# Horus Swift: identification, plumage variation and distribution

*Justin J F J Jansen & Gerald Driessens*

Horus Swift *Apus horus* is endemic to sub-Saharan central and southern Africa (figure 1). It breeds in sandy banks, where it uses abandoned burrows excavated by other birds. In this respect, Horus differs from all other *Apus* swifts. Breeding has also been observed in artificial holes, such as drainage pipes (eg, at Maputo, Mozambique; Gary Allport in litt). Horus shares its breeding habitat with other burrow-nesting species like bee-eaters Meropidae, martins Hirundinidae and starlings Sturnidae (although with no or only little overlap in breeding season). Breeding colonies are often small, with up to c 40 pairs. Non-breeding parties are comparatively small as well, rarely numbering up to a few 100 birds (Fry et al 1988, Gary Allport in litt).

Identification issues may obscure (or have obscured) the status of Horus Swift, especially away from breeding colonies (cf Harrison et al 1997). The paucity of records outside the breeding season may be related to the fact that swift flocks often escape the attention of birders and field ornithologists. A better insight into the identification of Horus may help to improve the knowledge of the species' distribution.

In January 2018, a breeding colony of c 18 Horus Swifts was discovered on the Doué riverbank (16°31'12"N, 14°42'05"W) in Gamadji Saré district, Podor department, Saint-Louis region, in northernmost Senegal (Bacuez 2018, Piot 2018, Piot & Bacuez 2021). At this site, as many as 58 birds were counted on 14-15 December 2020. This discovery represents a northward breeding-range expansion of 1600 km. It is, however, uncertain whether the expansion is the result of a recent event or may have occurred earlier, and gone undetected (Piot & Bacuez 2021).

Fry & Elgood (1968) and, more recently, Amezian (2018) already hinted at the possibility of Horus Swift occurring in the Western Palearctic (WP). A swift photographed on Schiermonnikoog, Friesland, the Netherlands, on 26-27 September 2019 (Dutch Birding 41: 612-613, plate 585-586, 2019) may, if accepted, constitute the first record of Horus for the Palearctic region (currently being assessed by the Dutch rarities committee). A swift photographed and initially believed to most likely be a White-rumped Swift *A caffer* on North Bull Island, Dublin, Ireland, on 25 December 2002 (Persson 2003) might have been a Horus as well (Mullarney et al in prep). A record of an alleged Horus on Agaléga, one of the outer islands of Mauritius, on 28 June 1974 (Brooke & Steyn 1979, Cheke & Lawley 1983, Anthony Cheke pers comm) might be an earlier indication of the species' vagrancy potential. Variation in Horus has been discussed in more detail by, amongst others, Roberts (1929), Chapin (1939), Lack (1955), Brooke (1971a) and Clancey (1984). Unfortunately, the data relating to the variation shown by Horus summarised in books relevant to African birds (for instance, Fry et al 1988, Hockey et al 2005, del Hoyo & Collar 2014) are of little practical use, given the critical and nuanced assessment required for reliable identification. Chantler & Driessens (1995a, 2000) described variation in Horus in a more satisfactory way but their description was by no means complete. Field guides rarely illustrate the variation in birds adequately (cf Töpfer 2018) and this can lead to overly simplistic identification claims by observers who are unaware of the complexities.

In this paper we focus on the plumages of Horus Swift but also of all other white-rumped *Apus* swifts of the world. This includes two hybrids White-rumped Swift x Little Swift *A caffer x affinis* at Chipiona, Cádiz, Spain, from 2015 to at least 2019 (Jansen et al 2023), depicted here in figure 13. A summary can be found in appendix 1.

**Taxonomy**

Horus Swift is considered a polytypic species (cf Dickinson & Remsen 2013, del Hoyo & Collar 2014, Gill et al 2023), comprising the nominate subspecies *horus* (von Heuglin 1869), of which the (lost) 'type specimen' was collected in South Africa, and the subspecies *fuscobrunneus* (Brooke 1971a) that is only known from a single series of 10 specimens collected in the coastal plain of Namibe, Angola, in May 1966 (cf figure 5) (holotype ISCED 16.161). Known specimens of the latter are kept at the Instituto Superior de Ciências da Educação (Luanda, Angola) (eight) and at the Zoologisches Forschungsmuseum Alexander

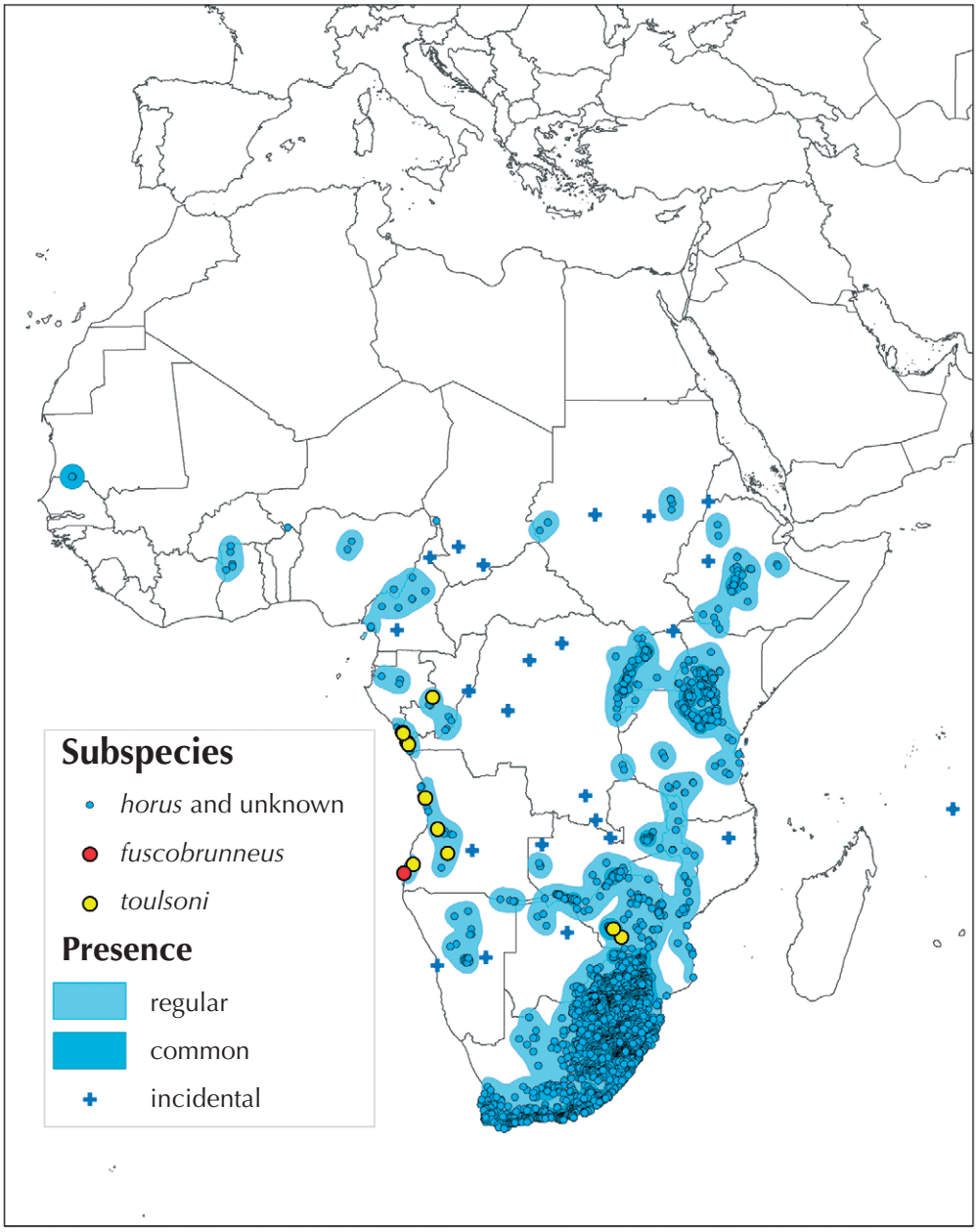


FIGURE 1 Distribution of Horus Swift / Horusgierzwaluw *Apus horus*. Based on eBird, observation.org, vertnet.org, Macaulay Library, southern African bird atlas project [digital resources accessed 19 June 2022], Nikolaus 1987, Fry et al 1988, Chantler & Driessens 1995a, 2000, Kelly 1996, Roberson 1996, Anonymus 1998ab, Stevenson & Fanshawe 2002, Crisler et al 2003, Hoff 2003, Sinclair et al 2004, Carswell et al 2005, Languy et al 2005, Dowsett-Lemaire & Dowsett 2006, 2014, Boix 2010, Borrow 2011, King 2011, Mason & Mason 2013, David et al 2015, Karr 2017, Vasapolli 2018, Stevenson & Brinkley 2019; Gary Allport in litt, Guido Keijl pers comm (n=10 174 observations, including specimens). Shown are breeding ranges of subspecies *A h horus* and *A h fuscobrunneus* and distribution of dark morph *'toulsoni'*.

Koenig (Bonn, Germany) (two). However, in the absence of records of the subspecies *fuscobrunneus* since the early 1970s (Dean et al 2019), its distributional status is uncertain. This may also apply to its taxonomic status.

The form '*toulsoni*' ('Loanda Swift') (Bocage 1877) is now considered a dark colour morph of nominate Horus Swift (cf Rosa Pinto 1973, Snow 1978, Dean 2000, Dickinson & Remsen 2013, Stead et al 2013, del Hoyo & Collar 2014, Sinclair et al 2020) (figure 5, plate 88-90); 10 dark-morph birds were examined, eight from Angola and two from Zimbabwe (the type from Angola is lost). In addition, there are at least five distinct locations where dark-morph birds were recorded; at three locations, these birds were photographically documented (one in Angola and two in Congo-Brazzaville). Recently, it has also been recorded in Namibia (Chittenden et al 2016).

The following three Palearctic *Apus* swift clades have been proposed (Leader 2011, Päckert et al 2012): ***1*** Pacific *A pacificus* (with the subspecies *pacificus* and *kurodae* (including '*kanoi*'; *kurodae* was not examined for this study)), Salim Ali's *A salimalii,* Blyth's *A leuconyx* and Cook's Swift *A cooki*; ***2*** Little *A affinis* (with the subspecies *galilejensis*, *bannermani*, *aerobates*, *theresae*, *affinis* and *singalensis*), House *A nipalensis* (with the subspecies *nipalensis*, *subfurcatus*, *furcatus* and *kuntzi*), Horus (with the subspecies *horus* and *fuscobrunneus*) and White-rumped Swift *A caffer*; and ***3*** Pallid Swift *A pallidus* (with the subspecies *brehmorum*, *illyricus* and *pallidus*) and Common Swift *A apus* (with the subspecies *apus* and *pekinensis*). The taxonomy followed in this paper is consistent with the proposed clade arrangement.

## General notes on identification of swifts

### Morphological differences

Size and shape are difficult to establish in flying swifts (table 4). Shape and flight action of swifts are the combined result of body mass, wing length, moult, behaviour and flight conditions, like rain and wind (cf Brooke 1993, Chantler 1993, Chantler & Driessens 1995a, 2000, Lentink et al 2007, Jukema et al 2015, Hedenström & Åkesson 2017). Wing and tail angles change all the time, shifting, for instance, from bulging (plate 92) to streamlined non-bulging primaries (plate 87, 91) in a fraction of a second (Lentink et al 2007, Muir et al 2017). The best way to establish the structure of a flying swift is to study, if available, long series of photographs or high-speed video-recordings of the bird involved.

The elasticity of a swift's feather can also affect its shape; for instance, when the wing or tail is spread in a manoeuvring bird, the feather-webs can stretch out to a surprising degree (plate 86). In windy conditions, a swift can look, when gliding, more rakish (plate 87) (Ahmed et al 2010, Muir et al 2017) while, only a split second later, it can appear heavier while manoeuvring.

It should be kept in mind that *Apus* swifts moult the remiges and rectrices symmetrically. Especially during the early moult stages, missing inner rectrices may give the tail a more forked appearance while missing outer rectrices may give the tail a less forked look.

When studying photographs of flying Horus Swifts, one should always be aware that most have been taken at breeding colonies, often at close range when they are about to enter the nest burrow. Then, they tend to glide more on stretched wings (thus broader), sometimes with spread-out tail to reduce speed. This is less often seen in flying individuals away from breeding sites. Photographs of Horus may often show birds with a proportionately bigger head than other white-rumped *Apus* swifts. However, as pointed out above, most flight photographs are of adults flying to the nest to feed the young and thus having a full crop. Indeed, such birds may look bigger headed (as confirmed by an examination of more than 20 photographed birds). More distantly taken (away from the nesting locations) flight photographs of Horus show birds with normal head proportions.

### Plumage differences

When observing flying swifts, especially in various light conditions, it is difficult to describe the plumage in a satisfactory way. Changing angles of light can have a dramatic effect on their colouration (cf Gilardoni 2016). Also, wear and bleaching can have a distinct effect on the colouration (Chantler & Driessens 1995a, 2000, Ahmed & Adriaens 2010). The bird's hormonal balance is another factor that may affect both colouration (van Diek & van Grouw 2020, Duquet & Reeber 2020) and moult (Jukema et al 2015). It should always be remembered that birds can show individual plumage differences as well (cf Fitzpatrick 1998).

When confronted with a swift that shows characters suggestive of Horus Swift, not only other white-rumped *Apus* swifts (and their presumed hybrids) must be considered but also aberrantly plumaged Pallid Swifts and Common Swifts (Britton 1970, Catley 1978, Sharrock 1978, Vinicombe

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**86** Horus Swift / Horusgierzwaluw *Apus horus*, Gamadji Saré district, Podor department, Saint-Louis region, Senegal, 12 January 2020 *(Nicholas Vinciguerra)*. Note shape of wings and tail, illustrating how feather-webs can stretch in manoeuvring bird. In left half of tail, one rectrix (t2) missing. Throat-patch extending onto upperbreast. Pale head sides barely darker than throat-patch, so hardly any demarcation. Pale band across median under primary coverts and pale-fringed lesser underwing-coverts enhance contrast between pale outer and dark inner underwing. **87** Horus Swift / Horusgierzwaluw *Apus horus*, Gamadji Saré district, Podor department, Saint-Louis region, Senegal, 15 December 2019 *(Jérémy Calvo)*. Note broad hips, pale head with dark eye-patch (somewhat recalling pattern in Pallid Swift *A pallidus*) and medium-forked tail. Longest pale rump feathers (bordering dark uppertail) show diffusely pale tip, as in 23.1% of scored specimens. **88** Horus Swift / Horusgierzwaluw *Apus horus*, Kouilou, Congo-Brazzaville, 14 October 2013 *(Niall Perrins)*. Considered to belong to dark '*toulsoni*' morph. Note dark throat and rump. Keep in mind that throat-patch in dark-morph birds may be as pale as in normal morph Horus. **89** Horus Swift / Horusgierzwaluw *Apus horus*, Tchimpounga National Nature Reserve, 50 km north of Pointe-Noire, Congo-Brazzaville, 22 July 2014 *(Malcolm Wilson)*. Considered to belong to dark '*toulsoni*' morph. Underwing uniformly black-brown, so lacking pale band across median coverts, as many dark-rumped Horus do. Throat-patch small and poorly demarcated and head only slightly paler than rest of body.

1978, Morgan 1990, Blincow et al 1992, Chantler & Driessens 1995b, Meijer 1995, Stegmann 1995, Jacobs 1999, McGuigan 1999, Tenovuo 2003). In a (partially) leucistic *Apus* swift, all leucistic feathers (including the downy feathers) are pure white (van Grouw 2021; Hein van Grouw in litt) as they lack any pigmentation. This contrasts with the feathers of normally coloured white-rumped *Apus* swifts where the downy feathers are darker and may create an off-white colour. The oddest aberrantly plumaged birds we found are shown in plate 105-107.

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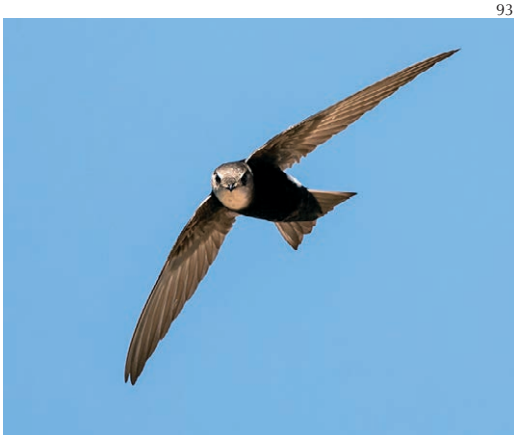

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**90** Horus Swift / Horusgierzwaluw *Apus horus*, Tchimpounga National Nature Reserve, 50 km north of Pointe-Noire, Congo-Brazzaville, 22 July 2014 *(Malcolm Wilson)*. Considered to belong to dark '*toulsoni*' morph. Same bird as in plate 89. Head only slightly paler than blackish saddle. Saddle is darkest part of body. Dark bird with almost blackish rump-patch. **91** Horus Swift / Horusgierzwaluw *Apus horus*, Gamadji Saré district, Podor department, Saint-Louis region, Senegal, 12 January 2020 *(Nicholas Vinciguerra)*. Same bird (from recently discovered colony) as in plate 86. Not all birds have contrasting oily-black saddle. Lower border of rump-patch shows greyish-buff intergrading between pale rump-patch and dark brown uppertail-coverts, which often shows messy paler patches. In photographs, pale trailing edge to secondaries is often overexposed to light and appears more prominent than it really is. Note how broad rump-patch broadens towards rear flank. Sharp tail corners as in this individual are usually result of slightly notched inner web, as in 7.1% of scored specimens. **92** Horus Swift / Horusgierzwaluw *Apus horus*, Sordore, Ethiopia, May 2016 *(Thomas Varto)*. Taken near breeding colony, showing bird gliding on stretched wings (thus broader), as it is most often photographed. Note large white throat-patch with typical trapezium-shaped extension reaching upperbreast (like 44.6% of examined birds), broadly pale-tipped median coverts (showing no visible shaft-streaks) and broadly pale-edged lesser coverts, adding to effect of paler outer-wing. Also, note typical tail shape with fully pointed (and straight-edged) outermost rectrix. Fully stretched wing when gliding often appearing broader than when in more regular feeding flight. **93** Horus Swift / Horusgierzwaluw *Apus horus*, Lüneburg, South Africa, December 2008 *(Warwick Tarboton)*. Taken near breeding colony. In this individual, forehead rather brown, partly taking away pale-faced impression; nevertheless, throat-patch running out smoothly upwards behind eye to add to species' pale-headed impression. Pale-tipped median under primary coverts showing distinct shaft-streaks while lesser under primary coverts are distinctly pale fringed, enhancing effect of paler outer underwing. Rump-patch is seen even from this angle.

