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Extensive diversification across islands in the echolocating *Aerodramus* swiftlets

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Abstract. Taxa that are known as "great speciators" are characterised by a rare combination of a potential to disperse coupled with a tendency not to, because extensive dispersal leads to gene flow counteracting differentiation, and too little dispersal leads to an inability to colonise new areas. Here we investigate the phylogenetic history of the genus *Aerodramus*, a group of echolocating swiftlets that has diversified throughout the Indo-Pacific region, to gauge the level of differentiation and ascertain if traditional taxonomy provides an accurate assessment of species diversity, and find several phylogenetic relationships that challenge traditional taxonomy, especially within the *A. vanikorensis* species complex. We also suggest that the genus may be considered a "great speciator", which has undergone a recent rapid radiation involving the colonisation of most islands in the Indian and Pacific oceans.

Key words. biogeography, Australo-Papuan region, swifts, "great speciator"

INTRODUCTION

Vagility is an important factor in island bird diversification (Mayr & Diamond, 2001). Because of their ability to cross large water barriers in flight, birds have been successful in colonising isolated regions and diversifying in new habitats and niches. Birds have dispersed to virtually all oceanic island groups, many of which would have remained uninhabited by reptiles, mammals, and amphibians if human-mediated introductions had not occurred (Wallace, 1887). Examples of genera that have diversified across remote islands are *Zosterops* white-eyes (Warren et al., 2006; Phillimore et al., 2008; Moyle et al., 2009; Clegg & Phillimore, 2010; Melo et al., 2011), *Acrocephalus* warblers (Cibois et al., 2007, 2008, 2010, 2011a, 2011b), and *Alopecoenas* ground-doves (Jønsson et al., 2011).

Conversely, high vagility may also counter diversification as it facilitates connectivity among populations across a species range. For example, whereas some seabird species nest on small and isolated islets in the Pacific Ocean, they nevertheless maintain demographic cohesion across thousands of kilometers of open ocean (e.g., Morris-Pocock et al., 2011). There are also a number of terrestrial birds that range across far-flung archipelagoes; imperial pigeons of the genus *Ducula* are prone to eruptive flights during tree-fruiting events and are known to congregate in large flocks to cross long distances between islands (Pratt, 2010).

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The most speciose genera of island birds are those that combine a non-dispersive lifestyle with a capability for dispersive and eruptive movements in times of adverse ecological conditions (Mayr & Diamond, 2001). These groups are the ones that have the potential to found new populations on distant islands on infrequent occasions and subsequently remain isolated from further gene flow with the parent population. White-eyes (*Zosterops*) have been termed a "great speciator" having diversified into nearly 100 mostly insular species over a timespan of perhaps as little as 2 million years (Moyle et al., 2009). Sometimes high levels of diversification are obscured by uniform phenotypes as in *Acrocephalus* warblers, in which DNA data have revealed cryptic species diversity across islands in the Pacific (Cibois et al., 2007, 2008, 2010, 2011a, 2011b).

Swiftlets of the genus *Aerodramus* constitute a complex avian radiation that has diversified into c. 22 species (Table 1), colonising most islands in the Pacific and Indian oceans and several adjacent, mostly coastal, mainland regions (Chantler, 1999). Many *Aerodramus* species are known to breed colonially in caves. All members of this genus use echolocation to navigate through caves, crevices, and the darkness of dusk (Chantler, 1999). Unlike bats, however, they have not perfected echolocation to the point of using it for catching their insect prey. The ability to echolocate sets *Aerodramus* apart from the closely related genera *Hydrochous* and most members of *Collocalia* (Lee et al., 1996; Thomassen et al., 2003; Price et al., 2004, 2005).

Because of their aerial lifestyle, *Aerodramus* swiftlets are considered to be excellent island colonisers, and a number of species are thought to extend over vast archipelagic regions: for instance, the distributional range of the uniform swiftlet *A. vanikorensis* stretches from Sulawesi to the Vanuatu Islands (Chantler, 1999; Table 1). Other *Aerodramus* species are

Table 1. Swiftlet species in the genus *Aerodramus* and their geographic and elevational breeding distribution (after Chantler, 1999). A species is considered montane if it breeds mostly >1,000 m. Taxonomy follows Chantler (1999) with the exception of *A. vulcanorum*, which is considered here to be a species separate from *A. brevirostris* based on widely different ranges and habits (see also Chantler, 1999). Those species sampled in the present study are printed in bold.

Species (bold if represented in study)	Geographic Breeding Distribution	Elevational Breeding Distribution
***A. elaphrus* (Seychelles swiftlet)**	**Seychelles Islands (Indian Ocean)**	**To sea level**
***A. francicus* (Mascarene swiftlet)**	**Mauritius and Réunion (Indian Ocean)**	**To sea level**
A. unicolor (Indian swiftlet)	SW India, Sri Lanka	To sea level
A. infuscatus (Moluccan swiftlet)	Sulawesi, Moluccas	To sea level
***A. mearnsi* (Philippine swiftlet)**	**Philippines (incl. Palawan)**	**Montane**
***A. hirundinaceus* (mountain swiftlet)**	**New Guinea**	**Montane**
***A. spodiopygius* (white-rumped swiftlet)**	**Bismarck Archipelago, Solomons, Vanuatu, Fiji, New Caledonia, Samoa, Tonga**	**Mostly montane**
***A. terraereginae* (Australian swiftlet)**	**Queensland (Australia)**	**To sea level**
A. brevirostris (Himalayan swiftlet)	Himalayas, SW China, N Indochina	Montane
***A. vulcanorum* (volcano swiftlet)**	**W Java**	**Montane**
***A. whiteheadi* (whitehead's swiftlet)**	**Luzon, Mindanao**	**Montane**
A. nuditarsus (bare-legged swiftlet)	S New Guinea	Montane
A. orientalis (Mayr's swiftlet)	Bismarck Archipelago, Solomons	Montane
***A. vanikorensis* (uniform swiftlet)**	**Philippines, Sulawesi, Moluccas, New Guinea, Bismarck Archipelago, Solomons, Vanuatu**	**To sea level**
***A. salangana* (mossy-nest swiftlet)**	**Borneo, Sumatra, Java**	**To sea level**
A. pelewensis (Palau swiftlet)	Palau Islands (Micronesia)	To sea level
***A. bartschi* (Guam swiftlet)**	**S Mariana Islands (Micronesia)**	**To sea level**
A. inquietus (Caroline swiftlet)	Caroline Islands (Micronesia)	To sea level
***A. sawtelli* (Atiu swiftlet)**	**Atiu Island (Cook Islands; Polynesia)**	**To sea level**
A. leucophaeus (Polynesian swiftlet)	Society and Marquesas Islands (Polynesia)	To sea level
***A. maximus* (black-nest swiftlet)**	**Thai-Malay Peninsula, Sumatra, Borneo, Java**	**To sea level**
***A. fuciphagus* (edible-nest swiftlet)**	**Hainan, Indochina, Andamans, Thai-Malay Peninsula, Sumatra, Borneo, Java, Bali, Lesser Sunda Islands, Philippines**	**To sea level**
***A. papuensis* (Papuan swiftlet)**	**New Guinea**	**Mostly montane**

