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

shaft-streaks to a uniformly dark-rumped subspecies, across a transition zone in the south where individuals of both patterns were mixed. Although shown below to be erroneous, this interpretation by a respected ornithologist proved influential on subsequent opinion.

Stresemann (1931) also applied the name *vestita* to dark-rumped specimens from Borneo, of which he saw six in the Berlin Museum from Tamaluang cave, East Kalimantan, and ten in the Raffles Museum from eastern North Borneo (now Sabah). He found no valid name for the dark-rumped white-nest swiftlets of Java, which he described as a new subspecies *C. francica javensis*, type locality Ceribon (Stresemann 1931: 89–90), distinguished by rump 'a little paler than the back but by no means as light as in *germani*', wing 109–116 mm, tail 49–53 mm, furcation 4–7 mm (n=6). He also noted that a series of eight swiftlets collected by Chasen in Singapore had 'mostly a very great similarity with the Javanese *C. f. javensis*', wing 113–118 mm, tail 47–52 mm, furcation 4–7 mm (Plate 2D).

The first modification of Stresemann's (1931) scenario followed a survey of the birds'-nest caves of Sabah by Chasen (1931). New specimens, not seen by Stresemann, showed that grey-rumped swiftlets occupied small caves and grottoes on the Mantanani Islands (Plate 1D), off the west coast, and Berhala Island in Sandakan harbour, on the east coast (Plate 1E), while the white-nest swiftlets in caves at Gomantong, 'only a few miles away and within sight of Berhala', were dark-rumped (Plate 2F). On the grounds that, despite the close proximity of Berhala and Gomantong, the grey-rumped and dark-rumped white-nest swiftlets remained distinct, Chasen (1935) treated the two populations as separate species. The grey-rumped swiftlets from Sabah islands he considered to be to be 'absolutely inseparable from true *germani*' (Chasen 1935), and followed Stresemann (1931) in listing these under the trinomial *C. francica germani*. He also recognised that the distinct dark shaft-streaks of the dull brownish grey rump of *C. francica perplexa* Riley, 1927 of Maratua Islands, East Kalimantan, Indonesia, confirmed affinity with *germani* and therefore included this as a subspecies among the grey-rumped swiftlets. For the dark-rumped birds, he raised the name *vestita* to species rank, with the English name Brown-rumped Swiftlet. He also noted that Brown-rumped Swiftlets occurred at other inland caves in Sabah, at Baturong, Madai, Tapadong and, once again not far from the coast, near Lahad Datu.

In Sarawak, white-nest swiftlets of the two kinds were recorded by Banks (1935), again separated by habitat but nonetheless treated as a single species. Grey-rumped Swiftlets (as *C. francica germani*) occurred 'in several suitable places around the coast, such as the two Pulo Satang and Pulo Lakei, nesting in the soft sandstone crevices'. At inland localities in Sarawak, Banks (1935) recorded dark-rumped white-nest swiftlets (as *C. francica vestita*) in limestone caves of the Middle Baram. The only other locality for *vestita* in Sarawak known to Banks (1935) was a small colony in a sandstone cave in Ulu Suai, yielding 'a couple of katties' of nests (i.e., around 140 nests).

In Peninsular Malaysia all nesting records of white-nest swiftlets were from coastal or island locations. No occupied inland caves were known (and none has since been discovered). On the west coast Chasen (1935, 1939) and his successor at the Raffles Museum, Gibson-Hill (1948, 1949), agreed that white-nest swiftlets from peninsular Thailand and islands of northern Peninsular Malaysia were identical with topotypes of Germain's Swiftlet (Plate 1A, 1B), displaying a pale grey rump, almost white, with distinct, broad dark longitudinal stripes that involve both shafts and vanes of the rump feathers. The west coast range of these 'Northern Grey-rumped Swiftlets' (*C. francica germani*) included Penang and Selangor. On the evidence of Allen (1948), Gibson-Hill (1949) provisionally added the Sembilan Islands, Perak.

White-nest swiftlets of the south of Peninsular Malaysia, including east coast islands and rocky stacks of the Pahang-Johor archipelago (specifically, Tioman, Tinggi and Tokong Gantong), were characterised by Chasen (1939) as having the rump darker than Northern Grey-rumped Swiftlets. Judging that this character justified separation at subspecies level, Chasen (1939: 123) called these birds 'Southern Grey-rumped Swiftlets', and 'found it convenient to use for them the name proposed by Dr H. C. Oberholser, *amechana*'. At the same time, echoing Stresemann (1931), he reiterated the mixed appearance of the swiftlets in south Peninsular Malaysia: 'There is a considerable amount of variation in the colour of the rump: in some birds it is almost as pale as in the northern subspecies, *C. f. germani*, but in other specimens it is much darker and only slightly paler than the back'. In a later survey of the east coast islands Gibson-Hill (1948) found white-nest swiftlet colonies from Pulau Nyireh in the Tenggol group, Terengganu, through the Tioman archipelago, Pahang, to the Pulau Tinggi group and Pulau Batu Gajah, Johor. Following Chasen, he too identified these as *C. francica amechana* (Gibson-Hill 1949).

To be consistent with his discoveries in Borneo, Chasen (1935, 1939) recognised dark-rumped birds sympatric with Southern Grey-rumped Swiftlets in the south of Peninsular Malaysia as a second species, Brown-rumped Swiftlet *Collocalia v. vestita*, conspecific with those of interior caves of Borneo to which he applied the trinomial *C. vestita maratua* Riley, 1927. However, he was unwilling to overturn the views of Stresemann on the north–south cline in Peninsular Malaysia. Commenting on his decision to recognise the species *C. vestita*, Chasen (1935) wrote: 'but otherwise, in our arrangement of this very difficult genus, we follow the latest reviewer, Dr E. Stresemann in *Bull. Raffles Mus.* 6. 1931, p. 83.' Gibson-Hill (1949: 110) took a narrower view, identifying Brown-rumped Swiftlet 'only from Tioman [island], where it is breeding in the neighbourhood of Juara Bay, and the adjacent coast of Johore'.

Opinion subsequently remained unsettled on species limits and nomenclature of the white-nest swiftlets of territories now comprising Malaysia. In Borneo, Smythies (1957) recognised two species, noting that among the grey-rumped group Hume's Swiftlet *Collocalia inexpectata* Hume, 1873, type locality Andaman Islands, had priority and therefore naming the birds of Sarawak and Sabah *C. inexpectata germani*, restricting *C. i. perplexa* to the type locality, Maratua Island. For the Brown-rumped Swiftlets, Smythies (1957) restricted *Collocalia vestita vestita* to the Natuna Islands, Indonesia, and *C. v. maratua* to Maratua Island, applying *C. vestita mearnsi* Oberholser, 1912 to birds of mainland Borneo. Later, Smythies (1960) retained this treatment of Brown-rumped Swiftlets, but placed the Grey-rumped Swiftlets in *Collocalia francica*, and subsequently in *C. fuciphaga* (Smythies 1968).

Meanwhile, Medway (1966a) showed that the type of nest is a reliable taxonomic indicator among swiftlets, and that an unmistakable illustration of a white edible nest accompanied the description of *Hirundo Fuciphaga* Thunberg, 1812, overlooked by Stresemann (1914). This is therefore the oldest available systematic name for white-nest swiftlets of Java, reducing Stresemann's *javensis* to synonymy. Nuclear and mitochondrial DNA sequencing has subsequently confirmed that Mascarene Swiftlet (now *Aerodramus francicus*) is a distinct species, confined to Mauritius and Réunion, Indian Ocean (Johnson & Clayton 1999). Medway (1966a) accepted the existence of a north–south cline through Peninsular Malaysia to Singapore, linking Germain's or Northern Grey-rumped Swiftlets with the dark-rumped swiftlets of Java, but differed from previous opinion by proposing that sympatry of grey-rumped and brown-rumped taxa in north and north-west Borneo could be explained if the two forms were the ends of a *Rassenkreis* or 'circle of overlap' (Mayr 1942), thereby justifying their inclusion in a single 'ring' species.

Plate 1. Grey-rumped Swiftlets *Aerodramus inexpectatus* from caves.
(**1A**) Topotype *A. i. germani* from Pulau Condore, Vietnam. 1882, USNM. (**1B**) Koh Phangan, Thailand. 1912, AMNH. (**1C**) Satang Kechil, Sarawak. 1932, RMBR. (**1D**) Manttanani, Sabah. 1931, RMBR. (**1E**) Berhala, Sabah. 1931, RMBR. (**1F**) *A. i. perplexus* from Maratua. 1927, RMBR.

