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Short Communication

# Systematics and biogeography of Indo-Pacific ground-doves

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ABSTRACT

Ground-doves represent an insular bird radiation distributed across the Indo-Pacific. The radiation comprises sixteen extant species, two species believed to be extinct and six species known to be extinct. In the present study, we present a molecular phylogeny for all sixteen extant species, based on two mitochondrial markers. We demonstrate that the *Gallicolumba* as currently circumscribed is not monophyletic and recommend reinstalling the name *Alopecoenas* for a monophyletic radiation comprising ten extant species, distributed in New Guinea, the Lesser Sundas and Oceania. *Gallicolumba* remains the name for six species confined to New Guinea the Philippines and Sulawesi. Although our phylogenetic analyses fail to support a single origin for the remaining *Gallicolumba* species, we suspect that the addition of nuclear sequence data may alter this result.

Because a number of ground-dove taxa have gone extinct, it is difficult to assess biogeographical patterns. However, the *Alopecoenas* clade has clearly colonized many remote oceanic islands rather recently, with several significant water crossings. The *Gallicolumba* radiation(s), on the other hand, is significantly older and it is possible that diversification within that group may in part have been shaped by plate tectonics and corresponding re-arrangements of land masses within the Philippine and Sulawesi region.


## 1. Introduction

*Gallicolumba* comprises a group of medium to small sized ground-doves with relatively short wings and tails. They are terrestrial and associated with various kinds of wooded habitat including coastal thickets and mangroves. The sixteen extant species occur in New Guinea (three species), the Pacific (nine species, two of which are shared with New Guinea), the Philippine archipelago (four species), Sulawesi (one species) and the Lesser Sundas (one species) (Gibbs et al., 2001). Two species, *G. salamonis* from Makira and Ramos in the southern Solomon archipelago and *G. menagei* from Tawi-Tawi in the southern Philippines are believed to be extinct, with the latter known from a single specimen. Additionally, six species from the Pacific are known to be extinct (Steadman, 2006): *G. ferruginea* from Tanna in the southern Vanuatu archipelago; *G. longitarsus* from New Caledonia; *G. nui* widespread in eastern Polynesia; *G. leonpascoi* from Henderson island in the Pitcairn group; an undescribed *Gallicolumba* species from the Marianas; and *G. norfolciensis* from Norfolk Island. Nearly all extant species have undergone considerable range contractions and in several cases appear to now have relictual distributions (Steadman, 2006). Thus, any biological interpretations based on a phylogeny of the extant species of *Gallicolumba* will have to take into account a significant number of known extinctions.

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

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may be closer to Australasian genera such as *Geopelia*, *Phaps* and *Leucosarcia* than to the "bleeding-hearts" of the Philippines.

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

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

## 2. Material and methods

### 2.1. Taxon sampling and laboratory procedures

To examine relationships within *Gallicolumba* we included all sixteen extant species along with *Geopelia cuneata*, *Phaps chalcoptera*, *Geophaps plumifera*, *Ocyphaps lophotes* and *Leucosarcia melanoleuca*. The mtDNA study of Shapiro et al. (2002) indicated that *Gallicolumba* may be polyphyletic with respect to these genera. For outgroup comparison we used sequence data on *Zenaida macroura* and *Hemiphaga novaeseelandiae* obtained from GenBank.

We sequenced the first 525 base pairs (bp) of the mitochondrial marker NADH dehydrogenase subunit 2 (ND2) and all of subunit 3 (ND3) and some flanking tRNA. Fresh tissue (blood, liver, muscle) was extracted using the DNeasy Tissue kit (Qiagen, Valencia, CA), following the manufacturer's protocol. Corresponding laboratory procedures for study skins are detailed in Irestedt et al. (2006). Primer pairs used for the amplification of ND2 were Lmet (Hackett, 1996)/H6312 (Cicero and Johnson, 2001) and for ND3-L10755/ND3-H11151 (Chesser, 1999). Additionally, we designed new internal primers for ND2 specifically for this study: ND2gal330F: ATTCCACCTCTGATTCCCAGAAGT; ND2per340R: CCTTGTAGTACTTC TGGGAATCA; ND2gal530R: GAGGARAARGCYAARATTTTTCG.