restricted to single islands (Chantler, 1999; Table 1). However, because of their invariably drab colouration and uniform morphology, species delimitation and taxonomic treatment in *Aerodramus* are uncertain (see e.g., Salomonsen, 1983). Given recent discoveries of crypsis and underestimation of diversity on islands (Cibois et al., 2007, 2008, 2010, 2011a, 2011b; Moyle et al., 2009), the level of species diversification within the genus may be under-estimated and the vagility over-estimated.

Aerodramus has been subjected to previous mtDNA analyses (Lee et al., 1996; Thomassen et al., 2003; Price et al., 2004, 2005) including largely independent datasets that were not combined between author groups. We have combined sequences of the single overlapping locus, cytochrome-*b*, across all studies and added additional samples, including sequences of two taxa that have not previously been included in molecular comparisons. This gives our dataset the largest taxonomic coverage hitherto reported for DNA studies of this genus, spanning 15 of the 22 species recognised by Salomonsen (1983) and Chantler (1999). We analysed this dataset to improve our understanding of systematic relationships within *Aerodramus* and assess the extent of diversification and vagility across the various lineages.

METHODS

We sequenced a 406 bp fragment of the mitochondrial coding gene cytochrome-*b* (cytb) from muscle tissue of one *Aerodramus terraereginae*, muscle tissue of one *A. vanikorensis yorki*, and liver tissue of two individuals of *A. hirundinaceus*. The latter two taxa have never been included in molecular analyses (Table 2). Genbank sequences were available for another 47 *Aerodramus* individuals (Table 2). They derived from five different studies (Lee et al., 1996; Johnson & Clayton, 2000; Thomassen et al., 2003; Price et al., 2004, 2005; Braun & Huddleston, 2009; Rahman & Azmi, unpublished). Identity, collection localities, and Genbank accession numbers of all sequences are listed in Table 2. As outgroups, we used an individual of *Hirundapus caudacutus* for which we sequenced cytb as well as three *Collocalia* species (*C. linchi*, *C. esculenta*, *C. troglodytes*) for which cytb sequences were available on Genbank. *Collocalia* is closely related to *Aerodramus*, while *Hirundapus* is known to be more distantly related (Price et al., 2004). The non-echolocating monotypic genus *Hydrochous* is widely thought to be sister to *Aerodramus* although recent studies have left it unclear whether it may be embedded within *Aerodramus* (e.g., Lee et al., 1996; Price et al., 2005). Therefore we also

Table 2. Identity of the study samples, Genbank accession numbers, localities, and the source study (unless sequence produced for this study). * indicates a sequence of *A. fuciphagus vestitus* identified as an introgressed haplotype of *A. salangana natunae* by Lee et al. (1996).