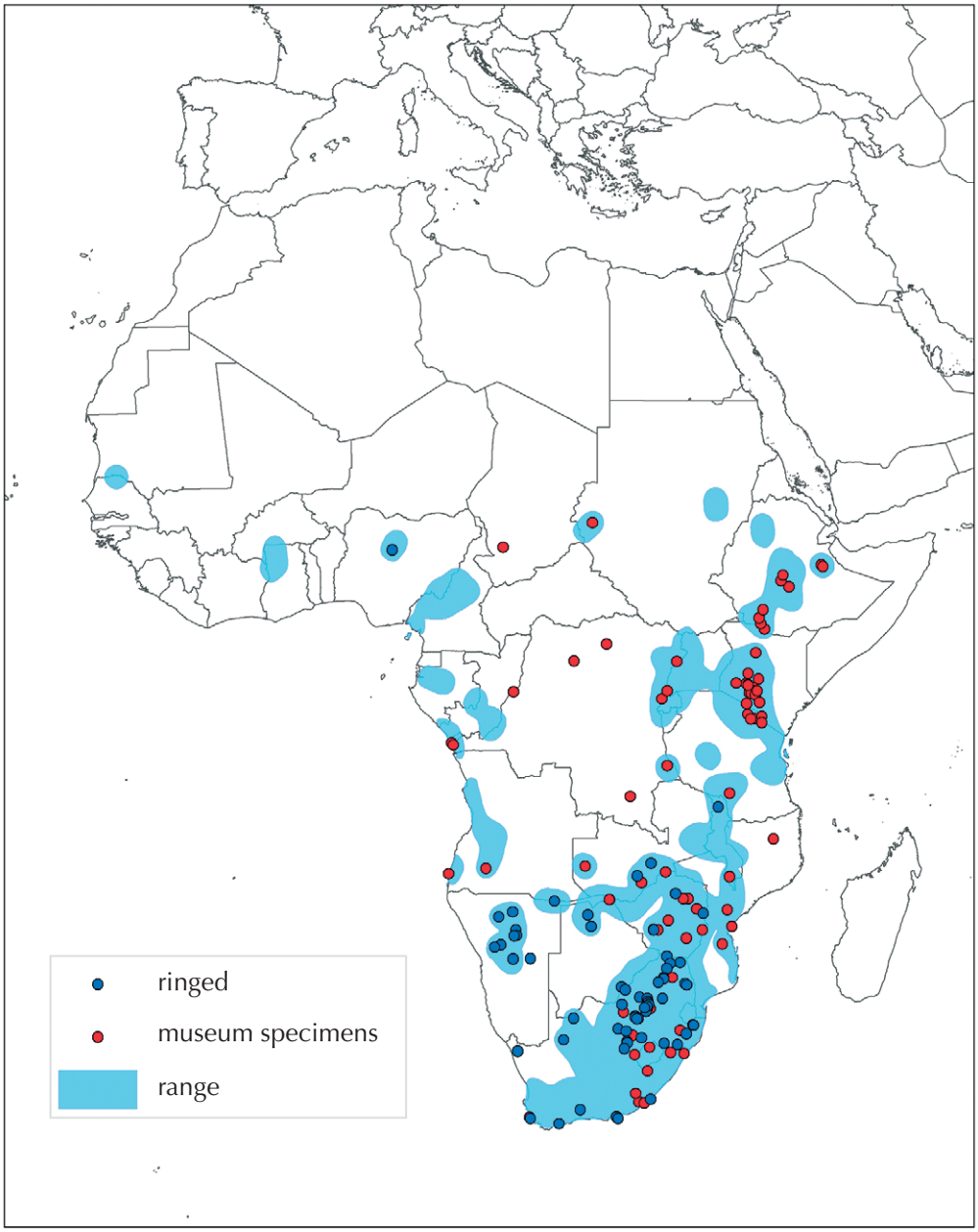


FIGURE 2 Collecting sites and ringing locations of Horus Swift / Horusgierzwaluw *Apus horus* specimens used in this study

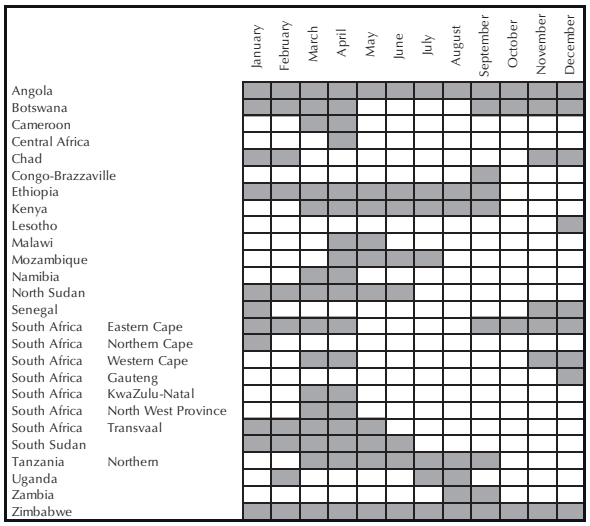


FIGURE 3 Timing of known breeding season of Horus Swift / Horusgierzwaluw *Apus horus* throughout Africa. Based on Taylor 1949, Clancey & Holliday 1951, Dickin 1952, Brooke 1971a, Clancey 1984, Nikolaus 1987, Fry et al 1988, Brown 1989, Lewis & Pomeroy 1989, Ash 1990, Chantler & Driessens 1995a, 2000, Zimmerman et al 1999, Languy et al 2005, Ash & Atkins 2010, Dowsett-Lemaire & Dowsett 2014, Hancock & Weiersbye 2015, López Velasco & Kalema 2018, Chantler & Boesman 2020, Piot & Bacuez 2021; Gary Allport in litt, Max Berlijn in litt, Michael Mills in litt.

**Age differences**

It is not known how long the juvenile plumage is kept in many *Apus* swifts, especially in tropical species including Horus Swift. Tropical species may be less well adapted to winter-season conditions (Foster 1975). Thus, ageing of white-rumped *Apus* swifts is hindered by incomplete, sometimes confusing, information in the literature. According to Brooke (1971a), juvenile Horus have blunt-tipped outermost rectrices, and tend to have a smaller white rump-patch and show dark shaft-streaks in the white body parts. Fry et al (1988) pointed out that juvenile Horus can be distinguished from adults by their pale-fringed body feathers. However, recently moulted adults may also have narrow white fringes to the fresh underpart feathers (Chantler & Driessens 1995a, 2000).

**Hybrids**

Relatively little is known about hybridisation and hybrids in swifts. Although the rather recent developments in digital photography have increased possibilities to document field characters in detail, the limited time that swifts spent roosting, prevents a detailed field study of subtle differences and colours.

There are some cases of proven hybridisation in swifts in WP species: there is a case of hybridisation between White-rumped Swift and Little Swift (two individuals) in one of the rare Spanish colonies of Little (Jansen et al 2023). Secondly, a DNA study in Corsica, France, demonstrated that hybridisation between Pallid Swift and Common Swift is far more common than was previously assumed (Cibois et al 2022).

In the field as well as on photographs, both hybrids White-rumped x Little Swift showed some quite 'obvious' characteristics referring to both parent species. These hybrids proved to be morphologically very close to Horus Swift (Jansen et al 2023). It is, however, a well-known phenomenon that hybrids often resemble a third species rather than the parents (Driessens & van Grouw 2017). Recognition of hybrids Pallid x Common Swift will prove to be extremely difficult based on field observations or photographs since characters of both species are subtle and their variation is considerable.

Due to a lack of information and research, it was impossible to deal with all potential swift hybrids in this study. However, if well documented, we assume that it will usually be possible to establish whether an aberrant individual shows mixed characters of two species (indicating a hybrid), or whether all characters fit within the expected variation of one species.

## Variation in Horus Swift

**Measurements**

For the purposes of our study, we divided Horus Swift into three regional groups: ***1*** eastern Africa: Ethiopia, Kenya, Tanzania and west to Congo-Kinshasa; ***2*** southern Africa: Zimbabwe, Mozambique and South Africa; and ***3*** western Africa: south to Namibia. Horus from southern African populations have, on average, longer wings than those from more northern populations (Clancey 1984) but we found this difference far too small to be used in separating southern birds from northern ones, even in the hand.

**Moult**

Knowledge of the moult of Horus Swift is still incomplete. Primary moult may last 6-7 months (based on the assumption that it is comparable with that of the migratory Common Swift) (De Roo

TABLE 1 Number of examined specimens of *Apus* swift species per museum (with their acronyms). For Horus Swift *A horus*, numbers are divided over subspecies/colour morphs.

| Museum | Acronym | Horus | | | Little | House |
|---|---|---|---|---|---|---|
| | | ***A h horus*** | ***A h fuscobrunneus*** | ***A h 'toulsoni'*** | ***A affinis ssp*** | ***A nipalensis ssp*** |
| American Museum of Natural History, New York, USA | AMNH | 21 | – | 1 | 123 | 28 |
| Academy of Natural Sciences, Philadelphia, USA | ANSP | 2 | – | – | 12 | – |
| Canadian Museum of Nature, Ottawa, Canada | CMN | – | – | – | 1 | – |
| Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA | CM | 1 | – | – | – | – |
| Cornell University Museum of Vertebrates, Ithaca, New York, USA | CUMV | 1 | – | – | – | – |
| Ditsong Transvaal Museum, Pretoria, South Africa | DNMNH | 14 | – | – | – | – |
| Durban Natural Science Museum, Durban, South Africa | DM | 7 | – | – | – | – |
| East London Museum, East London, South Africa | ELM | 5 | – | – | – | – |
| Field Museum of Natural History, Chicago, USA | FMNH | 6 | – | – | – | – |
| Florida Museum of Natural History, Gainesville, USA | FLMNH | – | – | – | – | 15 |
| Instituto Superior da Ciências e Educação, Lubango, Angola | ISCED | 3 | 8 | 4 | – | – |
| Lee Kong Chian Natural History Museum, Singapore | ZRC | – | – | – | – | – |
| Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana, USA | LSUMZ | 2 | – | – | – | – |
| Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA | MCZ | 1 | – | – | – | – |
| Muséum national d'Histoire naturelle, Paris, France | MNHN | 1 | – | – | – | – |
| Museu Nacional de História Natural e da Ciência, Lisboa, Portugal | MUHNAC | – | – | 1 | – | – |
| Museum für Naturkunde, Berlin, Germany | ZMB | 6 | – | – | 14 | 4 |
| Naturalis Biodiversity Center, Leiden, Netherlands | Naturalis | – | – | – | 7 | 48 |
| Natural History Museum, Tring, England | NHMUK | 22 | – | 1 | 257 | 79 |
| Natural History Museum of Los Angeles County, Los Angeles, USA | LACM | 12 | – | – | – | – |
| National Museum of Scotland, Edinburgh, Scotland | NMS | – | – | – | 16 | 1 |
| Nationale Museum, Bloemfontein, South Afrika | NMBV | 3 | – | – | – | – |
| Naturhistorisches Museum Wien, Wien, Austria | NMW | 3 | – | – | – | 2 |
| Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe | NMZB | 55 | – | 3 | – | – |
| Naturhistoriska Riksmuseet, Stockholm, Sweden | NRM | 1 | – | – | – | – |
| Royal Museum for Central Africa, Tervuren, Belgium | RMCA | 7 | – | – | 40 | – |
| Royal Ontario Museum, Toronto, Canada | ROM | 2 | – | – | – | – |
| Smithsonian Institution, National Museum of Natural History, Washingon, USA | USNM | 10 | – | – | 22 | 110 |
| Übersee-Museum, Bremen, Germany | UMB | – | – | – | 6 | – |
| University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA | UMMZ | 2 | – | – | – | – |
| University of Washington Burke Museum, Seattle, Washington, USA | UWBM | 1 | – | – | – | – |
| Western Foundation of Vertebrate Zoology, Camarillo, California, USA | WFVZ | 1 | – | – | – | – |
| Yale Peabody Museum, New Haven, Connecticut, USA | YPM | 1 | – | – | – | – |
| Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany | ZFMK | 2 | 2 | – | 4 | 1 |
| **Totals** | | **192** | **10** | **10** | **502** | **288** |

TABLE 1 (continued)

| Acronym | White-rumped *A caffer* | Pacific *A pacificus* | Blyth's *A leuconyx* | Salim Ali's *A salimalii* | Cook's *A cooki* | Pallid *A pallidus* ssp | Common *A apus* ssp |
|---|---|---|---|---|---|---|---|
| AMNH | 37 | 62 | – | – | 13 | 111 | 247 |
| ANSP | 2 | 23 | – | – | – | 4 | 20 |
| CMN | – | – | – | – | – | – | – |
| CM | – | – | – | – | – | – | – |
| CUMV | – | – | – | – | – | – | – |
| DNMNH | – | – | – | – | – | – | – |
| DM | – | – | – | – | – | – | – |
| ELM | – | – | – | – | – | – | – |
| FMNH | – | – | – | – | – | – | – |
| FLMNH | 12 | – | – | – | – | – | 30 |
| ISCED | – | – | – | – | – | – | – |
| ZRC | – | 4 | – | – | – | – | – |
| LSUMZ | – | – | – | – | – | – | – |
| MCZ | – | – | – | – | – | – | – |
| MNHN | – | – | – | – | – | – | – |
| MUHNAC | – | – | – | – | – | – | – |
| ZMB | 15 | 14 | 2 | 3 | 3 | 19 | 73 |
| Naturalis | 8 | 27 | – | – | – | 16 | 25 |
| NHMUK | 72 | 80 | 18 | 25 | 26 | 130 | 379 |
| LACM | – | – | – | – | – | – | – |
| NMS | – | – | – | – | – | – | – |
| NMBV | – | – | – | – | – | – | – |
| NMW | 5 | 38 | – | – | – | – | – |
| NMZB | – | – | – | – | – | – | – |
| NRM | – | – | – | – | – | – | – |
| RMCA | 35 | – | – | – | – | – | – |
| ROM | – | – | – | – | – | – | – |
| USNM | 14 | 38 | – | – | 17 | 33 | 57 |
| UMB | 1 | – | – | – | – | – | 11 |
| UMMZ | – | – | – | – | – | – | – |
| UWBM | – | – | – | – | – | – | – |
| WFVZ | – | – | – | – | – | – | – |
| YPM | – | – | – | – | – | – | – |
| ZFMK | – | – | – | – | – | – | – |
| | **201** | **286** | **20** | **28** | **59** | **313** | **842** |

TABLE 2 Number of examined specimens and ringed individuals of Horus Swift *Apus horus* per country (latter supplied by Safring database)

| **Country of origin** | **Specimens in museums** | | | **Ringed individuals** |
|---|---|---|---|---|
| | *A h horus* | *A h 'toulsoni'* | *A h fuscobrunneus* | *A h horus* |
| Angola | 5 | 8 | 10 | – |
| Botswana | 1 | – | – | 3 |
| Chad | 1 | – | – | – |
| Congo-Kinshasa | 10 | – | – | – |
| Ethiopia | 23 | – | – | – |
| Kenya | 47 | – | – | – |
| Lesotho | 1 | – | – | – |
| Malawi | 2 | – | – | – |
| Mozambique | 9 | – | – | 2 |
| Namibia | 1 | – | – | 16 |
| Nigeria | – | – | – | 1 |
| South Africa | 24 | – | – | 71 |
| South Africa, KwaZulu-Natal | 3 | – | – | – |
| Sudan | 1 | – | – | – |
| Tanzania | 13 | – | – | – |
| Uganda | 4 | – | – | – |
| Zambia | 3 | – | – | 2 |
| Zimbabwe | 40 | 2 | – | 5 |
| Unknown | 4 | – | – | – |
| **Totals** | **192** | **10** | **10** | **100** |

1966, Herroelen 1998). No primary moult was shown by 16 birds trapped in southern Africa in November-December but two birds trapped there in January-April were in active primary moult (Safring database). Birds actively moulting their primaries have also been recorded in February (Senegal), June (Tanzania), October (Congo-Brazzaville) and December (Senegal) (Piot & Bacuez 2021; eBird [accessed 28 August 2021]). A combination of moulting/not-moulting Horus with their known local breeding periods revealed that most adults start moulting their body feathers at the end of their breeding season (which varies a lot geographically, see figure 3) or shortly after. Later, usually when the last body feathers are being replaced, it is followed by the moult of the flight feathers, starting with the inner primaries. Because breeding can occur in two or even more different time blocks in some areas, it is difficult to estimate the exact timings of moult; however, the whole moult cycle probably takes c 3-4 months. Note that wear (accelerated by the species' habit of nesting and sleeping in burrows) and bleaching (due to prolonged exposure to solar radiation as in other *Apus* swifts) have marked effects on its plumage (Brooke 1971a, Fry et al 1988).