The thermocycling conditions included a hotstart at 95 °C for 5 min, followed by 32 cycles at 95 °C for 40 s, 54–63 °C for 40 s, and 72 °C for 60 s, and was completed by a final extension at 72 °C for 8 min. One microliter of the amplification products was electrophoresed on a 1.5% agarose gel and viewed under UV light with ethidium bromide to check for correct fragment size and to control for the specificity of the amplifications. PCR products were purified using ExoSap enzymes (Exonuclease and Shrimp Alkaline Phosphatase). Purified PCR products were cycle-sequenced using the Big Dye terminator chemistry (ABI, Applied Biosystems) in both directions with the same primers as used for PCR amplification and run on an automated AB 3100 DNA sequencer.

Sequences were assembled with SeqMan II (DNASTAR Inc.). Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC code. GenBank accession numbers are provided in Table 1.

### 2.2. Alignment and phylogenetic analyses

Alignment was performed using MegAlign with some minor manual adjustments. The concatenated alignment consisted of 921 bp comprising 525 bp of ND2 and 396 bp of ND3. Both genes were checked for the presence of stop codons or insertion/deletion events that would have disrupted the reading frame.

**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 |

We used Bayesian inference (e.g., Holder and Lewis, 2003; Huelsenbeck et al., 2001), as implemented in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2003; Ronquist and Huelsenbeck, 2003) to estimate phylogenetic relationships. The most appropriate substitution models were determined with MrModeltest 2.0 (Nylander, 2004), using the Akaike Information Criterion (Akaike, 1973; Posada and Buckley, 2004). Bayesian analyses for the concatenated data set were performed using a mixed-models approach (Ronquist and Huelsenbeck, 2003; Nylander et al., 2004) allowing for different parameters (base frequencies, rate matrix or transition/transversion ratio, shape parameter, proportion of invariable sites) to vary between the four partitions (1st, 2nd, 3rd codon positions and tRNA). In all MrBayes analyses, Markov Chain Monte Carlo (MCMC) was run using Metropolis-coupling, with one cold and three heated chains, for 15 million iterations with trees sampled every 500 iterations. The number of iterations discarded before the posterior probabilities (i.e. the length of the 'burn-in' period) were graphically estimated using AWTY (Nylander et al., 2008; Wilgenbusch et al., 2004) by monitoring the change in cumulative split frequencies. Two independent runs initiated from random starting trees were performed for each data set, and the log-likelihood values and posterior probabilities for splits and model parameters were checked to ascertain that the chains had reached apparent stationarity.

Maximum likelihood analyses were performed using GARLI 0.95 (Zwickl, 2006). Five independent analyses (20 million generations) were performed both for the individual analyses and for the analysis of the concatenated dataset. Nodal support was evaluated with 100 nonparametric bootstrap pseudoreplications.

Because of stop codons present in the ND2 and ND3 sequences of *G. tristigmata* we ran separate analyses in MrBayes and GARLI excluding this taxon.

To estimate the relative divergence times within ground-doves, we used BEAST v.1.4.6 (Drummond et al., 2002, 2006; Drummond and Rambaut, 2007). We assigned the best fitting model, as estimated by MrModeltest 2.0 (Nylander, 2004), to each of the partitions. We assumed a Yule Speciation Process for the tree prior and an uncorrelated lognormal distribution for the molecular clock model (Drummond et al., 2006; Ho, 2007). We used default prior distributions for all other parameters and ran MCMC chains for 50 million generations. We used the program Tracer (Rambaut and Drummond, 2007) to assess convergence diagnostics.

## 3. Results

Sequence alignment for all taxa and genes was straight-forward. The ND3 sequences contained an extra nucleotide at position 174 found in some reptiles and birds, which is not translated and

