Accepted Manuscript

Short communication

Systematics and biogeography of Indo-Pacific ground-doves

Knud A. Jønsson, Martin Irestedt, Rauri C.K. Bowie, Les Christidis, Jon Fjeldså
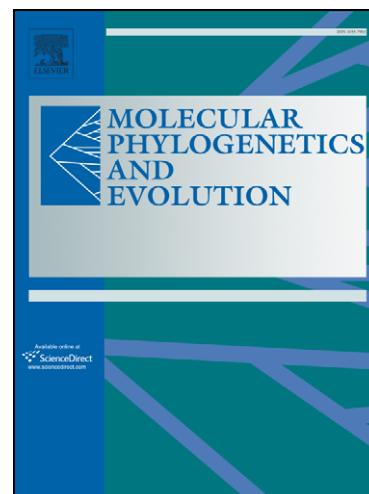
Please cite this article as: Jønsson, K.A., Irestedt, M., Bowie, R.C.K., Christidis, L., Fjeldså, J., Systematics and biogeography of Indo-Pacific ground-doves, *Molecular Phylogenetics and Evolution* (2011), doi: 10.1016/j.ympev. 2011.01.007

1 **Systematics and biogeography of Indo-Pacific ground-doves**

2

3 Knud A. Jønsson[1,2], Martin Irestedt[3], Rauri C. K. Bowie[2], Les Christidis[4,5] and Jon Fjeldså[1]

4

5 [1] Center for Macroecology, Evolution and Climate at the Zoological Museum, University of

6 Copenhagen, 2100 Copenhagen Ø, Denmark.

7 [2] Museum of Vertebrate Zoology and Department of Integrative Biology, 3101 Valley Life

8 Science Building, University of California, Berkeley CA 94720-3160.

9 [3] Molecular Systematic Laboratory, Swedish Museum of Natural History, P.O. Box 50007,

10 SE-10405 Stockholm, Sweden.

11 [4] National Marine Science Centre, Southern Cross University, Coffs Harbour, New South

12 Wales 2450, Australia.

13 [5] Department of Genetics, University of Melbourne, Parkville, Victoria 3052, Australia

14

15 **Corresponding author**

16 Knud Andreas Jønsson, Center for Macroecology, Evolution and Climate at the Zoological

17 Museum, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark.

18 Phone: +45 22 32 04 63. Email: kajonsson@snm.ku.dk

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34

35 **Abstract**

36 Ground-doves represent an insular bird radiation distributed across the Indo-Pacific. The

37 radiation comprises sixteen extant species, two species believed to be extinct and six species

38 known to be extinct. In the present study, we present a molecular phylogeny for all sixteen

39 extant species, based on two mitochondrial markers. We demonstrate that the *Gallicolumba* as

40 currently circumscribed is not monophyletic and recommend reinstalling the name

41 *Alopecoenas* for a monophyletic radiation comprising ten extant species, distributed in New

42 Guinea, the Lesser Sundas and Oceania. *Gallicolumba* remains the name for six species

43 confined to New Guinea the Philippines and Sulawesi. Although our phylogenetic analyses

44 fail to support a single origin for the remaining *Gallicolumba* species, we suspect that the

45 addition of nuclear sequence data may alter this result.

46 Because a number of ground-dove taxa have gone extinct, it is difficult to assess

47 biogeographical patterns. However, the *Alopecoenas* clade has clearly colonized many remote

48 oceanic islands rather recently, with several significant water crossings. The *Gallicolumba*

49 radiation(s), on the other hand, is significantly older and it is possible that diversification

50 within that group may in part have been shaped by plate tectonics and corresponding re-

51 arrangements of land masses within the Philippine and Sulawesi region.

52

53 **Keywords:** Biogeography, *Gallicolumba*, Ground-dove, Oceania, Pacific, Pigeons,

54 Systematics

55

56

57 **Introduction**

58 *Gallicolumba* comprises a group of medium to small sized ground-doves with relatively short

59 wings and tails. They are terrestrial and associated with various kinds of wooded habitat

60 including coastal thickets and mangroves. The sixteen extant species occur in New Guinea

61 (three species), the Pacific (nine species, two of which are shared with New Guinea), the

62 Philippine archipelago (four species), Sulawesi (one species) and the Lesser Sundas (one

63 species) (Gibbs *et al*. 2001). Two species, *G. salamonis* from Makira and Ramos in the

64 southern Solomon archipelago and *G. menagei* from Tawi-Tawi in the southern Philippines

65 are believed to be extinct, with the latter known from a single specimen. Additionally, six

66 species from the Pacific are known to be extinct (Steadman, 2006): *G. ferruginea* from Tanna

67 in the southern Vanuatu archipelago; *G. longitarsus* from New Caledonia; *G. nui* widespread

68 in eastern Polynesia; *G. leonpascoi* from Henderson island in the Pitcairn group; an

69 undescribed *Gallicolumba* species from the Marianas; and *G. norfolciensis* from Norfolk
70 Island. Nearly all extant species have undergone considerable range contractions and in
71 several cases appear to now have relictual distributions (Steadman, 2006). Thus, any
72 biological interpretations based on a phylogeny of the extant species of *Gallicolumba* will
73 have to take into account a significant number of known extinctions.