Taxon	Genbank Accession Number	Locality	Source	Voucher Information
A. bartschi	U49984	Hawaii (introduced from Guam)	Lee et al. (1996)	specimen or blood (DHC77); collector Dale Clayton
A. elaphrus	U49988	Seychelles	Lee et al. (1996)	specimen or blood (DHC63); collector Dale Clayton
A. francicus	U49991	Mauritius	Lee et al. (1996)	specimen or blood (DHC54); collector Dale Clayton
A. fuciphagus amechanus	EU594264	Selangor (Pen. Malaysia)	A. Rahman & N.S. Azmi (unpublished)	specimen or blood (SB33BP3); collectors A.R. Mustafa and W.L. Goh
A. fuciphagus	AY135631	?	Thomassen et al. (2003)	blood sample (label F4)
A. fuciphagus amechanus	EU594263	Selangor (Pen. Malaysia)	A. Rahman & N.S. Azmi (unpublished)	specimen or blood (SB31P2); collectors A.R. Mustafa and W.L. Goh
A. fuciphagus germani	U49995	Balambangan Island (off Sabah)	Lee et al. (1996)	specimen or blood (DHC04); collector Dale Clayton
A. hirundinaceus hirundinaceus	KF691790	Southern Highland Province (Papua New Guinea)	this study	specimen (Y28); voucher at Australian Museum
A. hirundinaceus hirundinaceus	KF691791	Southern Highland Province (Papua New Guinea)	this study	specimen (Y68); voucher at Australian Museum
A. maximus lowi	U50000	Sabah	Lee et al. (1996)	specimen or blood (DMT040); collector Dan Tompkins
A. maximus lowi	AY135624	Borneo	Thomassen et al. (2003)	blood sample (label M6)
A. mearnsi	AY294441	Philippines	Price et al. (2004)	specimen (SEA116); collector Sarah Al-Tamimi
A. papuensis	AY950787	Eastern Highland Province (Papua New Guinea)	Price et al. (2005)	specimen or blood (SEA-389); collector Sarah Al-Tamimi
A. salangana natunae	AY294424	mainland Sabah	Price et al. (2004)	specimen (DMT002); collector Dan Tompkins
A. salangana natunae	AY294425	mainland Sabah	Price et al. (2004)	specimen (DMT047); collector Dan Tompkins
A. salangana natunae	U50006	mainland Sabah	Lee et al. (1996)	specimen or blood (DMT001); collector Dan Tompkins
A. salangana natunae	U50008	mainland Sabah	Lee et al. (1996)	specimen or blood (DMT048); collector Dan Tompkins
"A. fuciphagus vestitus" = *A. salangana natunae* *	U49994	mainland Sabah	Lee et al. (1996)	specimen or blood (DMT028); collector Dan Tompkins
A. sawtelli	U50012	Atiu Island (Polynesia)	Lee et al. (1996)	specimen or blood (W3); collector Graham Wragg
A. spodiopygius assimilis	AY294435	Fiji	Price et al. (2004)	specimen (DHC36); collector Dale Clayton
A. spodiopygius assimilis	AY294436	Fiji	Price et al. (2004)	specimen (DHC37); collector Dale Clayton
A. spodiopygius assimilis	U50002	Fiji	Lee et al. (1996)	specimen (DHC36); collector Dale Clayton
A. spodiopygius assimilis	U50010	Fiji	Lee et al. (1996)	specimen or blood (W13); collector Graham Wragg
A. spodiopygius assimilis	U50009	Fiji	Lee et al. (1996)	specimen or blood (W12); collector Graham Wragg
A. spodiopygius spodiopygius	U50013	West Samoa	Lee et al. (1996)	specimen (DHC31); collector Dale Clayton
A. spodiopygius spodiopygius	U50014	West Samoa	Lee et al. (1996)	specimen or blood (DHC35); collector Dale Clayton
A. spodiopygius spodiopygius	AY294437	West Samoa	Price et al. (2004)	specimen (DHC31); collector Dale Clayton
A. terraereginae	U50016	Queensland	Lee et al. (1996)	specimen (DHC28); collector Dale Clayton
A. terraereginae	KF691789	Kaban (Queensland)	this study (voucher: C645)	specimen (C645); voucher at Australian National Wildlife Collection
A. terraereginae	AY294451	Queensland	Price et al. (2004)	specimen (DHC20); collector Dale Clayton
A. terraereginae	AY294453	Queensland	Price et al. (2004)	specimen (DHC28); collector Dale Clayton
A. terraereginae	AY294452	Queensland	Price et al. (2004)	specimen (DHC30); collector Dale Clayton

Table 2. Cont'd.

Taxon	Genbank Accession Number	Locality	Source	Voucher Information
A. vanikorensis lugubris	AY294444	Rennell Island (Solomons)	Price et al. (2004)	specimen (UWBM58708); voucher at University of Washington Burke Museum
A. [vanikorensis] palawanensis	AY294439	Balambangan Island (off Sabah)	Price et al. (2004)	specimen (DHC01); collector Dale Clayton
A. [vanikorensis] palawanensis	AY294440	Balambangan Island (off Sabah)	Price et al. (2004)	specimen (DHC06); collector Dale Clayton
A. "salangana natunae" = A. [vanikorensis] palawanensis	U50004	Balambangan Island (off Sabah)	Lee et al. (1996)	specimen (DHC01); collector Dale Clayton
A. "salangana natunae" = A. [vanikorensis] palawanensis	AF182681	Balambangan Island (off Sabah)	Johnson & Clayton (2000)	specimen (DHC01); collector Dale Clayton
A. vanikorensis pallens	FJ588453	New Ireland (Bismarck Archipelago)	Braun & Huddleston (2009)	specimen (USNM 608672; B04039); voucher at United States National Museum (Smithsonian)
A. vanikorensis yorki	KF691788	Kokoda (Papua New Guinea)	this study	specimen (E530); voucher at Australian National Wildlife Collection
A. vulcanorum	AY135634	Java	Thomassen et al. (2003)	blood sample (label V1)
A. vulcanorum	U50017	Java	Lee et al. (1996)	specimen or blood (DHC65); collector Dale Clayton
A. vulcanorum	AY294450	Java	Price et al. (2004)	specimen (DHC66); collector Dale Clayton
A. whiteheadi	AY294454	Mindanao (Philippines)	Price et al. (2004)	specimen (CMNH37000); voucher at Cincinnati Museum of Natural History
Collocalia esculenta	AY294466	outgroup	Price et al. (2004)	specimen (MSP068); collector Michael Putnam
Collocalia linchi	AY294467	outgroup	Price et al. (2004)	specimen (DHC72); collector Dale Clayton
Collocalia troglodytes	U50027	outgroup	Lee et al. (1996)	specimen or blood (SL12); collector Scott Lanyon
Collocalia troglodytes	U50028	outgroup	Lee et al. (1996)	specimen or blood (SL13); collector Scott Lanyon
Collocalia troglodytes	AY294468	outgroup	Price et al. (2004)	specimen (FMNH358312); voucher at Field Museum of Natural History
Hydrochous gigas	AY135626	?	Thomassen et al. (2003)	blood sample (label H2)
Hydrochous gigas	U50035	Java	Lee et al. (1996)	specimen or blood (CTC18); collector Charlie Collins
Hydrochous gigas	AY135625	?	Thomassen et al. (2003)	blood sample (label H1)
Hirundapus caudacutus	KF691792	outgroup (locality: Canberra, Australia)	this study	specimen (B563); voucher at Australian National Wildlife Collection

included three individuals of *Hydrochous gigas* to confirm its position relative to *Aerodramus*.

DNA extraction, PCR amplification, and sequencing procedures followed those of Norman et al. (1998), with PCR annealing temperatures of 52–58°C. The primers, CeCb-L (CCAAATATCMTTCTGAGGYG) and CeCb-H (TTCTGGTTTGATRTGGGGG), were designed for amplification of a related species, *Collocalia esculenta*, using sequences from Lee et al. (1996). Sequences were checked for stop codons and reading frame. Sequence alignment was generally straightforward on account of a lack of indels. Codon usage was explored using the Codon Usage tool at the Gene Infinity webpage (http://www.geneinfinity.org/sms/sms_codonusage.html).

