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A morphological revision of Mascarene Swiftlet *Aerodramus francicus*, with the description of a new subspecies from Reunion

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Summary.—In light of speculation in the recent literature concerning the species' intraspecific taxonomy and personal observations, we examined specimens of the Mascarene Swiftlet *Aerodramus francicus* from both range islands, Mauritius and Reunion, with the aim of documenting any geographical variation in morphology. We found that specimens from Reunion clearly differ from those collected on Mauritius (the type locality) in multiple plumage and biometric characters, and that at least some of these differences are also visible in the field. As a result, we describe the Reunion population as a new subspecies under the Biological Species Concept. Taken together, these insular forms are treated by BirdLife International as Near Threatened, but the declining nominotypical Mauritian population might require a reassessment of its conservation status according to IUCN criteria should future taxonomic research applying an integrative approach indicate that species rank is more appropriate.

Mascarene Swiftlet *Aerodramus francicus* (J. F. Gmelin, 1789) is endemic to the south-west Indian Ocean, where it occurs on two islands, Mauritius and Reunion. Vague historic reports of this swiftlet from far northern Madagascar (Milne-Edwards & Grandidier 1879) are considered to be unfounded and little more than rumours (Safford 2013). The only species of tiny swift in Madagascar is Madagascar Spinetail *Zoonavena grandidieri* (J. Verreaux, 1867). At present, *A. francicus* is considered Near Threatened by BirdLife International (2017) given its restricted range, moderately small population (estimated at 6,000–15,000 mature individuals), comparative paucity of available nesting sites and their vulnerability to human disturbance and vandalism.

One other species of *Aerodramus* Oberholser, 1906, is also endemic to this region of the Indian Ocean, Seychelles Swiftlet *A. elaphrus* (Oberholser, 1906), which is confined to the granitic islands of the Seychelles. It has been speculated to be merely a subspecies of *A. francicus* (Peters 1940: 223, Gaymer *et al*. 1969). All other members of the genus *Aerodramus* as currently constituted (*c*.20 species) occur in tropical and subtropical Asia, northern Australasia, and on various islands in the western and central Pacific (*cf*. Dickinson & Remsen 2013). Like many other swiftlets, Mascarene and Seychelles Swiftlet were frequently placed in the genus *Collocalia* G. R. Gray, 1840, prior to the realisation that the latter genus could be separated into two clades on the basis of genetic data (Price *et al*. 2005, Thomassen *et al*. 2005). Despite being geographical outliers, both *A. elaphrus* and *A. francicus* are clearly embedded deep within the well-supported *Aerodramus* clade according to multilocus molecular data (Lee *et al*. 1996, Price *et al*. 2004, 2005, Thomassen *et al*. 2005). The two species are, unsurprisingly, closely related to one another, having diverged *c*.500,000 years ago based on 1% divergence in the mitochondrial marker cytochrome *b* (Johnson & Clayton 1999). In all of these studies, molecular samples for Mascarene Swiftlet are exclusively from

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Mauritius (Johnson & Clayton 1999, Lee *et al*. 1996, Price *et al*. 2004, 2005). Other intra-generic relationships are not well known.

Mascarene Swiftlet has always been considered monotypic, although an examination by M. R. Browning (*in litt*. to Chantler & Driessens 2000) of four specimens of this species from the island of Reunion held in the National Museum of Natural History, Washington DC, has led to fairly widespread speculation that more than one subspecies might be involved (Chantler 1999, Safford 2013, del Hoyo & Collar 2014). Browning reported that the specimens are 'duller (browner, less green) above and darker-rumped than birds of similar museum age from Mauritius. The Reunion series also appears slightly darker on the underparts, especially the undertail-coverts. Browning considered that Reunion birds should be a separate subspecies, but no name was available' (Chantler & Driessens 2000: 129).

During extensive field work throughout the Mascarene Islands in November–December 1999 and March–April 2004, but especially in December 2013–January 2014 and November–December 2014, one of us (HS) observed *A. francicus* on both Mauritius and Reunion, documenting apparent differences between the two insular populations photographically. As a result, we reviewed much of the available specimen material, including the Washington series, and the previous literature, with the aim of determining whether Browning was correct in his belief that more than one subspecies should be recognised.