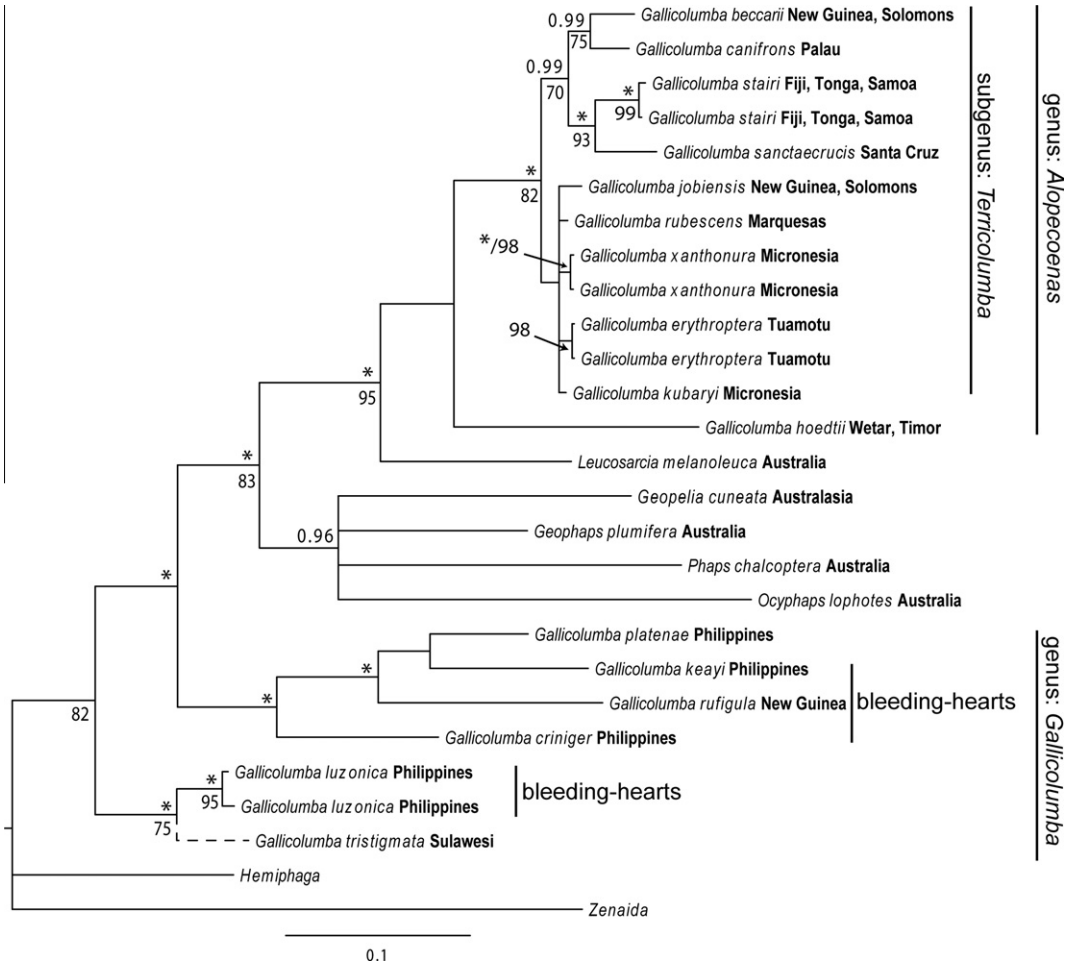


**Fig. 1.** 50% majority-rule consensus tree obtained from Bayesian analysis of the combined ND2 and ND3 data sets. Support values are indicated to the left of the nodes. Above the branch is the posterior probability (only $\geqslant$0.90 are shown, asterisks indicate posterior probabilities of 1.00) and below the branch is the maximum likelihood bootstrap value (only values $\geqslant$70% are shown) from 100 pseudoreplicates. Present distributions are indicated after the taxon name. Note that *Gallicolumba tristigmata* has a stop codon in both the ND2 and ND3 sequences indicative of a pseudogene. We have therefore indicated its systematic position by a dashed line and remain cautious about its placement in the phylogeny.

thus does not disrupt the reading frame (Mindell et al., 1998). This nucleotide position was excluded in all phylogenetic analyses. We found one stop-codon in both the ND2 and the ND3 sequence of *G. tristigmata*. This would cause a disruption of the reading frame and is indicative of the presence of a pseudogene. Although, we included the sequences from this individual in our phylogenetic analyses, we remain cautious about its systematic placement. All other mitochondrial data contained neither insertions, deletions nor anomalous stop-codons. Additional analyses excluding *G. tristigmata* did not change the relationships or the support values in any of the trees.

Model based analyses performed on the concatenated dataset (four partitions: 1st, 2nd, 3rd codon positions and tRNA; maximum likelihood (ML): −ln 5358.29, Bayesian inference (BI) harmonic mean: −ln 5098.91) yielded a 50% majority-rule consensus tree (BI) that was topologically congruent with the ML tree (Fig. 1), (for well-supported nodes receiving posterior probabilities > 0.95 or bootstrap values > 70%). Scores of the best likelihood trees were within 0.5 likelihood units of the best tree recovered in each of the other four GARLI runs, suggesting that the five runs had converged.

