same set of markers by which to calibrate time.

459

460 **Conclusion**

461 We hope that we have shown an important role of molecular data in unravelling the interplay
462 between the evolutionary history and present-day biology of malurids. We are confident that this has
463 now reached the point where a solid framework is in place for the evolutionary relationships within
464 the family. Questions remain, especially at the species and population levels, but much progress has
465 been made. We take the opportunity to emphasize that this stage would not have been reached without
466 the diverse resources provided by museum collections. Similarly, we stress that continued growth and
467 diversification of those resources through collection of new kinds of specimens will enable areas such
468 as gene-environment interactions in changing environments to be pursued more thoroughly. Odeen *et*
469 *al.*'s (2011) work cited above on *SWS1* opsin gene variation is a hint of where this work might go.
470 Only then will we continue teasing apart history and present-day biology in developing a full
471 understanding of the most remarkable birds that are the Maluridae.

472

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484

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Figure Captions

Fig. 1. (a) Species tree of the Maluridae from Lee *et al.* (2012). Species names with asterisks indicate those depicted in figures to the right, in order from top to bottom. Prepared by Angela Frost. Bird figures by Peter Marsack as in Rowley and Russell (1997). *Amytornis woodwardi* and *Sipodotus wallacei* were not available for inclusion but see Fig. 1 (b). Reproduced with permission. (b) Maximum likelihood tree for the Malurinae from Driskell *et al.* (2011). Numbers at the nodes are in the order of: maximum parsimony bootstrap value/maximum likelihood bootstrap value/Bayesian posterior probability. Bootstrap values and posterior probabilities >98% are indicated by * and a dash denotes the node was not present in the bootstrap tree. Reproduced with permission. Note that both trees were used to develop arguments that *Chenoramphus* should be retained for *M. grayi*/*M. campbelli*. See text for details.

Fig. 2. Distribution of the widespread Variegated Fairy-wren *M. lamberti* and its subspecies, and the Lovely Fairy-wren *M. amabilis*, redrawn from Schodde and Mason (1999). Hatching indicates putative zones of intergradations discussed in the text.

Fig. 3. *Left*: Phylogenetic relationships of *M. l. assimilis* (Clade 1) and *M. l. lamberti* (Clade 2) estimated in MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003) based on Bayesian inference from unique mitochondrial ND2 haplotypes (sample size per haplotype if >1 shown in parentheses). LaAs specimen codes in bold are from the *M. l. lamberti*-*M. l. assimilis* zone of intergradations between the two (see map at right). LQ and LN are shorthand for samples of the species *M. lamberti* from Queensland and New South Wales. Maximum parsimony, posterior probabilities and maximum likelihood bootstrap values are indicated at the nodes. An asterisk represents values less than 85 / 0.85 / 85 respectively. *Right*: Central eastern Australian distribution of *M. l. lamberti* (white circles), *M. l. assimilis* (black) and zone of morphological intergrades (grey, between dashed lines) based on examination of all available specimens.