Methods and materials

GMK (and in some cases HS) examined and measured 28 study skins of *Aerodramus francicus* as follows: the Natural History Museum, Tring (NHMUK; *n* = 4, Mauritius), Cambridge University Museum of Zoology, Cambridge, UK (CUMZ; *n* = 4, Mauritius, *n* = 1, Reunion), the Muséum national d'Histoire naturelle, Paris (MNHN; *n* = 8, Reunion, *n* = 2, Mauritius) and Museum für Naturkunde, Berlin (ZMB; *n* = 1, Mauritius), as well as those at the Museum d'Histoire naturelle de Genève (*n* = 3, Mauritius) and National Museum of Natural History, Smithsonian Institution, Washington DC (USNM; *n* = 4, Reunion), which were sent on loan to NHMUK. In addition, HS alone examined material at the American Museum of Natural History (AMNH; *n* = 1, Reunion), and specimens at the University of Michigan Museum of Zoology, Ann Arbor (UMMZ; *n* = 4, Reunion, *n* = 3, Mauritius) were measured and photographed on our behalf by J. Hinshaw. This gave totals of 17 specimens from Mauritius and 19 from Reunion. A juvenile from Reunion held at MNHN (1886.716) was excluded from all analyses. Material of *A. francicus* is comparatively uncommon in museum collections. In addition to the material studied by us, we are aware of the following specimens: Royal Belgian Institute of Natural Sciences, Brussels (*n* = 6, Reunion), Kansas State University, Lawrence (*n* = 2, Mauritius) and two old specimens, one collected on Mauritius sometime between March 1801 and December 1803, held in Paris (MNHN-ZO-2014-429) and the other, NMW 35205 (Naturhistorisches Museum Wien), labelled Reunion, but of otherwise unknown provenance. Photographs of NMW 35205 were provided by A. Gamauf; the older of the two labels on the specimen has an inscription that cites Bonaparte, suggesting that it was collected sometime later than that held in Paris. The most interesting fact concerning this specimen is that the upperparts gloss suggests that it might actually have been collected on Mauritius (see Results). Photographs of the Brussels specimens were made available by A. Folie.

The type specimen of *A. francicus* does not appear to be extant. The species was described by Gmelin (1789: 1017), who clearly stated its type locality to be 'insula Franciae' (= Mauritius). Gmelin cited as authorities for his species the works of Buffon (1779: 345–346)

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and Latham (1783: 582). Both of these previous works also mentioned the Île de France as terra typica for this bird, but all three texts (including Gmelin) further cited a depiction of the 'Hirondelle de l'isle de Bourbon' (a reference to Reunion) in Buffon *et al*. (1765–80) as a basis for Gmelin's species. This illustration is clearly attached to a bird that Buffon (1779: 344–345) considered to be a 'variety' of 'la grande hirondelle brune à ventre tacheté' and which Gmelin (1789: 1017) named *Hirundo borbonica* (= Mascarene Martin *Phedina borbonica*), again with type locality 'insula Franciae', although he referred to the same depiction of the 'Hirondelle de l'isle de Bourbon', among other authorities, as the basis for his new name *Hirundo francica*. The plate (544, https://www.biodiversitylibrary.org/item/109398#page/95/mode/1up) in Buffon, however, is clearly a closer match for the *Phedina* than a swiftlet, by virtue of its clearly streaked underparts and the pale-tipped tertials (which are characteristic of its plumage when fresh). Nevertheless, to allay any doubt, we searched unsuccessfully for the type of Gmelin's name, by means of both specific queries of certain museums and a general request via the electronic bulletin board for relevant European curators, eBEAC. In particular, J. J. F. J. Jansen (*in litt*. 2018) confirmed that neither Paris nor Leiden, two obvious repositories for material studied by Buffon (and thus subsequently utilised by Gmelin), holds any specimen of *A. francicus* dating from the 18th century. As noted above, the oldest specimens that we have been able to locate clearly date from the 19th century. Thus, without any evidence to the contrary, we must accept Gmelin's type locality designation of Mauritius. It is also worth mentioning that, to date, ourselves and others have been unable to locate a copy of Buffon's *Histoire naturelle des oiseaux* with identical pagination to that cited by Gmelin, although the potential exists that the citation in the latter reflects a typesetting error.

In addition to plumage comparisons conducted under natural light, the following measurements were taken according to standard protocols (Svensson 1999) using dial callipers and a metal wing-rule with a perpendicular stop at zero: wing length (from carpal joint to tip while applying gentle pressure to the primary-coverts), tail length (from the distal end of the pygostyle to the tip), bill length (from the tip of the maxilla to skull, and separately from the tip of the maxilla to the feathers), bill depth (at the distal edge of feathering), tail fork (as the distance between the tips of r1 and r5, i.e. the longest and shortest rectrices, measured along the axis of the tail) and the width of the white rump patch. The latter measurement is difficult to take and we eventually elected to use the mean value of the sum of its max. width (measured as the broadest extent of pale feathering, which we believe would be visible in the field) and its minimum width (the depth of the pure white feathering forming the rump's 'core'). All measurements were taken by GMK, other than the single specimen at AMNH (by HS), the seven specimens at UMMZ (J. Hinshaw) and tail fork alone for the MNHN material (R. Stopiglia). Field work in 2012–14 (see above), by HS alone, which was undertaken on both islands, involved observations of *c*.200 individuals on Reunion and *c*.150 individuals in Mauritius, of which small numbers of both were photographed, and the photographs subsequently compared both with each other and other images available online (e.g. at www.hbw.com/ibc/species/mascarene-swiftlet-aerodramus-francicus), and with specimen material.