74 Based on plumage patterns there is a natural divide between the extant species
75 distributed on either side of New Guinea. The "bleeding-hearts", which are characterized by
76 pale underparts and a red-orange breast patch, occur in the Philippines (*keayi, criniger,*
77 *platenae, luzonica*). An assemblage of ground-doves, which are brown with purplish/bronzy
78 reflection and a white or grey breast and head, occur on Pacific islands and New Guinea
79 (*beccarii, canifrons, xanthonura, kubaryi, jobiensis*, *santeaecrucis*, *stairi*, *erythroptera*,
80 *rubescens*) extending as far to the east as the Marquesas archipelago. The species on Wetar
81 and Timor in the Indonesian archipelago (*G. hoedtii*) has variously been included with the
82 Pacific ground-dove clade (Wolters, 1975-1982) or treated as a separate lineage (Peters,
83 1937). Similarly, the positions of *G. tristigmata* and *G. rufigula* are poorly understood.
84 Wolters (1975-1982) aligned both with the "bleeding-hearts" whereas Peters (1937) treated
85 the former as a distinct lineage. Shapiro *et al*. (2002) included three representatives of
86 *Gallicolumba* (*tristigmata*, *luzonica*, *beccarii*) in their mtDNA study and their rather limited
87 data suggested that the New Guinean-Pacific *Gallicolumba* assemblage may be closer to
88 Australasian genera such as *Geopelia*, *Phaps* and *Leucosarcia* than to the "bleeding-hearts" of
89 the Philippines.

90 The distribution of the *Gallicolumba*, makes it an interesting group for
91 investigating island biogeography, dispersal and speciation. Several molecular studies on a
92 range of mammals and birds within the Indonesian and Philippine archipelagos have revealed
93 complex patterns of dispersal between islands and continental land masses, and have
94 furthermore demonstrated that present-day distributions are strongly influenced by a
95 combination of historic terrane movements, Plio-Pleistocene water-level changes and
96 variation in life strategies (Steppan *et al*., 2003; Filardi and Moyle, 2005, Heaney, 2005; Jansa
97 *et al*., 2006; Cibois, 2007, Irestedt *et al*., 2008, Esselstyn *et al*., 2009; Jønsson *et al*., 2010a,b).

98 In the present study we construct the first molecular phylogeny (based on two
99 mitochondrial loci) for all extant members of *Gallicolumba* in order to address questions
100 pertaining to their systematic relationships, historical biogeography and dispersal patterns.

101
102

103 **Material and Methods**

104

105 *Taxon Sampling and Laboratory Procedures*

106 To examine relationships within *Gallicolumba* we included all sixteen extant species along

107 with *Geopelia cuneata*, *Phaps chalcoptera*, *Geophaps plumifera*, *Ocyphaps lophotes* and

108 *Leucosarcia melanoleuca*. The mtDNA study of Shapiro *et al*. (2002) indicated that

109 *Gallicolumba* may be polyphyletic with respect to these genera. For outgroup comparison we

110 used sequence data on *Zenaida macroura* and *Hemiphaga novaeseelandiae* obtained from

111 GenBank.

112 We sequenced the first 525 base pairs (bp) of the mitochondrial marker NADH

113 dehydrogenase subunit 2 (ND2) and all of subunit 3 (ND3) and some flanking tRNA. Fresh

114 tissue (blood, liver, muscle) was extracted using the DNeasy Tissue kit (Qiagen, Valencia,

115 CA), following the manufacturer's protocol. Corresponding laboratory procedures for study

116 skins are detailed in Irestedt *et al*. (2006). Primer pairs used for the amplification of ND2

117 were Lmet (Hackett, 1996)/H6312 (Cicero and Johnson, 2001) and for ND3-L10755/ND3-

118 H11151 (Chesser, 1999). Additionally, we designed new internal primers for ND2

119 specifically for this study: ND2gal330F: ATTCCACCTCTGATTCCCAGAAGT;

120 ND2per340R: CCTTGTAGTACTTCTGGGAATCA; ND2gal530R:

121 GAGGARAARGCYAARATTTTTCG.

122 The thermocycling conditions included a hotstart at 95°C for 5 min, followed by

123 32 cycles at 95°C for 40s, 54–63°C for 40s, and 72°C for 60s, and was completed by a final

124 extension at 72°C for 8 min. One microliter of the amplification products was electrophoresed

125 on a 1.5% agarose gel and viewed under UV light with ethidium bromide to check for correct

126 fragment size and to control for the specificity of the amplifications. PCR products were

127 purified using ExoSap enzymes (Exonuclease and Shrimp Alkaline Phosphatase). Purified

128 PCR products were cycle-sequenced using the Big Dye terminator chemistry (ABI, Applied

129 Biosystems) in both directions with the same primers as used for PCR amplification and run

130 on an automated AB 3100 DNA sequencer.