**Breeding**

Breeding of Horus Swift has been observed in all months of the year, and the rainy season may have no or only a limited effect on breeding (figure 3). In addition to the countries listed in figure 3, the species (possibly) breeds in Burundi, Eritrea, Eswatini (formerly named Swaziland), Gabon, Ghana, Niger, Nigeria and Rwanda (Elsgood et al 1994, Crisler et al 2003, Borrow & Demey 2004, Dowsett-Lemaire & Dowsett 2014). It is unknown at what age Horus breed for the first time.

Horus Swift is supposed to be an intra-African migrant (eg, Chantler & Driessens 1995a, 2000). Birds reported at locations away from breeding areas (for instance, in the Ethiopian Highlands and in coastal areas of Ghana and Namibia) (figure 1) may involve migrants. However, little is known about its migratory or dispersive movements. This also applies to the species' non-breeding ranges (Hockey et al 2005).

## Materials and methods

**General approach**

This study's focus was on Horus Swift and other white-rumped *Apus* swifts in the world, with emphasis on WP species. However, because of the existence of aberrantly plumaged birds, also some dark-rumped *Apus* swifts (Pallid Swift and Common Swift) were (partly) investigated, although, despite investigating 313 specimens of

**94** Horus Swifts / Horusgierzwaluwen *Apus horus*, Eastern Cape province, South Africa, 7 January 2019 *(Michael Buckham)*. Note tail with medium-sized fork on right-hand bird. Grey-brown graduation (or 'graduated tone') between pale rump-patch and dark brown uppertail-coverts is visible in right-hand bird. Also, note how shadow can darken pale throat-patch easily; pale head-sides with dark eye-patch and pale supercilium remain visible to form paler brown head. **95** Horus Swift / Horusgierzwaluw *Apus horus*, Gamadji Saré district, Podor department, Saint-Louis region, Senegal, 12 January 2020 *(Nicholas Vinciguerra)*. Note extremely well-patterned underwing, showing important (but variable) character of Horus: pale band across outer underwing, formed by broad pale tips to median underwing-coverts. Pale-edged lesser and marginal underwing-coverts add to effect of pale outer underwing, standing out against darker innerwing. Also, note paler head with dark eye-patch, and throat-patch merging with browner cheek behind eye in this individual.

Pallid (table 1), we do not report on those species here because its general plumage colouration prevents confusion with Horus. Our study lasted from September 2019 to March 2023.

For white-rumped *Apus* swifts, we have tried to meet the minimum sample size of 59 specimens for each trait (Sangster 2021). The basis for these findings are 39 traits and their individual patterns (table 3). Each discussed taxon was compared with Horus Swift and the three traits with the highest sensitivity/importance to distinguish both taxa are shown. We illustrate our findings in illustrations and tables (figure 4-5, 9-12 and 15) that complement each other. Furthermore, the numbers of examined specimens are given (table 1).

**Examined material**

In total, 212 Horus Swift specimens (originating from 27 museums) were examined (figure 2, table 1-2). For the acronyms of the museums, see table 1. From the examined specimens, 93 male and 82 female Horus specimens were sexed (sexing as on label). Most specimens were collected in February-March and May-July. Ringing data of eight pulli, 23 juveniles or immatures and 67 adults (10 unaged) (up to 22 February 2021), supplied by the Safring database, were used (figure 2, table 2). Horus (74) specimens and other *Apus* specimens from AMNH, ANSP, Naturalis, NHMUK, RMCA, USNM, ZFMK and ZMB were examined in situ (specimens were randomly chosen, not pre-selected). At other museums, staff were requested to photograph the Horus specimens in their collections (preferably, from dorsal, ventral and lateral positions).

Six Horus Swift specimens (five from Naturalis and one from AMNH) appeared to be misidentified White-rumped Swifts, and one specimen

TABLE 3 Traits and their patterns used to characterise the *Apus* swifts examined for this study

| Feature | Trait | Pattern |
|---|---|---|
| **1** | **Upperhead**: colour difference between forehead and crown | 1 Cream to pale brown, paler than crown<br>2 Brown to brown-grey as crown<br>3 Darker than crown |
| **2** | **Supercilium**: presence and contrast | 1 Broadly white/pale grey edged and brownish centred<br>2 Narrowly white/pale grey edged and brownish centred<br>3 Edged paler brown<br>4 Uniformly blackish-brown |
| **3** | **Orbital feathers**: presence of black mark | 1 C-shaped velvet mark front of the eye<br>2 Dark mark enclosing eye<br>3 Not prominently present |
| **4** | **Crown**: colour differences between nape and ear-coverts | 1 Uniform with or slightly paler than ear-coverts<br>2 Darker than ear-coverts but paler than mantle |
| **5** | **Crown**: scaling | 1 No scaling to crown feathers<br>2 Narrow scaling to crown feathers |
| **6** | **Nape and hindneck**: differences between crown and mantle | 1 Darker than crown<br>2 Nape/hindneck uniform to crown<br>3 Paler than crown |
| **7** | **Lore**: colour difference with forehead | 1 Darker than forehead<br>2 Uniform with forehead<br>3 Paler brown than forehead |
| **8** | **Lore and face**: pale-faced impression | 1 Contiguous with paler face<br>2 Browner, not conitiguous with pale face |
| **9** | **Ear coverts**: colour and pattern | 1 Pale brown, at most slighly darker than throat<br>2 Mid brown, merging with moustachial area<br>3 Mid brown, pale tips creating barred effect<br>4 Mid brown, sharply defined from moustachial area<br>5 Dark brown, slighly merging with throat patch<br>6 Dark brown, sharply contrasting with throat patch |
| **10** | **Throat**: colour | 1 Uniformly whitish<br>2 Uniformly creamy<br>3 Slightly greyish<br>4 Brownish |
| **11** | **Throat**: moustachial demarcation from throat-patch | 1 Sharply contrasting patch (dark/white impression)<br>2 Rather contrasting patch<br>3 Not sharply defined throat patch<br>4 Throat patch hardly defined |
| **12** | **Throat**: length | 1 Small patch (restricted to throat)<br>2 Patch covering throat area, not reaching upper breast<br>3 Large patch, extending onto upper breast |
| **13** | **Throat**: shape | 1 Oval/egg shaped<br>2 Rather triangular shaped (broadest towards breast)<br>3 Slightly pointed towards breast<br>4 Trapezium-shaped extension towards breast |
| **14** | **Throat**: width | 1 Broad patch (pale head from below)<br>2 Broad patch, brown cheeks just visible<br>3 Narrow patch (dark cheeks from below) |
| **15** | **Throat**: shaft-streaks | 1 Shaft-streaks probably visible in field photographs<br>2 No (clear) shaft-streaks |
| **16** | **Chin**: colour | 1 White or whitish<br>2 Greyish or creamy white<br>3 Brownish |
| **17** | **Breast**: chest-area | 1 Uniformly black-brown as central underparts<br>2 Slightly paler dark grey-brown band<br>3 Mottled blackish and dark brown band<br>4 Rather pale brown, scalloped dark and pale-fringed |
| **18** | **Flank**: pattern | 1 White of rump extending near legs<br>2 White of rump extending to rear flank<br>3 White of rump does not reach rear flanks<br>4 Lacking or ghostly brown impression on rear flanks |
| **19** | **Flank and rump from below**: pattern | 1 Rump-patch visible from below<br>2 Rump-patch not visible from below |
| **20** | **Belly**: colour | 1 Brown with subterminal markings and pale tips (scalloped)<br>2 Dark brown with subterminal markings<br>3 Uniform black-brown<br>4 Ghostly scaled brown and dark brown (juvenile type)<br>5 Glossy black-brown |
| **21** | **Undertail-coverts**: colour | 1 Uniformly coloured black-brown<br>2 Uniformly coloured mid brown<br>3 Black-brown with browner feather bases<br>4 Black-brown, narrowly fringed whitish (<1 mm)<br>5 Black-brown, clearly and broadly fringed white (>1 mm) |
| **22** | **Undertail-covert panel**: contrast | 1 Clearly paler than belly<br>2 Slightly paler than belly<br>3 Uniform with belly colour |

TABLE 3 (continued)

| | | |
|---|---|---|
| **23** | **Rump**: shape | 1 C-shaped, broader towards flanks<br>2 C-shaped white, parallel shaped<br>3 Rectangular white<br>4 Ghostly impression of rump-patch<br>5 No rump-patch |
| **24** | **Rump**: colour | 1 Rump whitish<br>2 Rump slightly washed creamy of buffish<br>3 Rump with messy buffy-brown areas<br>4 Rump dark brown as lower rump area |
| **25** | **Rump**: patterns | 1 Shaft-streaks probably visible on field photographs<br>2 No shaft-streaks in rump-patch |
| **26** | **Lower rump**: contrast of border | 1 Well defined<br>2 Ill defined |
| **27** | **Lower rump**: colour | 1 Blackish as saddle<br>2 Slightly browner than saddle<br>3 Slightly browner, showing paler fringes |
| **28** | **Lower rump and shortest uppertail-coverts**: pattern | 1 Uniform black-brown<br>2 Somewhat paler brown, no paler tips<br>3 Feathers paler and diffusely tipped near rump<br>4 Feathers dark brown and narrowly tipped near rump<br>5 Sharp white/pale fringes near rump |
| **29** | **Lower rump and shortest uppertail-coverts**: contrast | 1 Contrastingly black-brown<br>2 Merging area near rump is smooth<br>3 Merging area near rump is patchy |
| **30** | **Saddle effect**: colour | 1 Uniform with hindneck and lower rump<br>2 Darkest part on upperparts and dull black-brown<br>3 Darkest part on upperparts and glossy black-brown |
| **31a** | **Outer rectrices**: shape left | 1 Rounded feather<br>2 Rounded feather slighly tapering<br>3 Pointed feather with rounded point<br>4 Pointed feather with tapering point<br>5 Fully pointed tip (straight webs)<br>6 Pointed, sligtly emarginated inner-web<br>7 Spiky but bluntly tipped (juvenile *caffer* type)<br>8 Streamered, clearly emarginated |
| **31b** | **Outer rectrices**: shape right | 1 Rounded feather<br>2 Rounded feather slighly tapering<br>3 Pointed feather with rounded point<br>4 Pointed feather with tapering point<br>5 Fully pointed tip (straight webs)<br>6 Pointed, sligtly emarginated inner-web<br>7 Spiky but bluntly tipped (juvenile *caffer* type)<br>8 Streamered, clearly emarginated |
| **32** | **Upperside tail**: colour | 1 Deep black<br>2 Uniform dark-brown<br>3 Dull black-brown with blackish fringe |
| **33** | **Primaries**: fringing | 1 No visible primary fringes<br>2 Clear but fragmented primary fringes<br>3 Clear and contiguous primary fringes |
| **34** | **Greater upper primary coverts**: fringing | 1 No or hardly visible paler fringe<br>2 Faint but visible grey-brown edge<br>3 Easily visible, broader edge (grey-brown) |
| **35** | **Pale tip to longest tertial**: colour and width | 1 No trailing edge whatsoever<br>2 Brown trailing edge<br>3 Grey-white trailing edge<br>4 Broad white trailing edge >1 mm |
| **36** | **Trailing edge to secondaries**: colour | 1 No trailing edge whatsoever<br>2 Brown traling edge < 1 mm<br>3 Grey-white trailing edge<br>4 Broad clear white trailing edge >1 mm |
| **37** | **Lesser under primary coverts**: fringe colour | 1 No fringing at all<br>2 Pale fringes showing weak contrast<br>3 Clear but narrow fringing, inconspicuous compared to dark parts<br>4 Obvious creamwhite tips, probably visible in the field |
| **38** | **Median underwing-coverts**: pattern | 1 Unmarked black-brown (as belly)<br>2 Unmarked mid brown to brown-grey, paler than belly<br>3 Brown tot black-brown with narrow pale tips<br>4 Brown based with broad merging whitish-grey distal part |
| **39** | **Median underwing-coverts**: shaft-streaks | 1 No shaft-streaks<br>2 Narrow to obvious dark brown shaft-streak |

(from CMN) was a Little Swift. Conversely, a specimen from NRM labelled as White-rumped was a Horus.

Museum staff were requested to photograph specimens of other *Apus* species in their collections to meet a lower sample-size threshold of 59 specimens, if possible (cf Sangster 2021). A larger series was examined whenever possible (table 1). Photographs were received from FMNH, NHMUK, NMS, NMW and ZRC. Material included specimens of Blyth's, Salim Ali's and Cook's Swift. These three species have never occurred in the WP and their identification is being discussed in more detail in appendix 2 for the sake of completeness (cf Leader 2011, Leader et al 2020). We only sampled a limited number of specimens of these species mainly due to their restricted availability or because of time constraints.

Photographs of more than 30 Horus Swifts, taken in Ethiopia, Senegal, South Africa and Uganda were examined. Also, photographs of three birds considered to belong to the dark '*toulsoni*' morph were examined: one (by Niall Perrins) of a bird at Kouilou, Congo-Brazzaville, on 14 October 2013 (plate 88); two (by Malcolm Wilson) of an adult ringed at Tchimpounga National Nature Reserve, 50 km north of Pointe-Noire, Congo-Brazzaville, on 22 July 2014 (plate 89-90); and several (by Callan Cohen and Derek Engelbrecht) of a bird at Kanjonde, at the foot of Mount Moco, Angola, on 18 May 2018.

**Definition of ageing criteria**

Our examination of juvenile characters was often hindered by the worn state of the specimens. Hence, museum collections were screened for the presence of nestlings wearing a juvenile or near-juvenile plumage. Fully grown juveniles strongly resemble such nestlings because they still wear the same feathers, already present in nestlings. In the end, we identified combinations of characters that often allowed ageing of white-rumped *Apus* swifts in the field.

**Scoring system**

After a testing phase with all white-rumped *Apus* swifts, we established 39 traits and added variation patterns to the individual traits (varying between two and eight, see table 3). The specimens were designated (if the trait could be assessed) to one of the patterns. All specimens were examined by Gerald Driessens to deduct differences in the scores.

Scoring the limited number of plumage colours found in the studied *Apus* specimens can be perceived as arbitrary. To objectively determine the non-existing (relative) limits, we categorised the field characters or plumage variations. Fortunately, in several patterns, these limits are absolute (for instance, *paler than* or *darker than*, *uniform with …*, *the presence of* or *the absence of* …). In several other patterns, however, these limits were more diffuse, and one pattern transited into the other (for instance, an oval-shaped or slightly pointed throat-patch, rectrices being pointed or with a slightly tapering point). If a field character fell between two patterns, we chose the one it would probably resemble the most in field conditions.

We furthermore defined three mensural characters encompassing details of the tail and primaries. The wing length was measured to the nearest 0.5 mm. The tail length was determined by inserting a pair of dividers down to the shaft-base of the central rectrices (t1) and measuring from that point to the tips to the other rectrices (cf Svensson 1992). The measurements of the wing (and the primaries) were taken by GD and those of the tail (and the rectrices) by Justin Jansen. It should be noted that measurements of specimens do not always match those of live birds because of the possibility of shrinking, especially in old skins (Vepsäläinen 1968).

The selected patterns could not be examined in all specimens, mainly because some specimens were too damaged, or due to preparatory state or photographed angle. For some specimens, only a few patterns could be examined. We thus mention the number (n) of Horus Swift specimens examined for each pattern. For examined traits and patterns, see table 3. Percentage values were rounded to one decimal.

We performed a principal component analysis (PCA) using the hetcor function in the R package (R core team 2022) 'polycor' on 20 categorical morphological traits of eight morphologically similar *Apus* species (figure 20). Before analysis, we scaled the ordinal variables (Pearson correlation used for ordinal variables) and used the two nominal variables as factors, filling a heterogeneous correlation matrix using a mixture of polychoric, polyserial and Pearson correlations for the PCA. The results reveal a 39.7% of explained variance for the first two principal components.

A chi-square test was used to establish differences in sex and region for Horus Swift. However, we did not find diagnosable differences.

# Results

## Characters

The examined characters of adult Horus Swift are treated in the following order: head and neck, underparts, upperparts, tail, upperwing, underwing and measurements. Additionally (although exceptionally), we discuss juveniles, and if so, this is clearly mentioned.

### Head and neck (character 1-16)

1 UPPERHEAD: COLOUR DIFFERENCE BETWEEN FOREHEAD AND CROWN (N=92) In most specimens (73.9%), the forehead was paler than the crown, cream-coloured to pale brown, enhancing a 'pale-faced' impression (like in a flying bird when viewed head on). In 26.1%, the forehead and crown were uniformly coloured. No Horus Swift was found with a forehead darker than the crown (0%).

2 SUPERCILIUM: presence and contrast (n=98). In most specimens (85.7%), the dark-based and white- to grey-edged feathers of the supercilium, varying in width from narrow to broad, showed a distinct contrast with the dark eye-patch. In 14.3%, especially in worn specimens, the supercilium was edged paler brown. Female specimens showed a narrower supercilium more often (80%) than male specimens (50%).

3 ORBITAL FEATHERS: PRESENCE OF BLACK MARK (N=118) All specimens showed a distinct c-shaped black mark and a browner central part of the eye-patch, which separates the dark mark from the eye. This character may be visible in birds photographed at close distance or in ideal light conditions but, in most circumstances, it will prove to be hidden by shadow. Only one out of 10 juvenile specimens (10.0%) showed indistinct orbital feather markings.

4 CROWN: COLOUR DIFFERENCES BETWEEN NAPE AND EAR-COVERTS (N=118) In most specimens (66.9%), the crown and ear-coverts were similarly coloured while the crown was slightly darker than the ear-coverts (but still paler than the nape in 33.1%).

5 CROWN: SCALING (N=118) Most specimens (95.8%) showed no pale scaling on the crown; the crown feathers were narrowly pale tipped in only 4.2%. Nine out of 11 juvenile specimens (81.8%) showed pale scaling on the crown (a pattern also seen in juveniles of most other white-rumped *Apus* swifts).