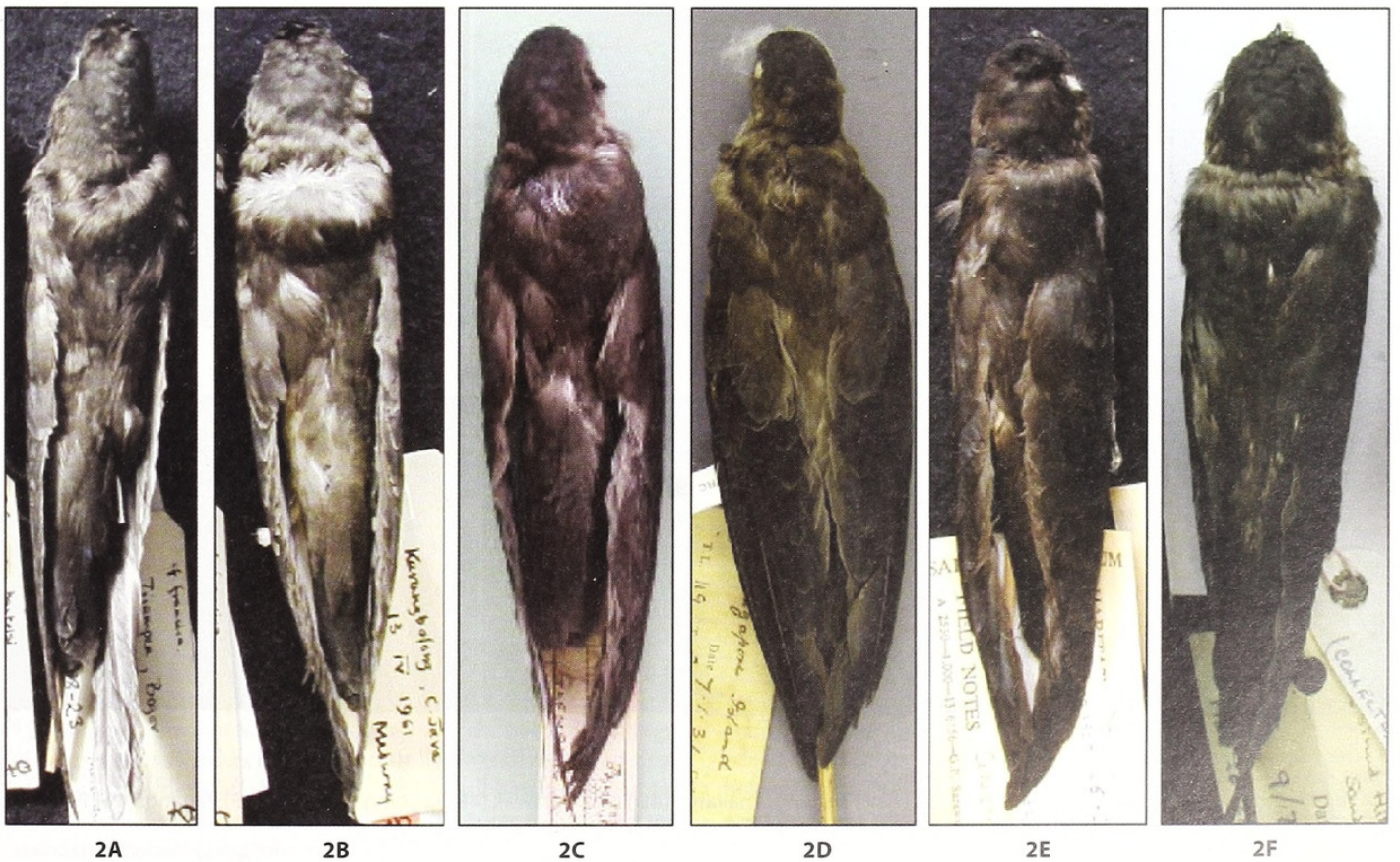
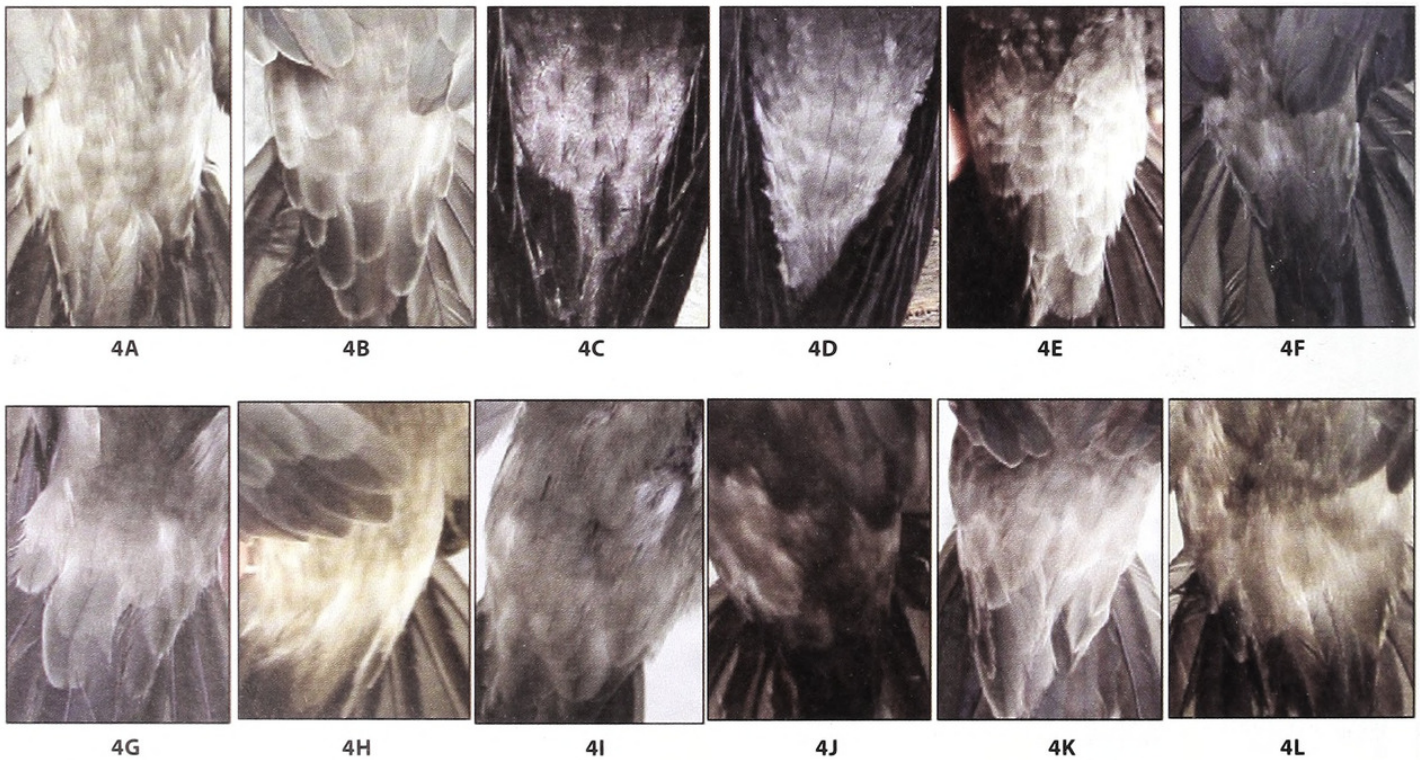


Plate 2. Thunberg's Swiftlet *A. f. fuciphagus* and Brown-rumped Swiftlets *A. f. vestitus* from caves.
(**2A**) Thunberg's Swiftlet from inland cave at Jampea, Java. 1960, NHMUK. (**2B**) Thunberg's Swiftlet from coastal cave at Karangbolong, Java. 1960, NHMUK. (**2C**) Topotype of Brown-rumped Swiftlet from Sumatra. USNM. (**2D**) Thunberg's Swiftlet from Singapore. 1931, RMBR. (**2E**) Brown-rumped Swiftlet from Baram, Sarawak. 1957, NHMUK. (**2F**) Brown-rumped Swiftlet from Gomantong, Sabah. 1958, NHMUK.

3A 3B 3C 3D 3E 3F

Plate 3. Sympatric specimens of Grey-rumped Swiftlet and Thunberg's Swiftlet collected around 3°N in Peninsular Malaysia.
(**3A**) *A. inexpectatus germani* from Malacca. 1953, RMBR. (**3B**) *A. inexpectatus* from Selangor. 1879, NHMUK. (**3C**) *A. fuciphagus* from Selangor. 1887, NHMUK. (**3D**) *A. inexpectatus* from Tioman. 1907, RMBR. (**3E**) *A. fuciphagus* from Tioman. 1907, RMBR. (**3F**) *A. amechanus* topotype from Anamba Is., Indonesia. 1899, USNM.



4A 4B 4C 4D 4E 4F

4G 4H 4I 4J 4K 4L

Plate 4. Variations in rump shade in house-farm birds.
(**4A**) Bukit Imbiah, Singapore. (**4B**) Sajira, Java. (**4C**) Pak Phanang, Thailand. (**4D**) Miri, Sarawak (**4E**) Kuching, Sarawak. (**4F**) Penang. (**4G**) Penang. (**4H**) Kota Bharu. (**4I**) Pusing, Perak. (**4J**) Johor Bahru. (**4K**) Johor Bahru. (**4L**) East Kalimantan.