Statistical analyses of morphometric data were performed in R 3.3.3 (R Core Team 2017). Overall variation was explored with principal component analyses (PCA) applying the function prcomp of the package 'stats'. To test whether the swiftlets from Reunion and Mauritius can be separated by the measured traits and to maximise separation between them, flexible discriminant analyses were performed using the package 'mda' (Hastie & Tibshirani 2015). The discriminant power of the seven measured traits was assessed using Wilks' lambda estimated in the package 'DiscriMiner' (Sanchez 2013). Only specimens for

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which a complete set of measurements was available were included (n = 14 for Reunion, n = 13 for Mauritius) and all measurements were log-transformed prior to the analyses.

Results

Plumage.—Our comparison of the available specimen material confirmed the differences initially suggested by the field observations made by HS and the prior comments by Ralph Browning, but also brought to light additional features, some of which might require confirmation via a longer series of specimens or trapped birds. The three most obvious plumage differences are: (1) the depth of the white rump patch and the number of pure white feathers therein, and thereby its degree of visibility; (2) the browner, less glossed upperparts, especially the wings of Reunion birds, and (3) underparts pattern. We can discount that the differences we highlight are significantly influenced by moult, wear or the age of the specimens concerned (some more than 100 years old), given that we viewed specimen material and live birds from a range of months and years. For example, compare the plumage gloss in the specimens shown in Figs. 4–6, which display consistent differences despite the varying ages of the Mauritian specimens in NHMUK, MNHN and UMMZ, respectively. Nevertheless, all of them are considerably older than those from Reunion, suggesting that fading is not an issue. These and other features are discussed in more detail below (see Diagnosis).

Biometrics.—The biometric data we acquired are shown in Table 1 (see also Appendix). In most morphometric characters the populations on the two islands are basically indistinguishable, and it is only in the depth of the white rump patch and the degree of graduation in the rectrices (tail fork) that major differences were found.

There was no consistent separation between the specimens of Reunion from those of Mauritius in the PCA (Fig. 1). Only the length of the tail fork and the width of the white rump patch contributed significantly to the discriminant function according to Wilks' lambda. All 14 specimens from Reunion and 12 of the 13 specimens from Mauritius were correctly assigned in the flexible discriminant analyses to their respective origin.

The morphological differences between the two populations described above indicate to us that a new taxon is involved that we elect to treat at subspecies level (i.e. under a modern interpretation of the Biological Species Concept, e.g. Helbig *et al*. 2002). We describe herewith the new taxon as follows:

TABLE 1

Biometric data for 17 specimens of *Aerodramus f. francicus* from Mauritius and 18 specimens from Reunion taken from museum specimens according to standard measuring protocols (see Methods and materials). Mass data from specimen labels. See the Appendix for complete mensural data for all relevant specimens.

Biometric ↓ / Locality →	**Mauritius**	**Reunion**
Wing length	103.0–117.0 mm (111.3 mm; n = 17)	107.0–115.0 (110.3 mm, n = 18)
Tail length	46.0–52.0 mm (49.6 mm, n = 17)	45.0–53.0 mm (50.1 mm, n = 17)
Bill to feathers	2.8–4.2 mm (3.5 mm, n = 17)	3.0–4.1 mm (3.6 mm, n = 16)
Bill to skull	4.1–6.3 mm (5.2 mm, n = 17)	4.4–6.1 mm (5.4 mm, n = 17)
Bill depth at feathers	1.4–2.7 mm (1.8 mm, n = 14)	1.5–2.5 mm (1.8 mm, n = 17)
Tail fork	4.1–8.4 mm (6.6 mm, n = 17)	3.5–6.9 mm (5.3 mm, n = 17)
Depth of white rump patch	12.9–17.3 mm (15.0 mm, n = 14)	9.6–15.5 mm (11.8 mm, n = 17)
Mass	9.0–9.3 g (9.17 g, n = 3)	7.9–11.8 g (9.04 g, n = 8)

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Figure 1. Dorsal, ventral and lateral views of the (USNM 486962) and three paratypes (USNM 486964–966) of Mascarene Swiftlet *Aerodramus francicus saffordi* (holotype, at left), collected in northern Reunion, in November 1964, compared to four specimens (NHMUK 1844.10.19.3, 1844.10.19.3, 1890.12.16.39, 1890.12.16.40) of *A. f. francicus*, collected on Mauritius on unknown dates in the 19th century (Hadoram Shirihai, © Natural History Museum, London)