131 Sequences were assembled with SEQMAN II (DNASTAR Inc.). Positions where

132 the nucleotide could not be determined with certainty were coded with the appropriate IUPAC

133 code. GenBank accession numbers are provided in Table 1.

134

135 **Alignment and phylogenetic analyses**

136 Alignment was performed using MEGALIGN with some minor manual adjustments. The

137 concatenated alignment consisted of 921 bp comprising 525 bp of ND2 and 396 bp of ND3.

138 Both genes were checked for the presence of stop codons or insertion/deletion events that

139 would have disrupted the reading frame.

140 We used Bayesian inference (e.g., Holder and Lewis, 2003; Huelsenbeck *et al*.,

141 2001), as implemented in MRBAYES 3.1.2 (Huelsenbeck and Ronquist, 2003; Ronquist and

142 Huelsenbeck, 2003) to estimate phylogenetic relationships. The most appropriate substitution

143 models were determined with MRMODELTEST 2.0 (Nylander, 2004), using the Akaike

144 Information Criterion (Akaike, 1973, Posada and Buckley, 2004). Bayesian analyses for the

145 concatenated data set were performed using a mixed-models approach (Ronquist and

146 Huelsenbeck, 2003; Nylander *et al*., 2004) allowing for different parameters (base

147 frequencies, rate matrix or transition/transversion ratio, shape parameter, proportion of

148 invariable sites) to vary between the four partitions (1st, 2nd, 3rd codon positions and tRNA). In

149 all MRBAYES analyses, Markov Chain Monte Carlo (MCMC) was run using Metropolis-

150 coupling, with one cold and three heated chains, for 15 million iterations with trees sampled

151 every 500 iterations. The number of iterations discarded before the posterior probabilities (i.e.

152 the length of the 'burn-in' period) were graphically estimated using AWTY (Nylander *et al*.,

153 2008a; Wilgenbusch *et al*., 2004) by monitoring the change in cumulative split frequencies.

154 Two independent runs initiated from random starting trees were performed for each data set,

155 and the log-likelihood values and posterior probabilities for splits and model parameters were

156 checked to ascertain that the chains had reached apparent stationarity.

157 Maximum likelihood analyses were performed using GARLI 0.95 (Zwickl,

158 2006). Five independent analyses (20 million generations) were performed both for the

159 individual analyses and for the analysis of the concatenated dataset. Nodal support was

160 evaluated with 100 nonparametric bootstrap pseudoreplications.

161 Because of stop codons present in the ND2 and ND3 sequences of *Gallicolumba*

162 *tristigmata* we ran separate analyses in MRBAYES and GARLI excluding this taxon.

163 To estimate the relative divergence times within ground-doves, we used BEAST

164 v.1.4.6 (Drummond et al., 2002, 2006; Drummond & Rambaut, 2007). We assigned the best

165 fitting model, as estimated by MRMODELTEST 2.0 (Nylander, 2004), to each of the partitions.

166 We assumed a Yule Speciation Process for the tree prior and an uncorrelated lognormal

167 distribution for the molecular clock model (Drummond et al., 2006; Ho, 2007). We used

168 default prior distributions for all other parameters and ran MCMC chains for 50 million

169 generations. We used the program Tracer (Rambaut & Drummond, 2007) to assess

170   convergence diagnostics.

171

172   **Results**

173   Sequence alignment for all taxa and genes was straight-forward. The ND3 sequences

174   contained an extra nucleotide at position 174 found in some reptiles and birds, which is not

175   translated and thus does not disrupt the reading frame (Mindell *et al*., 1998). This nucleotide

176   position was excluded in all phylogenetic analyses. We found one stop-codon in both the

177   ND2 and the ND3 sequence of *Gallicolumba tristigmata*. This would cause a disruption of the

178   reading frame and is indicative of the presence of a pseudogene. Although, we included the

179   sequences from this individual in our phylogenetic analyses, we remain cautious about its

180   systematic placement. All other mitochondrial data contained neither insertions, deletions nor

181   anomalous stop-codons. Additional analyses excluding *Gallicolumba tristigmata* did not

182   change the relationships or the support values in any of the trees.

183   Model based analyses performed on the concatenated dataset (four partitions:

184   1st, 2nd, 3rd codon positions and tRNA; maximum likelihood (ML): –ln 5358.29, Bayesian

185   inference (BI) harmonic mean: –ln 5098.91) yielded a 50% majority-rule consensus tree (BI)

186   that was topologically congruent with the ML tree (Fig. 1), (for well-supported nodes

187   receiving posterior probabilities >0.95 or bootstrap values >70%). Scores of the best

188   likelihood trees were within 0.5 likelihood units of the best tree recovered in each of the other

189   four GARLI runs, suggesting that the five runs had converged.