Brooke (1970, 1972) divided the swiftlets into three genera, recognising the Giant Swiftlet (now Waterfall Swift) as monotypic *Hydrochous gigas* and, among the remainder, restricting *Collocalia* to the small swiftlets with glossy plumage and separating as *Aerodramus* the group of middle-sized drab blackish-brown species, to which white-nest swiftlets belong. Until the discovery that the Pygmy Swiftlet *Collocalia troglodytes* utters an echolocating call (Price *et al.* 2004), it was thought that the capacity to orientate in darkness by echolocation was a further defining character of *Aerodramus*. Monroe & Sibley (1993), Inskipp *et al.* (1996) and, following these checklists, regional field guides by Lim & Gardner (1997) and Robson (2002) continued to combine all species except the Waterfall Swift in the genus *Collocalia*. However, molecular studies have confirmed genetic boundaries between *Hydrochous*, *Aerodramus* and *Collocalia* (Lee *et al.* 1996, Thomassen *et al.* 2003, 2005), and these genera were recognised by Chantler (1999), Smythies (1999), Wells (1999), Strange (2001), Mann (2008) and Phillipps & Phillipps (2009).

Salomonsen (1983: 65) suggested that there could be three white-nest species: *Collocalia fuciphaga* (with *vestita*, *dammermani*, *micans* and *inexpectata* as subspecies), *C. germani* (with *amechana*) and possibly *C. perplexa* with *amelis* of the Philippines. Monroe & Sibley (1993) recognised two species: *Collocalia fuciphaga* (including *inexpectata* and *vestita*) and *C. germani*. In recent publications, Robson (2002) and Phillipps & Phillipps (2009) followed, listing two species: Grey-rumped (*germani*) and Brown-rumped (*vestita* grouped with *fuciphaga*), whereas others including Chantler (1999), Smythies (1999), Wells (1999) Lim & Cranbrook (2002) and Jeyarajasingam (2012) have treated all white-nest swiftlets as a single species under the prior name *Aerodramus fuciphagus*. Wells (1999: 459) criticised the arbitrary nature of species boundaries within clines of changing rump colouration, and called for more research where different-looking populations meet.

Origins of house-farming and house-farm white-nest swiftlets

The propensity of swiftlets to select hollows, rock-shelters or caves as nest sites is reflected throughout their range by many instances of occupation of similar man-made structures, such as culverts, multi-storey car-parks, houses, barns or other buildings. White-nest swiftlet 'farming' began with the spontaneous occupation of buildings by birds and the responses of people. The earliest instances arose in Java, with the first reputedly in 1880 at Sedayu, East Java (Lim & Cranbrook 2002). In western Java, in 1960 Medway (1961) was told that the birds nesting in outbuildings around three sides of a courtyard of a large country house, near Jakarta, had been present for about 60 years. Elsewhere in Java by that time there were already many buildings, domestic or industrial, in which colonising swiftlets had been encouraged by a variety of modifications to thrive and increase. From such beginnings, enterprises steadily developed. The buildings involved, whether modified from existing structures or purpose-built, have become known in English as 'house-farms', and the management of the swiftlet colonies within them as 'house-farming' (e.g. Nugroho & Whendatro 1994). The swiftlets occupying house-farms are normally allowed free egress to forage for food and water (Marzuki 1994). An important advance in Java was the discovery that eggs of house-farm swiftlets could successfully be transferred to nests of Linchi Swiftlet *Collocalia linchi*, which will hatch and rear the fostered chicks. The procedure was widely promoted and became standard practice (Nugroho *et al.* 1994).

In Peninsular Malaysia, an early house-farm colony in Penang was studied by Langham (1980). Although wildlife protection legislation covered all swiftlets, thereby rendering illegal any operation involving the handling of the birds or interference with their nests, clandestine house-farm developments continued. Trailing the process in Indonesia, the great expansion of swiftlet house-farming in Peninsular Malaysia was a phenomenon of the last decade of the twentieth century. The town of Sitiawan, Perak, became the foremost mainland centre, with more than 50 shophouses undergoing conversion by the end of 1999 (Ng 2000a). Simultaneously, public health and nuisance concerns were being raised (Ng 2000b). It was claimed that the repeal of Malaysia's Rent Control Act with effect from 1 January 2000 incentivised the process (Tan 2000).

At present, in 2013, few towns are without modified or specially constructed premises and, with government encouragement, others have been erected in rural areas. On the internet, many sites provide video clips of the birds and bird-houses, and several offer consultancies on management and manuals in English, Bahasa Malaysia and Chinese. Active associations of bird-house owners and nest traders have been established in most Malaysian States. A report on the industry by Merican (2007) provided guidance through current complexities and, following an initiative of the Federal Veterinary Department (Fadzilah A'ini 2007), in 2009 the Malaysian Department of Standards published provisional guidelines on good husbandry practice (MS2273:2009P). In the history of the relationship between humans and animals, house-farming of swiftlets has become a prominent and novel form of domestication. Where a systematic name is required, it has been customary to identify house-farm birds as *Aerodramus fuciphagus* or *Collocalia fuciphaga*.

The multiplication of house-farms has not been restricted to Malaysia. Through much of tropical South-East Asia there have been entrepreneurial developments in the adaptation of existing structures and the construction of new, purpose-designed buildings, coupled with practices to attract and hold new colonists, especially the use of recorded vocalisations. Many urban house-farms now exist in Vietnam, notably in Khanh Hoa and Tien Giang provinces and Ho Chi Minh City (Phach & Voisin 2007), and between 2003 and 2009 activity developed in Cambodia (Poole 2010).

The increase in numbers and expanding geographical range of house-farm white-nest swiftlets raise questions on the origins of these birds and their relations with natural wild populations. In Vietnam, Phach & Voisin (2007) found that urban house-farms swiftlets were not the native Germain's Swiftlets of island caves (Phach *et al.* 2002), but resembled the house-farm birds of Sumatra and Malaysia. They concluded that immigration and colonisation of buildings in towns occurred spontaneously during the 1970s. Occupying separate nesting habitats, with different breeding seasonality and dissimilar diets, the two forms behave as separate species. Yet in southern Thailand Aowphol *et al.* (2008), finding very low genetic diversity of mtDNA among swiftlets of ten house-farms along the coasts of the Gulf of Thailand and the Andaman Sea, concluded that this was a single panmictic population, and attributed the observed genetic homogeneity to regular mixing by natal dispersal between wild population in natural sites on coastal islands and house-farm birds on the adjoining mainland. It is an aim of the present paper to discover which, if either, of these contrasting scenarios prevails in Malaysia.

Since the skies are now crowded with house-farm swiftlets, evidence to determine the identity of potential wild ancestors must rely on collections made before the practice was so prevalent, i.e. before the mid-twentieth century. Thanks to good curation, many specimens on which taxonomic judgments can be based still exist in museums in USA, Europe and South-East Asia. A review of historic museum specimens, notably from the overlap zone in southern Peninsular Malaysia, leads to clarification of the original geographic boundaries of wild species and subspecies. A photographic survey of house-farm swiftlets of Malaysia has

illustrated plumage variation within and between colonies that can be compared with museum skins. The extent to which this variation is matched by genetic diversity was investigated by sequencing mtDNA cytochrome-*b* (cyt-*b*). From the combined data, it becomes possible to form a view of the relations of house-farm white-nest swiftlets of Malaysia with putative source species.

Other than countries, provinces or states, localities mentioned are listed in a gazetteer (Appendix 1).

METHODS

Morphometric studies

Skins of swiftlets collected in the nineteenth and twentieth centuries, before the expansion of house-farming, were examined in the following museums: American Museum of Natural History, New York (AMNH), United States National Museum, Washington (USNM), National Museum of Natural History, Paris (MNHN), Naturalis, Leiden (RMNH), Sarawak Museum, Kuching (SM), Raffles Museum of Biodiversity Research, University of Singapore (RMBR), and the Natural History Museum, Tring (NHMUK), where loans from the Academy of Natural Sciences, Philadelphia (ANSP) were also seen. Particularly crucial have been skins in RMBR which include those originally seen by Stresemann (1931), Chasen (1935, 1939) and Gibson-Hill (1949). These are now very fragile, and liable to shed feathers at the lightest touch. It has been possible to take photographs but not to risk the handling necessary to check wing or tail measurements.

Between 2003 and 2010, with the agreement of owners or managers, juvenile house-farm birds were photographed on the nest at Pak Phanang, Thailand, and Miri and Kuching, Sarawak. To ensure that they were fully fledged, other birds were caught in flight inside, emerging from or returning to house-farms located in Peninsular Malaysia in the states of Penang, Perak, Kelantan, Terengganu and Johor, and in Sarawak at Miri, Bintulu and Sarikei; also in Indonesia at Sajira, Banten, Java and southern East Kalimantan. The number of swiftlets caught at each house-farm varied from one to four. Birds were held singly in cloth bags for short periods. Standard procedure was then to measure wing-length and tail, closed, note the state of moult in the primary tract and rectrices, photograph the dorsal and ventral aspects, and the feet, and then to release the bird. A dead bird from a new house-farm in Sulawesi was also measured and photographed. In addition, swiftlets in natural colonies occupying the former underground military works at Bukit Imbiah, Sentosa Island, Singapore, were caught and handled by these procedures.