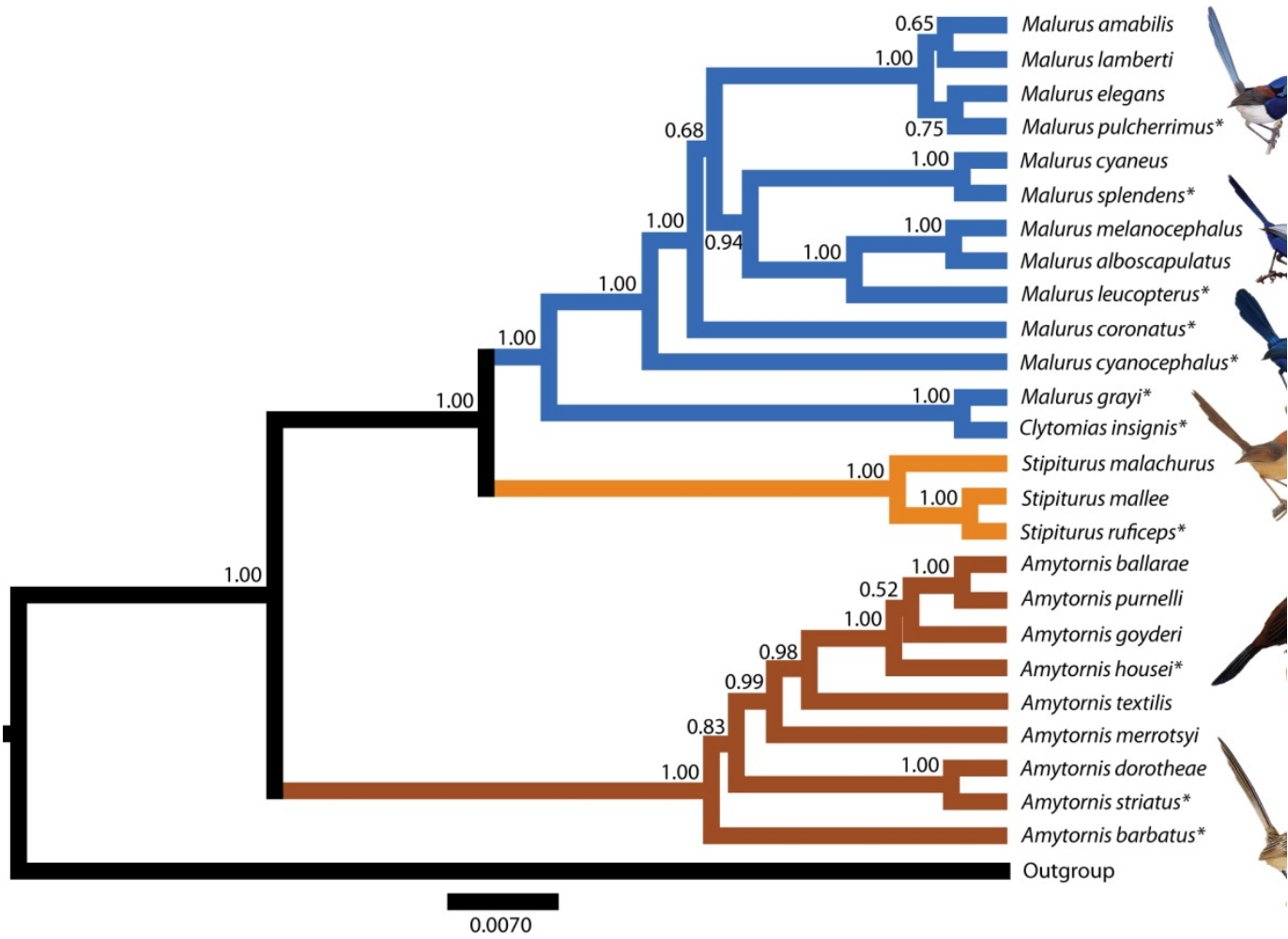
780 Fig. 4. Alternative hypotheses of relationships among CSFW from (a) Lee *et al.* (2012) inferred using
781 BEST from 1 mitochondrial gene, 5 anonymous nuclear loci, 5 nuclear introns and 7 nuclear
782 exons; numbers on branches indicate posterior probabilities, and (b) Driskell *et al.* (2011)
783 using maximum likelihood from four mitochondrial genes and three nuclear introns; numbers
784 at the nodes are in order of: maximum parsimony bootstrap value / maximum likelihood
785 bootstrap value / Bayesian posterior probability. See text for discussion.

786 Fig. 5. Inference of ancestral distributions of CSFW as implemented in RASP (Reconstruct Ancestral
787 Ancestral State in Phylogenies) v 2.0 (Yu *et al.* 2011) by Bayesian binary MCMC (BBM)
788 analysis. BBM offers a statistical procedure for inferring states, including geographic
789 distributions, at ancestral nodes using a full hierarchical Bayesian approach (Ronquist 2004).
790 Distributional regions are colour coded and were assigned *a priori* based on known
791 distributions (shown on map); undetermined distributions are shaded black. Seven
792 geographical regions that were used in the analysis are shown on the map as A to H (*sensu*
793 Cracraft 1991). Pie charts at nodes of the tree above the map show relative probabilities of
794 alternative ancestral distributions; the inset shows the most likely states at nodes. The
795 outgroup, *M. splendens melanotus*, occurs in two of the regions occupied by *M. l. assimilis* (E
796 and F) and was coded (EF). Further division of region E did not alter marginal probabilities at
797 the nodes. 25,000 trees previously produced by BEST v2.3 (Liu 2008) were loaded and the
798 analysis was run for 100,000 cycles using 30 chains with the maximum number of areas kept
799 at seven.