190   The phylogenetic analyses demonstrate that *Gallicolumba* is not monophyletic.

191   One clade consists of a mostly Pacific radiation (subgenus: *Terricolumba*, Fig. 1) with its

192   members distributed in Melanesia, Polynesia and Micronesia as well as in New Guinea.

193   *Gallicolumba hoedtii* of Wetar and Timor with a similar plumage as members of

194   *Terricolumba* is sister to this Pacific radiation (together they form the genus: *Alopecoenas*,

195   Fig. 1) although support is low. Sister to the *Alopecoenas* is *Leucosarcia melanoleuca* from

196   Australia and sister to the *Alopecoenas* and *Leucosarcia* is a group of mostly Australian

197   pigeon species. The other *Gallicolumba* species, which occur in the Philippines, Sulawesi and

198   New Guinea are found in two clades sister to the aforementioned groups. However, low ML

199   values indicate that additional nuclear sequence data may alter this result.

200   Results from the BEAST dating analyses provides relative diversification times,

201   which indicate that the *Terricolumba* clade (*beccarii*, *canifrons*, *xanthonura*, *kubaryi*,

202   *jobiensis*, *sanctaecrucis*, *stairi*, *erythoptera*, *rubescens*) is about five times younger than the

203   early radiation of the basal *Gallicolumba* clades (*keayi*, *criniger*, *platenae*, *luzonica*, *rufigula*,

204   *tristgmata*). Despite the lack of appropriate calibration points to obtain absolute

205   diversification time estimates, another molecular study on Columbiformes dates the basal split

206   for the *Gallicolumba/Geopelia/Phaps/Geophaps/Leucosarcia* radiation to approximately 36

207   My (Pereira *et al.*, 2007). With this in mind the *Alopecoenas* may have started diversifying in

208   the late Miocene/early Pliocene.

209

210   **Discussion**

211

212   *Phylogenetics, systematics and taxonomy*

213   The phylogenetic analyses demonstrate that *Gallicolumba* as currently circumscribed is

214   polyphyletic. One well supported clade restricted to New Guinea and Oceania corresponds to

215   the subgenus *Terricolumba* Haschisuka 1931 as circumscribed by Peters (1937). Hence, of the

216   species examined in the present study, the *Terricolumba* includes: *beccarii*, *canifrons*,

217   *xanthonura*, *kubaryi*, *jobiensis*, *sanctaecrucis*, *stair*, *erythoptera* and *rubescens*. Sister to this

218   assemblage, but with no support is *hoedtii*, which was kept in the monotyic subgenus

219   *Alopecoenas* Sharpe 1899 by Peters (1937), whereas Wolters (1975-1982) included

220   *Terricolumba* within *Alopecoenas*. Both treatments are compatible with the branching

221   patterns of the our molecular phylogeny, although we note that Gibb and Penny (2010) have

222   pointed out that in terms of relative molecular divergences, Australasian pigeons are oversplit

223   at the generic level. Consequently, we advocate that *Alopecoenas*, as the oldest name, be

224   reinstated as the genus name for the *Terricolumba* assemblage and *hoedtii*. According to

225   Wolters (1975 - 1982) the extinct species *salamonis*, *ferruginea* and *norfolciensis* are also part

226   of *Alopecoenas*. It is also highly likely that that the Oceanic species described from fossil

227   remains (Steadman, 2006); *longitarsus*, *nui*, *leonpascoi* and the as yet unnamed form from the

228   Marianas; are also part of *Alopecoenas*. Consequently, the genus *Alopecoenas* comprises

229   sixteen named species, restricted to islands and archipelagos, distributed across the Lesser

230   Sundas, New Guinea and Oceania (see map in Fig. 2). The subgenus *Terricolumba* is retained

231   for all species excluding *hoedtii*.

232   The clade comprising the genus *Alopecoenas* is strongly linked with the large

233   ground-dwelling *Leucosarcia melanoleuca* from the coastal forests of eastern Australia. (PP

234   =1.00, ML bootstrap = 95) and this group is in turn linked to an assemblage comprising the

235   Australian genera: *Phaps*, *Ocyphaps, Geophaps* and *Geopelia* (PP =1.00, ML bootstrap = 83).

236   The remaining members of *Gallicolumba* do not form a monophyletic clade but

237   support values for most associations are low. Wolters (1975-1982) restricted *Gallicolumba* to

238   the Phillipine bleeding-hearts (*menagei*, *keayi*, *criniger*, *platenae*, *luzonica*) along with

239   *rufigula* of New Guinea and *tristgmata* of Sulawesi of which the latter species was separated

240   into the subgenus *Diopezus*. Wolters (1975-1982) also separated *rufigula* at the subgeneric

241   level but did not ascribe a name to it. The DNA phylogeny is only partially in agreement with

242   Wolters (1975-1982). Bleeding-hearts are not recovered as monophyletic. Instead they fall in

243   two clades, with *rufigula* in one clade and *tristigmata* in the other clade.