We used the Akaike Information Criterion as implemented in the program jModelTest (Posada, 2008) to find that the best of 88 evolutionary models for our data was a GTR + G + I model with user-specified substitution rates (1, 16.9826, 1, 1, 5.671, 1), assumed nucleotide frequencies of A=0.3018, C=0.3913, G=0.0940, T=0.2129, an assumed proportion of invariable sites of 0.644, a gamma shape parameter of a=2.48, and four rate categories.

We employed maximum parsimony (MP), maximum likelihood (ML), and Bayesian methods using the programs PAUP* 4.0b10 (Sinauer Associates, Inc.; see also Swofford, 2002) and MRBAYES 3.1.2 (Ronquist & Huelsenbeck, 2003). For heuristic ML and MP searches, we ran PAUP's tree-bisection-reconnection method for tree-swapping by stepwise addition using random addition sequence. Support for individual nodes was estimated through heuristic bootstrap re-sampling (2,000 replicates in MP; 150 replicates in ML). We incorporated the parameters of the most-likely evolutionary model, as given by jModelTest, into our ML runs in PAUP.

In MRBAYES analyses, we conducted two runs with four chains each (one hot, three cold) over 20,000,000 generations, sampling trees every 1,000 generations for the evaluation of posterior probabilities. For the evolutionary model used in MRBAYES, we only specified the number of substitution types and the presence of a gamma shape parameter. In Bayesian analysis, there is a moderate computational penalty associated with estimating parameters as opposed to fixing them prior to analysis (Ronquist & Huelsenbeck, 2003). Therefore, we let MRBAYES estimate the particular parameters of the evolutionary model (such as base frequencies, the rate matrix and the value of the gamma shape parameter). Likelihood versus generation plots were inspected in Tracer Version v1.4.1 (Rambaut & Drummond, 2008) to ascertain how many generations each run required to reach a likelihood plateau. In this fashion we determined that a burn-in of 12% was appropriate for both runs. We evaluated convergence using Tracer, making sure that Bayesian runs reached an effective sample size greater than 200 at burn-in.

Genetic divergence among taxa was computed with the program MEGA5 (Tamura et al., 2011) using a Tamura-Nei model of evolution as it most closely approaches the GTR model provided by jModelTest.

RESULTS

A reading frame and stop codon check demonstrated that all 52 sequences in the 406 bp alignment were potentially functional. Adding up differences from majority codon usage in the alignment, three aberrant sequences (see Discussion) exhibited the highest accumulative deviation of codons in usage (not shown). Genetic divergences between *Aerodramus* species range between 0–16.8% (Table 3). Different modes of analysis (ML, MP, Bayesian) provided similar tree topologies (Fig. 1). Importantly, highly supported clades were identical among analytical modes (Fig. 1). Many nodes on the tree lacked strong support from any of the analytical modes and must be considered tentative. Nevertheless, strongly supported clades always comprised members of one taxon each, with three exceptions.

1. An individual of *A. fuciphagus vestitus* was nested with strong support (87–98 bootstrap or posterior probability depending on analysis) inside a clade containing four *A. salangana natunae* individuals (Fig. 1). This sample of *A. fuciphagus vestitus*, which breeds inside a large cave that also hosts a sizeable colony of *A. salangana natunae* (Gomantong Cave, Sabah), was identified by Lee et al. (1996) as having an introgressed genotype from the latter species.

2. The five individuals of *A. spodiopygius assimilis* examined, all from Fiji, formed two widely separated clades of two and three individuals that differed by a genetic distance of 7.0% (Table 3).

3. The three individuals of *A. vulcanorum* examined, all from Java, formed two widely separated clades of one and two individuals that differed by a genetic distance of 4.6–5.2% (Table 3).

DISCUSSION

Pseudogene sequences in *Aerodramus* swiftlets? Surprisingly, five Fijian individuals of *A. spodiopygius assimilis* emerge in two fairly well-supported clades (Fig. 1). These clades are deeply diverged (7%; Table 3) and are separated by several nodes of low support. One of these clades, which we call the 'aberrant *spodiopygius* clade', forms the well-supported sister group of a single aberrant individual of the Javan volcano swiftlet *A. vulcanorum* (Fig. 1), an arrangement that makes little biogeographic sense. The aberrant *A. vulcanorum* individual is widely divergent (4.6–5.2%; Table 3) from a well-supported clade of two other *A. vulcanorum* specimens (Fig. 1). The two other specimens of *A. vulcanorum* form a strongly supported clade with the black-nest swiftlet *A. maximus*, an arrangement that agrees with traditional taxonomic and biogeographic assumptions (Chantler, 1999). The clade including the 'aberrant' *A. vulcanorum* and *A. spodiopygius assimilis* individuals emerges basal to and deeply diverged from all other