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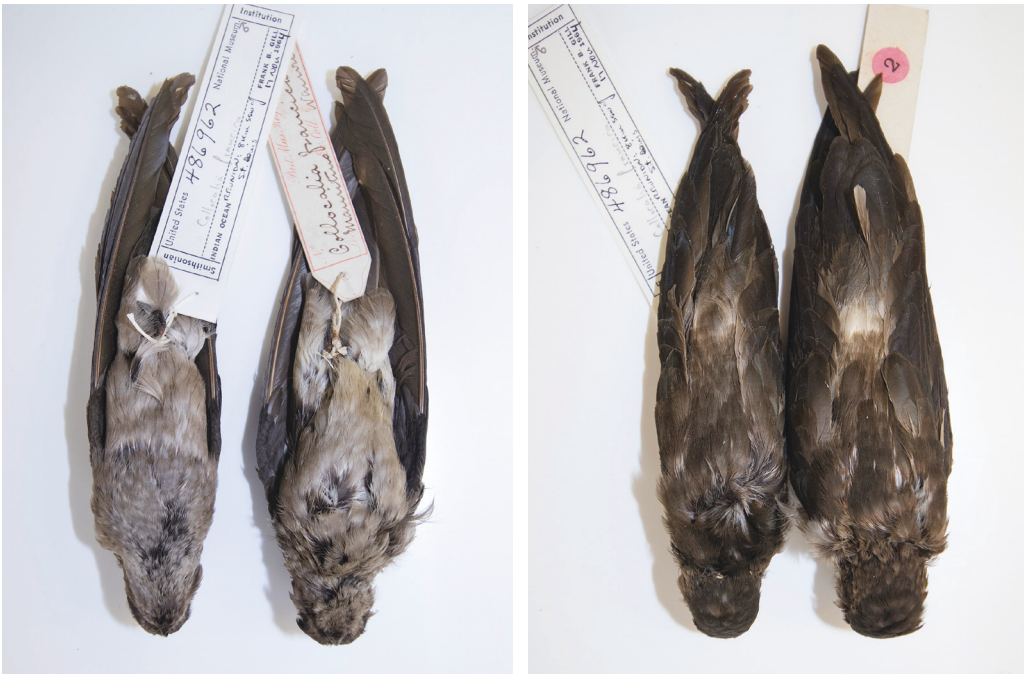

Figure 2. Ventral, dorsal and lateral views of the holotype (USNM 486962) of Mascarene Swiftlet *Aerodramus francicus saffordi*, collected 8 km south-southwest of Saint-Denis (20°52′44″S, 55°26′53″E), northern Reunion, on 17 November 1964, compared to a specimen (NHMUK 1844.10.19.5) of *A. f. francicus*, collected on Mauritius on an unknown date in the 19th century; USNM 486962 is on the left in the first two images and above in the lateral view (Hadoram Shirihai, © Natural History Museum, London)

Aerodramus francicus saffordi subsp. nov.

Holotype.—National Museum of Natural History, Washington DC (USNM 486962), male collected by F. B. Gill, at 1,100 m elevation, 8 km south-southwest of Saint-Denis (20°52′44″S, 55°26′53″E), northern Reunion, in the south-west Indian Ocean, on 17 November 1964 (Figs. 1–2).

Paratypes.—USNM 486964, female collected by F. B. Gill, at Nez de Bœuf (21°12′20″S, 55°37′14″E), Reunion, on 22 November 1964; USNM 486965, male collected by F. B. Gill, at Nez de Bœuf, Reunion, on 22 November 1964; and USNM 486966, male collected by F. B. Gill, 6 km north-northwest of Le Vingt-Septième (*c*.21°11′38″S, 55°29′47″E), on 23 November 1964 (Fig. 1).

Diagnosis.—Based on the rather small sample sizes available, *saffordi* is separable from nominate *francicus* using plumage characters and biometrics (see Table 1, Fig. 3). For biometrics, *saffordi* has an on average smaller / narrower pale rump patch than nominate