6 NAPE AND HINDNECK: DIFFERENCES BETWEEN CROWN AND MANTLE (N=133) In most specimens (51.2%), the nape and hindneck were darker than the crown, but there was no contrast between the nape and hindneck and the crown in 48.1%. In one specimen (0.7%) (AMNH 810057 from Kenya), nape and hindneck appeared paler than the crown (unlike other specimens collected at the same localities). There were more 'darker-naped' females than males.

7 LORE: COLOUR DIFFERENCE WITH FOREHEAD (N=118) In most specimens (70.3%), the lore was marginally paler than the forehead but the lore and forehead were similarly coloured in 29.7%.

8 LORE AND FACE: PALE-FACED IMPRESSION (N=121) In most specimens (85.1%), the pale forehead, paler lore and throat-patch enhanced a pale-faced impression but in 14.9% the slightly darker lore reduced the pale-faced impression. Hence, in frontal view, the bill usually stood out as an isolated dark mark.

9 EAR-COVERTS: COLOUR AND PATTERN (N=120) Most specimens (77.5%) had mid brown ear-coverts that merged with the washed-out buffy-grey moustachial area. In 11.7%, the similarly coloured ear-coverts were sharply demarcated from the paler moustachial area but the pale brown ear-coverts were only a shade darker than the throat-patch and moustachial area in 9.2%, representing the palest and most strikingly patterned specimens. Two specimens (BMNH 1946.5.368, Chikwawa, Southern Region, Malawi; and BMNH 1857.4.42, sine loco) showed darker brown ear-coverts only slightly merging with the throat-patch (1.6%). This may result in a contrasting throat-patch in the field.

10 THROAT: COLOUR (N=169) Most specimens (76.3%) showed a uniform cream-coloured hue over the whitish throat-patch (usually matching the colour of the rump-patch) while 14.2% showed a whiter throat-patch. In 9.5%, the throat-patch was more brownish or greyer, compared with the rump-patch, resulting in a more pale-headed appearance with a less striking throat-patch.

11 THROAT: MOUSTACHIAL DEMARCATION FROM THROAT-PATCH (N=157) In most specimens (66.2%), the throat-patch was well defined with a smooth border but it was ill defined in 17.2%. Some specimens had either a contrasting throat-patch (in 14%) or even a sharply contrasting one (in 2.6%), resulting in a 'dark-and-white' impression that approached the appearance of other white-rumped *Apus* swifts.

12 THROAT: LENGTH (N=170) In most specimens (65.9%), the throat-patch covered the entire throat area but did not reach the upper breast; however, it covered the entire throat area and extended onto the upper breast in 34.1%.

13 THROAT: SHAPE (N=168) Most specimens (44.6%) had a large throat-patch, with a distinct trapezoid to rectangle towards or on the upper breast. In 26.2%, the throat-patch was triangular and broadest towards the breast. In 16.1%, the throat-patch was slightly pointed towards the breast while it was oval- or egg-shaped and restricted to the throat-patch area in 13.1%.

14 THROAT: WIDTH (N=165) Most specimens (66.1%) had a broad throat-patch; such birds will look pale headed when viewed from below. 31.5% showed a slightly narrower throat-patch, with the brown ear-coverts showing along the head-side. In four specimens (2.4%), the brown ear-coverts were obvious because of the distinctly narrower throat-patch.

15 THROAT: SHAFT-STREAKS (N=161) Most specimens (82.0%) had no dark shaft-streaks to the pale throat feathers but 18.0% showed scattered narrow dark shaft-streaks on the throat-patch (probably not visible in photographs taken in the field).

16 CHIN: COLOUR (N=169) Most specimens (76.3%) showed a slightly cream-coloured or greyish chin; other specimens showed either a whitish (13.6%) or a brownish chin (10.1%).

FIGURE 4 Horus Swift / Horusgierzwaluw *Apus horus (Gerald Driessens)*. *Idealised* version ('majority vote' of all characters combined) of adult Horus Swift showing all diagnostic and near-diagnostic features in dorsal and ventral postures. Within white-rumped swift group, Horus has palest head. The most striking birds have pale head down to upperbreast, throat-patch showing hardly any contrast with browner side of head (even surpassing effect known from many Pallid Swifts *A pallidus*). Note that broad rump-patch is wrapped around body and quite easily seen from below. Horus is unique in (usually) showing faint to obvious pale band over distal half of median under primary coverts.

**Underparts (character 17-22)**

17 BREAST: CHEST-AREA (N=156) In most specimens (80.8%), a dark grey-brown band contributed to a subtly greyer transition zone between the pale throat-patch and the dark to blackish belly. However, the breast was dark brown and showed blackish mottling in 11.5%, while it was uniform black-brown and was uniform with the belly in 7.7%. This character is very subtle and not visible in field photographs.

18 FLANK: PATTERN (N=151) In most specimens (70.9%), the white of the rump-patch extended to the thigh but the extended white of the rump-patch was (only a little) more restricted up to the rear flank in 29.1%. This is an arbitrary difference, especially in worn specimens.

FIGURE 5 Horus Swift / Horusgierzwaluw *Apus horus fuscobrunneus*/'*toulsoni*' *(Gerald Driessens)*. *Idealised* version ('majority vote' of all characters combined) of both *fuscobrunneus* and dark morph '*toulsoni*'. This subspecies and dark morph are not separable based on morphology. Both should be considered as dark (brown) colour morph of Horus Swift, with darker head and lacking rump-patch being main difference. Although some individuals show classical throat-patch as in nominate *horus*, most birds have more restricted oval throat-patch (figure 7) and in general much darker underwing (figure 8). Note that some birds can look markedly blacker than depicted individual.

FIGURE 6 Horus Swift / Horusgierzwaluw *Apus horus (Gerald Driessens)*. Nine adult phenotypes (10th is shown in figure 4). Note 'pale-faced' impression when viewed head on and variation in head, wing and tail shape depending on posture. Note broad hips in figures bottom left and right. Some different throat-patch shapes and underwing patterns (uniform, faint pale band, and clear pale band across median under primary coverts/central hand) are depicted as well. Central figure on right shows Horus with less contrasting throat-patch (can as well be a result of light conditions); complete head can look rather uniform pale brown in such birds/circumstances. These variations can occur in various combinations individually.

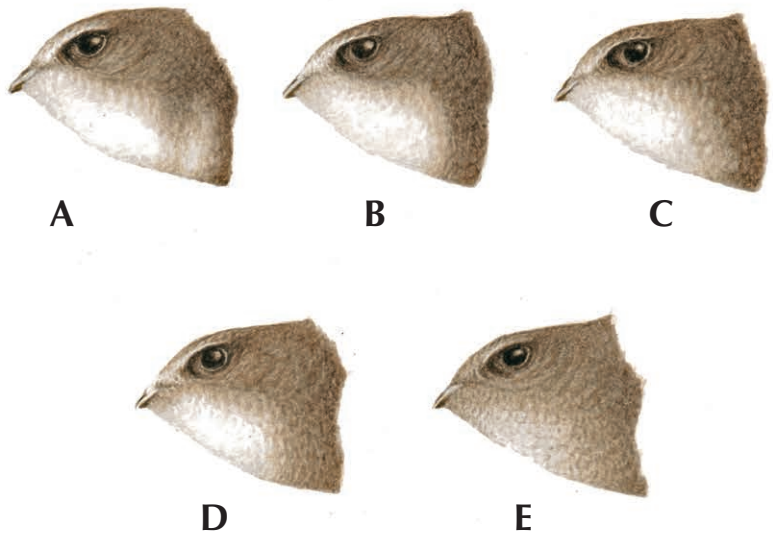


FIGURE 7 Horus Swift / Horusgierzwaluw *Apus horus (Gerald Driessens)*. Variation in head (and throat-patch) pattern: **A** with trapezium/rectangular-shaped extension on upperbreast; **B** triangular shaped; **C** slightly pointed towards upperbreast; **D** rather oval shaped; **E** with restricted oval throat-patch. This last type is often seen in dark-rumped Horus and was included in category D when scoring skins.

FIGURE 8 Horus Swift / Horusgierzwaluw *Apus horus (Gerald Driessens)*. Variation in underwing pattern. Left two variations can mostly be found in *A h fuscobrunneus* and *A h 'toulsoni'*, right three only in *A h horus*.

FIGURE 9 Pacific Swift / Siberische Gierzwaluw *Apus pacificus* (including *A p 'kanoi'*) *(Gerald Driessens)*. *Idealised* version ('majority vote' of all characters combined) of adult Pacific showing all diagnostic and near-diagnostic features in dorsal and ventral postures. All species in Pacific group (thus, including Salim Ali's *A salimalii*, Blyth's *A leuconyx* and Cook's Swift *A cooki*) are unique within white-rumped swifts group in showing obvious scaling to entire underparts. They all differ in same way from Horus Swift *A horus*. Head is usually browner than body and crown shows some faint scaling. Deeply forked tail shows full pointed feathers to tip. Pacific has broadest and whitest rump-patch within its group (see also figure 21); in Salim Ali's and Blyth's, it is generally slightly narrower with tendency to show more and broader shaft-streaks. Cook's has by far narrowest rump within this group, showing obvious and broad (to very broad) shaft-streaks, darkening rump-patch, especially its borders.

FIGURE 10 Little Swift / Huisgierzwaluw *Apus affinis* (including subspecies *A a galilejensis*, *A a bannermani*, *A a aerobates*, *A a theresae*, *A a affinis* and *A a singalensis*) *(Gerald Driessens)*. *Idealised* version ('majority vote' of all characters combined) of adult Little showing all diagnostic and near-diagnostic features in dorsal and ventral postures. Little is the most compact white-rumped swift and only one showing square tail (when closed), often with slight cleft in centre. Paler subspecies/individuals show highly translucent tail (especially when spread) and somewhat pale-fringed uppertail- and undertail-coverts. This species can look strikingly pale faced but throat-patch is always defined sharply from breast, resulting in more pale-faced impression rather than pale-headed effect of Horus Swift *A horus*.

FIGURE 11 House Swift / Grote Huisgierzwaluw *Apus nipalensis* (including subspecies *A n nipalensis*, *A n subfurcatus*, *A n furcatus* and *A n kuntzi*) *(Gerald Driessens*). *Idealised* version ('majority vote' of all characters combined) of adult House showing all diagnostic and near-diagnostic features in dorsal and ventral postures. Extremes of this species (with longest tail and deepest fork) are structurally closest to Horus Swift *A horus*. Apart from highly separated distribution range, it differs in its darker plumage, lacking paler head and large throat-patch (often with dark chin), and with darker hind body and narrower and less wrapped-around rump-patch. Outer tail feathers never looking sharply pointed but rather rounded or (at most) slightly tapering.

19 FLANK AND RUMP FROM BELOW: PATTERN (N=150) In most specimens (96.7%), the rump-patch was visible when viewed from below but it was not in 3.3% (however, this may be attributed to the way the specimens were prepared or preserved).
20 BELLY: COLOUR (N=163) Two types were found, a glossy black-brown belly (in 58.9% of the specimens) and a duller black-brown belly (in 41.1%). However, a third type found in juvenile specimens was characterised by a slightly scaled or clouded browner belly (see also the section on 'Ageing of juvenile Horus Swifts and other white-rumped *Apus* swifts').
21 UNDERTAIL-COVERTS: COLOUR (N=126) All specimens had black-brown undertail-coverts. In 80.2%, the undertail-coverts were not uniformly coloured (because of the browner feather bases) but they were uniformly coloured in 19.8% (this is not or barely visible in the field).
22 UNDERTAIL-COVERT PANEL: CONTRAST (N=128) In most specimens (75.0%), the undertail-covert panel was slightly paler than the belly but, in 24.2%, there was no colour contrast between the undertail-covert panel and the belly, especially in specimens with a paler belly. In one specimen (0.8%), an adult female (ISCED 29473, Angola), the undertail-covert panel was distinctly paler than the belly.

**Upperparts (character 23-30)**
23 RUMP: SHAPE (N=82) Most specimens (86.6%) had a C-shaped, broad rump-patch, broadening towards the rear flank, while the rump-patch was more parallel edged in 11.0%. Two specimens had a different pattern (2.4%). One had a rectangular-shaped rump-patch (RMCA 3174, N'Goma, Kivu, Congo-Kinshasa) (unlike two other specimens collected at the same location) and another (BMNH 1901.2.22.359, Irrigo, Kenya) had an aberrantly shaped rump-patch (see figure 16). Photographic effects, light conditions and the state of some skins hampered an objective assessment of this character.
24 RUMP: COLOUR (N=154) In most specimens (74.7%), the white rump-patch showed a slightly creamy wash but, in 22.7%, it was mixed with a messy buffy-brown tone. Only 2.6% showed a white rump-patch.
25 RUMP: PATTERNS (N=148) In most specimens (76.4%), the whitish rump-patch was unstreaked but it showed faint shaft-streaks in 23.6% (probably not visible in photographs taken in the field).
26 LOWER RUMP: CONTRAST OF BORDER (N=152) Most specimens (80.3%) showed a well-defined contrast on the lower rump-patch border but the contrast was only ill defined in 19.7%.
27 LOWER RUMP: COLOUR (N=149) In most specimens (66.4%), the lower rump was black-brown (like the uppertail-coverts), appearing slightly browner than the saddle. In 21.5%, the lower rump was as blackish as the saddle; it looked slightly browner and showed paler fringes in 12.1%.
28 LOWER RUMP AND SHORTEST UPPERTAIL-COVERTS: PATTERN (N=147) Most specimens (68.7%) had paler brown feathers bordering the rump-patch, feathers which showed no pale tip. In 23.1%, the paler feathers showed

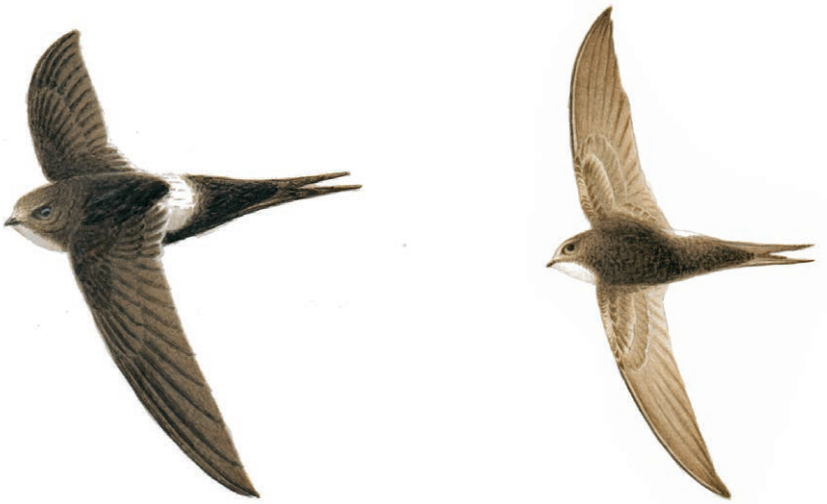

FIGURE 12 White-rumped Swift / Pijlstaartgierzwaluw *Apus caffer (Gerald Driessens)*. *Idealised* version ('majority vote' of all characters combined) of adult White-rumped showing all diagnostic and near-diagnostic features in dorsal and ventral postures. White-rumped shows narrowest rump-patch, always sharply demarcated and highly contrasting, and not wrapped around body and thus not (or hardly) visible from below. This is the only species with streamered tail feathers. Dark brown ear-coverts contrasting sharply with clearly defined white throat-patch. Underwing-pattern of some White-rumped may recall pattern of typical Horus Swift *A horus* but pale band is much narrower and can be described as obvious pale tips rather than 'half a feather'.

a diffusely pale tip. In six specimens (4.1%), however, these feathers were more contrastingly black-brown with a narrow pale tip, increasing the contrast with the rump-patch and more resembling the effect of other white-rumped swifts. Five other specimens showed uniform black-brown feathers (3.4%) and one (AMNH 296822, Lukolela, Congo-Kinshasa) (0.7%) showed sharp whitish fringes here (unlike three other specimens collected at the same location).

29 LOWER RUMP AND SHORTEST UPPERTAIL-COVERTS: CONTRAST (N=144) Most specimens (66.0%) showed a smooth (not sharp) intergrade from the pale rump-patch to the dark lower rump-patch and uppertail-coverts, creating a buffy-grey band; 18.7% had a contrastingly black-brown contrast here, while 15.3% showed a patchy merging area.

30 SADDLE EFFECT: COLOUR (N=131) In most specimens (82.5%), the glossy black-brown saddle (including the mantle, back and scapulars) formed the darkest part of the body but the saddle was dull coloured in 16.0%. Two specimens (1.5%) showed a dull brown saddle that was uniform with the hindneck and uppertail-coverts (NMZB 66397, Esigodini, Matabeleland South province, Zimbabwe and CM 213492 Juja Farm, Athi river, Kenya). A plain brown saddle is usually indicative of a juvenile but other characters in this bird were more consistent with an adult (NMZB 66397) (see also the section on 'Ageing of juvenile Horus Swifts and other white-rumped *Apus* swifts').

**Tail (character 31-32)**

31AB OUTERMOST RECTRICES (T5): SHAPE (LEFT N=144) (RIGHT N=109) (LEFT AND RIGHT TAIL-HALVES COMBINED: N=253) 43.1% had fully pointed and straight-edged outermost rectrices, while the tip to the outermost rectrices was slightly rounded or slightly tapering in 39.1%. In 10.7%, the outermost rectrices had a distinctly rounded tip, which is usually indicative of a juvenile; in 7.1%, the tip was sharply pointed, with a slightly notched inner web (figure 17).

32 UPPERTAIL: COLOUR (N=117) Most specimens (82.0%) had a uniform dark brown uppertail but it showed indistinct blackish fringes in 12.0%, and only 6.0% showed a deep black uppertail.

**Upperwing (character 33-36)**

33 PRIMARIES: FRINGING (N=117) Most specimens (52.1%) showed no fringes to the primaries but 45.3% had distinct but fragmented fringes to the primaries, especially to the inner ones. Three specimens (2.6%) were recently moulted adults and showed distinct and contiguous fringes to the primaries like most juvenile specimens (see also the section on 'Ageing of juvenile Horus Swifts and other white-rumped *Apus* swifts').