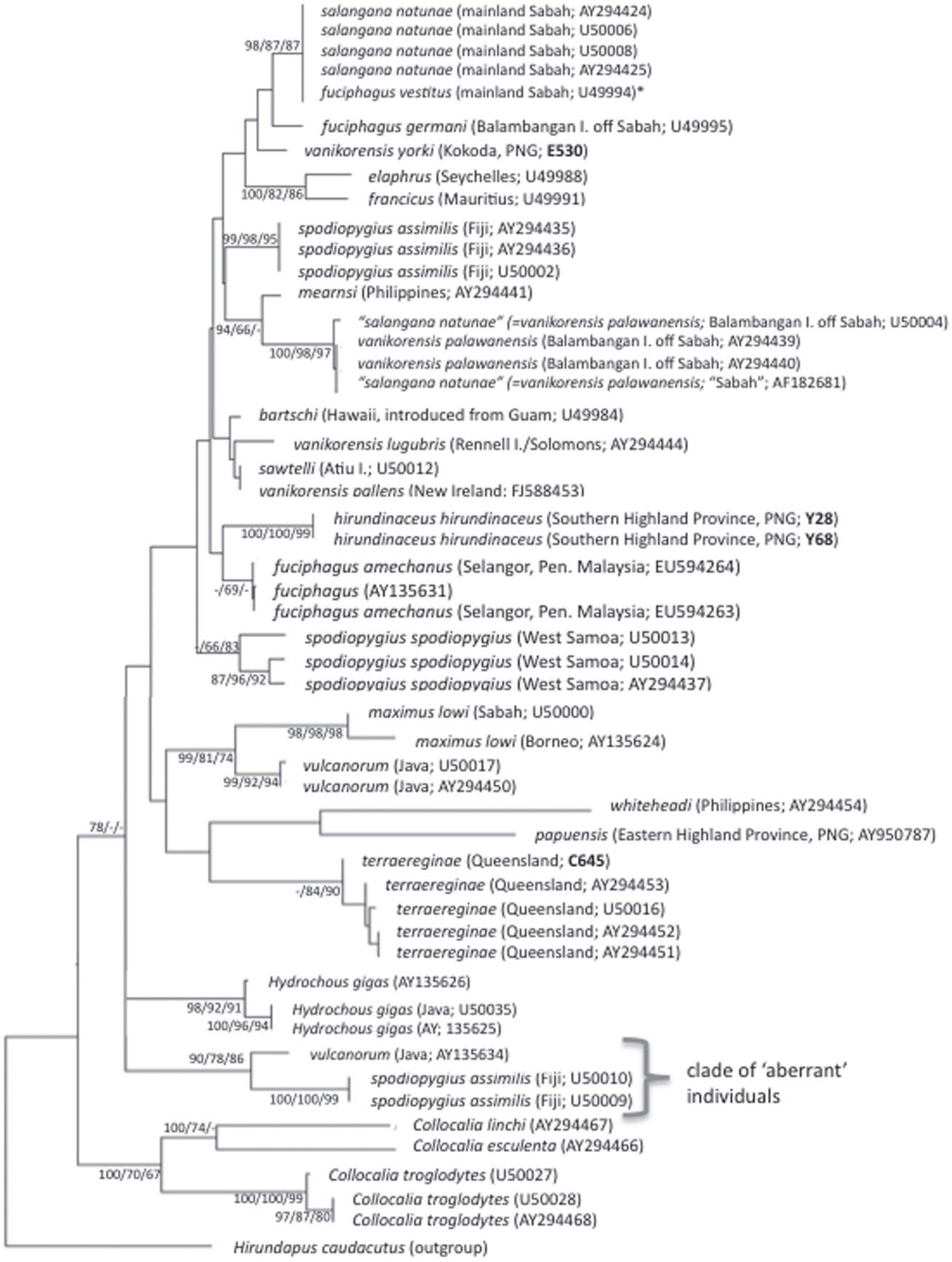

Fig. 1. Cytochrome-*b* maximum-likelihood tree topology. Branch support is given as Bayesian posterior probability (multiplied by 100 for ease of reading) / Maximum Likelihood bootstrap / Maximum Parsimony bootstrap. Only posterior probabilities >75 and bootstrap values >65 are given. Asterisk refers to a specimen of *A. fuciphagus vestitus* which possesses an introgressed mtDNA haplotype from *A. salangana natunae* (see text).

Table 3. Pairwise cytochrome-b sequence divergences between *Aerodramus* taxa using a Tamura-Nei model (see Methods). Grey cells indicate intra-taxon divergences.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
(1) *Hirundapus caudatus* (outgroup)	n/a																							
(2) 3 *Collocalia* species (outgroup)	0.09–0.114	0.005–0.097																						
(3) *Hydrochous gigas*	0.99–0.101	0.091–0.109	0–0.015																					
(4) *A. whiteheadi*	0.158	0.111–0.138	0.123–0.124	n/a																				
(5) *A. hirundinaceus*	0.090	0.085–0.120	0.051–0.065	0.102	0.000																			
(6) *A. elaphrus*	0.106	0.099–0.124	0.070–0.077	0.168	0.042	n/a																		
(7) *A francicus*	0.102	0.099–0.117	0.070–0.077	0.127	0.046	0.015	n/a																	
(8) *A. mearnsi*	0.091	0.085–0.110	0.061	0.116	0.035	0.034	0.023	n/a																
(9) *A. [vanikorensis] palawanensis*	0.083	0.084–0.115	0.066–0.067	0.124–0.145	0.045	0.046–0.051	0.034–0.04	0.015–0.02	0.005															
(10) *A. vanikorensis yorki*	0.098	0.081–0.116	0.054–0.065	0.118	0.029	0.023	0.032	0.023	0.039	n/a														
(11) *A. vanikorensis pallens / lugubris*	0.08–0.091	0.069–0.110	0.055–0.064	0.116	0.020–0.023	0.029–0.037	0.023–0.032	0.015–0.018	0.026–0.035	0.014–0.023	0.008													
(12) *A bartschi*	0.076	0.066–0.102	0.051–0.058	0.103	0.023	0.032	0.026	0.018	0.023–0.029	0.017	0.002–0.01	n/a												
(13) *A sawtelli*	0.080	0.069–0.106	0.055–0.061	0.116	0.020	0.029	0.023	0.015	0.026–0.032	0.014	0–0.008	0.002	n/a											
(14) *A. maximus*	0.098–0.11	0.098–0.144	0.071–0.087	0.091–0.102	0.069–0.079	0.09–0.1	0.089–0.099	0.072–0.082	0.071–0.081	0.06–0.07	0.059–0.079	0.056–0.065	0.059–0.068	0.008										
(15) *A. vulcanorum* (main clade)	0.085–0.089	0.083–0.110	0.052–0.061	0.103–0.113	0.056–0.059	0.062–0.065	0.062–0.065	0.05–0.055	0.052–0.064	0.042–0.045	0.044–0.059	0.041–0.046	0.044–0.049	0.027–0.037	n/a									
(16) *A. vulcanorum* (aberrant specimen)	9.1	0.076–0.121	0.034–0.051	0.137	0.065	0.074	0.074	0.058	0.064–0.07	0.058	0.052–0.062	0.049	0.052	0.075–0.085	0.046–0.052	n/a								
(17) *A. terraereginae*	0.091–0.102	0.087–0.131	0.064–0.086	0.053–0.092	0.054–0.058	0.08–0.095	0.076–0.088	0.058–0.071	0.062–0.074	0.066–0.07	0.049–0.061	0.045–0.055	0.049–0.058	0.055–0.074	0.055–0.068	0.072–0.09	0–0.005							
(18) *A. papuensis*	0.123	0.118–0.145	0.088–0.095	0.081	0.097	0.111	0.111	0.089	0.088–0.089	0.089	0.087–0.094	0.083	0.087	0.115–0.126	0.096–0.103	0.088	0.104–0.122	n/a						
(19) *A. salangana*	0.098	0.082–0.125	0.070–0.077	0.113	0.032	0.026	0.026	0.023	0.04–0.046	0.014	0.018–0.026	0.021	0.018	0.062–0.71	0.046–0.052	0.067–0.068	0.066–0.081	0.101–0.103	n/a					
(20) *A. s. spodiopygius*	0.073–0.083	0.066–0.117	0.058–0.071	0.138–0.156	0.039–0.042	0.043	0.043	0.035–0.036	0.034–0.041	0.034–0.036	0.024–0.033	0.021–0.022	0.024–0.025	0.068–0.079	0.047–0.053	0.043–0.061	0.064–0.083	0.09–0.098	0.032–0.015	0.005–				
(21) *A. spodiopygius assimilis* (main clade)	0.077	0.078–0.098	0.058–0.064	0.103	0.029	0.032	0.026	0.024	0.023–0.028	0.023	0.018–0.026	0.015	0.018	0.062–0.072	0.053–0.059	0.062	0.058–0.074	0.086	0.026	0.026	0			
(22) *A. spodiopygius assimilis* (aberrant specimens)	0.098	0.078–0.119	0.048–0.066	0.135	0.071	0.09	0.09	0.073	0.072–0.079	0.071	0.06–0.07	0.057	0.06	0.083–0.093	0.061–0.067	0.023	0.078–0.099	0.094	0.082	0.051–0.07	0.07	0		
(23) *A. fuciphagus amechanus*	0.067–0.083	0.078–0.124	0.064–0.067	0.091	0.02–0.023	0.026–0.035	0.034–0.039	0.021–0.022	0.026–0.031	0.016–0.017	0.015–0.019	0.013–0.015	0.015–0.016	0.053–0.072	0.043–0.049	0.056–0.058	0.041–0.058	0.086–0.099	0.018–0.019	0.024–0.03	0.018–0.023	0.066–0.068	0.000	
(24) *A. fuciphagus germani*	0.095	0.091–0.127	0.07–0.077	0.114	0.029	0.026	0.026	0.023	0.037–0.042	0.011	0.018–0.026	0.021	0.018	0.068–0.078	0.046–0.052	0.067	0.065–0.074	0.103	0.010	0.037–0.038	0.026	0.082	0.018	n/a