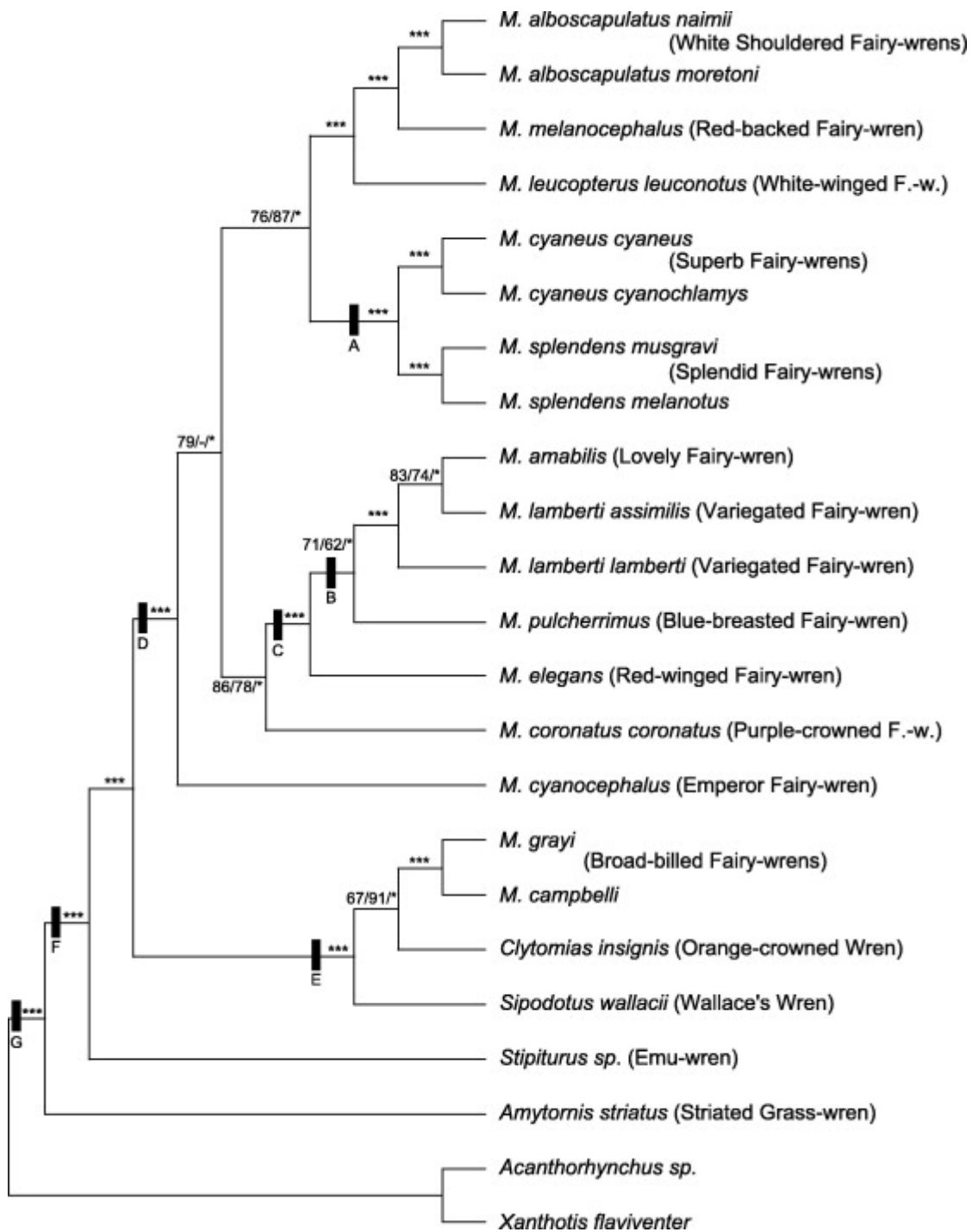
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801 **Figure 1 a**



