The species of white-nest swiftlets (Apodidae, Collocaliini) of Malaysia and the origins of house-farm birds: morphometric and genetic evidence

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The taxonomy of South-East Asian swiftlets (Apodidae, Collocaliini) has proved challenging because of their limited variation in size and plumage colouration. Of particular interest are 'white-nest' swiftlets, whose nests, built almost entirely of hardened secretions from paired sublingual salivary glands, are valued in the edible birds'-nest trade. The natural breeding sites of white-nest swiftlets are caves or grottoes but, for over a century, there has been a progressive increase in numbers occupying man-made structures. Through most of South-East Asia there is now a developed industry, utilising sophisticated practices to attract and retain white-nest swiftlets in purpose-made buildings, known as 'house-farms'—a novel form of domestication. A review of the systematics of wild populations based on museum skins collected in late nineteenth and early twentieth centuries, before the expansion of house-farms, concludes that there are two largely allopatric species of white-nest swiftlet in Malaysia, identified as Grey-rumped Swiftlet Aerodramus inexpectatus, with subspecies A. i. germani and A. i. perplexus, and Thunberg's or Brown-rumped Swiftlet Aerodramus fuciphagus, with subspecies A. f. fuciphagus and A. f. vestitus. During 2003 to 2010, house-farm swiftlets in southern Thailand, east and west coasts of Peninsular Malaysia, Sarawak, Java and southern East Kalimantan, Indonesia, were photographed to show variability in plumage of the rump. House-farm birds of Sarawak resembled neither of the wild species occurring naturally in the state. Tissue samples from embryos in eggs were collected for genetic studies from house-farms in Medan, Sumatra, west and east coasts of Peninsular Malaysia, and Sibu, Sarawak. Results of phylogenetic analyses, AMOVA and pairwise F_{ST} comparison based on the partial cytochrome-b sequence are presented. Of the 11 haplotypes identified, two are restricted to a wild population of Brown-rumped Swiftlets A. f. vestitus of Middle Baram, Sarawak, thereby shown to be genetically distinct from house-farm birds. One haplotype is common among all house-farm birds, two are unique to Medan, three and one to Kuantan and Endau-Rompin, respectively. The birds from Sarawak share haplotypes with all other house-farm populations in Peninsular Malaysia and Medan, Sumatra. The evidence for two clades within house-farm samples indicates that Peninsular Malaysian birds combine genetic components from north (A. inexpectatus germani) and south (A. f. fuciphagus). Sarawak house-farm birds are similar to east coast Peninsular Malaysian populations in plumage characters and genes, and apparently arrived by spontaneous immigration from Peninsular Malaysia. If hybrids have arisen among Malaysian house-farm white-nest swiftlets, they are excluded from regulation by the International Code of Zoological Nomenclature.

INTRODUCTION

Swiftlets are small swifts Apodididae, subfamily Apodinae, tribe Collocaliini (Chantler 1999), inhabiting the Indo-Pacific region and reaching greatest diversity in South-East Asia. A shared character of most swifts, including swiftlets, is the production of a dense secretion from a pair of sublingual salivary glands that serves as structural or binding material to form the nest (Chantler 1999). Termed 'nest-cement', this salivary secretion is the edible component, and is sufficiently copious in the nests of some swiftlets to make them commercially valuable. Edible birds'-nests have been esteemed in Chinese society since at least the late sixteenth century, and there is a long history of harvesting from natural wild colonies (Medway 1963, Lim & Cranbrook 2002). Most sought-after and expensive are 'white' nests, composed wholly of the edible salivary material with, at most, the incorporation of a few small feathers from the body plumage of the adult birds, probably adhering accidentally.

Sequencing of genetic material (mitochondrial DNA; mtDNA) derived from commercial edible birds'-nests has distinguished authentic nests of Indonesian white-nest swiftlets from counterfeit products derived from nests of House Swift *Apus affinis = nipalensis* (Lin *et al.* 2009). However, this study did not attempt to discriminate between the nests of different swiftlet species.

One, two or three species of white-nest swiftlet?

Lack of distinctive external characters has caused persistent difficulty in defining species limits among swiftlets. For many years all were included in a single genus *Collocalia*. A series of papers by Stresemann (1914, 1925, 1926) culminated in a revision of species in the Malaysian subregion (Stresemann 1931). In this paper, the

author acknowledged the loan of swiftlet skins from the Raffles Museum, Singapore, supplemented by specimens in the museums at Tring, Leiden and Berlin. Basing his taxonomy chiefly on wing length, tail length and furcation, and tarsal feathering, Stresemann (1931) combined a group of dull blackish-brown swiftlets in a single widespread Indo-Malayan species for which the prior name was *Collocalia francica* (Gmelin, 1789), the Mascarene Swiftlet. He noted that the type of nest was variable within this species, as defined, and listed subspecies building white nests: *germani*, *inexpectata*, *javensis*, *vestita* and *micans*. Of these, three occurred in localities now within Malaysia and Singapore.

First, Germain's Swiftlet Collocalia francica germani Oustalet, 1876, type locality Pulau Condore (=Con Son island), Vietnam (Plate 1A), was seen by Stresemann (1931) in the form of skins collected in 1913 by H. C. Robinson on Koh Pennan (= Koh Phangan), east coast of peninsular Thailand (Plate 1B). He characterised these birds as having tarsus invariably unfeathered, and rump much paler than the back, 'whitish grey with blackish shafts'; wing 113-121 mm, tail 5-53 mm, furcation 5-7 mm. Thus defined, C. f. germani extended through southern (peninsular) Thailand and Peninsular Malaysia 'nearly as far as Johore'. At this point, Stresemann considered that C. f. germani intergraded with a subspecies having rump 'as a rule of the same colour as the back'. However, in the transition zone, 'individual variation is great in some localities, specimens with dark rumps being found together with light-rumped ones' (Stresemann 1931: 87). The dark-rumped subspecies was identified as C. f. vestita (Lesson, 1843), type locality Sumatra, and the variable population in the transition zone as *germani* >< *vestita*. This nomenclature indicated a north-south cline among white-nest swiftlets in Peninsular Malaysia, from a subspecies that was pale grey-rumped with dark