Aerodramus swiftlets and potentially falls outside the genus (Fig. 1, Table 3). There are several potential explanations for this aberrant clade.

a. There may be cryptic diversification in *A. vulcanorum* and *A. spodiopygius assimilis* such that both species emerge as two different lineages each. We consider this possibility very unlikely. These sequence divergences are amongst the highest found between any *Aerodramus* individuals sampled in our study despite the lack of any morphological indication of cryptic speciation in these taxa (Salomonsen, 1983). Especially in the case of *A. vulcanorum*, there is little ecological space for two nearly identical species to coexist in such a small distributional range.

b. The aberrant clade may be a consequence of the usage of different lab protocols or different lab personnel. However, all three aberrant samples have counterparts, collected at identical sites and analysed by identical authors (Lee et al., 1996; Thomassen et al., 2003), that fall into clades of expected phylogenetic position (Fig. 1, Table 2). This aberrant clade is therefore not due to artifacts that can be attributed to different lab protocols or personnel.

c. The aberrant clade may be related to misidentifications of specimens in the field. All three samples in question are derived from studies that used unvouchered blood samples, often collected in the field from birds that were subsequently released (Lee et al., 1996; Thomassen et al., 2003). These unvouchered blood samples are problematic because, if a caught bird was misidentified, there is no subsequent possibility to ascertain its true identity based on morphology. However, we doubt that a field misidentification applies to this case, because there is only a limited number of *Aerodramus* species sympatric to the two species in question, and our dataset includes them all, such that the misidentified birds would have had to cluster with other *Aerodramus* specimens rather than form a divergent lineage of their own.

d. The aberrant clade may result from an ancestral mitochondrial polymorphism originating from before the *Aerodramus* radiation occurred. Incomplete lineage sorting is a ubiquitous side product of the coalescent process of diversification. However, its effect in fast-evolving loci (e.g., mtDNA) in species with comparatively low effective population sizes (e.g., birds) over time scales on the order of hundreds of thousands of years is limited (Edwards & Beerli, 2000). Thus we do not think that incomplete lineage sorting could have caused this pattern.

e. The three aberrant sequences may be based on nuclear pseudogenes ('numts') rather than actual mtDNA. 'Numts' are nuclear paralogs of mtDNA genes that may have been transferred to the nuclear genome a long time ago (Bensasson et al., 2001). Blood samples, as opposed to muscle tissue samples, are a particularly rich source of 'numts' (Sorenson & Quinn, 1998). As all three aberrant sequences derived from blood, this makes their identity as 'numts' particularly likely. A check for stop codons revealed that these sequences have retained their full functional potential, but this may be due to a stochastically based lack of mutations that would have introduced novel stops codons. An analysis of codon usage showed that these three sequences exhibited the highest accumulative deviation of codons in usage amongst all individuals in the alignment, corroborating that their origin may be paralogous.

The likely identification of aberrant sequences as 'numts' underscores the importance of sampling several individuals per taxon. Beyond the three aberrant sequences, we do not think our dataset contained any other 'numt'-based sequence because none of the other sequences emerged in such a widely divergent and basal position and because multiple individuals were available for most taxa, all of which grouped together.