Genetic studies

Eggs or nestlings of white-nest swiftlets were collected from: house-farms at Medan, Sumatra, Indonesia (nine individuals); the west coast of Peninsular Malaysia at Sitiawan, Perak, and Selangor (12 individuals); the east coast of Peninsular Malaysia at Kuantan (11 individuals) and Rompin (five individuals), Pahang, and Endau, Johor (six individuals); and Sibu, Sarawak (four individuals). Six samples were also taken from wild white-nest swiftlets occupying Salai cave, Middle Baram, Sarawak. The collected specimens were kept in 70% ethanol at room temperature at the sampling site and later at –20°C in the laboratory.

Total genomic DNA was extracted from tissue using Promega Wizard® Genomic DNA Purification Kit following manufacturer's instructions. The partial cyt *b* sequence was amplified using the primers Cyt523 (forward) and Thr (Reverse) (Thomassen *et al.* 2003). The polymerase chain reaction (PCR) mixture contains a final concentration of 0.5 µM of each primer, 1 × reaction buffer, 2.5 µM $MgCl_2$, 0.2 µM of each dNTP, and 2.5 unit of *Taq* polymerase and ~60 ng of DNA template. The reaction was run using a Perkin Elmer GeneAmp 9600 Thermocycler with the programme set at 94°C for 3 minutes; 29 cycles of 94°C for 35 seconds, 55°C for 45 seconds and 72°C for 1 minute; 72°C for 5 minutes; hold at 4°C. The PCR products were purified using the Promega PCR Clean-Up System following the manufacturer's instructions. Direct sequencing was commercially done by First Base Laboratories Sdn. Bhd. (Malaysia) (Goh 2007).

The DNA sequences were trimmed to readable bases on both ends of the strands. In most cases the scoring of the bases started by the light-strand complementing the light-strand towards the centre. All sequences obtained were deposited with GenBank (JF269226–JF269236). The cyt *b* haplotypes were defined by ARLEQUIN 3.1 (Excoffier *et al.* 2005) and DNaSP (Rozas *et al.* 2003). Haplotype sequences were aligned using the ClustalX v1.81 (Thompson *et al.* 1997).

The neighbour-joining (NJ) and most parsimonious (MP) trees were reconstructed using 1,000 bootstrap replicates in Molecular Evolutionary Genetic Analysis (MEGA) 4 (Tamura *et al.* 2007) and Phylogenetic Analysis Using Parsimony (PAUP) v4.0b (Swofford 2002), respectively, based on the cyt *b* haplotype matrix. The cyt *b* sequence of two white-nest swiftlet individuals, named as *Aerodramus fuciphagus germani* (DHC04; Price *et al.* 2004) and *Aerodramus fuciphagus vestitus* (DHC40; Price *et al.* 2004), were retrieved from GenBank (accession numbers AY294429 and AY294428, respectively) and incorporated into the phylogenetic analyses. Black-nest Swiftlet *Aerodramus maximus lowi* (Thomassen *et al.* 2003; Genbank accession number AY135623) was included as the outgroup in the phylogenetic trees. The genetic structure of the white-nest swiftlets was estimated using the analysis of molecular variance (AMOVA; Excoffier *et al.* 1992) and the pairwise comparison F_{ST}. Both analyses were performed using 10,000 permutations in the ARLEQUIN software.

RESULTS

Plumage characters and species limits

Historic collections confirm the presence of Grey-rumped Swiftlets on the Mantanani Islands (Plate 1D) and Berhala (Plate 1E) and Brown-rumped Swiftlets in Gomantong caves (Plate 2F), Sabah (NHMUK, RMBR, USNM). Further observations have found only Grey-rumped Swiftlets on other islands of north-west and north Borneo. Sabah records have confirmed Mantanani Islands (Sheldon *et al.* 1983), and Francis (1987) added Batu Mandi, off Kudat, Balambangan Island, and Gaya (Bodgaya) and Si Amil, Sempurna bay. Francis (1987) also noted that birds from the Mantanani Islands had a slightly paler back and whiter rump than those of Berhala, assigning the former to the subspecies *germani* and the latter, by implication, to *perplexus* (Plate 1F). No specimens are available of grey-rumped swiftlets from Gaya or Si Amil, but on geographical grounds these are also likely to be attributable to *perplexus*.

RMBR holds two skins taken in 1932 by Banks on Pulau Satang Kecil, Sarawak (Plate 1C), confirming his record of *germani* from this group of islands (Banks 1935). A specimen was obtained on Satang Kecil in 1957 (NHMUK); it is poorly skinned but nonetheless shows a distinct whitish rump. Tom Harrisson, quoted by Smythies (1957: 653), reported that 'about fifty pairs [have nested] most years since 1947 on Satang Besar and Kechil (two sea caves)'. Repeated searches around both islands from 1998 to 2008 by Lim & Cranbrook (pers. obs.) have failed to find occupied sea caves. Pulau Lakei, a site also mentioned by Banks (1935), and the nearby islet Batu Sarang, were investigated by Lim & Cranbrook (pers. obs.), but only Black-nest Swiftlets were found. These Sarawak colonies of grey-rumped white-nest swiftlets may now be extinct.

Banks's (1935) record of Brown-rumped Swiftlets in limestone caves of the Middle Baram is confirmed by specimens (Plate 2E). Lim (in Lim & Cranbrook 2002) has provided many photographs of this population. In November 1957, Cranbrook visited the sandstone cave in Ulu Suai noted by Banks (1935), and confirmed the presence of white nests. Two skins collected (NHMUK) are indistinguishable from Middle Baram Brown-rumped Swiftlets. In the altered landscape of modern Sarawak, the site has not since been rediscovered.

Skins in RMBR collected in 1953 at Melaka (Malacca), although faded and foxed, show the characteristic pale rump with dark shaft-streaks (Plate 3A), thereby extending the historic range of Germain's or Northern Grey-rumped Swiftlet southwards of previous records on the west coast of Peninsular Malaysia. In April 2009, on a brief visit to the Sembilan Islands, Cranbrook saw no swiftlets around Pulau Rembia, the site of Allen's (1948) observations. However, on the rocky islet known as Batu Putih, underneath the tumble of huge, angular granite boulders, there were separate groups of seven black nests and 11 white nests. There were no eggs, and (around midday) no swiftlets present in the vicinity, leaving the identity of the white-nest builders unverified. Further south and east, a specimen from Horsburgh Light considered a stray by Gibson-Hill (1949) is still in RMBR. This lighthouse (now commonly known at Pedra Branca) was visited on 28 August 2012 when about 40 nests, with young, were present in the building. All were Black-nest Swiftlets and there was no evidence of any other resident swiftlet species (Geoffrey Davison pers. comm.).

Skins in NHMUK are from Selangor around latitude 3°N, near the coast at Kelang and at interior locations. Of six collected (presumably shot in flight) in the vicinity of Kelang by W. Davison in 1879, mostly part of the Hume collection (Collar & Prys-Jones 2012), three (reg. nos 1887.8.1.297, 298 and 299), although faded and foxed with age, show pale rumps with distinct, dark longitudinal shaft-streaks, identifying them as Grey-rumped Swiftlets (Plate 3B). In three others, (1887.8.1.272, 300 and 301), the rump is uniformly coloured with the back, or slightly paler, with only the feather shafts dark, and no dark colour extending to the vanes (Plate 3C). Two other skins from interior Selangor also have dark rumps: 1887.8.1.296 collected April 1879 in Ulu Langat and 1908.12.15 collected in March 1907 (by H. C. Robinson) on Mengkuang Lebar at 4,300 ft (1,310 m) elevation.

On the east coast islands, three birds were collected in Juara bay, Tioman Island, Pahang, in September 1907 (RMBR), of which two have the characteristic streaked rump of Grey-rumped Swiftlets (Plate 3D) but one is dark-rumped (Plate 3E), likely to be the specimen identified by Gibson-Hill (1949) as Brown-rumped Swiftlet. Despite the assertion of breeding by Gibson-Hill, there is no indication on the labels that any of these birds was taken at the nest. Medway (1966b) was told that white-nest swiftlets nested on Tioman in sea-caves, but failed to find any, and Lee (1977) repeated this assertion, again without location. There is also in RMBR a dark-rumped bird collected by Robinson in 1915 on Tokong Gantong, Johor, presumably the specimen noted by Chasen (1939).