244

245   ***Biogeography***

246   Comparisons between the relative divergences within the *Terricolumba* component of

247   *Alopecoenas* and *Gallicolumba sensu stricto* suggest a recent radiation for the former and a

248   much older one for the latter. Resolution within *Gallicolumba* was low which precludes

249   detailed interpretation of its biogeographical history. Nevertheless, it is possible that the

250   diversification of *Gallicolumba* may in part have been shaped by the tectonic movements and

251   corresponding extensive re-arrangements of land masses within the Philippine and Sulawesi

252   region throughout the Neogene (23 -2.5 MYA) (Hall 1998, 2002), in accordance with other

253   studies in the region for both birds (Jønsson *et al.*, 2010) and mammals (Steppan *et al.*, 2003;

254   Heaney, 2005; Jansa *et al.*, 2006).

255   With the exception of the Hawaiian Islands, all evidence, modern or pre-

256   historic, points to Australo-Papuan affinities for landbirds in Oceania (Mayr and Diamond,

257   2001; Steadman, 2006). The rich Neotropical avifauna has had no influence on Pacific islands

258   west of Juan Fernandez, Galapagos, Cocos and the various Mexican islands. Furthermore,

259   there is no evidence of colonization by landbirds from New Zealand and Hawaii. Thus, it

260   seems fair to assume that the origin of *Alopecoenas* is within the Australo-Papuan region.

261   This is consistent with the relatively close association between *Alopecoenas* and other mostly

262   Australian pigeon species in the phylogeny. Although *Alopecoenas* is absent from Australia, it

263   could be argued that *Leuscosarcia* represents this clade within Australia. In ecology and

264   body-shape it can almost be considered a giant *Alopecoenas*. Accordingly, we postulate that a

265   number of ocean dispersal events across the Pacific archipelagos from Australo-Papua

266   accounts for the distributional pattern observed in *Alopecoenas*. There is clearly evidence for

267   long-distance ocean dispersal to Palau (*canifrons*) and Micronesia (*xanthonura, kubaryi*) and

268   also dispersal to the Santa Cruz archipelago (probably via the Solomons) and onwards to Fiji,

269   Tonga (*sanctaecrucis* and *stairi*) and the remote Tuamotu archipelago (*erythroptera*) and

270   Marquesas (*rubescens*).

271   The fact that members of *Alopecoenas* have colonized islands across significant

272   water gaps is intriguing. Although, there are no sightings of ground-doves crossing water

273   barriers between islands, there is evidence of the colonization of recent *de novo* environments,

274   for example of islands after volcanism in Melanesia implying that ground-doves will cross

275   minor water barriers (Mayr and Diamond, 2001). For example, *A. beccarii* is now resident on

276   six small islands in the Bismarck archipelago, which were defaunated by seventeenth and

277   nineteenth century volcanic explosions. Similarly, *A. jobiensis* has colonized one Holocene

278   volcanically defaunated island in the Bismarcks and also colonized Vuatom off New Britain

279   between 1910 and 1936 (Mayr and Diamond, 2001).

280   Most of the islands in the Pacific are true oceanic islands (formed *de novo*) that

281   have never been connected to any continent even during glacial times (Steadman, 2006).

282   Consequently, it is clear that members of *Alopecoenas* colonized the remote Pacific islands

283   numerous times by means of long-distance ocean dispersal. For example, to reach the eastern

284   part of the main chain of the Solomon islands from Papua and the Bismarcks would only

285   require a 174 km water crossing (157 during Pleistocene glacial intervals) whereas to proceed

286   from the Solomons to Fiji, via the Santa Cruz group and Vanuatu would require an ocean

287   crossing of 840 km (530 during glacial times). Most islands within West Polynesia can be

288   reached from Fiji by crossing no more than 300 km of water but then it requires a crossing of

289   at least 1100 km to reach East Polynesia (Cook Islands) from West Polynesia (Niue) and a

290   further 520 km to get across from the Cook Islands to Tahiti. To reach the Marquesas from

291   the Society Islands and Tuamotus requires an additional water crossing of about 400 km

292   (Steadman, 2006). Although extinctions seriously hampers our understanding of

293   biogeographical patterns for Pacific land birds, the phylogenetic relationships and

294   distributions of members of *Alopecoenas* make for a good example of the important role that

295   long-distance dispersal has played in shaping the land avifauna of oceanic islands.

296

304

305 **References**

306 Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle,

307 in: Petrov, B.N., Csaki, F. (Eds.), Second International Symposium on Information Theory

308 Akademiai Kiado, Budapest, pp. 276-281.

309

310 Cibois, A., Thibault, J.-C., Pasquet, E., 2007. Uniform phenotype conceals double

311 colonization by reed-warblers of a remote Pacific archipelago. J. Biogeogr. 34, 1150-1166.