Taxonomic implications. Although many nodes of our phylogenetic tree (Fig. 1) lacked strong support, others were highly supported and allow for the following taxonomic inferences:

1. Philippine members of the uniform swiftlet *A. vanikorensis* group:
   Four specimens from Balambangan Island off the coast of Sabah (Malaysia) derived from three different studies (Lee et al., 1996; Johnson & Clayton, 2000; Price et al., 2004), in which they were variably identified as mossy-nest swiftlet *A. salangana natunae* or as uniform swiftlet *A. vanikorensis palawanensis*. In our analyses, all four specimens shared near-identical mtDNA sequences and clustered in a highly supported clade that was distinct from another Balambangan specimen identified as edible-nest swiftlet *A. fuciphagus germani* (3.7–4.2% divergence; Table 3). The latter was separated from the former clade by several partly well-supported nodes (Fig. 1). This result confirms the conclusion by Lee et al. (1996) and Price et al. (2004) of the existence of two *Aerodramus* species on Balambangan Island, one belonging to the edible-nest swiftlet complex (*A. fuciphagus*) and the other belonging to the uniform swiftlet complex (*A. vanikorensis*), whose Greater Sunda members are usually distinguished as mossy-nest swiftlets *A. salangana* (e.g., Salomonsen, 1983; Chantler, 1999).

   Our analysis indicates that the Balambangan swiftlets belonging to the uniform swiftlet complex have a mtDNA haplotype highly distinct from that of mossy-nest swiftlets *A. salangana natunae* collected on the adjacent Sabah mainland (4–4.6% divergence; Table 3). Our well-supported clade of mainland Sabah mossy-nest swiftlets, which is separated from the Balambangan birds by several partly well-supported nodes (Fig. 1), includes individuals from two different studies (Lee et al., 1996; Price et al., 2004) that have identical mtDNA haplotypes. Although an individual of *A. fuciphagus* is included in this clade, Lee et al. (1996) stated that this individual had an introgressed mtDNA haplotype of *A. salangana*. Lee et al. (1996) did not actually carry out analyses to test the hypothesis if this sequence may be a product of genetic

introgression (see e.g., Rheindt & Edwards, 2011), leaving it uncertain whether they examined the specimen to detect a morphological affinity with *A. salangana* or whether they merely inferred that this specimen was misidentified. As the Balambangan birds obviously form a clade distinct from that of confirmed mainland *A. salangana*, we agree with Price et al. (2004) about attributing Balambangan birds to the taxon *palawanensis* (otherwise known from adjacent Palawan and surrounding islands). Although *palawanensis* has been subsumed by Chantler (1999) under the uniform swiftlet *A. vanikorensis*, it deserves species-level recognition, either on its own, or together with the taxon *amelis* (from the main Philippine islands) as a subspecies of the latter, based on the phylogenetic arrangement in our study (Fig. 1). We note that our *palawanensis* samples do not cluster closely with other samples of *A. vanikorensis* that are geographically much closer to the type specimen from Vanuatu, such as New Guinean (*yorki*) or Melanesian (*lugubris*, *pallens*), and are separated from them by 2.6–3.9% divergence (Table 3). In fact, within the sampling regime of our study, the Philippine swiftlet *A. mearnsi* emerges as the most closely related taxon to *palawanensis* (Fig. 1, Table 3), providing evidence for scenarios of intra-regional speciation rather than speciation by long-distance dispersal. We therefore propose that *palawanensis* should no longer be considered conspecific with *A. vanikorensis*. Although we lack molecular data of *amelis* to determine its phylogenetic position, we propose that—in the interest of conservatism—*amelis* and *palawanensis* be united into one species *A. amelis*, for which the English name "gray swiftlet" or (preferably in our opinion) "Ameline swiftlet" has previously been suggested (Chantler, 1999).

2. The edible-nest swiftlet *A. fuciphagus* complex:
Disregarding the specimen of *A. fuciphagus vestitus* that was identified by Lee et al. (1996) as having the introgressed mtDNA haplotype of *A. salangana*, our dataset included a sample of *A. fuciphagus germani* from Balambangan Island (off Sabah) as well as three presumable samples of *A. fuciphagus amechanus* collected on the coast of Selangor (West Malaysia). Note that there has been great uncertainty about the subspecific identity of peninsular Malaysian birds in the past, with many authors attributing most peninsular populations to the taxon *germani* (type locality: Condore Island in southern Vietnam) rather than *amechanus* (type locality: Anambas Islands off peninsular Malaysia; for a summary, see Cranbrook et al., 2013). While the three mtDNA sequences of the peninsular Malaysian specimens were identical, the single Balambangan specimen was 1.8% divergent (Table 3) and was several nodes removed from the three *amechanus* samples, with none of these nodes receiving strong branch support (Fig. 1). Aditionally, both the Balambangan and the peninsular specimens exhibited comparatively limited mtDNA differentiation from the sympatric mossy-nest swiftlet *A. salangana* (1–1.8%; Table 3) and *salangana*'s eastern Indonesian and Pacific counterparts (i.e., *A. vanikorensis yorki/pallens/lugubris, A. bartschi, A. sawtelli*; mtDNA divergence from edible-nest swiftlets at 1.1–2.6%; see Table 3). Two conclusions emerge: a) Given the comparatively low mtDNA divergence of edible-nest swiftlets from mossy-nest swiftlets and their close relatives, and given the claims of genetic introgression between both species in Sabah's caves (Lee et al., 1996), occasional hybridisation events between the two species are likely to have led to mtDNA sweeps (Rheindt & Edwards, 2011), making low mtDNA divergences between these taxa an unreliable taxonomic indicator. Future studies using whole-genomic data will be necessary to elucidate patterns of gene flow among these taxa; b) Both *amechanus* and *germani* are variously subsumed under *A. fuciphagus* (e.g. Chantler, 1999) or raised to species level owing to their lighter rump and belly coloration (see Cranbrook et al., 2013, for a summary). However, on the Malaysian Peninsula and beyond, there is a broad cline between lighter-rumped and darker-rumped birds, and individuals across the whole spectrum of rump darkness are known to breed in the same colonies, often in commercial house-farms (Cranbrook et al., 2013). Given their limited mtDNA divergence, it is still an open question whether light and dark-rumped birds were ever on the way towards different species trajectories. However, both our study (Table 3, Fig. 1) and Cranbrook et al.'s (2013) results (e.g., their table 1, which enables the reader to compute divergence estimates) conclusively demonstrate low mtDNA divergences between light and dark-rumped birds, including both recent specimens from human-maintained house farms and old museum specimens from a time when house-farms probably did not exist. Hence, whatever limited incipient differentiation there may or may not have been between lighter and darker-rumped birds in the past, the present practice of swiftlet farming is quickly eroding its signal. It becomes clear, therefore, that all edible-nest swiftlet populations should be merged into one biological species, *A. fuciphagus*.