In Java, wild white-nest swiftlets collected in caves at coastal and inland sites in 1960 (Plate 2A & 2B) have rump feathers the same colour as the back or slightly paler, without prominent dark shaft-streaks, matching the description of *C. francica javensis* Stresemann, 1931, now recognised as a junior synonym of Thunberg's Swiftlet *Aerodramus fuciphagus fuciphagus*. Although old and faded, the dark-rumped swiftlets of southern mainland and islands of Peninsular Malaysia, identified by Chasen and Gibson-Hill as *vestita* (RMBR), are similar. As noted by Stresemann (1931), skins collected by Chasen in Singapore, in 1930–1931 (RMBR) are indistinguishable from Javan Thunberg's Swiftlets. Photographs of white-nest swiftlets occupying former military underground emplacements at Bukit Imbiah, Sentosa Island, Singapore (Kang *et al.* 1991, Kang & Lee 1993: 18) and measurements and photographs of living adults mist-netted at this site in 2005 (Plate 4A) show that, by plumage character, these white-nest swiftlets of a natural colony are also identifiable as Thunberg's Swiftlet.

Re-examination of historic collections has therefore confirmed that, as in the Borneo States, there are two original wild white-nest swiftlet species in Peninsular Malaysia, grey-rumped and dark-rumped, evidently sharing the same diurnal habitat in a zone around 3°N on the mainland and east coast islands. The former are confirmed as nesting on the Pahang-Johor islands of Peninsular Malaysia, but not at Horsburgh Light (Pedra Branca). The latter nest on Singapore, but there is no confirmation that they do also on the most southerly Johor rocky stacks.

The white-nest swiftlets of house-farms

Java was the site of multiple early instances of spontaneous occupation of buildings by white-nest swiftlets of the native population of Thunberg's Swiftlets. House-farm swiftlets of western Java, such as those handled in 2005 at Sajira, Banten (Plate 4B), are similar in size, plumage characters and tarsal feathering to wild Thunberg's Swiftlets from caves at interior sites, such as Jampea (Plate 2A), or on the south coast at Karangbolong (Plate 2B). By the transportation and cross-species fostering of eggs in the nests of Linchi Swiftlets, the distribution of house-farm swiftlets has been enlarged to many new areas within the island of Java. Eggs from Java have also been traded, to an unrecorded and unknown extent, to localities beyond the natural range of the subspecies *A. f. fuciphagus*. In Kalimantan successful fostering of eggs from Java by White-bellied Swiftlets *Collocalia esculenta cyanoptila* is known as far north on the west coast as Singkawang, West Kalimantan (Charles Leh pers. comm. 2006) and on the east coast at Bayangkara, East Kalimantan (Lim & Cranbrook 2002: 149).

In Singapore, Chasen observed prospecting swiftlets in the 1930s: 'In January of two years I have found large numbers seeking the shady shelter of large stone-walled rooms, or vaults in buildings, in the late afternoon for roosting purposes: they were then easily caught with a large butterfly net.' In a footnote he added: 'Later. There is now a breeding colony of these birds in a much-frequented large building in Singapore' (Chasen 1939: 119). These remarks are supported by skins in RMBR, collected on Singapore Island at various dates in January 1931, with a note on one label: 'Taken in a large building'. The dark rumps of these skins, concolorous with or slightly paler than the back, identify them as Thunberg's Swiftlets. Later, Gibson-Hill (1948, 1949) reported swiftlets occupying an office building on Robinson Road, Singapore. The fate of this colony is not known but it is clear that in Singapore, by this time, there had been more than one spontaneous occupation of buildings by Thunberg's Swiftlets.

In north-west Peninsular Malaysia the pioneer birds occupying buildings were grey-rumped swiftlets. Gibson-Hill (1949: 110) reported Northern Grey-rumped Swiftlets (as *C. francica germani*) nesting in a godown in Penang, first noticed in 1947, and 'Southern Grey-rumped Swiftlets' in the Federal Survey Office, Kuala Lumpur, along with grey-rumped swiftlets of uncertain subspecies in a building in Teluk Anson, Perak. In the 1960s, white-nest swiftlets (identity not determined) occupied government buildings in (then) Mountbatten Road, Kuala Lumpur, ultimately being excluded by the advent of air-conditioning and hence the glazing of all apertures (Cranbrook pers. obs. 1968). In the 1970s a small colony, defiantly persistent in the face of repeated nest removal, occupied the porch of Kuala Lumpur Town Hall (Medway & Wells 1976); no specimens were collected. On the east coast of Peninsular Malaysia, by 1974 swiftlets were nesting in six sea-front shophouses

in Kuala Terengganu (Cranbrook pers. obs.). Specimens were not collected at that time, but the presumed origin of these birds would be 'Southern' Grey-rumped Swiftlets of the Redang or Tenggol groups of islands (Gibson-Hill 1949, Wells 1999).

Swiftlet house-farming is a private and confidential enterprise, and in Peninsular Malaysia there is no authoritative data source for innovation or development in husbandry. There is, however, no evidence that the progressive increase in house-farm colonies in Malaysia has involved egg-transfer and fostering to a significant extent. One case of cross-species fostering in the nests of White-bellied Swiftlets reported to us was carried out at the town of Bentong, Pahang, around 2000–2002. An established population persisted in 2012 in the building used. In addition, other colonies have established themselves in this town, probably involving birds fledged from this source.

There are no colonies of wild white-nest swiftlets in interior Peninsular Malaysia and, so far, no confirmed instance of swiftlets of the house-farm type establishing breeding colonies in natural sites. For instance, in the environs of Ipoh, Perak, there are numerous house-farms and abundant limestone caves that so far remain unoccupied (Cranbrook pers. obs., Tou Jing Yi *in litt.* 2011). The expanding population of house-farm swiftlets into new areas in Peninsular Malaysia therefore reflects an upsurge in recruits from pre-existing house-farms, reinforced by the imprinting of buildings as potential nest sites and the attraction of acoustic stimulus in the form of recorded swiftlet calls, now universally employed. No doubt, the increasing architectural sophistication of house-farm design also plays a part. But, essentially, Malaysian-fledged house-farm white-nest swiftlets seek familiar constructions to occupy, and do not look for natural sites. This behavioural trait can lead to ecological separation within common activity space, as has occurred in Vietnam (Phach & Voisin 2007).

As among house-farm birds in Vietnam (Phach & Voisin 2007), throughout their range from southern Thailand, at Pak Phanang ('Birds nest city'), through Peninsular Malaysia, and in Sarawak, at Miri and Kuching, nestling house-farm swiftlets in their first plumage have pale grey rumps (Plate 4C, 4D & 4E). Among adult house-farm swiftlets of Malaysia, our accumulated photo-record shows variability in rump colouration between and within colonies. At Penang, three from the same farm-house showed minor variation in rump shade, in all cases with moderately defined shaft-streaks (Plate 4F & 4G). At Kota Bharu, Kelantan, all three birds caught showed similar pale, brownish rumps with lightly defined shaft-streaks (Plate 4H). At Kuala Terengganu, poor pictures of four birds are sufficient to confirm similar rump patterns, varying slightly in lightness of shade. On the west coast, at Pusing, Perak, the general tone was darker, with two of four birds showing rump the same shade as the back but one paler, with dark shaft-streaks (Plate 4I). In southern Peninsular Malaysia, five birds from house-farms in the neighbourhood of Kota Tinggi and Johor Bahru, Johor, all had rumps more or less mottled with darker feather centres; one was distinctive, with a uniformly pale band and narrow dark shaft-streaks (Plate 4J & 4K).

In Sarawak, although there is anecdotal report of successful hand-rearing in Kuching of nestlings from an outside source (reputedly from Pontianak, West Kalimantan), house-farm owners have testified that there have been no transfers of eggs from Java or elsewhere. The dramatic spread of house-farm swiftlets into this state initially occurred in coastal locations, starting in the north-east. The first house in Miri was occupied in the mid-1990s. In Bintulu the first colonists noted were a pioneer group of 18 nests in the eaves of the MAS building in 1997 (Lim and Cranbrook pers. obs.), and by 2000 Mukah was colonised. These three towns now support many large colonies. The spread to south-west Sarawak was later: in 2000, an informant went every weekend all the way along the coast from Kuching westward to Sematan, testing with sound replay, and found no evidence of swiftlets (Tsai Mui Leong *in litt.* 2010). By 2011, this coastline contained at least five house-farms with substantial colonies.

Adult house-farm swiftlets in Miri, Bintulu, Sarikei and Kuching do not resemble either of the wild species of Sarawak, i.e. Germain's or Grey-rumped on the islands, or Brown-rumped of interior caves. The house-farm swiftlets of Sarawak appear to be generally uniform in appearance, in rump colouration resembling most closely those of east coast Peninsular localities such as Terengganu and southern Johor. The similarity in appearance and size points to a common origin, leading to the conclusion that pioneer birds crossed the South China Sea from west to east, i.e. from Peninsular Malaysia to northern Sarawak.

In the Kalimantan provinces of Indonesia, outside Malaysian borders, specialised house-farms have been constructed at many localities, urban and rural, not infrequently on a trial basis. Swiftlets from a house-farm on the coast of southern East Kalimantan, near Balikpapan, resemble the house-farm swiftlets of Sarawak (Plate 4L). A carcass from Sulawesi, brought from a new house-farm by Anton Hoo, was similar in size and appearance, representing a further trans-marine range extension by swiftlets of house-farm type.