312

313 Cicero, C., Johnson, N.K., 2001. Higher level phylogeny of vireos (Aves: Vireonidae) based

314 on sequences of multiple mtDNA genes. Mol. Phylogenet. Evol. 20, 27-40.

315

316 Chesser, R.T., 1999. Molecular systematics of the rhinocryptid genus *Pteroptochos*. Condor

317 101, 439-446.

318

319 Darwin, C., 1859. On the origin of species by means of natural selection. Murray, London.

320

321 Diamond, J.M., 1972. Avifauna of the Eastern Highlands of New Guinea. Nuttall

322 Ornithological Club, Cambridge, MA.

323

324 Diamond, J.M., 1977. Continental and insular speciation in Pacific island birds. Syst. Zool.

325 26, 263-268.

326

327 Drummond, A.J., Rambaut, A. 2007. BEAST v.1.4.7. http://beast.bio.ed.ac.uk.

328

329 Drummond, A.J., Nicholls, G.K., Rodrigo, A.G., Solomon, W. 2002. Estimating mutation

330 parameters, population history and genealogy simultaneously from temporally spaced

331 sequence data. *Genetics* 161, 1307-1320.

332

333 Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A. 2006. Relaxed phylogenetics and

334 dating with confidence. *PLoS Biol.* 4, e88.

335

336 Esselstyn, J.A., Timm, R.M., Brown, R.M., 2009. Do geological or climatic processes drive

337 speciation in dynamic archipelagos? The tempo and mode of diversification in southeast

338 Asian shrews. Evolution 63, 2595-2610.

339

340   Gibb, G.C., Penny, F.D., 2010. Two aspects along the continuum of pigeon evolution: a

341   South-Pacific radiation and the relationships of pigeons within Neoaves. Mol. Phylogenet.

342   Evol. 56, 698-706.

343

344   Gibbs, D., Barnes, E., Cox, J., 2001. Pigeons and doves, a guide to the pigeons and doves of

345   the world. Pica Press. UK.

346

347   Filardi, C.E., Moyle, R.G., 2005. Single origin of a pan-Pacific bird group and upstream

348   colonization of Australasia. Nature 438, 216-219.

349

350   Hackett, S.J., 1996. Molecular phylogenetics and biogeography of tanagers in the genus

351   *Ramphocelus* (Aves). Mol. Phylogenet. Evol. 5, 368-382.

352

353   Hall, R., 1998. The plate tectonics of the Cenozoic SE Asia and the distribution of land and

354   sea, in: Hall, R., Holloway, J.D. (Eds), Biogeography and geological Evolution of SE Asia.

355   Backhuys Publishers, Leiden, The Netherlands, pp. 133-163.

356   Hall, R., 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW

357   Pacific: computer-based reconstructions, model and animations. J. Asian Earth Sci. 20, 353-

358   431.

359

360   Heaney, L.R., Walsh, J.S. Jr., Peterson, A.T., 2005. The roles of geological history and

361   colonization abilities in genetic differentiation between mammalian populations in the

362   Philippine archipelago. J. Biogeogr. 32, 229-247.

363

364   Ho, S.Y.W. 2007. Calibrating molecular estimates of substitution rates and divergence times

365   in birds. *J. Avian Biol.* 38, 409-414.

366

367   Holder, M.T., Lewis, P.O., 2003. Phylogeny estimation: traditional and Bayesian approaches.

368   Nat. Rev. Genet. 4, 275-284.

369

370   Huelsenbeck, J.P., Ronquist, F., 2003. MrBayes: a program for the Bayesian inference of phylogeny.

371   Version 3.1.2. Available at: http://mrbayes.scs.fsu.edu/index.php.

372

373   Huelsenbeck, J.P., Ronquist, F., Hall, B., 2001. MrBayes: Bayesian inference of phylogeny.

374   Bioinformatics 17, 754-755.

375

376   Irestedt, M., Ohlson, J.I., Zuccon, D., Källersjö, M., Ericson, P.G.P., 2006. Nuclear DNA

377   from old collections of avian study skins reveals the evolutionary history of the Old World

378   suboscines (Aves, Passeriformes). Zool. Script. 35, 567-580.

379

380   Irestedt, M., Fuchs, J., Jønsson, K.A., Ohlson, J.I., Pasquet, E., Ericson, P.G.P., 2008. The

381   systematic affinity of the enigmatic *Lamprolia victoriae* (Aves: Passeriformes) – An example

382   of avian dispersal between New Guinea and Fiji over Miocene intermittent landbridges. Mol.