The phylogenetic analyses demonstrate that *Gallicolumba* is not monophyletic. One clade consists of a mostly Pacific radiation (subgenus: *Terricolumba*, Fig. 1) with its members distributed in Melanesia, Polynesia and Micronesia as well as in New Guinea. *G. hoedtii* of Wetar and Timor with a similar plumage as members of *Terricolumba* is sister to this Pacific radiation (together they form the genus: *Alopecoenas*, Fig. 1) although support is low. Sister to the *Alopecoenas* is *Leucosarcia melanoleuca* from Australia and sister to the *Alopecoenas* and *Leucosarcia* is a group of mostly Australian pigeon species. The other *Gallicolumba* species, which occur in the Philippines, Sulawesi and New Guinea are found in two clades sister to the aforementioned groups. However, low ML values indicate that additional nuclear sequence data may alter this result.

Results from the BEAST dating analyses provides relative diversification times, which indicate that the *Terricolumba* clade (*beccarii*, *canifrons*, *xanthonura*, *kubaryi*, *jobiensis*, *sanctaecrucis*, *stairi*, *erythoptera*, *rubescens*) is about five times younger than the early radiation of the basal *Gallicolumba* clades (*keayi*, *criniger*, *platenae*, *luzonica*, *rufigula*, *tristgmata*). Despite the lack of appropriate calibration points to obtain absolute diversification time estimates, another molecular study on Columbiformes dates the basal split for the *Gallicolumba*/*Geopelia*/*Phaps*/*Geophaps*/*Leucosarcia* radiation to approximately 36 My (Pereira et al., 2007). With this in mind the *Alopecoenas* may have started diversifying in the late Miocene/early Pliocene.

## 4. Discussion

### 4.1. Phylogenetics, systematics and taxonomy

The phylogenetic analyses demonstrate that *Gallicolumba* as currently circumscribed is polyphyletic. One well supported clade restricted to New Guinea and Oceania corresponds to the subgenus *Terricolumba* Hachisuka 1931 as circumscribed by Peters (1937). Hence, of the species examined in the present study, the *Terricolumba* includes: *beccarii*, *canifrons*, *xanthonura*, *kubaryi*, *jobiensis*, *sanctaecrucis*, *stairi*, *erythoptera* and *rubescens*. Sister to this assemblage, but with no support is *hoedtii*, which was kept in the monotyic subgenus *Alopecoenas* Sharpe 1899 by Peters (1937), whereas Wolters (1975–1982) included *Terricolumba* within *Alopecoenas*. Both treatments are compatible with the branching patterns of the our molecular phylogeny, although we note that Gibb and Penny (2010) have pointed out that in terms of relative molecular divergences, Australasian pigeons are oversplit at the generic level. Consequently, we advocate that *Alopecoenas*, as the oldest name, be reinstated as the genus name for the *Terricolumba* assemblage and


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

*hoedtii*. According to Wolters (1975–1982) the extinct species *salamonis*, *ferruginea* and *norfolciensis* are also part of *Alopecoenas*. It is also highly likely that that the Oceanic species described from fossil remains (Steadman, 2006); *longitarsus*, *nui*, *leonpascoi* and the as yet unnamed form from the Marianas; are also part of *Alopecoenas*. Consequently, the genus *Alopecoenas* comprises sixteen named species, restricted to islands and archipelagos, distributed across the Lesser Sundas, New Guinea and Oceania (see map in Fig. 2). The subgenus *Terricolumba* is retained for all species excluding *hoedtii*.

The clade comprising the genus *Alopecoenas* is strongly linked with the large ground-dwelling *Leucosarcia melanoleuca* from the coastal forests of eastern Australia. (PP = 1.00, ML bootstrap = 95) and this group is in turn linked to an assemblage comprising the Australian genera: *Phaps*, *Ocyphaps, Geophaps* and *Geopelia* (PP = 1.00, ML bootstrap = 83).