34 GREATER PRIMARY COVERTS: FRINGING (N=126) Most specimens (65.1%) showed faint and narrow paler edges, barely visible as grey-brown fringing to the outer web of the greater primary coverts. In 30.2%, there was no visible fringing (thus, the feathers looked uniform black-brown). Six specimens showed more easily visible, broader grey-brown edges (4.7%).

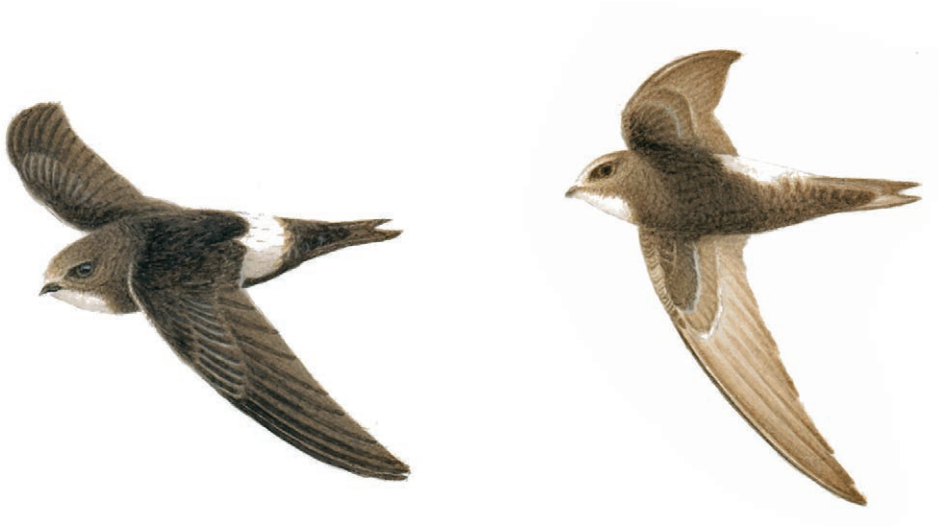

FIGURE 13 Hybrid White-rumped Swift x Little Swift / hybride Pijlstaartgierzwaluw x Huisgierzwaluw *Apus caffer x affinis (Gerald Driessens)*. Based on at least one of two birds staying at Chipiona, Cádiz, Spain, from 2015 to at least 2019 (see appendix 1 and Jansen et al 2023). Mixed characters of White-rumped and Little result in impression highly like Horus Swift *A horus*. Nevertheless, throat-patch is oval and highly contrasting with dark moustachial area and underparts, uppertail- and undertail-coverts are paler than rest of body, and only outer tail feathers looking pointed and are translucent, referring to Little parentage. Underwing pattern does not show broad pale band over median under primary coverts as in most Horus. First impression is that of Little with longer, slightly forked tail.

FIGURE 14 Common Swift / Gierzwaluw *Apus apus (Gerald Driessens)*. Adult bird illustrated here in more traditional way, thus not showing *idealised* version.

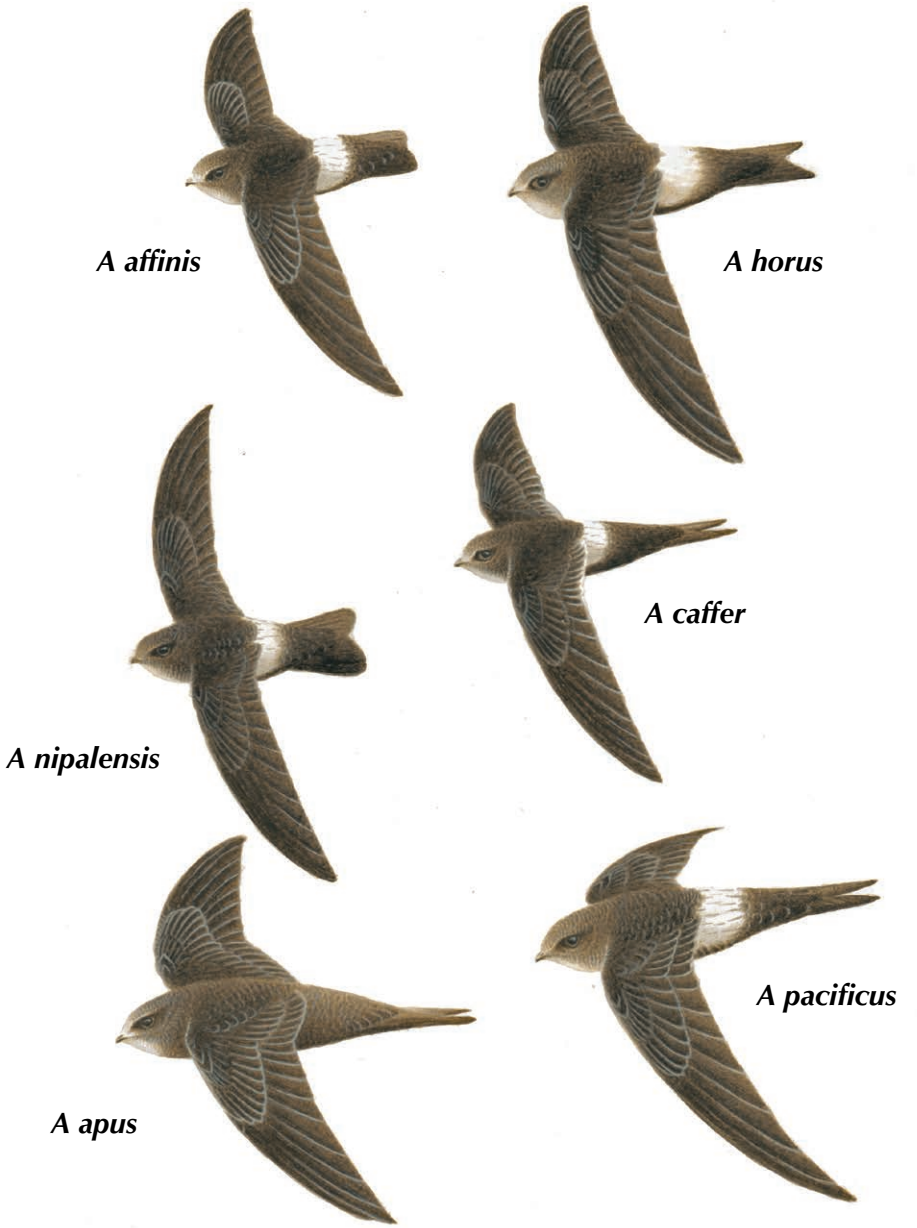


FIGURE 15 Little Swift / Huisgierzwaluw *Apus affinis*, Horus Swift / Horusgierzwaluw *A horus*, House Swift / Grote Huisgierzwaluw *A nipalensis*, White-rumped Swift / Pijlstaartgierzwaluw *A caffer*, Common Swift / Gierzwaluw *A apus* and Pacific Swift / Siberische Gierzwaluw *A pacificus (Gerald Driessens)*. *Idealised* versions ('majority vote' of all characters combined) of juveniles of each species and combination of different subspecies of depicted species. Based on specimens of Little (n=16), Horus (n=14), House (n=20), White-rumped (n=10), Common (n=20) and Pacific Swift (n=10). Juvenile plumage is kept for only relatively short period of time. Generally, body moult into adult-type plumage presumably starts c 1-2 months after fledging. Note generally browner plumage in most juveniles, presence of subtle fringing on crown and pale fringing to wing feathers.

FIGURE 16 Horus Swift / Horusgierzwaluw *Apus horus (Gerald Driessens)*. Average rump pattern (left) and most extreme rump pattern encountered in this study (right; BMNH 1901.2.22.359, adult female, Irrigo, Kenya, 23 March 1901).

35 PALE TIP TO LONGEST TERTIAL: COLOUR AND WIDTH (N=165) Most specimens (44.3%) showed a pale brown tip to the longest tertial and 32.1% had a grey-white tip. However, in 23.6%, a paler feather tip was lacking. Seven out of 13 juvenile specimens showed a broader greyish-white trailing edge (see also the section on 'Ageing of juvenile Horus Swifts and other white-rumped *Apus* swifts').

36 TRAILING EDGE TO SECONDARIES: COLOUR (N=126) Most specimens (42.8%) showed a grey-white trailing edge to the secondaries. In 41.3%, the trailing edge was narrow (<1 mm) and brown, while it was missing or worn off in 15.9%. A trailing edge is prone to wear and may disappear rapidly, especially during the breeding season.

**Underwing (character 37-39)**

37 LESSER UNDER PRIMARY COVERTS: FRINGE COLOUR (N=75) Most specimens (38.7%) showed distinct cream-coloured white tips to the lesser under primary coverts while 33.3% had indistinct pale fringes to the under primary coverts; 17.3% of the specimens showed no fringing at all and in 10.7% the fringing was distinct but narrow (inconspicuous, compared with the dark centres). Most specimens could not be examined as they had been prepared (and/or photographed) with the wings closed.

38 MEDIAN UNDERWING-COVERTS: PATTERN (N=110) In most specimens (80.9%), the median under primary coverts showed a unique pattern: the brown-based and pale-tipped median underwing-coverts merged, roughly halfway each feather, to form a broad whitish-grey to greyish-brown band over the distal part of this feather-tract (thus, over the centre of the outer underwing). 14.6% showed unmarked mid brown to brown-grey feathers which were paler than the belly. 3.6% had brown to black-brown feathers with a narrow pale tip (nearly as dark as the belly) and one specimen had unmarked mid brown under median coverts, being paler than the belly

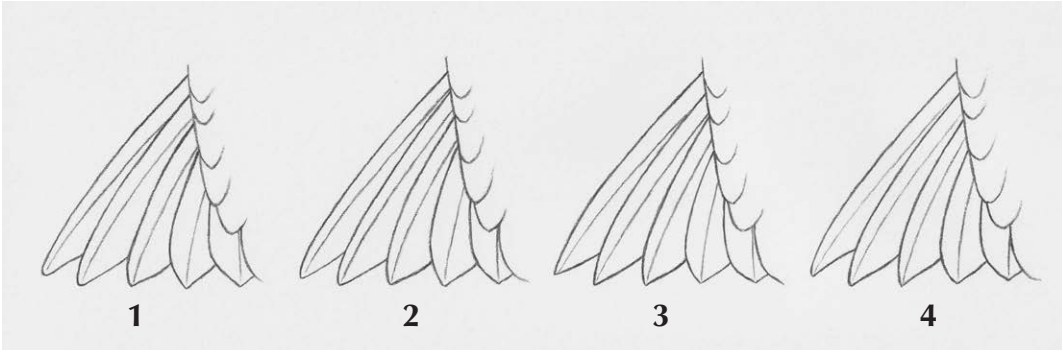


FIGURE 17 Horus Swift / Horusgierzwaluw *Apus horus horus (Gerald Driessens)*. Variation in outer rectrix (t5) in nominate Horus. Complete half of tail shown; 253 outer rectrices of adult birds examined (combined left and right), and 23 outer rectrices of juveniles (combined left and right). ***1*** outer rectrix with rounded point (10.7% of adult birds and 56.5% of juveniles); ***2*** outer rectrix pointed, with tapering point (39.1% of adult birds and 39.1% of juveniles); ***3*** outer rectrix with fully pointed tip (straight web) (43.1% of adult birds and 4.3% of juveniles); ***4*** outer rectrix pointed, with slightly emarginated inner web (7.1% of adult birds). Note that these four traits describe extremely subtle variation in rectrix shape.

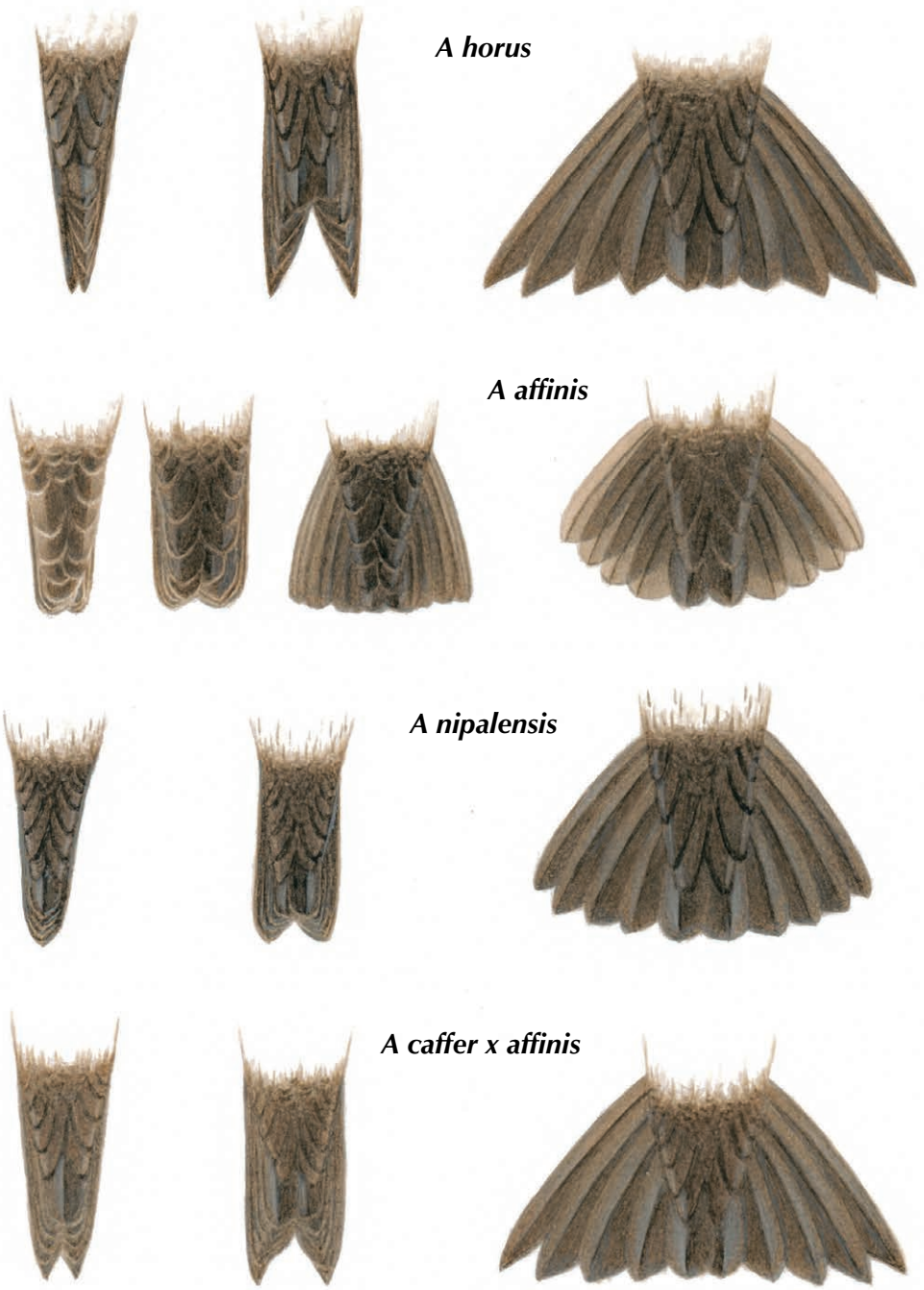


FIGURE 18 Horus Swift / Horusgierzwaluw *Apus horus*, Little Swift / Huisgierzwaluw *A affinis,* House Swift / Grote Huisgierzwaluw *A nipalensis* and hybrid White-rumped x Little Swift / hybride Pijlstaartgierzwaluw x Huisgierzwaluw *Apus caffer* x *affinis (Gerald Driessens)*. Tail closed, slightly opened and spread.

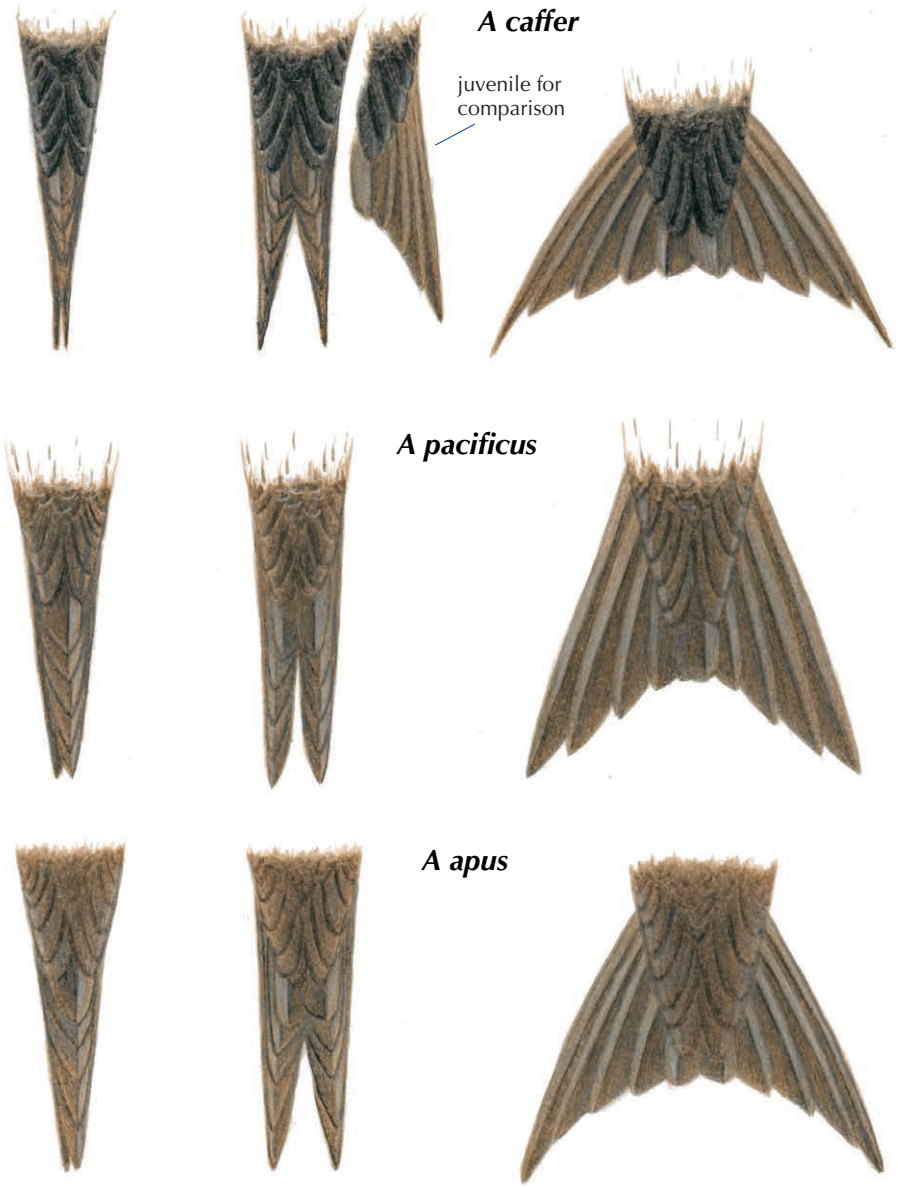


FIGURE 19 White-rumped Swift / Pijlstaartgierzwaluw *Apus caffer* (upper), Pacific Swift / Siberische Gierzwaluw *A pacificus* (centre) and Common Swift / Gierzwaluw *A apus* (lower) *(Gerald Driessens)*. Tail closed, slightly opened and spread.