383   Phylogenet. Evol. 48, 1218-1222

384

385   Jansa, S.A., Barker, F.K., Heaney, L.R., 2006. The pattern and timing of diversification of

386   Philippine endemic rodents: Evidence from mitochondrial and nuclear gene sequences. Syst.

387   Biol. 55, 73-88.

388

389   Jønsson, K.A., Bowie, R.C.K., Moyle, R.G., Christidis, L., Norman, J.A., Benz, B.W.,

390   Fjeldså, J., 2010. Historical biogeography of an Indo-Pacific passerine bird family

391   (Pachycephalidae): different colonization patterns in the Indonesian and Melanesian

392   archipelagos. J. Biogeogr. 37, 245-257.

393

394   Jønsson, K.A., Bowie, R.C.K., Nylander, J.A.A., Christidis, L., Norman, J.A., Fjeldså, J.,

395   (online) Biogeographical history of cuckoo-shrikes (Aves: Passeriformes): Trans-oceanic

396   colonization of Africa from Australo-Papua. J. biogeogr.

397

398   Keast, A., 1996. Avian Geography: New Guinea to the eastern Pacific, in: Keast, A., Miller,

399   S.E. (Eds.), The origin and evolution of Pacific island biotas, New Guinea to Eastern

400   Polynesia: patterns and processes. Academic Publishing, Amsterdam, pp. 373-398.

401

402   MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography.

403   Evolution 17, 373-387.

404

405   MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton, NJ.

406

407   Mayr, E., Diamond, J.M., 2001. The birds of Northern Melanesia: Speciation, Ecology, and

408   biogeography. Oxford University Press, New York.

409

410   Mindell, D.P., Sorenson, M.D., Dimcheff, D.E. 1998. An extra nucleotide is not translated in

411   mitochondrial ND3 of some birds and turtles. Mol. Biol. Evol. 15, 1568-1571.

412

413   Nylander, J.A.A., 2004. MrModeltest2. Available at: < http://www.abc.se/~nylander/>.

414

415   Nylander, J.A.A., Wilgenbusch, J.C., Warren, D.L., Swofford, D.L., 2008. AWTY (are we

416   there yet): a system for graphical exploration of MCMC convergence in Bayesian

417   phylogenetics. Bioinformatics 24, 581-583

418

419   Pereira, S.L., Johnson, K.P., Clayton, D.H., Baker, A.J., 2007. Mitochondrial and nuclear

420   DNA sequences support a Cretaceous origin of Columbiformes and a dispersal driven

421   radiation in the Paleogene. Syst. Biol. 56, 656-672.

422

423   Peters, J.L., 1937. Check-list of Birds of the World. Vol. 3.Museum of Comparative Zoology,

424   Harvard University Press, Cambridge, Massachusetts.

425

426   Polhemus, D.A., 1996 Island arcs, and their influence on Indo-Pacific biogeography, in:

427   Keast, A., Miller, S.E. (Eds.). The origin and evolution of Pacific island biotas, New Guinea

428   to Eastern Polynesia: patterns and processes. Academic Publishing, Amsterdam, pp. 51-66.

429

430   Posada, D., Buckley, T.R., 2004. Model selection and model averaging in phylogenetics:

431   advantages of Akaike information criterion and Bayesian approaches over likelihood ratio

432   tests. Syst. Biol. 53, 793-808.

433

434   Rambaut, A., Drummond, A.J. 2007. Tracer v.1.4. http://beast.bio.ed.ac.uk/Tracer.

435

436   Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under

437   mixed models. Bioinformatics 19, 1572-1574.

438

439   Schellart, W.P., Lister, G.S., Toy, V.G., 2006. A Late Cretaceous and Cenozoic
440   reconstruction of the Southwest Pacific region: Tectonics controlled by subduction and slab
441   rollback processes. Earth Sci. Rev. 76, 191-233.

442   Shapiro, B., Sibthorpe, D., Rambaut, A., Austin, J., Wragg, G. M., Bininda-Emonds, O. R. P.,
443   Lee, P.L.M., Cooper, A., 2002. Flight of the dodo. Science 295, 1683.

444

445   Steadman, D.W., 2006. Extinction and biogeography of tropical Pacific birds. University of
446   Chicago Press, USA.

447

448   Steppan, S.J., Zawadski, C., Heaney, L.R., 2003. Molecular phylogeny of the endemic rodent
449   *Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. Biol. J.
450   Linn. Soc. 80, 699-715.

451

452   Wilgenbusch, J.C., Warren, D.L., Swofford, D.L., 2004. AWTY: A system for graphical
453   exploration of MCMC convergence in Bayesian phylogenetic inference. Available at:
454   http://ceb.csit.fsu.edu/awty.

455

456   Wolters, H.E., 1975-1982.. Die Vogelarten der Erde. Paul Parey, Hamburg.

457

458   Zwickl, D.J., 2006. Genetic algorithm approaches for the phylogenetic analysis of large
459   biological sequence datasets under the maximum likelihood criterion. PhD dissertation, The
460   University of Texas at Austin.