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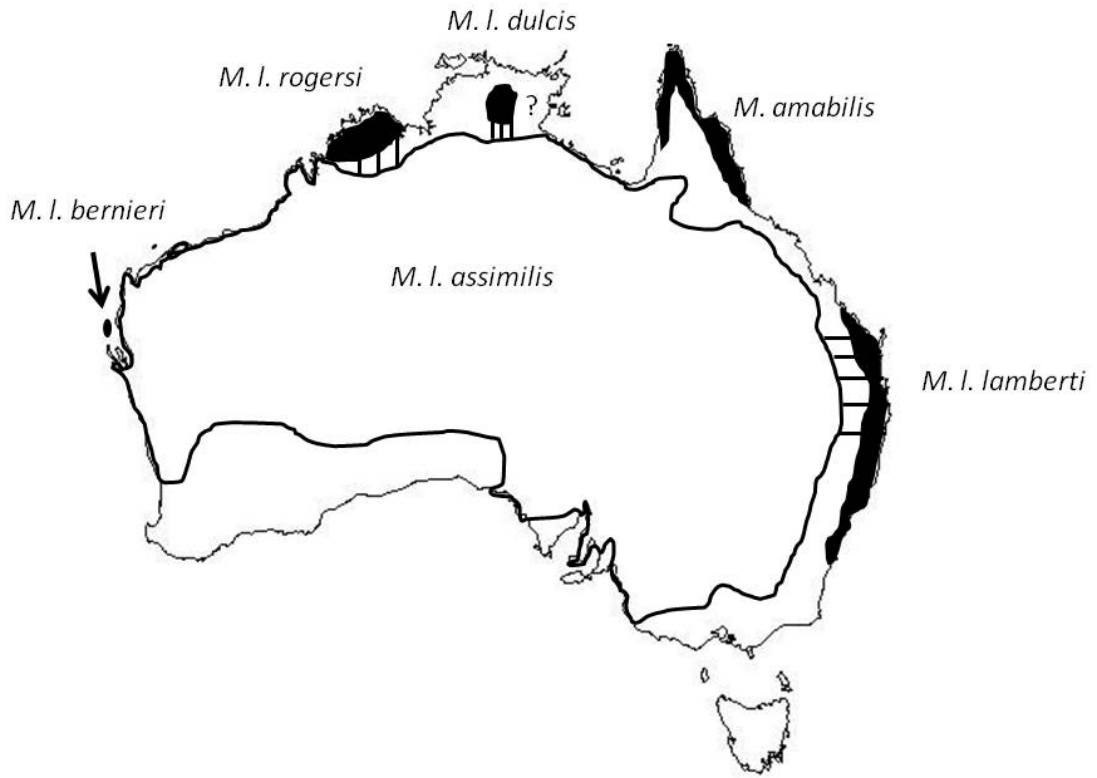