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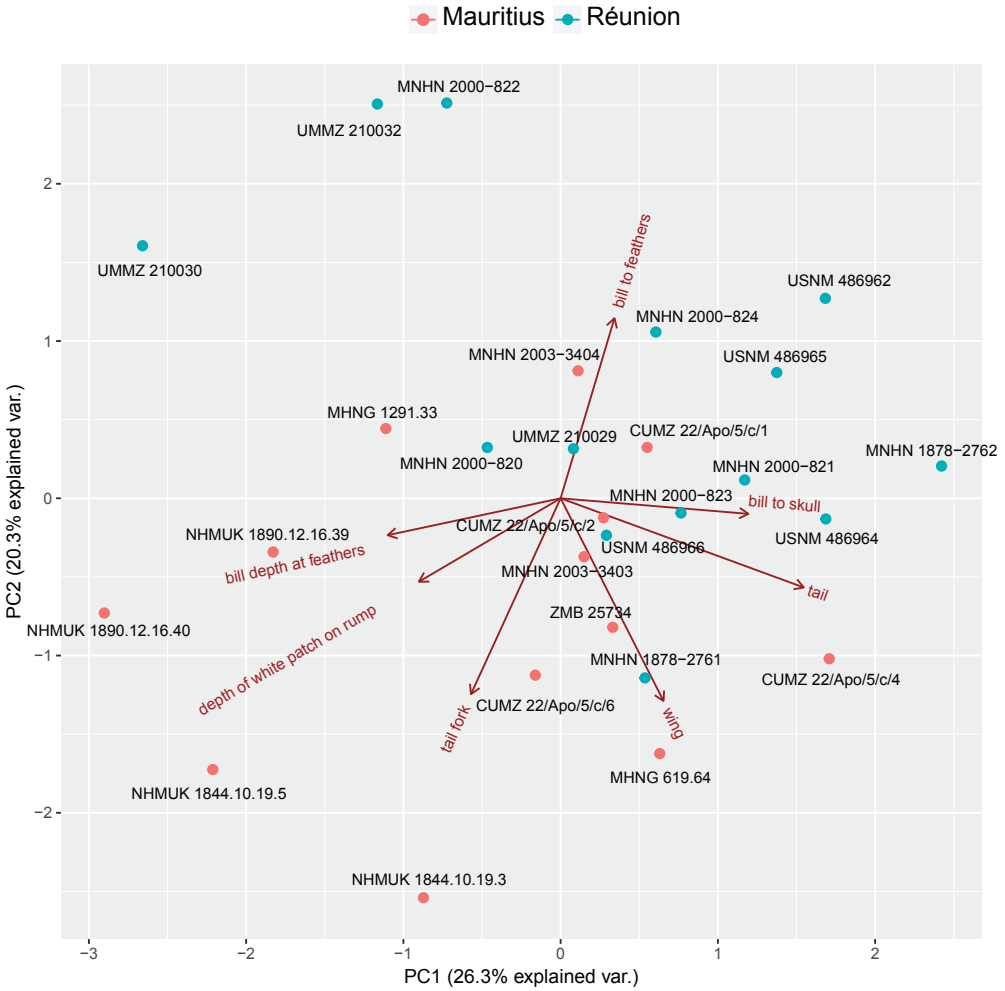

Figure 3. Plot of first two axes of a principal components analysis (PCA) showing the morphospace of *Aerodramus francicus* from Mauritius (n = 13) and Reunion (n = 14) based on seven measurements. Museum numbers are given for each specimen and the vectors indicate the direction and strength of the contributions of the different morphological variables to the overall distribution.

francicus. Additionally, tail fork is potentially a useful separating character, with that of *saffordi* being on average considerably (*c*.20%) shallower, although judging specimens in comparable states of feather wear unquestionably can limit the reliability of this feature in the museum. Nevertheless, it can be obvious when comparing images of live birds on the wing (Fig. 4). In plumage, the rump patch of *saffordi* is far less contrasting by virtue of the often many fewer pure or almost pure white feathers therein, in addition to its being narrower. As noted by M. R. Browning (*in* Chantler & Driessens 2000), the wings, especially the flight-feathers, of nominate *francicus* appear substantially more glossed (greenish in some lights, but bluer in others) than those of *saffordi*, and this remains obvious even in much older specimen material from Mauritius (see Fig. 1). The head-sides and ear-coverts of nominate *francicus* typically appear much more solidly dark than those of *saffordi*, with the result that its cap seems much larger, whereas *saffordi* appears to display much more of a paler and contrasting neck-collar. Finally, specimens of *saffordi* appear considerably more

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Figure 4. Comparative field photographs of the Reunion and Mauritius populations of Mascarene Swiftlet *Aerodramus francicus* in both fresh (lower line) and very worn plumages (middle line); the bird top left is at the extreme end of variation in the white rump patch of this island's population (Hadoram Shirihai)

patterned below than those of nominate *francicus*, displaying much more obvious shaft-streaks on the lower breast and belly, and a sharper division between the darker throat and breast vs. paler (and greyer) remainder of the underparts; in nominate *francicus* this pectoral band effect is much reduced, as well as being much higher on the breast. *A. f. saffordi* is separated from the similar but larger and darker *Aerodramus elaphrus* of the Seychelles by most of the same characters as can be used to distinguish the latter from nominate *francicus*, namely the shorter wings and bill of *saffordi* (*A. elaphrus* has wing 115–119 mm and bill to feathers 7.5–8.0 mm; Rocamora 2013), its narrower wing base and smaller eye. In contrast to nominate *francicus*, the rump patch of *saffordi* being rather less obvious within the otherwise dark upperparts, is more similar to *A. elaphrus*.