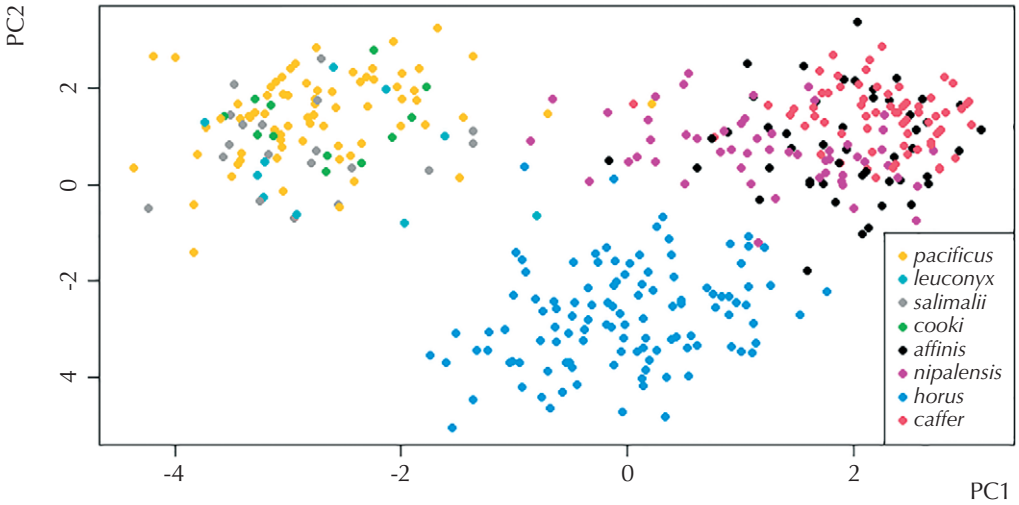


FIGURE 20 Principal component analysis (PCA) based on 20 morphological features of eight morphologically similar *Apus* species. First two PCA axes are shown, explaining 39.7% of variance.

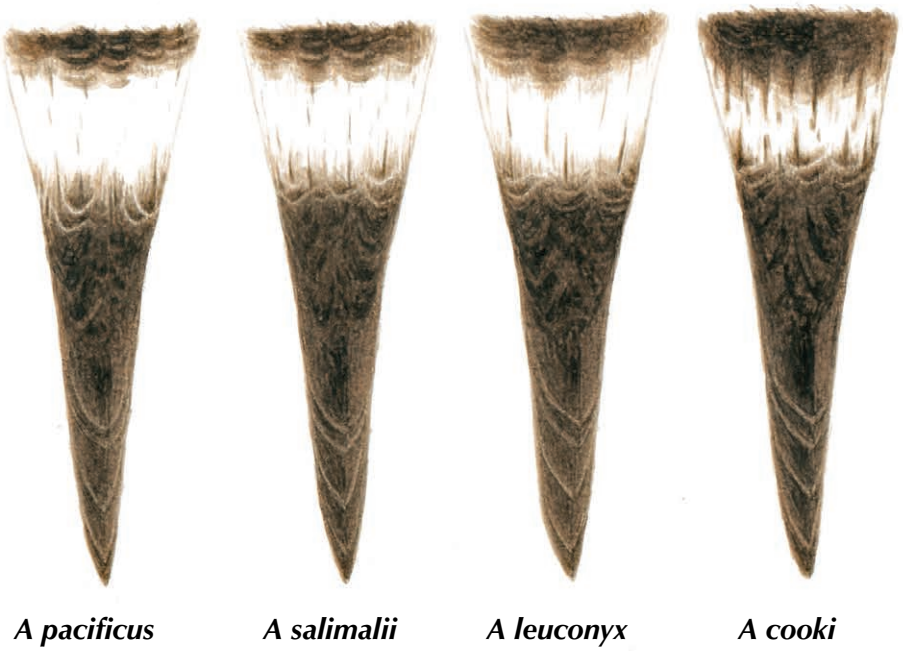


FIGURE 21 Pacific Swift / Siberische Gierzwaluw *Apus pacificus* (including *A p 'kanoi'*), Salim Ali's Swift / Salim Ali's Gierzwaluw *A salimalii*, Blyth's Swift / Blyths Gierzwaluw *A leuconyx* and Cook's Swift / Cooks Gierzwaluw *A cooki (Gerald Driessens)*. Variation in rump width and presence of shaft-streaks (see appendix 2).

(DNMNH TM14899, Dire-Dauur, Ethiopia, 19 June 1926) (0.9%).
39 MEDIAN UNDERWING-COVERTS: SHAFT-STREAKS (N=96) Most specimens (86.5%) showed narrow to distinct dark brown shaft-streaks (standing out in the paler band described in character 38) but there were no or only barely visible shaft-streaks in 13.5%.

**Measurements (character 40-42)**
40 TAIL: DEPTH (N=64) The tail-fork depth (the distance between the tip of short central rectrix and the long outer one on the closed tail) was 10-22 mm (mean 15.3 mm) (figure 18-19, 22).
41 TAIL: FORMULA (N=40) The relative spacing of the three outer rectrices (t3-5) showed variation but, in most specimens, the distances between their tips were similar, so with their length increasing evenly outwards, resulting in a practically straight profile of the tail-fork when spread (table 5). In some individuals, especially juveniles, the spacing between t4-5 is shorter than that between t3-4.
42 PRIMARIES: LENGTH (N=30) The length of the primaries showed a substantial variation (table 6). This variation differs from the variation in wing width as can be seen in the field, where it is more pronounced as the diagonal implantation of the primaries decreases towards the inner primaries. The variation was most pronounced in p4-6, thus, positioned halfway along the primaries, where Horus Swift may show a bulging trailing edge.

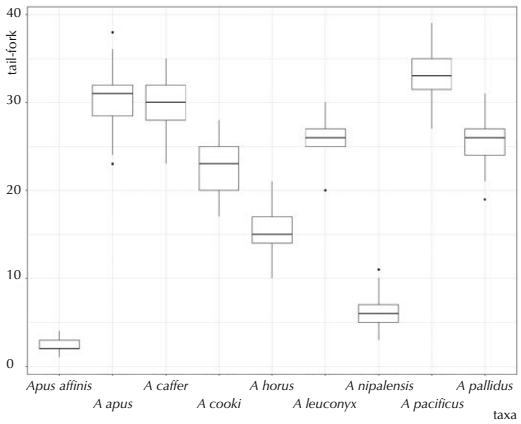


FIGURE 22 Box-whiskerplot showing results of 461 examined tail-forks. Measured are Little *A affinis* ssp (61), Common *A apus* ssp (59), White-rumped *A caffer* (59), Cook's *A cooki* (28), Horus *A horus* (64), Blyth's *A leuconyx* (10), House *A nipalensis* ssp (61), Pacific *A pacificus* (59) and Pallid Swift *A pallidus* ssp (59). For each species, 50% of all examined individuals fall within box, while whisker above and below both measure 25%. Dots show outliers.

## Ageing criteria for Horus Swift and other white-rumped *Apus* swifts

*Juvenile Horus Swift*
Plumage differences between juvenile and older specimens could be established but we found no sex-related differences (for illustrations of juvenile Horus Swift, see figure 15). The 14 examined juvenile specimens included two one-week-old nestlings (which were excluded from this research), four nestlings which were about to fledge (body feathers already fully grown) and eight fledged juveniles. All looked more uniform brown and 'softer' plumaged (figure 15) than the examined adult specimens, which were more contrasting and had a blacker and glossier mantle and belly (plate 96-97). Also, the shape of the outermost rectrices and the extent of the pale fringing appeared helpful. However, these characters should always be combined, as pale fringing in the wing or a slightly clouded belly can be shown by recently moulted adults as well. The following characters proved to be useful when identifying juvenile specimens.
SADDLE All juvenile specimens (still carrying only juvenile body feathers) had a brown saddle that did not con-

TABLE 5 Tail formula variation in 40 Horus Swifts *Apus horus* based on measurements of central (t1) to outermost (t5) rectrix. Length of each rectrix (mm) measured from estimated point of attachment to caudal vertebrae to rectrix tip. Median, shortest and longest measurements given for each rectrix.

| | median | shortest | longest |
|---|---|---|---|
| t5 | 54 | 43 | 62 |
| t4 | 50 | 39 | 57 |
| t3 | 46 | 36 | 51 |
| t2 | 41 | 31 | 47 |
| t1 | 39 | 29 | 45 |

TABLE 6 Primary length variation in 30 Horus Swifts *Apus horus*. Length of each primary measured from estimated point of attachment to bones of hand to primary tip. In Horus, p9 is longest and therefore 100% of wing length. Other primaries given as percentage of length of p9. Median, shortest and longest measurements given for each primary.

| | median | shortest | longest |
|---|---|---|---|
| p10 | 98 | 87.4 | 100 |
| p9 | 100 | 100 | 100 |
| p8 | 94.7 | 92.7 | 99.3 |
| p7 | 84.6 | 80 | 92.7 |
| p6 | 74.7 | 70.4 | 84.5 |
| p5 | 65.5 | 61.3 | 74.8 |
| p4 | 55.7 | 52.8 | 66.7 |
| p3 | 48 | 45.1 | 57.7 |
| p2 | 40,8 | 37.5 | 49.6 |
| p1 | 34.7 | 32.6 | 42.3 |

**96-97** Horus Swifts / Horusgierzwaluwen *Apus horus*. From right to left: juvenile female, Lukokela, Congo-Kinshasa, 10 October 1930 (AMNH 296824); juvenile female, Lukokela, Congo-Kinshasa, 10 October 1930 (AMNH 296822); adult male, Lukokela, Congo-Kinshasa, 10 October 1930 (AMNH 296821); adult male, Escarpment West of Kasenyi, Lake Albert, Congo-Kinshasa, 22 August 1926 (AMNH 262446); adult female, Lukokela, Congo-Kinshasa, 10 October 1930 (AMNH 296823); adult female, Escarpment West of Kasenyi, Lake Albert, Congo-Kinshasa, 22 August 1926 (AMNH 262447); American Museum of Natural History, New York, USA, 18 November 2022 *(Justin J F J Jansen/AMNH)*. Note difference between adult and juvenile birds. Note also scaly pattern to belly feathers and browner belly and saddle of juvenile, which both are blacker in adults.

**98** Horus Swifts / Horusgierzwaluwen *Apus horus*, Natural History Museum, Tring, England, 16 March 2020 *(Gerald Driessens/NHMUK)*. Sample showing well-marked to unmarked head to mantle contrast. **99** Horus Swifts / Horusgierzwaluwen *Apus horus*, Natural History Museum, Tring, England, 16 March 2020 *(Gerald Driessens/NHMUK)*. Sample showing most limited (absent) to broadest rump-patch. Bird on left is '*toulsoni*' (BMNH 1889.3.27.19).

**100** Horus Swifts / Horusgierzwaluwen *Apus horus*, Natural History Museum, Tring, England, 16 March 2020 *(Gerald Driessens/NHMUK)*. Sample showing dusky to whitish throat. **101** Horus Swifts / Horusgierzwaluwen *Apus horus*, Natural History Museum, Tring, England, 16 March 2020 *(Gerald Driessens/NHMUK)*. Sample showing smallest to largest white throat. Bird on left is *'toulsoni'* (BMNH 1889.3.27.19).

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**102** White-rumped Swift / Pijlstaartgierzwaluw *Apus caffer*, Vejby Strand, Sjælland, Denmark, 27 October 2020 *(Anders Sørensen)*. Spread tail-fork can look surprisingly shallow in White-rumped, especially in juveniles (compare tail in this plate with closed tail of same bird in Dutch Birding 42: 437, plate 578, 2020). Inner web of outermost rectrices (t5) only slightly notched, indicative of juvenile. Also note distinct white tips to secondaries and tertials (running up along outer webs), dark face with contrasting white supercilium and narrow U-shaped white rump-patch. **103** House Swift / Grote Huisgierzwaluw *Apus nipalensis nipalensis*, Hong Kong, China, 1 January 2021 *(John Holmes)*. Interesting photograph, showing how difficult swift identification can be when based on just one image. Head and upperparts perhaps slightly overexposed to light. Head showing no contrast (apart from shadowed throat-patch), while eye-patch more or less swallowed by dark head, leaving black bristle feathers in front of eye. Throat-patch small and oval shaped. Darker moustachial area running up to lower mandible (most House show dark chin). Rump-patch sharply demarcated from blackish uppertail-coverts, masked by sharp pale buff tips to shortest feathers. In House, uppertail and uppertail-coverts often looking as black as saddle. Tail shape impossible to establish but still looking square ended. **104** House Swift / Grote Huisgierzwaluw *Apus nipalensis nipalensis*, adult (collected in India; USNM 148977), Smithsonian Institution, National Museum of Natural History, Washington, USA, 16 November 2022 *(Justin J F J Jansen/USNM)*. This bird was confusing as it showed deep (14.5 mm) tail-fork, much longer than any other House measured. This length of tail-fork is not shown in figure 22. However, throat-patch rather small and underwing consistent with all examined House. T3-4 spade shaped and heavily curved to inner web; this shape/pattern is never present in Horus Swift *A horus* but is also extreme for House; therefore this is a very tricky bird. **105** Common Swift / Gierzwaluw *Apus apus*, Wassenaar, Zuid-Holland, Netherlands, 5 July 2011 *(Vincent van der Spek)*. Aberrantly coloured bird. Feathers all white and patchily distributed over back (indeed, little higher up than rump). In aberrantly plumaged Common, all leucistic feathers (including their downy bases) are pure white as they lack any pigmentation, as also shown in plate 106-107.

**106-107** Common Swift / Gierzwaluw *Apus apus*, East Chevington NWT Nature Reserve, Northumberland, England, 23 April 2016 *(Jonathan Farooqi)*. Aberrantly coloured bird; note patchy white feathers, with undefined, asymmetrical pattern. This may be result of progressive greying. See also comments in caption of plate 105.

trast strongly with the adjacent upperparts like in most adult specimens. However, 17.5% of the adult specimens had a dull black-brown saddle, although they showed more contrast with the adjacent upperparts than the average juvenile.

BELLY Eight juvenile specimens (carrying juvenile body feathers) had a belly pattern that differed from that of adult specimens, being paler and warmer brown with a 'ghostly clouded' impression. However, one juvenile specimen showed more distinct dark subterminal markings bordering pale tips to the central belly feathers and two other juvenile specimens showed a more uniform black-brown belly like in adult specimens (these two specimens might have been in a more advanced body moult). As a result of the browner plumage, the undertail-coverts were equally coloured as the belly.

SHAPE OF OUTERMOST RECTRICES (T5) When fresh, the (pointed) outermost rectrix had a rounded tip but, due to wear, this often showed a more tapering point. We found both types also in adult specimens but the outermost rectrices were never as straight edged and fully pointed in juveniles.

FRINGING TO PRIMARIES In 11 juvenile specimens, birds showed distinct and contiguous greyish-white fringes to the primaries. In adult specimens, this pattern was rare and only found in recently moulted birds. It should be remembered that adults replace their primaries in a consecutive order, while, in juveniles, they all grow simultaneously, resulting in a more even, uniform set of primaries and thus all showing obvious fringing at the same time. In one juvenile specimen, the pale fringes to the primaries were not present, they may have worn off completely.

FRINGING TO GREATER COVERTS In 10 juvenile specimens, birds showed distinct pale fringing to the greater primary coverts but, in two juveniles, the pale fringing was indistinct. Two juvenile specimens showed no pale fringing at all. In adults, the greater primary coverts showed indistinct or no fringing.

FRINGING TO CROWN FEATHERS Nine juvenile specimens showed narrow pale fringes to the crown feathers, resulting in pale scaling to the crown. This pattern could not be found in specimens of adult birds.

SPACING OF TAIL FEATHERS Two out of four examined juveniles showed spacing in the rectrices that differed from adult birds. They showed a smaller distance between t4-5 and t1-2 but a distance twice as large between t3-4 and t2-3.

Our comparisons between skins showing a full juvenile plumage and those showing different stages of body-moult, linked to the breeding periods in their respective ranges, indicate that the body moult probably starts c 1-2 months after fledging. Thus, juvenile Horus Swifts can be safely aged for only a relatively short period (c 1-2 months). However, the timing of moult may vary individually. As wear and bleaching increase, it becomes more difficult to confirm the age of suspected juvenile swifts. We expect that after a period of only a few months (probably after already two months), most body feathers will have been replaced by adult-type feathers and fringing has worn off, so birds cannot be aged easily or safely anymore.