The remaining members of *Gallicolumba* do not form a monophyletic clade but support values for most associations are low. Wolters (1975–1982) restricted *Gallicolumba* to the Phillipine bleeding-hearts (*menagei*, *keayi*, *criniger*, *platenae*, *luzonica*) along with *rufigula* of New Guinea and *tristgmata* of Sulawesi of which the latter species was separated into the subgenus *Diopezus*. Wolters (1975–1982) also separated *rufigula* at the subgeneric level but did not ascribe a name to it. The DNA phylogeny is only partially in agreement with Wolters (1975–1982). Bleeding-hearts are not recovered as monophyletic. Instead they fall in two clades, with *rufigula* in one clade and *tristigmata* in the other clade.

### 4.2. Biogeography

Comparisons between the relative divergences within the *Terricolumba* component of *Alopecoenas* and *Gallicolumba sensu stricto* suggest a recent radiation for the former and a much older one for the latter. Resolution within *Gallicolumba* was low which precludes detailed interpretation of its biogeographical history. Nevertheless, it is possible that the diversification of *Gallicolumba* may in part have been shaped by the tectonic movements and corresponding extensive re-arrangements of land masses within the Philippine and Sulawesi region throughout the Neogene (23–2.5 MYA) (Hall, 1998, 2002), in accordance with other studies in the region for both birds (Jønsson et al., 2010) and mammals (Steppan et al., 2003; Heaney et al., 2005; Jansa et al., 2006).

With the exception of the Hawaiian Islands, all evidence, modern or pre-historic, points to Australo-Papuan affinities for landbirds in Oceania (Mayr and Diamond, 2001; Steadman, 2006). The rich Neotropical avifauna has had no influence on Pacific islands west of Juan Fernandez, Galapagos, Cocos and the various Mexican islands. Furthermore, there is no evidence of colonization by landbirds from New Zealand and Hawaii. Thus, it seems fair to assume that the origin of *Alopecoenas* is within the Australo-Papuan region. This is consistent with the relatively close association between *Alopecoenas* and other mostly Australian pigeon species in the phylogeny. Although *Alopecoenas* is absent from Australia, it could be argued that *Leuscosarcia* represents this clade within Australia. In ecology and body-shape it can almost be considered a giant *Alopecoenas*. Accordingly, we postulate that a number of ocean dispersal events across the Pacific archipelagos from Australo-Papua accounts for the distributional pattern observed in *Alopecoenas*. There is clearly evidence for long-distance ocean dispersal to Palau (*canifrons*) and Micronesia (*xanthonura, kubaryi*) and also dispersal to the Santa Cruz archipelago (probably via the Solomons) and onwards to Fiji, Tonga (*sanctaecrucis* and *stairi*) and the remote Tuamotu archipelago (*erythroptera*) and Marquesas (*rubescens*).

The fact that members of *Alopecoenas* have colonized islands across significant water gaps is intriguing. Although, there are no sightings of ground-doves crossing water barriers between islands, there is evidence of the colonization of recent *de novo* environments, for example of islands after volcanism in Melanesia implying that ground-doves will cross minor water barriers (Mayr and Diamond, 2001). For example, *A. beccarii* is now resident on six small islands in the Bismarck archipelago, which were defaunated by seventeenth and nineteenth century volcanic explosions. Similarly, *A. jobiensis* has colonized one Holocene volcanically defaunated island in the Bismarcks and also colonized Vuatom off New Britain between 1910 and 1936 (Mayr and Diamond, 2001).

Most of the islands in the Pacific are true oceanic islands (formed *de novo*) that have never been connected to any continent even during glacial times (Steadman, 2006). Consequently, it is clear that members of *Alopecoenas* colonized the remote Pacific islands numerous times by means of long-distance ocean dispersal. For example, to reach the eastern part of the main chain of the Solomon islands from Papua and the Bismarcks would only require a 174 km water crossing (157 during Pleistocene glacial intervals) whereas to proceed from the Solomons to Fiji, via the Santa Cruz group and Vanuatu would require an ocean crossing of 840 km (530 during glacial times). Most islands within West Polynesia can be reached from Fiji by crossing no more than 300 km of water but then it requires a crossing of at least 1100 km to reach East Polynesia (Cook Islands) from West Polynesia (Niue) and a further 520 km to get across from the Cook Islands to Tahiti. To reach the Marquesas from the Society Islands and Tuamotus requires an additional water crossing of about 400 km (Steadman, 2006). Although extinctions seriously hampers our understanding of biogeographical patterns for Pacific land birds, the phylogenetic relationships and distributions of members of *Alopecoenas* make for a good example of the important role that long-distance dispersal has played in shaping the land avifauna of oceanic islands.

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