Description of holotype.—See also Figs. 1–2. Colours correspond to those in Smithe (1976). Very dusky above, and paler, slightly greyer below. Head basically shows four tones: the cap which is blacker (between Color 119 Sepia and 119A Hair Brown) and quite well demarcated reaching level with lowest part of eye; the lores which are even blacker (closest to Color 89 Jet Black); the paler greyish-brown ear-coverts (close to Color 119B Dark Drab) and chin (slightly paler than the ear-coverts); with the throat being the palest part of the head (closest to 119C Light Drab). Upperparts: largely dusky brown (Color 221 Vandyke Brown), contrasting with ill-defined paler grey rump (between Color 119C Light Drab and 119D Drab-Grey), with very few whitish bases and edges exposed; rectrices, remiges and some of the coverts and tertials are darkest part of wing, almost blackish brown (Color 119), with very slight greenish gloss/iridescence. Underparts: lower throat to breast 119C Light

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Figure 5. Two specimens of *Aerodramus f. francicus* (MNHN 2003-3403 and 2003-3404; top two) collected on Mauritius on unknown dates, previously in the Boucard collection, compared to a specimen of *A. f. saffordi* (MNHN 2000-823) collected on Reunion in July 1966 (Guy M. Kirwan, Muséum national d'Histoire naturelle, Paris)

Drab, or slightly darker (119B Dark Drab) forming a very broad and somewhat diffuse breast-band, below which the remainder of the underparts (belly to undertail-coverts) become paler (between 119C and 119D); especially from the mid-breast across the belly, shaft-streaks are very well pronounced and there are dark feather centres exposed between the lower throat and upper breast forming a broken mesial stripe. Underwing-coverts as top of head (nearest to Color 119), but underside of remiges marginally paler (between Color 119 Sepia and 119A Hair Brown). Bare parts all dark post-mortem (original colours unknown).

Measurements of holotype.—Wing 107.0 mm, tail 51.0 mm, bill (to skull) 5.8 mm, bill (to feathers) 3.3 mm, bill depth (at feathers) 1.5 mm, tail fork 4.9 mm, and depth of white rump patch 9.9 mm; mass 8.6 g.

Variation in the type series.—The three paratypes (Fig. 1) are very similar both to one another and to the holotype, but USNM 486965 has the most visible white on the rump, whereas the holotype and USNM 486966 show least.

Measurements of paratypes.—USNM 486964 (female): wing 109.5 mm, tail 52.0 mm, bill (to skull) 5.9 mm, bill (to feathers) 3.3 mm, bill depth (at feathers) 1.6 mm, tail fork 6.5 mm, and depth of white rump patch 10.3 mm; mass 8.9 g. USNM 486965 (male): wing 111.5 mm, tail 49.0 mm, bill (to skull) 6.1 mm, bill (to feathers) 3.7 mm, bill depth (at feathers) 1.5 mm, tail fork 5.2 mm, and depth of white rump patch 12.1 mm; mass 11.8 g. USNM 486966 (female): wing 110.0 mm, tail 50.0 mm, bill (to skull) 5.7 mm, bill (to feathers) 3.0 mm, bill depth (at feathers) 1.8 mm, tail fork 5.0 mm, and depth of white rump patch 12.6 mm; mass 8.5 g.

Geographic distribution.—Endemic to the island of Reunion (2,152 km^2), a French overseas territory, where it is widespread from sea level to the island's highest point (3,069 m, Piton des Neiges), although known breeding sites are comparatively few, and most support rather small numbers of birds. The largest are in the Ravine de la Grande Chaloupe, an Important Bird Area in the north-west of the island (Le Corre & Safford 2001) and at La

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Figure 6. Specimen of *Aerodramus f. francicus* (UMMZ 210026), collected on Mauritius, in September 1964, showing glossy wings and upperparts (Janet Hinshaw, © University of Michigan Museum of Zoology, Ann Arbor)

Chapelle, Cirque de Cilaos, in the centre of Reunion (Cheke & Hume 2008). However, at least some caves (potential breeding sites) are almost certainly inaccessible and detailed surveys do not appear to have been attempted, in contrast to the situation on Mauritius (Safford 2013).

Etymology.—In naming this new swiftlet subspecies, it is gratifying to be able to pay tribute to the many contributions of Roger Safford to our avifaunal knowledge of the south-west Indian Ocean islands, especially the Mascarenes. His work there began in the late 1980s and culminated recently in the co-authorship of a superb new field guide to the region (Hawkins *et al*. 2015) and, even more importantly, the eighth adjunctive volume in *The birds of Africa* series, of which he was both an editor and a primary author (Safford & Hawkins 2013). Safford is currently a Senior Programme Manager at BirdLife International with a special responsibility for threatened species conservation. The name *saffordi* is a noun declined in its genitive singular form.