We were not able to find photographs of definite juvenile Horus Swifts on the Internet from the African subcontinent (as per 17 January 2023).

*Ageing of other juvenile white-rumped Apus swifts*

The ageing criteria described for Horus Swift can be applied to related swift species as well. Juvenile white-rumped *Apus* swifts in the hand look more uniform brown, 'softer' plumaged and lack the glossy body parts (however, juvenile Little Swifts

can show a glossy belly and saddle as well, especially when their post-juvenile moult is in a more advanced stage). In juveniles, fringing to the upperwing-coverts and secondaries is often more pronounced than in adults. The outermost rectrices of White-rumped Swift are shorter and more blunt-tipped. The plate illustrating juvenile *Apus* swifts offers more clues to ageing (figure 15).

The following comments may be useful: ***1*** In juvenile Little Swifts, the darker belly and saddle often stand out against the otherwise paler brown plumage (especially in the subspecies *galilejensis*) and thus resemble the adult plumage more than that of other white-rumped *Apus* swifts. However, when using this appearance in combination with the distinctly fringed coverts (especially the greater primary coverts) and the uniformly fresh state of the plumage, the age of some juveniles can sometimes be confirmed. The shape of the outermost rectrices, however, seems not to be useful for ageing Little. ***2*** Of the white-rumped *Apus* swifts, House Swift is the most difficult species to age, as the usual subtle age-related plumage differences are difficult to discern in the uniformly dark plumage. No structural differences in the outermost rectrices were found. ***3*** Apart from being more blunt tipped, the outermost rectrix of juvenile White-rumped Swift is not emarginated like in adults. Therefore, a juvenile tail will resemble that of an adult Horus Swift even more (but the spacing of t4-5 is clearly longer than in juvenile Horus). Also, the throat-patch shape and demarcation, and the rump-patch width and shape remain useful characters to separate it from Horus, as well as the darker throat surroundings of White-rumped (which never shows a broad throat-patch or the pale-looking head-side of Horus). ***4*** White-rumped Swift has a narrow rump-patch, the depth being approximately half the size of that in Horus. The rump-patch depth is always a useful field character to separate White-rumped from Horus.

**Separating Horus Swift from related *Apus* swifts**

For each species, we illustrate the trait and pattern with the highest sensitivity/importance to distinguish both taxa are shown (appendix 3). Because eliminating related *Apus* swifts is an essential step in the identification process when confronted with a swift showing characters suggestive of Horus Swift, we illustrate (figure 9-12) an idealised version of each taxon. We again tried to measure 59 specimens for each taxon, the examined birds were randomly selected. The idealised version is the highest score (highest percentage) for each pattern per trait; all combined they represent the 'majority vote'. It should be stressed that such an idealised version does not necessarily represent an actual bird (cf Parker 2019) but is a construction to represent a typical example of the species. Therefore, we illustrate for Horus nine additional phenotypes to cover a large part of the individual variation (figure 6).

For each *Apus* taxon illustrated, the differences with Horus Swift are explained in the captions (figure 9-12).

## Conclusion

After examining 212 specimens, the range of variation in Horus Swift can be established. Illustrations of nine phenotypes are presented here as the visual representations of this variation (figure 6). Figure 4 shows an idealised version of Horus (the 'majority vote' of all characters combined). Figure 7-8 illustrate the variation in (only) head and underwing, while figure 16 illustrates the extreme and average rump pattern. The diagnostic characters (in relation to Horus) were documented for other white-rumped *Apus* swifts as well, resulting in illustrations of an idealised version of them as well (the 'majority vote' of all characters combined) (figure 4 and figure 9-12, see appendix 3).

Although our research shows minor regional differences, the examined characters (throat-patch and moustachial demarcation, throat-patch width, belly pattern, contrast in the undertail-covert panel, shape of the outermost rectrices (figure 17), and secondary trailing edge) do not support the existence of regional groups in Horus Swift. The white throat patch extending onto the upperbreast is only found in Horus (although in only a minority of the scored specimens) (plate 101).

Horus Swift was identified as a distinct cluster in our PCA based on 20 categorical morphological variables (figure 20).

The average tail-fork depth (15.3 mm; range 10-21 mm) is the most reliable feature separating Horus Swift from all similar *Apus* swifts (figure 18-19, 22). However, three House (10-11 mm) (bird in plate 104 is an additional specimen), five Cook's (20-21 mm), two Pallid (19, 21 mm) and a single Blyth's Swift (20 mm) show some overlap with the range measured for Horus. By using a combination of all characters, Horus can be safely and in fact quite easily distinguished from other white-rumped *Apus* swifts.

Both *fuscobrunneus* and '*toulsoni*' should be recognised as brown-rumped colour morphs from nominate Horus Swift; they do – in our opinion – not differ from each other and are probably one

and the same melanistic variation of Horus for the following reasons: ***1*** *fuscobrunneus* is only known from a series of 10 birds collected in May 1966 on one location within the '*toulsoni*-range', and has not been reported since; ***2*** '*toulsoni*' is, despite being widespread (figure 1), very rare and a nest and eggs have never been found; ***3*** the set of 20 examined birds did not show any distinct features separating them from each other. Based on this, we consider Horus monotypic.

The shape of t3-4 was not scored for this research but their shape, combined with the shape of t5 and the spacing between the rectrices and depth of the tail-fork, would be highly interesting. So, this could be subject for future research. The dimensions of the rump-patch of Horus Swift and comparable taxa could also be further researched (see for example the variation in plate 99).

Hopefully, readers will be more aware of the fact that Horus Swift is a species that shows greater variation than suggested in the literature. Birders and field ornithologists are encouraged to test the proposed identification criteria in the field and, whenever possible, photographically document the birds they see.

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## Samenvatting

HORUSGIERZWALUW: IDENTIFICATIE, KLEEDVARIATIE EN VERSPREIDING Tot op heden is nog maar weinig gepubliceerd over de herkenning en de variatie in het verenkleed van Horusgierzwaluw *Apus horus*. Ook illustraties en teksten in de diverse gidsen en handboeken helpen niet om de variatie binnen deze soort te begrijpen. Een gierzwaluw *Apus* met een witte stuit die op 26 en 27 september 2019 rondvloog op Schiermonnikoog, Friesland, was de aanleiding om dit onderzoek te starten. Er werden voor dit onderzoek (dat tussen september 2019 en maart 2023 liep) bezoeken gebracht aan diverse museumcollecties. Aan musea die niet te bezoeken waren werd gevraagd om foto's beschikbaar te stellen. Er werden 212 Horusgierzwaluwen onderzocht en daarnaast werden nog 2539 balgen van andere (vooral witstuitige) *Apus*-soorten onderzocht (zie tabel 1-2).

Voor alle *Apus* gierzwaluwen met witte stuit werd de variatie binnen 39 veerpartijen en/of kenmerken onderzocht door het toekennen van bij voorkeur objectieve scores. Getracht werd om voor de diverse gierzwaluwen met witte stuit (en de vorm en ondersoort van Horusgierzwaluw zonder witte stuit) van minimaal 59 vogels een score van elk lichaamsdeel te verkrijgen. Dit is gelukt voor Pijlstaartgierzwaluw *A caffer*, Grote Huisgierzwaluw *A nipalensis*, Huisgierzwaluw *A affinis*, Horusgierzwaluw (nominaat) en Siberische Gierzwaluw *A pacificus*. Vanwege het lage aanbod in musea en de beperkte tijd werden voor de vermeende *fuscobrunneus*-ondersoort en de melanistische kleurvorm *'toulsoni'* van Horusgierzwaluw en Cooks *A cooki*, Salimali's *A salimalii* en Blyths Gierzwaluw *A leuconyx* minder dan 59 individuen gescoord. Verder onderzochten we de kenmerken van één van de twee hybriden Pijlstaartgierzwaluw x Huisgierzwaluw *A caffer x affinis* die in 2015-19 in Spanje werden waargenomen (zie figuur 13 en Jansen et al 2023).

De resultaten zijn percentages die weergeven welke variatie het vaakst tot het minst vaak werd aangetroffen voor elke onderzochte veerpartij. Dit is specifiek uitgewerkt voor Horusgierzwaluw (zie hoofdstuk resultaten) en de andere taxa (appendix 3 en onderschrift bij figuur 4-5, 9-12). Deze herkenningsplaten weerspiegelen het resultaat van de hoogste scores van de 39 lichaamsdelen (de 'ideale vogel'), en de afbeelding met negen Horusgierzwaluwen (figuur 6) illustreert de hele variatie binnen één tekening. Figuur 4-5 zijn dus complementair.

Om de diverse taxa in het veld van elkaar te onderscheiden moet per taxon worden gekeken naar de combinatie van zoveel mogelijk kenmerken (zie figuur 9-12). Er is geen uniek kenmerk gevonden dat exclusief in alle Horusgierzwaluwen voortkomt. Wel is de middelmatig gevorkte staart (tussen 10-20 mm) een betrouwbaar kenmerk: alleen de minst ondiepe staartvorken van Horusgierzwaluw overlappen met de diepste staartvork bij drie Grote Huisgierzwaluwen (*subfurcatus*) en de minst diepe staartvork bij één Cooks Gierzwaluw en twee Vale Gierzwaluwen *A pallidus*. Een grote witte keelvlek die reikt tot op de bovenborst (vaak met een trapeziumvormige uitloper) werd alleen in Horusgierzwaluw aangetroffen maar komt maar in 34.1 % van de vogels voor.

Horusgierzwaluwen kunnen net als andere tropische soorten het jaar rond broeden binnen het verspreidingsgebied, dus jonge vogels kunnen het hele jaar opduiken. Op basis van alle beschikbare data werd een nieuwe en gedetailleerde verspreidingskaart opgemaakt van de soort (figuur 1).

Een belangrijke conclusie is dat op basis van dit onderzoek de variatie binnen de witstuitige *Apus*-gierzwaluwen groter is dan men zou verwachten, en dat individuele afbeeldingen of teksten uit een veldgids niet altijd 'de gemiddelde vogel' afbeelden en dus vaak niet de oplossing bieden. Aangezien gierzwaluwen zich moeilijk objectief laten beoordelen in het veld, is het uitgebreid fotograferen van afwijkende vogels zeer belangrijk. Mits er goede detailfoto's beschikbaar zijn, is elke Horusgierzwaluw te onderscheiden van andere *Apus*-gierzwaluwen met een witte stuit. Het is de volledige combinatie van kenmerken die de determinatie van witstuitige gierzwaluwen goed mogelijk maakt.

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*Justin J F J Jansen, Naturalis Biodiversity Center, Leiden, Netherlands (justin.jansen@naturalis.nl)*
*Gerald Driessens, Lier, Belgium (gerald.driessens@telenet.be)*

## APPENDIX 1 Identification of hybrid White-rumped x Little Swift *Apus caffer x affinis*

**White-rumped x Little Swift hybrid**

Two hybrids White-rumped x Little Swift *Apus caffer* x *affinis* stayed in a breeding colony of Little Swifts at Chipiona, Cádiz, Spain, from 2015 to at least 2019. The bird's identification is summarised in figure 13. Its mtDNA (as one bird was caught) ruled out Horus Swift *A horus* but was close to Little Swift (no anaysis of nuclear DNA was executed) (Jansen et al 2023).

Indeed, when confronted with a swift showing characters suggestive of Horus Swift, it might be a challenge to eliminate a hybrid White-rumped x Little Swift. Until now, no confirmed cases of hybridisation between any other white-rumped *Apus* species have been reported or published (cf McCarthy 2006, Pellegrino et al 2017), but hybridisation between Pallid Swift *A pallidus* and Common Swift *A apus* has recently been demonstrated genetically (Cibois et al 2022).

**Identification summary**

The bird's well-defined oval-shaped throat-patch, the slightly scaled uppertail-coverts and the paler undertail-coverts suggested a Little Swift parentage. On the other hand, the white tips to the secondaries and tertials and the emargination to the outermost rectrix indicated a White-rumped Swift parentage. The elongated hind body resembled that of White-rumped while the bird's general colouration was rather brown, like Little, not black and white as in White-rumped. Additionally, the more translucent (especially outer) rectrices are reminiscent of Little and are not seen in Horus Swift. While this bird bore a strong superficial resemblance to Horus, it differed from that species in several aspects, which are best assessed from photographs.

## APPENDIX 2 Separating Salim Ali's *Apus salimalii,* Blyth's *A leuconyx* and Cook's Swift *A cooki* from Horus Swift *A horus*

Leader (2011) proposed to split Blyth's *Apus leuconyx*, Salim Ali's *A salimalii* and Cook's Swift *A cooki* from Pacific Swift *A pacificus*. Apart from Pacific, these three species never occurred in the Western Palearctic and were thus not treated in the main text. As these three species are distinguished from Horus Swift *A horus* by the same characters as Pacific, and because of the small samples of specimens examined for Salim Ali's (25), Blyth's (17) and Cook's (22), we only present a small summary how these three species differ from Pacific, which is by far the most well known within this group. We feel this is the better way to guide readers through these relatively 'new' species.

**Salim Ali's Swift** is very similar to Pacific Swift, with a tendency to show a slightly narrower rump-patch with broader, thus more obvious shaft-streaks. The rump-patch looks whiter in Pacific as the narrow streaks are hardly discernible (figure 21). Salim Ali's generally has a less scaly crown, so that the crown looks a bit darker overall. In the throat-patch, most Salim Ali's show some distinct barring in the lowest part and the sides of the pale throat, resulting in a more restricted patch. In the most boldly marked Salim Ali's, the barring can even cover the whole patch.

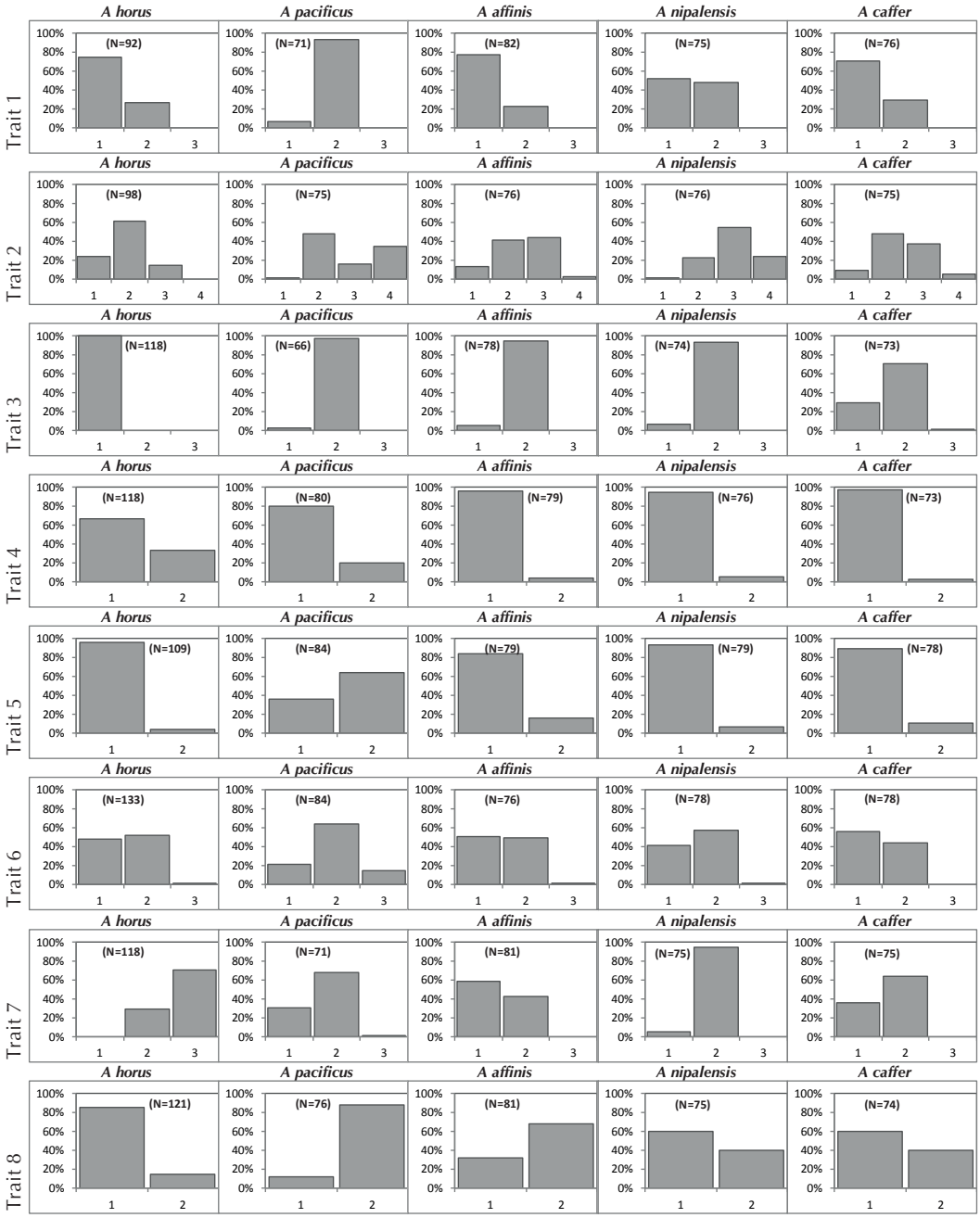
**Blyth's Swift** shows a much more variable throat pattern, from distinctly barred to a whitish throat-patch. In quite some individuals, though, the pale throat runs deeper down towards the breast, so that the underpart scaling starts much lower on de breast than the pattern known from typical Pacific Swift. The crown is somewhat paler than the back and thus like Pacific. Blyth's has in general a less broad rump-patch without or with similar shaft-streaks than Pacific (figure 21). This species is somewhat smaller than Pacific but this is not of any use in the field.