Genetic studies

Cyt-b haplotypes and data matrix

Eleven haplotypes are defined among the 55 sequences obtained (Table 1). Haplotype 5 (H05) is the most common, shared by 31 individuals from all house-farm populations, but not by wild Brown-rumped Swiftlets *A. f. vestitus* of Middle Baram, Sarawak. Haplotypes H04 and H07 are unique to the Medan house-farm population; H02, H03 and H11 unique to that of Kuantan; H07 to Endau-Rompin; and H09 and H10 to the wild swiftlets of Middle Baram. The Sibu birds share haplotypes with all other house-farm populations. The aligned DNA matrix is 558 bp in length, with 20 variable sites and no alignment gap. Among the variation sites, 10 sites are parsimony-informative (Table 1).

Phylogenetic analyses based on the cyt-b haplotypes

As the NJ tree shows no major topological difference from the MP tree, the NJ bootstrap values were mapped on the MP tree (Figure 1). Both NJ and MP trees recover two moderately supported major clades, Clade 1 and Clade 2, among the ingroups. Together, both clades include all haplotypes of house-farm birds, but none of the wild swiftlets of Middle Baram. Haplotypes H09 and H10 are exclusive to these swiftlets of Middle Baram. The specimen DHC04, which was identified as *A. fuciphagus germani* in Price *et al.* (2004), is included in Clade 2, while the specimen DHC40, which was identified as *A. f. vestitus* in Price *et al.* (2004), is unresolved among the ingroups (Figure 1).

AMOVA and pairwise F_{ST} comparison

As there are two major clades of house-farm swiftlets recovered in the phylogenetic analyses (Figure 1), pairwise F_{ST} comparison and AMOVA were used to test the genetic structure suggested by the clustering pattern in the phylogenetic trees. Individuals represented by the haplotypes in Clade II were combined to define a population, while the remaining individuals define the other six populations according to their sampling sites (which are combined into six area groups), i.e. (1) Middle Baram, Sarawak, (2) Medan, North Sumatra, (3) combined west coast locations in Perak and Selangor of Peninsular Malaysia, (4) Kuantan, the central east coast of Peninsular Malaysia, (5) Endau-Rompin, the southern east coast of Peninsular Malaysia, and (6) Sibu, Sarawak.

Pairwise comparison analysis shows that F_{ST} values are significant between the Middle Baram population and all other populations, and between the Clade 2 population and all other

Table 1. Summary of the parsimony-informative sites and the distribution of the cyt *b* haplotypes in white-nest swiftlet. Site numbers of the parsimony-informative characters are shown vertically; dots indicate identity with DHC04 sequence and letters designate base substitutions.

	Parsimony-informative characters										Sampling areas					
	3	1 0	1 1	1 3	1 7	2 4	2 9	3 5	3 8	4 7						
Haplotype	3	6	1	2	4	6	7	1	1	7	West Coast	Kuantan	Endau-Rompin	Sibu	Middle Baram	Sumatra
DHC04	G	T	G	A	T	C	C	G	G	C	–	-	-	-	-	-
H11	.	.	.	.	.	.	.	.	.	.	-	1	-	-	-	-
H01	.	.	A	G	C	T	T	.	A	T	2	2	3	1	-	-
H02	.	.	A	G	C	T	T	.	A	T	-	1	-	-	-	-
H03	.	C	A	G	C	.	.	A	A	T	-	1	-	-	-	-
H04	.	C	A	G	C	.	.	A	A	T	-	-	-	-	-	1
H05	.	C	A	G	C	.	.	A	A	T	10	7	5	3	-	7
H07	.	C	A	G	C	.	.	A	A	T	-	1	2	-	-	-
H08	.	C	A	G	C	.	.	A	A	T	-	-	1	-	-	1
H06	.	C	A	G	C	.	.	A	A	T	-	-	-	-	-	-
H10	.	.	A	G	C	.	.	A	A	T	-	-	-	-	5	-
H09	A	.	A	G	C	.	.	A	A	T	-	-	-	-	1	-
DHC40	A	.	A	.	C	.	.	A	A	T	-	-	-	-	-	-

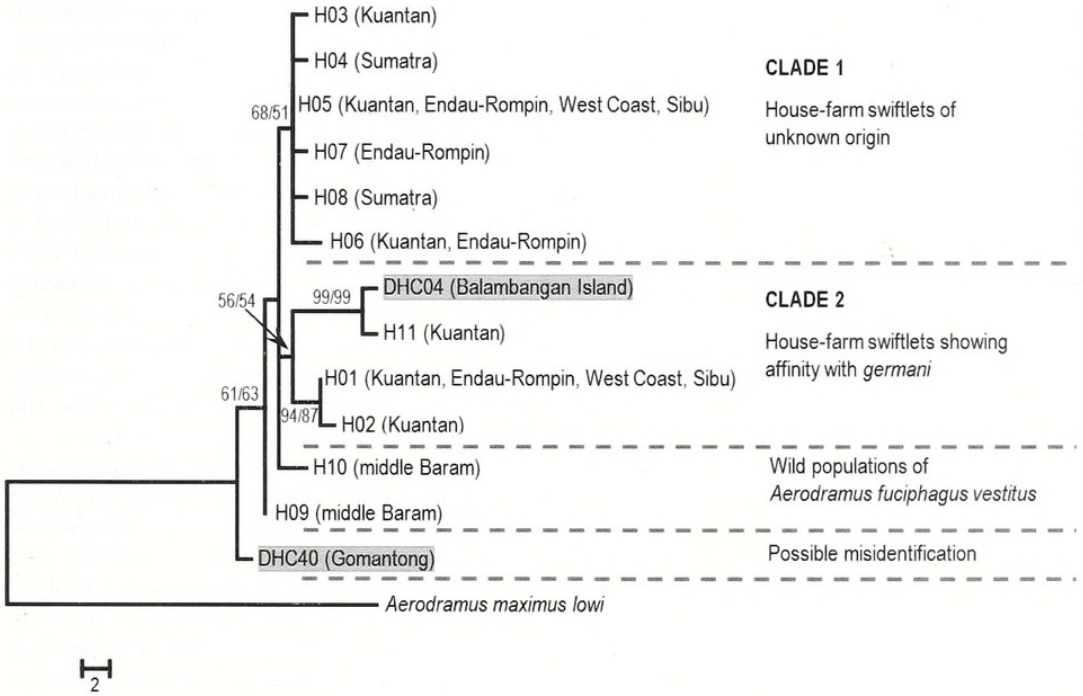


Figure 1. The phylogram of the most parsimonious (MP) tree based on cyt *b* haplotype sequence rooted by *A. maximus lowi*. Refer to **Table 1** for the haplotype distribution. Figures next to the nodes indicate the NJ bootstrap values / MP bootstrap values. DNA sequences obtained from Genbank are shown as highlighted individuals.

Table 2. Matrix of pairwise F_{ST} values among six populations of the white-nest swiftlets based on cyt *b* sequence. Figures with asterisk indicate the values which are significant at $p = 0.05$.

	Clade II	Endau-Rompin	Kuantan	Sibu	Sumatra	West Coast
Endau-Rompin	0.00010*					
Kuantan	0.00000*	0.71201				
Sibu	0.00356*	0.82398	0.99990			
Sumatra	0.00000*	0.16929	0.46481	0.99990		
West Coast	0.00000*	0.06871	0.08910	0.99990	0.20364	
Middle Baram	0.00000*	0.00020*	0.00040*	0.00980*	0.00010*	0.00010*

Table 3. Hierarchical AMOVA of the white-nest swiftlet populations. Fixation indices, i.e. the total variance (F_{ST}), the among population within group variance (F_{SC}) and among group variance (F_{CT}), are shown for the various structures tested. Figures with asterisk indicate the values which are significant at $p = 0.05$. The maximum F_{CT} is highlighted in bold.

Structure	Groups	F_{ST}	F_{SC}	F_{CT}
1	(Clade 2), (Endau-Rompin, Kuantan, Sibu, Sumatra, West Coast), (Middle Baram)	0.77595*	-0.02580	**0.78158***
2	(Clade 2), (Endau-Rompin, Kuantan, West Coast), (Sibu), (Sumatra), (Middle Baram)	0.69453*	0.00268	0.69371
3	(Clade 2), (Endau-Rompin, Kuantan), (West Coast, Sumatra), (Sibu), (Middle Baram)	0.67924*	-0.04615	0.69338*
4	(Clade 2), (Endau-Rompin, Kuantan, West Coast, Sumatra, Sibu), (Middle Baram)	0.74161*	0.60571*	0.34468

populations (Table 2). Among the various groupings tested in AMOVA, Structure 1 has the highest statistically significant F_{CT} value (Table 3), suggesting that it is the most plausible genetic structure among the white-nest swiftlets based on the cyt *b* sequence.