Taxonomic rank.—Employing a modern interpretation of the Biological Species Concept, we elect to describe *saffordi* at subspecies level based on the multiple but relatively modest morphological characters that distinguish the Reunion population of this swiftlet from that on Mauritius. This fulfils the notion expressed by Remsen (2010), in a defence of their usefulness in avian taxonomy, that subspecies should represent "geographic populations diagnosable by one or more phenotypic traits." Given that the discriminant analyses correctly assigned all but one of 27 specimens from the two islands to population, including all of the Reunion material (see Results, Biometrics), it appears that Patten & Unitt's (2002) advocacy of a 95% rule for assessing diagnosability of subspecies can be met in the case of *saffordi*. Despite that the sum of these differences might be considered comparatively significant within a morphologically extremely conservative group such as swiftlets, given our current lack of vocal, behavioural or genetic evidence of additional differentiation, we contend that subspecies rank is most appropriate for the Reunion population. For the present we have no basis to believe that, other than as a function of geography, the two populations would function as reproductively isolated units, and we have no evidence of potential pre-mating isolation mechanisms. Morphological characters demonstrate that there are qualitative and, to a lesser degree, quantitative differences between the two populations. Traditional genetic data would merely give an indication of a lack of gene flow over a certain time period.

Biogeographical considerations.—The landbird faunas of Mauritius and Reunion are strongly characterised by: (a) being highly depauperate (at least following several centuries of human impact); (b) extremely high rates of endemism among their native birds; and (c)

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the majority of species on both islands being introduced. None of these characters can be considered surprising given their comparative isolation, lying *c*.2,000 km from the African mainland and 175 km from each other; their volcanic and independent origins (Mauritius is *c*.8–9 million years old, Reunion *c*.2–5 million years old: see Safford & Hawkins 2013: 15); as well as their comparatively long periods of continuous human colonisation and importance to traders.

Discounting the introduced taxa, under most previous taxonomic arrangements Reunion boasted six extant endemic landbird species (a harrier *Circus maillardi*, a cuckooshrike *Coracina newtoni*, a bulbul *Hypsipetes borbonicus*, a stonechat *Saxicola tectes*, and two white-eyes, *Zosterops borbonicus* and *Z. olivaceus*), one endemic subspecies (*Terpsiphone b. bourbonnensis*, a monarch flycatcher) and two other native landbird species—*Aerodramus francicus* and *Phedina borbonica*. The latter is distinguished by being subdivided into separate races on Madagascar (*P. b. madagascariensis*) and in the Mascarenes (Mauritius and Reunion; nominate). The *Saxicola* is sometimes treated as a subspecies of a much wider Old World species-complex, or as a race of a purely Afrotropical species, but under either arrangement, the taxon concerned, *tectes*, is endemic to Reunion.

Extant Mauritian landbird endemicity was previously measured by eight species (a kestrel *Falco punctatus*, a pigeon *Nesoenas mayeri*, a parakeet *Psittacula eques*, a cuckooshrike *Coracina typica*, a bulbul *Hypsipetes olivaceus*, two white-eyes *Zosterops chloronothos* and *Z. mauritianus*, and a fody *Foudia rubra*) and one subspecies (*Terpsiphone bourbonnensis desolata*). The only other native landbirds were the two species shared with Reunion (i.e. *Phedina borbonica* and *Aerodramus francicus*).

It is worth remarking, however, that when considering overall known diversity, taking into account extinctions, the basic biogeographical differences between the two islands shrink, and it becomes obvious that their avifaunas are much more similar than might be apparent from the above (Cheke & Hume 2008, Safford & Hawkins 2013). Nevertheless, most populations are congenerics are clearly differentiated to some extent. Consequently, it is unsurprising that Mascarene Swiftlet should in fact conform to the same pattern of unique taxa on the different islands. This leaves the *Phedina* as the only landbird native to both Mauritius and Reunion that displays no named morphological differentiation between the two islands.