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807 **Figure 2**

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Figure 3

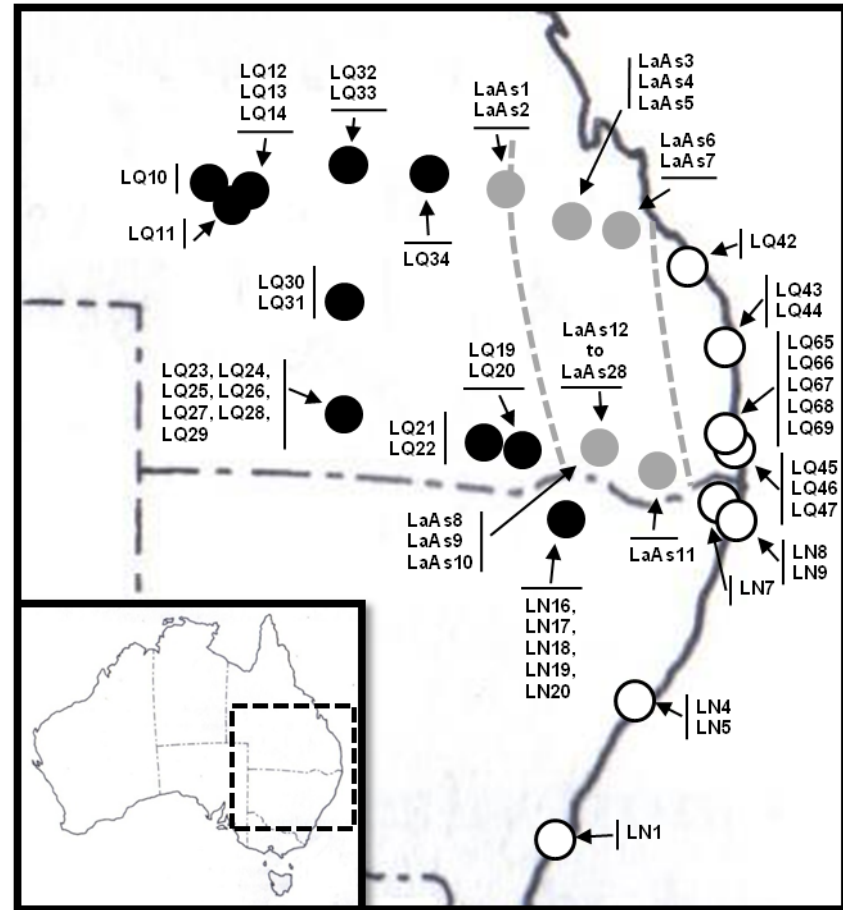
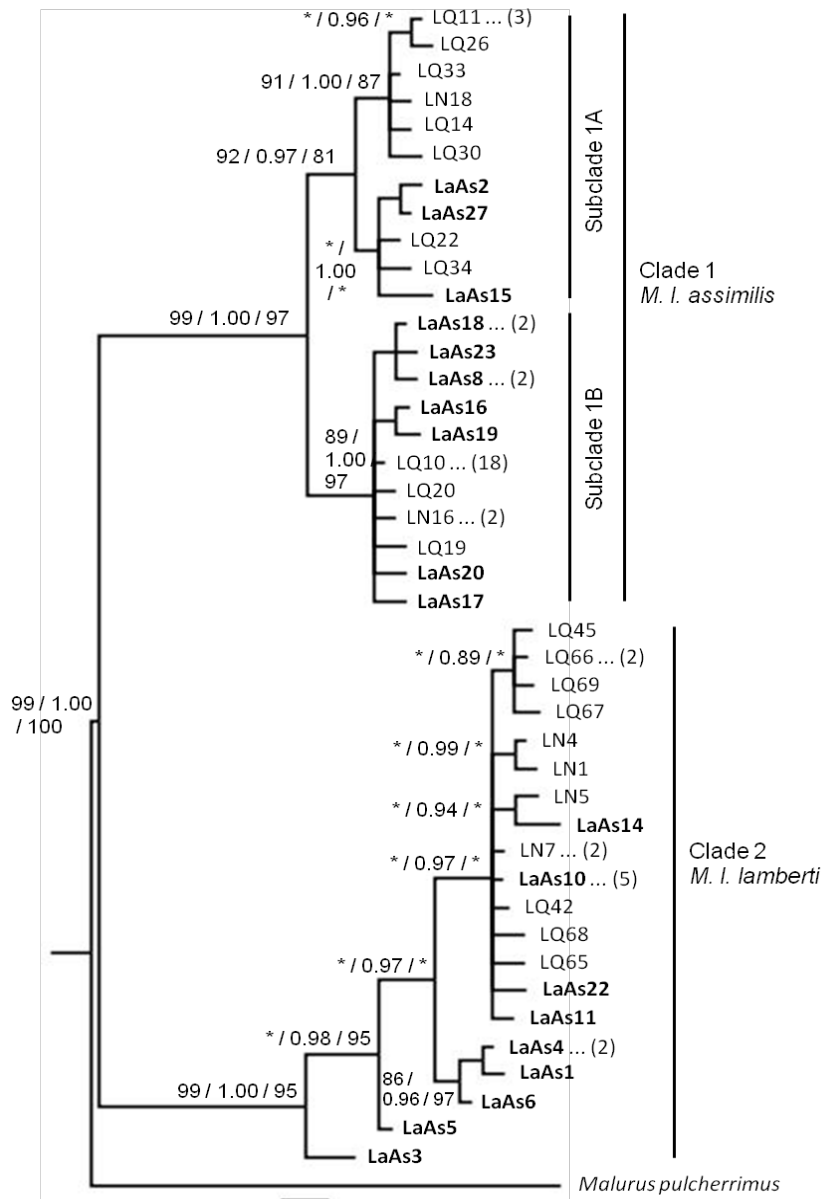


Figure 4

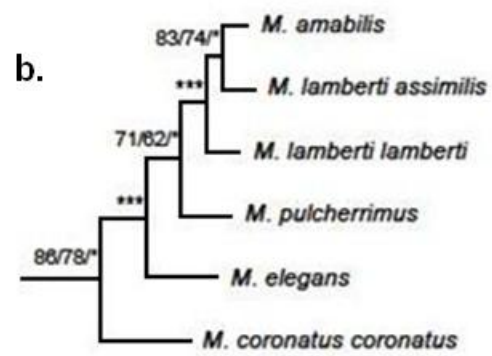
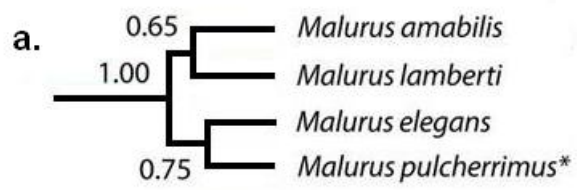


Figure 5.