DISCUSSION

Stresemann (1931) considered the variable population of white-nest swiftlets of the south of Peninsular Malaysia to be transitional members of a north–south cline, *germani* >< *vestita*. From experience in the field and with skins before them, Chasen, Gibson-Hill and Banks recognised two species of white-nest swiftlet in this area, as well as in the Borneo territories, Grey-rumped and Brown-rumped. Re-examination of historic museum specimens has confirmed that the two species overlapped in diurnal activity range in the south of Peninsular Malaysia. Rather than a clinal transition, a zone around 3°N therefore represents an area of contact where the two species shared a common feeding zone. Sympatric breeding ranges are not proven. The single dark-rumped bird shot on Tioman many years ago may have nested on that island as asserted by Gibson-Hill (1949) but, given the mobility and extensive daily foraging ranges of all swiftlets, it could equally have originated from Singapore or elsewhere within the range of Thunberg's Swiftlet. Medway's (1966a) suggestion that the situation in Borneo could be explained in terms of a *Rassenkreis* is redundant. Moreover, the classic example of a supposed ring species, the Great Tit *Parus major*, has been invalidated by morphological, acoustic and molecular data (cyt-*b* sequences) by Päckert *et al.* (2005), thereby strengthening doubts about the place of this mechanism in speciation (Mayr 2002: 183).

Available molecular evidence reinforces this conclusion. With samples from Sabah, Grey-rumped Swiftlets of Balambangan Island (as *A. f. germani*) and Brown-rumped (*A. f. vestitus*) from Gomantong caves, Lee *et al.* (1996) showed separation equivalent to the genetic distance between morphological species (with an anomalous result suggesting possible misidentification). Thomassen (2005: 161, Fig. 1) amplified the results of Price *et al.* (2004), again showing as great or greater genetic distance between the two as between many clades recognised on behavioural and morphological grounds as distinct species.

The prior specific name for the dark- or brown-rumped swiftlets is *Aerodramus fuciphagus*. The observations of Stresemann (1931) are supported by historic specimens and recent photographs, confirming that Singapore white-nest swiftlets are indistinguishable from those of Java, and are therefore *A. fuciphagus fuciphagus*. The dark-rumped swiftlets in historic collections from the south of Peninsular Malaysia, in NHMUK and RMBR, are also identifiable as *A. f. fuciphagus*. The type of *Collocalia vestita maratua* Riley, 1927 has been shown to be a Mossy-nest Swiftlet *Aerodramus salanganus* (Medway 1966a). This name is therefore not available for a Borneo subspecies of white-nest swiftlets, as proposed by Chasen (1935). Measurements and plumage characters do not distinguish the Brown-rumped Swiftlets of Borneo from those of interior Sumatra, type locality of *Salangana vestita* Lesson. Although nominate *fuciphagus* appears to intervene between these two separate populations, many authors, including latterly Smythies (1999) and Mann (2008), have used the name *A. fuciphagus vestitus* for Borneo Brown-rumped Swiftlets. Further clarification, particularly genetic evidence, is needed to define the relationship of Bornean Brown-rumped Swiftlets with Thunberg's Swiftlets of Java and topotypical *vestitus* of Sumatra.

In Peninsular Malaysia, both Chasen (1935, 1939) and Gibson-Hill (1949) observed a darker and more variable rump-band among grey-rumped swiftlets of the east coast islands. As a subspecific name, Chasen (1935, 1939) chose *Collocalia fuciphaga amechana*, described by Oberholser (1912: 13) on the basis of two skins collected on Pulau Jemaja, Anamba Islands, Indonesia, by Dr W. L. Abbott in 1899. Oberholser compared these birds with white-nest swiftlets of Java (known by him as typical *Collocalia fuciphaga*), noting in particular that they were darker on the upperparts, with a metallic greenish sheen. This green sheen is clearly evident in a third skin, also from Pulau Jemaja (therefore a topotype), kindly loaned by ANSP (Plate 3F). Although Oberholser described the rump as 'decidedly paler' than the back, there is no demarcated pale rump-band with dark shaft-streaks. As Oberholser remarked, *amechana* is characterised by its unusual glossy colouration and, until details of its biology are known including the type of nest built, it is best regarded as an endemic of the Anamba Islands. If separable, the 'Southern Grey-rumped Swiftlet' of Peninsular Malaysia lacks a systematic trinomial.

Among the grey-rumped swiftlets, while the diagnostic dark shaft-streaks remain distinctive, there is a peripheral cline from the palest, most contrasting pattern of the rump of *germani* of Vietnam and peninsular Thailand to a darker background shade of grey of the rump-band. In northern Borneo this is evident from the Mantanani group, Sabah, eastwards to *perplexus* in the Maratua Islands, Indonesia, and in Peninsular Malaysia from west and north to the southern islands of the Pahang-Johor archipelago. An extreme westerly outlier, with the rump marked by the distinctive blackish shaft-streaks on a dark grey background colour, is Hume's (Edible Nest) Swiftlet *Aerodramus inexpectatus* of the Andaman and Nicobar Islands. As Smythies (1957) recognised, *inexpectatus* has priority as species name of the grey-rumped swiftlets. Malaysian representatives are therefore Germain's or Northern Grey-rumped Swiftlet *Aerodramus inexpectatus germani* and, on the eastern islands of Sabah, Riley's Swiftlet *Aerodramus inexpectatus perplexus*.

Historical sources show that, in the region, wild white-nest swiftlets spontaneously colonised urban buildings at multiple sites. In Singapore, colonies of Thunberg's Swiftlet were established in the 1930s. In Peninsular Malaysia, by 1949 grey-rumped swiftlets *Aerodramus inexpectatus* already occupied buildings in Penang, Telok Anson and Kuala Lumpur, and at Kuala Terengganu before 1974. There is no evidence that similar events occurred in the Borneo states and, in plumage characters, the house-farm swiftlets appearing in Sarawak during the 1990s resemble neither of the wild species of Borneo.

Although receiving only moderate statistical support, the genetic comparisons using mitochondrial cyt *b* sequence emphasise the distinctiveness of Brown-rumped Swiftlets from the Middle Baram caves, Sarawak (Figure 1). The uniqueness of this wild population is reflected in the pairwise distance matrix (Table 2) and the observation that the Middle Baram population shares no haplotypes with house-farm populations. Molecular analysis therefore matches plumage comparisons, and serves to stress that the lineage of house-farm swiftlets of Sarawak is distinct from the inland wild population of Bornean Brown-rumped Swiftlets. It is, however, of note that these results show a more distant relationship between the Middle Baram Brown-rumped Swiftlets and the Genbank specimen DHC40 from Gomantong, Sabah (identified as *A. f. vestitus* by Price *et al.* 2004). This apparent anomaly is possibly due to limitations of sampling design and molecular methods, but could also indicate misidentification of the specimen DHC40. It is not easy to distinguish in the hand between Brown-rumped and Mossy-nest Swiftlet *A. salanganus*, both of which occur at Gomantong, and the possibility of erroneous identification of the specimen from which the Genbank sequence derived has been raised elsewhere (Lee *et al.* 1996).

Among the sample of 49 house-farm individuals, phylogenetic and population genetic structure analyses show substantial gene-flow, but also suggest the existence of two clades. These clades, 1

and 2 (Figure 1), represent the grouping of house-farm swiftlets in the most plausible genetic structure (Table 3). Clade 1 includes house-farm swiftlets from the entire geographical range sampled, broadly between 2–4°N and 99–114+°E, covering North Sumatra, across Peninsular Malaysia and Sarawak, but excludes haplotypes of all wild birds, represented by Brown-rumped Swiftlets of Middle Baram, Sarawak, and the two GenBank sequences from Sabah. This result is evidence that the wild swiftlet population of the Borneo states was not implicated in the ancestry of this clade.

Clade 2 is significantly different from all separate populations sampled (Table 2). This clade includes nine house-farm swiftlets from the west and east coasts of Peninsular Malaysia and Sibu, Sarawak, i.e. approximately 2–4°N 100–114°E, along with specimen DHC04, collected on Balambangan Island, Sabah, 7.267°N 116.917°E, and reported to be Germain's Swiftlet (as *A. f. germani*) by Price *et al.* (2004). One individual from Kuantan (haplotype H11) shows a strong genetic relationship with DHC04, while the other eight from both coasts of Peninsular Malaysia and Sibu (haplotypes H01 and H02) show a moderately close relationship with DHC04 (Figure 1). The inference is that Germain's Swiftlet was implicated in the ancestry of Clade 2.