461

462

463   **Figure 1**. 50% majority rule consensus tree obtained from Bayesian analysis of the combined
464   ND2 and ND3 data sets. Support values are indicated to the left of the nodes. Above the
465   branch is the posterior probability (only ≥ 0.90 are shown, asterisks indicate posterior
466   probabilities of 1.00) and below the branch is the maximum likelihood bootstrap value (only
467   values ≥ 70% are shown) from 100 pseudoreplicates. Present distributions are indicated after
468   the taxon name. Note that *Gallicolumba tristigmata* has a stop codon in both the ND2 and

469   ND3 sequences indicative of a pseudogene. We have therefore indicated its systematic

470   position by a dashed line and remain cautious about its placement in the phylogeny.

471

472

473   **Figure 2**. Map of Oceania. Note that the Pitcairn islands are outside the map to the southeast

474   of Tuamotu.

Table 1. List of taxa included in this study. Acronyms are: AMNH, American Museum of Natural History, New York, USA; AM, Australian Museum, Sydney, Australia; BMNH, British Museum of Natural History; FMNH, Field Museum of Natural History, Chicago, USA; MNHN EP, Eric Pasquet, Muséum National d´histoire Naturelle, Paris, France; MTI = Museum of Tahiti and Islands; MV, Museum Victoria, Melbourne, Australia; MVZ, Museum of Vertebrate Zoology, Berkeley, USA; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; and ZMUC, Zoological Museum, Copenhagen, Denmark. All ingroup taxa are vouchered. Toe-pad samples are indicated by *.

Species	Voucher	Origin of sample	ND3	ND2
Gallicolumba beccarii	ZMUC139335	Solomon Islands	HQ630241	HQ630220
*Gallicolumba canifrons**	AMNH331986	Palau		HQ630232
*Gallicolumba criniger**	ZMUC57467	Captivity	HQ630246	HQ630225
*Gallicolumba hoedtii**	BMNH 1904.7.21.47	Wetar	HQ845210	HQ845209
Gallicolumba jobiensis	AM0.40119	New Guinea		HQ630213
*Gallicolumba keayi**	FMNH209778	Philippines	HQ630256	HQ630236
*Gallicolumba kubaryi**	FMNH410387	Caroline Islands	HQ630255	HQ630235
Gallicolumba luzonica	ZMUC113832	Philippines		HQ630214
Gallicolumba luzonica	ZMUC114354	Philippines		HQ630215
*Gallicolumba platenae**	AMNH789931	Philippines	HQ630253	HQ630233
*Gallicolumba rubescens**	MVZ52047	Marquesas	HQ630237	HQ630216
*Gallicolumba rufigula**	AM55328	New Guinea	HQ630238	HQ630217
*Gallicolumba sanctaecrucis**	AMNH216850	Santa Cruz	HQ630251	HQ630230
*Gallicolumba stairi**	NRM570048	Fiji	HQ630240	HQ630219
*Gallicolumba stairi**	MVZ46741	Fiji	HQ630239	HQ630218
*Gallicolumba tristigmata**	AMNH298616	Sulawesi	HQ630252	HQ630231
*Gallicolumba xanthonura**	AMNH332258	Mariana Islands	HQ630243	HQ630222
*Gallicolumba xanthonura**	FMNH410389	Mariana Islands	HQ630254	HQ630234
Gallicoumba erythroptera	MTI	Marquesas	HQ630244	HQ630223
Gallicoumba erythroptera	MTI	Marquesas	HQ630245	HQ630224
*Geopelia cuneata**	ZMUC134117	Captivity	HQ630242	HQ630221
*Geophaps plumifera**	ZMUC56845	Captivity	HQ630247	HQ630226
*Leucosarcia melanoleuca**	ZMUC64468	Captivity	HQ630250	HQ630229
*Ocyphaps lophotes**	ZMUC68040	Captivity	HQ630249	HQ630228
*Phaps chalcoptera**	ZMUC56837	Captivity	HQ630248	HQ630227
Outgroup				
Zenaida macroura	GenBank	North America	AF076379	
Zenaida macroura	GenBank	North America		EF373359
Hemiphaga novaeseelandiae	GenBank	New Zealand	NC_013244	NC_013244

Philippines

Hawaii

Mariana Islands

Palau

Caroline Islands

Micronesia

Sulawesi

Bismarck
Archipelago

Nauru

Kiribati

Wetar

New Guinea

Solomon Archipelago

Polynesia

Timor

Tuvalu

Samoa

Melanesia

Vanuatu

Fiji

Cook Islands

Marquesas Islands

Tahiti

Tonga

Niue

Australia

New Caledonia

Tuamotu

Norfolk Island

New Zealand

1000 km

Research highlights

Phylogeny of all 16 Indo-Pacific ground-dove species

Polyphyly of Indo-Pacific ground doves

The new genus name Alopecoenas proposed for Pacific ground-dove clade