3. Papuan and Melanesian members of the uniform swiftlet *A. vanikorensis* group and related species:
Even after exclusion of Philippine *A. amelis* (see above) from the uniform swiftlet *A. vanikorensis*, the taxon still spans the region from Sulawesi to the Vanuatu Islands. Our sampling from this vast region is limited and only encompasses one *yorki* individual from New Guinea, a *lugubris* from Rennell Island (Solomons) and a *pallens* from New Ireland (Bismarck Islands). The New Guinean *yorki* is moderately differentiated from the two Melanesian samples on the tree (1.4–2.3% and several nodes removed; Fig. 1, Table 3). However, none of the nodes involving this arrangement is well-supported. Future analyses of the uniform swiftlet complex should include Wallacean subspecies (such as *moluccarum* from the Moluccas or *aenigma* from Sulawesi). In the meantime, we note that the Melanesian subspecies of *A. vanikorensis* clustered closely with two Micronesian/Polynesian swiftlet species, the Guam swiftlet *A. bartschi* and the Atiu swiftlet *A. sawtelli*. Although the clade comprising these taxa was not strongly supported, the two Micronesian/Polynesian species differed from Melanesian taxa of *A. vanikorensis*

by only 0–1.0% (Table 3), suggesting recent gene flow between these taxa. Note also that the mtDNA divergence between *A. salangana* and the geographically closest sampled member of *A. vanikorensis* (i.e., *yorki*) is at the lower end of intra-*vanikorensis* mtDNA divergences (1.4%; Table 3). The low mtDNA differentiation of *A. vanikorensis* from both *A. salangana* to the west and various Pacific island taxa to the east calls into question their status as independent species as rare but regular gene flow may prevent deep mtDNA divergence from building up. We postulate that limited differentiation may also involve other Micronesian swiftlet species not sampled but traditionally considered closely related to uniform swiftlets (Chantler, 1999), such as Caroline swiftlet *A. inquietus* and Palau swiftlet *A. pelewensis*. For now we refrain from subsuming all these species under *A. vanikorensis* pending further specimen and locus sampling, even though we find it likely that they will all prove to be members of one highly vagile species.

4. The white-rumped swiftlet *A. spodiopygius* complex: We discussed above that two sequences of *A. spodiopygius assimilis* are characterised by an aberrant phylogenetic position and are probably numts. Meanwhile, the fairly deep divergence between the three 'non-aberrant' individuals of *A. spodiopygius assimilis* and the Samoan nominate *A. s. spodiopygius* individuals is likely to be reliable (2.6%; Table 3). Morphologically, the two taxa differ only in the darkness of their underparts and rump band, while other (unsampled) subspecies of *A. spodiopygius* are separable by much more diagnostic morphological differences, such as feathered versus unfeathered tarsi, pronounced color differences or a ~9% difference in size (Salomonsen, 1983). By inference, if nominate *spodiopygius* and the neighbouring *assimilis* show such deep mtDNA divergence, other taxa that are even more distinct morphologically would be expected to be more deeply divergent genetically. Re-drawing the species boundaries in the white-rumped swiftlet complex requires much denser taxon sampling, but our dataset provides preliminary evidence that the complex may in fact contain multiple species.

Diversification in *Aerodramus* swiftlets. Our results suggest a rapid diversification of the genus *Aerodramus*, as evidenced by a cytb mitochondrial tree with many shallow branches between sister species (Fig. 1; Table 3). Although divergence values range up to 16.8% between the most distant congeners, most are as low as 0–3% between closely related species (Table 3). This range of divergence between species is low compared to other avian cytb divergences, suggesting potential mtDNA sweeps at least between sympatric species pairs (Rheindt & Edwards, 2011). For example, we found two widely sympatric species (*A. fuciphagus amechanus* and *A. salangana*) to have diverged by as little as 1.8–1.9%, while two adjacent but allopatric species *A. francicus* and *A. elaphrus* exhibit a divergence of 1.5% (Table 3). Furthermore, several widely-recognised species in the Pacific, including *A. bartschi*, *A. sawtelli*, and *A. vanikorensis* (ssp *pallens* and *lugubris*) are characterized by (near-) zero divergences (0 – 1%; Table 3). Whereas low mtDNA divergences between some species pairs (such as A. fuciphagus and A. salangana) may be caused by other processes, such as genetic introgression (Rheindt & Edwards, 2011), their pervasive occurrence in Aerodramus suggests a rapid pace of diversification over the past ~1 million years, during which members of the genus colonised most islands and archipelagoes in the Indian and Pacific Oceans. The area of origin of *Aerodramus* is difficult to ascertain in the absence of a better-resolved topology and knowledge of outgroup relationships. Considering that *Collocalia* and *Hydrochous*, the sister genera of *Aerodramus*, are centered in the Indo-Malayan Archipelago, however, it is likely that *Aerodramus* originated there, too, and only recently colonised the western Indian Ocean and the more distant regions of the Pacific.

Aerodramus swiftlets probably combine all the attributes that characterise a good speciator (see Moyle et al., 2009): they are extremely good fliers that are highly dispersive when foraging, enabling them to colonise far-flung islands, but they are also strongly tied to their home caves and other natural or man-made cavities for nesting. Indeed, they are known for their natal philopatry as they often occur in breeding colonies in large caves (Chantler, 1999). So despite their formidable colonisation abilities, they are unlikely to maintain gene flow over large areas on account of their special nesting requirements, thereby facilitating speciation.

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