**Cook's Swift** is the smallest and darkest species within this group. The darker colour generally creates more marked scallops on the underparts and it has very dark upperparts (usually lacking any pale markings on the saddle, which are usually – but far from always – present in Pacific) and an evenly dark crown (darkest within this group). The throat patch is often heavily marked with barring on the sides, and well-marked with bold shaft-streaks in the centre. It has the narrowest rump-patch of the four, often showing bold shaft-streaks, running out in a subterminal arrow mark towards the dark uppertail-coverts (figure 21).

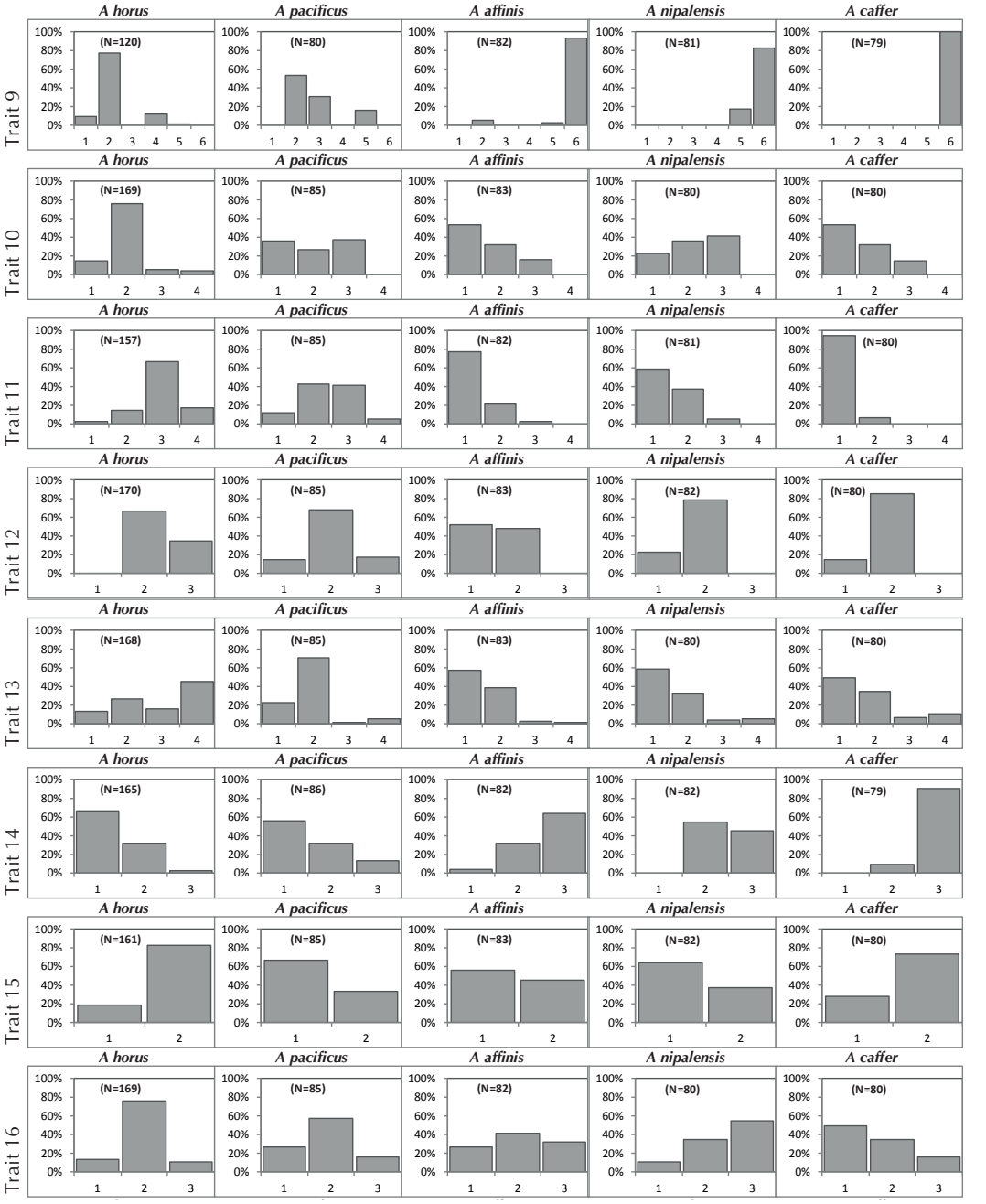
*Important note*

All four species within this group can look surprisingly unmarked brown when extremely worn (and bleached). In the most extreme individuals, pale feather tips are completely worn off and dark subterminal marks have bleached to form – in the most extreme individuals – uniform brown underparts. Usually, some scaling is still present but visible only under good circumstances in such worn birds, but the pattern will resemble the soft scaling of Pallid Swift *A pallidus*, rather than the striking scalloping of typical Pacific.

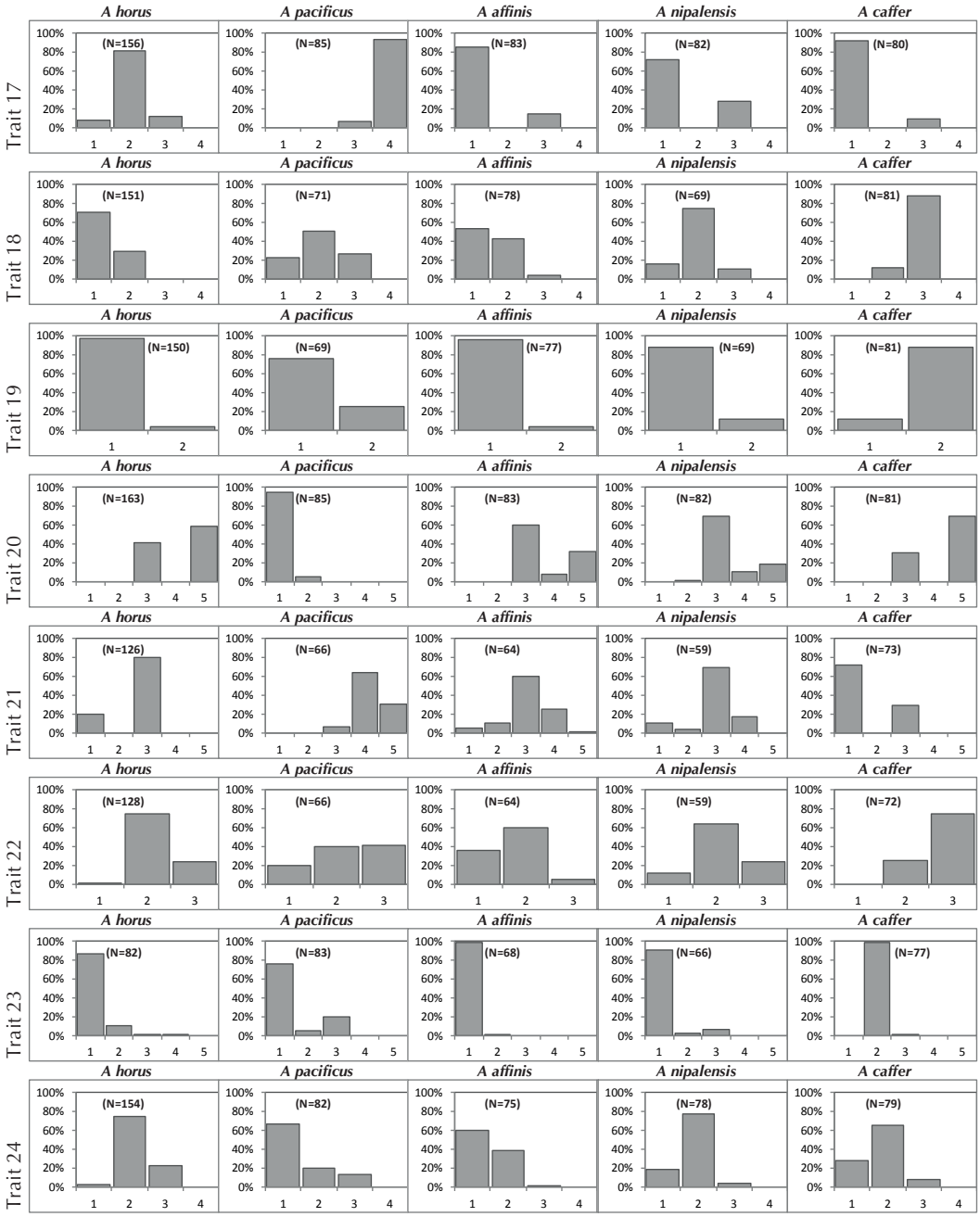
APPENDIX 3 The bar graphs show the physical scores we performed. We include the bars from Horus Swift *Apus horus* as discussed in the main text for completeness. Each row shows a trait as shown in table 3. The y-axis per trait shows the score for each of the numbered patterns on the x-axis shown in table 3 in the column Pattern. The N number shows the number of specimens researched for this trait used to produce the bar graphs.



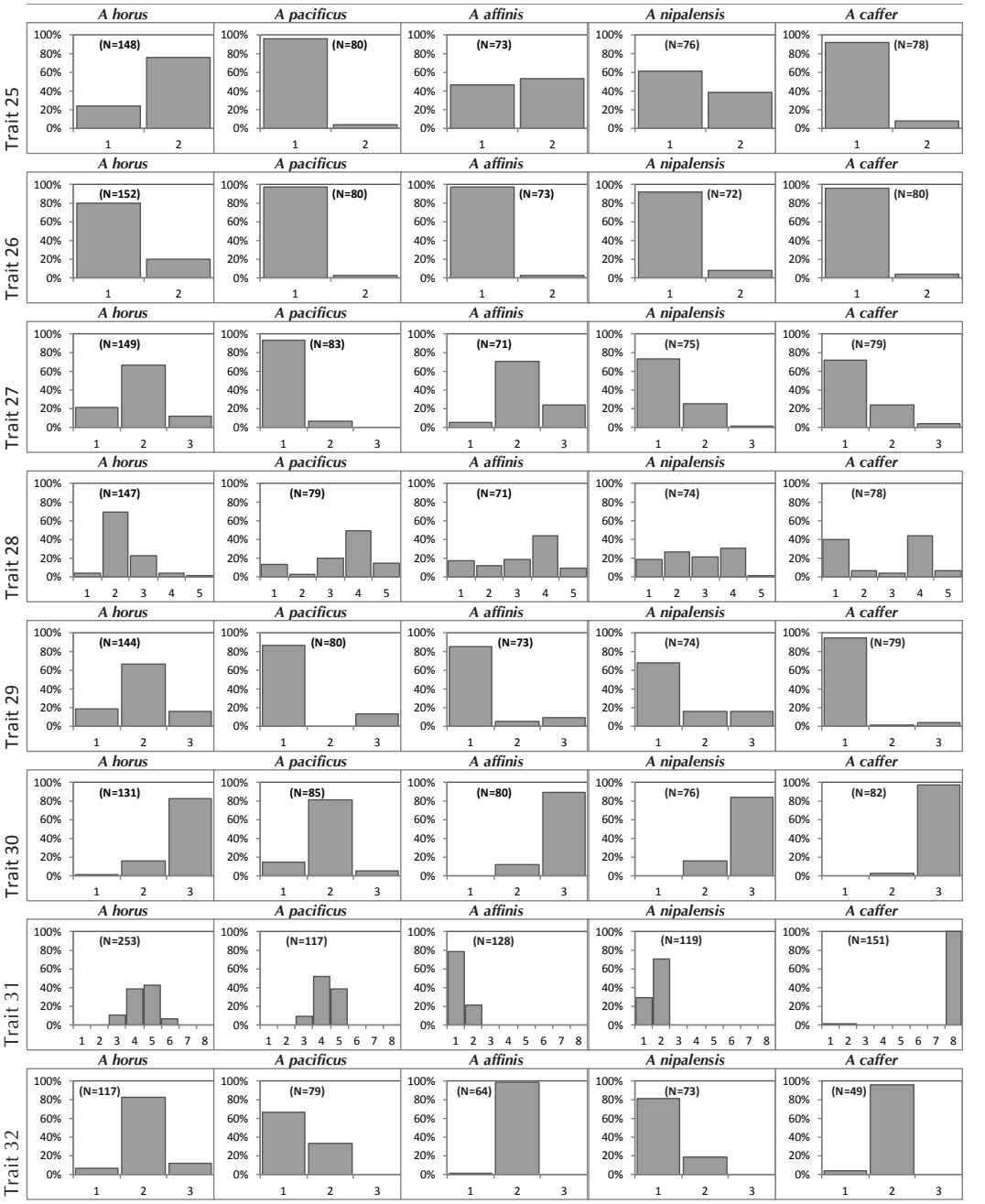
APPENDIX 3 (continued)



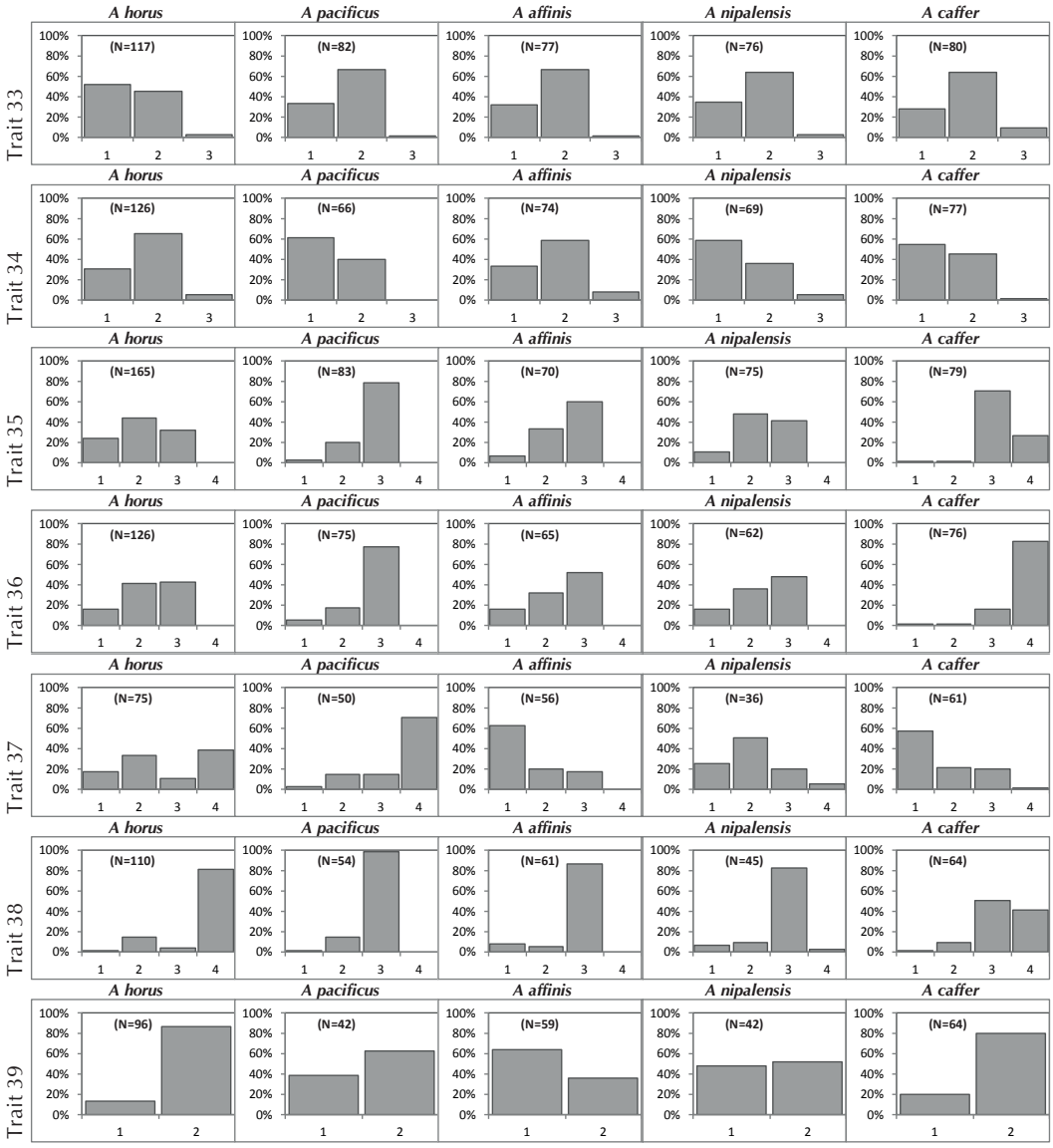
APPENDIX 3 (continued)



APPENDIX 3 (continued)



APPENDIX 3 (continued)



## Addendum

TABLE 4 Mean body length and weight of examined *Apus* swift species as found in literature

| | **Mean body length** | **Source** | **Mean weight (min-max; n)** | **Source** | **Remark** |
|---|---|---|---|---|---|
| Horus | 15 | Chantler & Driessens 1995a, 2000 | 26.2 (17-31.3; 214) | Fry et al 1988 | based on southern African birds |
| Little | 12 | Cramp 1985 | 25 (18-30; 64) | Cramp 1985 | several African subspecies |
| House | 15 | Chantler & Driessens 1995a, 2000 | – (20-35; 14) | Brooke 1971b | average male 21.1 (n=5) and female 26.13 (n=9) |
| White-rumped | 14 | Cramp 1985 | 22.1 (18-30; 170) | Fry et al 1988 | |
| Pacific | 17-18 | Cramp 1985 | – (38-54) | Gao & Zhou 1985 | average male (48.1 n=7) and female 42.5 (n=2) |
| Salim Ali's | 17-18 | Leader 2011 | – | | unknown |
| Blyth's | 17-18 | Leader 2011 | – | | unknown |
| Cook's | 17-18 | Leader 2011 | 53 (50-56; 2) | Cramp 1985 | |
| Pallid | 16-17 | Cramp 1985 | 41.3 | Cramp 1985 | Gibraltar, breeding season, weights |
| Common | 16-17 | Cramp 1985 | – (26-58) | Cramp 1985 | varies enormously in weight in season |