The existence of two clades is likely to reflect diversity of origins among the house-farm swiftlets. As well as Java, where houses were first occupied more than a century ago and many innovative management processes originated, the range of Thunberg's Swiftlets included Singapore, where buildings were occupied in the 1930s, and (at least in diurnal activity) southern Peninsular Malaysia to about 3°N as well. It is therefore expected that Thunberg's Swiftlets contributed to the genetic diversity of modern Malaysian house-farm populations, possibly augmented by the transportation of Javan genetic material as eggs or fostered young. At the same time, or a little later, on the west coast of Peninsular Malaysia the first records of white-nest swiftlets occupying buildings, in Penang, and at inland localities in Perak and at Kuala Lumpur, were attributed to Grey-rumped Swiftlets of two subspecies by Gibson-Hill (1949). Peninsular Malaysia, therefore, appears to have become a mixing ground where house-farm lineages from two species have met. Such a mixed ancestry is reflected in observed variation in plumage, notably in rump colouration (Plate 4), and is supported by the recognition of two genetic lineages.

In the Kalimantan provinces of Borneo, it is known that genes of Thunberg's Swiftlets were introduced in house-farms by the transfer of eggs for fostering in the nests of the local White-bellied Swiftlet at more than one location. Nonetheless, Sarawak house-farm swiftlets resemble those of Peninsular Malaysia, and genetic studies confirm that this is the case. It appears that Sarawak birds arrived by immigration from west to east across the South China Sea, not later than 1990. After the immigration event (or events) to the north-east of Sarawak, the population of house-farm genotypes expanded south-westwards along the coast. It is no longer possible to test the extent to which the progressive increase in the population of swiftlets drew solely on locally bred recruits or was augmented by supplementary immigration.

Long-distance movements across seas are not unexpected among swiftlets. The global distribution of *Aerodramus* species, embracing many remote islands from the western Indian Ocean to the Pacific (Chantler 1999), illustrates the natural mobility of this group of birds. The inclusion of Medan house-farm swiftlets in Clade 2 confirms genetic exchange across the Straits of Malacca. Phach & Voisin (2007) concluded that the colonisation of urban buildings in Vietnam by house-farm swiftlets was unassisted, representing a displacement of some 1,000 km, possibly including a sea-crossing. Further expansion in continental South-East Asia is shown by the appearance of house-farm birds in Cambodia (Poole 2010), in one direction, and eastwards to Sulawesi, Indonesia, again involving a sea crossing if not assisted by human intervention.

In Sarawak, there has been one observation of one pair of swiftlets of the house-farm type being found nesting in caves, in Batu Lebik at Bukit Sarang, Tatau. However, the pair did not return the following season. In Peninsular Malaysia, there is so far no confirmed record of white-nest swiftlets of the house-farm type occupying caves. That this has not occurred in more than half a century suggests decisive imprinting of many successive house-farm generations, to seek only buildings as nesting sites.

FUTURE PROSPECTS

This study has shown the potential of the mtDNA cyt-*b* gene as a marker in assessing genetic relationships among swiftlets, including comparisons between wild and house-farm populations. Firmer conclusions on the ancestry of Malaysian house-farm swiftlets could be achieved by sampling wild colonies of Grey-rumped Swiftlets of the east coast islands of Peninsular Malaysia and Sabah islands. As openness develops in the industry, it is to be hoped that there will be greater appreciation of the value of research and forthcoming sponsorship. As it was, our studies were self-funded, and therefore under-resourced. Results generated were limited, partly due to the small number of molecular markers and the lack of comprehensive sampling.

Further sampling of adult birds is needed to test the relations between plumage character and genetics. Investigation is needed to determine the number of independent entries from wild sources in different parts of Malaysia, and to discover the extent to which these have generated genetically distinct lineages of house-farm birds. Future studies should incorporate longer DNA sequences and more DNA regions so that the bootstrap support values can be improved.

Understanding the genetics of house-farm swiftlets could assist stakeholders in other ways. In the scenario of this newest domestication, with the backing of sound husbandry and good science, rational planning will be beneficial to ensure the perpetuation and sustainable management of this important avian resource. It may become possible to identify and propagate genotypes that show advantageous characters—for instance, those that are particularly productive, make nests of exceptional size or quality, or display strong fidelity to their home site. With disease inevitably threatening any birds kept in large numbers in close quarters, lineages offering genetic resistance may be identifiable. With enhanced understanding of the genome, it may even prove feasible to engineer deliberate crosses and thereby introduce other desirable characters.

An aspiration of this study was to decide the correct systematic name for house-farm swiftlets of Malaysia. A firm decision is prevented by evidence that the original pioneers were drawn from at least three wild sources of two species: Northern Grey-rumped Swiftlets *Aerodramus inexpectatus germani* in Penang and Southern Grey-rumped Swiftlets *A. inexpectatus* subsp. in Kuala Terengganu, and Thunberg's Swiftlet *A. fuciphagus fuciphagus* in Singapore, as also in Java. Further genetic evidence is needed, in particular from wild colonies of these three taxa. Future research may then provide a clearer understanding of the genetic relations between wild progenitors and, possibly, between local stocks of house-farm birds. Nuclear DNA markers will also be informative in determining whether house-farm swiftlets are products of hybridisation. If hybrids have been generated, they are excluded from regulation under the International Code of Zoological Nomenclature (ICZN 1999) Art. 1.3.3. Nonetheless, as a fertile, stable domesticate, a distinctive new form could be identified by an informal varietal name. We leave the choice of this name to the discretion of stakeholders.

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Appendix 1. Gazetteer: the coordinates of localities mentioned in the text.

Balambangan I., Sabah	7.267°N	116.917°E	Kuala Lumpur (Mountbatten Road)	3.133°N	101.683°E	Redang I., Terengganu	5.717°N	103.800°E
Batu Mandi, Kudat, Sabah	6.917°N	116.950°E	Kuala Terengganu (sea front)	5.317°N	103.150°E	Robinson Road, Singapore	1.267°N	103.833°E
Batu Putih, Sembilan I.	4.000°N	100.500°E	Kuantan, Pahang	3.817°N	103.317°E	Rompin, Pahang	2.800°N	103.483°E
Baturong caves, Sabah	4.700°N	118.017°E	Kuching, Sarawak	1.550°N	110.350°E	Sajira, Banten, Java	6.483°S	106.367°E
Bayangkara, East Kalimantan	2.850°N	117.283°E	Lahad Datu, Sabah	5.117°N	118.300°E	Sarikei, Sarawak	2.117°N	111.517°E
Belitung I., Indonesia	2.900°S	107.933°E	Lakei I., Sarawak	1.750°N	110.483°E	Satang Besar I., Sarawak	1.783°N	110.150°E
Bentong, Pahang	3.517°N	101.900°E	Malacca (Melaka)	2.250°N	102.233°E	Satang Kecil I., Sarawak	1.750°N	110.150°E
Berhala I., Sandakan, Sabah	5.867°N	118.133°E	Mantanani I., Sabah	6.700°N	116.333°E	Sematan, Sarawak	1.800°N	109.767°E
Bintulu, Sarawak	3.167°N	113.033°E	Maratua I., East Kalimantan	2.233°N	118.567°E	Sembilan I., Perak	4.000°N	100.533°E
Bukit Imbiah, Sentosa I., Singapore	1.250°N	103.800°E	Medan, Sumatra	3.583°N	98.667°E	Si Amil I., Sabah	4.283°N	118.850°E
Bukit Sarang (Batu Lebik), Sarawak	2.650°N	113.033°E	Mengkuang Lebar, Genting Highlands	3.433°N	101.783°E	Sibu, Sarawak	2.300°N	111.317°E
Endau-Rompin, Johor	2.667°N	103.600°E	Middle Baram, Sarawak	3.650°N	114.417°E	Singkawang, West Kalimantan	0.900°N	108.983°E
Gaya (Bodgaya) I., Sabah	4.617°N	118.733°E	Miri, Sarawak	4.250°N	113.950°E	Sitiawan, Perak	4.200°N	100.700°E
Gomantong caves, Sabah	5.533°N	118.067°E	Pak Phanang, Nakhon Si Thammarat	8.350°N	100.200°E	Suai, Sarawak	3.783°N	113.617°E
Horsburgh Light (Pedra Branca)	1.333°N	104.400°E	Pontianak, West Kalimantan	0.033°S	109.317°E	Tapadong caves, Sabah	5.083°N	108.133°E
Ipoh, Perak	4.600°N	101.100°E	Pulau Batu Gajah, Johor	2.483°N	103.850°E	Tamaluang cave, East Kalimantan	0.100°S	115.700°E
Jakarta, Indonesia	6.283°S	106.833°E	Pulau Jemaja, Anamba Is., Indonesia	2.917°N	105.750°E	Teluk Anson (Teluk Intan), Perak	4.000°N	101.033°E
Johor Bahru, Johor	1.550°N	103.800°E	Pulau Nyireh, Terengganu	4.867°N	103.067°E	Tenggol I., Terengganu	4.783°N	103.950°E
Koh Phangan, Surat Thani	9.750°N	100.017°E	Pulau Rembia, Sembilan I., Perak	4.000°N	100.533°E	Tioman I., Pahang	2.783°N	104.167°E
Kota Bharu, Kelantan	7.417°N	102.250°E	Pulau Tinggi, Johor	2.300°N	104.117°E			
Kota Tinggi, Johor	1.717°N	103.900°E	Pusing, Perak	4.467°N	101.000°E			