Conservation.—The following is largely based on Safford (2013). In the mid 1990s the Reunion population of *Aerodramus francicus* was estimated to be in excess of 10,000 individuals (whereas Barré *et al*. 1996 thought numbers to be approximately 5,000 birds); indeed, the colony at La Chappelle (see Geographic distribution) was estimated to comprise more than 10,000 nests alone. This was believed to reflect a genuine increase in numbers since the 1970s (when the species was thought to be much less numerous on Reunion compared to Mauritius), rather than merely improved coverage. Several colonies on Reunion were considered to be threatened by the caving activities of speleologists, while the species' nests have recently acquired a reputation for enhancing effects of cannabis (M. Le Corre *in* Chantler & Driessens 2000, Cheke & Hume 2008). On Mauritius, *A. francicus* declined between the early 20th century and the 1970s, but by the time of the first detailed survey, in 1998, it was believed to be increasing. At this time, numbers were estimated at just 2,244–2,610 individuals, with no cave holding more than 600–700 and 19 of 34 caves known to harbour the species held fewer than 30 swiftlets (Middleton 1999). Varied forms of human persecution and exploitation, which certainly was ongoing in the 1990s, as well as the deliberate blocking of cave entrances, suggest that the Mauritian population is not only considerably rarer but also at greater risk than that on Reunion. Consequently, should any future taxonomic work determine that *saffordi* and *francicus* merit species rather than

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subspecies rank, then it appears certain that *francicus sensu stricto* would automatically be listed as globally threatened.

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Appendix: mensural data for adult specimens of Mascarene Swiftlet *Aerodramus francicus* measured by the authors and others; the AMNH specimen was handled by HS, the UMMZ material was measured by J. Hinshaw, and all other specimens were measured by GMK. Measuring techniques are described under Methods and materials. Blank fields represent missing data that were impossible to take for various reasons.

	wing	tail	bill to skull	bill to feathers	bill depth at feathers	tail fork	depth of white patch on rump
Mauritius							
NHMUK 1890.12.16.39	106.0	48.0	5.7	3.3	1.9	8.1	17.05
NHMUK 1890.12.16.40	111.0	46.0	4.1	3.1	1.7	7.1	15.8
NHMUK 1844.10.19.3	114.5	49.0	5.4	2.8	2.0	7.8	13.35
NHMUK 1844.10.19.5	113.0	49.0	4.4	3.3	2.1	8.4	15.35
MNHN 2003-3404	108.5	50.0	5.1	3.8	1.4	5.8	16.5
MNHN 2003-3403	110.5	52.0	5.5	3.7	1.9	6.3	15.8
MHNG 1291.33	110.0	49.0	4.6	3.1	1.9	4.1	13.9
MHNG 619.64	116.0	50.0	5.5	3.0	1.7	5.6	13.1
MHNG 1291.32	115.5	52.0	5.5	3.2		4.8	14.1
CUMZ 22/Apo/5/c/6	113.0	51.0	5.4	3.6	1.9	7.0	15.9
CUMZ 22/Apo/5/c/4	117.0	51.5	5.5	3.7	1.5	6.1	13.5
CUMZ 22/Apo/5/c/2	111.0	50.0	6.3	3.9	1.9	6.7	15.5
CUMZ 22/Apo/5/c/1	107.0	51.5	5.3	3.7	1.5	7.9	12.9
ZMB 25734	114.0	50.0	5.8	3.5	1.7	5.5	17.3
UMMZ 210028	103.0	46.5	5.1	3.6	2.7	5.7	
UMMZ 210027	109.5	48.5	5.0	4.2		8.1	
UMMZ 210026	112.5	50.0	4.6	3.6		6.7	
Reunion							
MNHN 1878-2761	113.0	53.0	5.6	3.5	2.3	6.6	12.1
MNHN 2000-821	112.0	52.0	5.1	3.5	1.6	5.0	12.5
MNHN 2000-823	113.0	50.0	5.5	3.6	1.9	6.4	9.8
MNHN 2000-820	108.0	50.0	4.8	3.4	1.8	6.9	10.9
MNHN 2000-824	112.0	51.0	5.1	4.1	1.9	4.8	12.3
MNHN 2000-822	107.5	47.0	5.7	3.8	2.0	3.5	13.9

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	wing	tail	bill to skull	bill to feathers	bill depth at feathers	tail fork	depth of white patch on rump
MNHN 1878-2762	115.0	53.0	5.2	3.5	1.5	3.9	11.5
MNHN 1878-2765	110.5	50.5			2.0	3.5	9.6
AMNH 815847	109.0	51.0	6.0		2.5		15.5
USNM 486964	109.5	52.0	5.9	3.3	1.6	6.5	10.3
USNM 486966	110.0	50.0	5.7	3.0	1.8	5.0	12.6
USNM 486965	111.5	49.0	6.1	3.7	1.5	5.2	12.1
USNM 486962	107.0	51.0	5.8	3.3	1.5	4.9	9.9
CUMZ 22/Apo/5/c/3	110.0		6.0	3.1	1.55		
UMMZ 210031	111.0	47.5	4.4	3.6		6.1	11.0
UMMZ 210032	107.0	47.5	4.8	4.0	1.9	4.4	12.75
UMMZ 210030	108.0	45.0	4.6	3.7	2.1	5.7	12.2
UMMZ 210029	111.5	51.5	4.7	3.8	1.9	5.7	12.25

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