

JOURNAL OF AVIAN BIOLOGY

Article

Recognition of a new generic-level swallow taxon from central Africa

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Journal of Avian Biology

2018: e01698

doi: 10.1111/jav.01698

Subject Editor: Martin Paekert

Editor-in-Chief: Thomas Alerstam

Accepted 10 April 2018

The forest swallow *Petrochelidon fuliginosa* is a little-known species endemic to lowland forests in central Africa; for lack of access to high-quality genetic material, the species has been omitted from all previous molecular phylogenetic studies of the swallows. The species is currently placed in the genus *Petrochelidon*, within the ‘mud-nester’ clade of swallows, yet its plumage, morphology, and nesting behavior do not align well with those of other major swallow lineages. As a consequence, upon securing recent specimens and high-quality tissue samples, we sequenced DNA from two mitochondrial genes and one nuclear marker to place this species in the swallow phylogenetic tree. Our results placed the forest swallow firmly within the ‘mud nester’ clade, but outside of the clade corresponding to *Petrochelidon*. This outcome led us to document and describe formally a distinct, generic-level lineage of swallow endemic to the Lower Guinean forest region of central Africa.

Keywords: molecular phylogenetics, atronanus forest swallow, avian systematics and taxonomy

Introduction

The swallows (Hirundinidae) have been the focus of several detailed molecular phylogenetic studies that have provided a backbone for a stable taxonomic arrangement that reflects evolutionary history (Sheldon and Winkler 1993, Sheldon et al. 1999, 2005, Whittingham et al. 2002, Dor et al. 2010). The most complete molecular tree for the family (Sheldon et al. 2005) indicated major clades corresponding to 1) a few lineages lacking close relatives; 2) the ‘core martins’, a mostly New World clade; and 3) the ‘mud nesters’, a globally distributed clade of swallows, including monophyletic lineages corresponding to the genera *Ptyonoprogne*, *Hirundo*, *Delichon*, *Petrochelidon*, and *Cecropis*.



A few taxa were omitted from previous analyses for lack of high-quality tissue samples; these taxa have been placed taxonomically based on plumage morphology and nest characteristics (Turner and Rose 1989). One enigmatic taxon missing from the molecular phylogenetic studies was the forest swallow *Petrochelidon fuliginosa* (Sheldon et al. 2005, Gill and Donsker 2014). Despite its *Psalidoprocne*-like plumage, the forest swallow lacks the characteristic ‘saw-wing’ of that genus, and is unique in its rufous-tinged throat, ‘broader stouter bill’, and ‘slightly forked tail’ (Chapin 1925) (Fig. 1). Forest swallows are unique in their nesting habits, in that their mud nests with tunnel entrances (like those of *Cecropis*) are located in forested habitats, usually under large rocks; habitat choice is similar to that of grey-necked picathartes *Picathartes oreas* (Borrow and Demey 2001). Restricted to lowland forests, this species is endemic to a relatively narrow zone of central Africa from southeastern Nigeria to northern Angola (Turner and Rose 1989, Mills and Tebb 2015). The plumage, morphology, and nesting behavior of this species do not align well with those of any other major swallow lineage (Earlé 1987); nonetheless, it was originally placed in the genus *Lecythoplastes* with another central African ‘mud nester’, Preuss’s cliff swallow *Petrochelidon preussi* (note that *P. preussi* is the type species in *Lecythoplastes*). Both are now placed in the global ‘mud nester’ group, in the genus *Petrochelidon*.

On a recent expedition in Southwest Region, Cameroon (March–April 2015), we encountered forest swallows in mixed flocks with square-tailed saw-wings *Psalidoprocne nitens* along streams in primary, lowland forest at Chimpanzee Camp, in Korup National Park (5.0708°N, 8.8598°E). We collected four specimens (KU131409-11, KU131607), all accompanied by high-quality tissue samples. Upon realizing that this taxon was not represented in world tissue holdings, we sequenced DNA from two mitochondrial and one



Figure 1. Adult male forest swallow *Petrochelidon fuliginosa* (KU 131410).

nuclear gene markers to place the species on the swallow phylogenetic tree (Sheldon et al. 2005). Our unexpected results lead us to describe a new genus for this unique swallow lineage.

Methods

As part of a general survey of the avifauna at Korup National Park during 5–10 March 2015, 4 forest swallows were collected. Three were prepared as study skins and another as a fluid-preserved specimen, all with associated tissue samples preserved in 70% ethanol. Total DNA was extracted using DNeasy Blood & Tissue Kits (Qiagen, Valencia, CA) following manufacturer’s protocols. Each DNA sample was quantitated using a Qubit double-stranded DNA Assay Kit (Thermo-Fisher Scientific). DNA was amplified for two mitochondrial protein-coding genes (nicotinamide adenine dinucleotide dehydrogenase subunit 2 [ND2], 1041 bp; cytochrome b [Cyt b], 1143 bp) and one nuclear intron (seventh intron of the beta-fibrinogen gene [Fib7], 938 bp), following protocols from our previous studies (De Silva et al. 2017). PCR products were submitted to GENEWIZ (South Plainfield, NJ) for purification and single pass sequencing. Forward and reverse strands of the sequences were examined for complementary chromatograms, and were cleaned and assembled into contigs in Geneious 8.1.6 (Biomatters, Auckland, New Zealand).

In addition to new forest swallow DNA sequences, we gathered sequence data from the most comprehensive previous analysis (Sheldon et al. 2005) – in particular, we referred to Fig. 7 in that paper, and obtained sequences for the entire lower clade (Table 1) (crag martins through saw-wings, plus *Cheramoeca* and *Pseudhirundo*). Because of some confusion with the sequences corresponding to the Genbank accession numbers in the Sheldon et al. (2005) paper, some sequence data had to be discarded, particularly for Fib7, which reduced our taxon representation somewhat. We obtained sequences from single representatives of each of the remaining clades, prioritizing specimens for which complete sequences for all three segments were available. Sequences were aligned individually in MUSCLE (Edgar 2004), using default settings. The best-fitting partitioning scheme and evolutionary models were chosen using the corrected Akaike information criterion (AICc) (Posada and Buckley 2004), and the greedy algorithm implemented in PartitionFinder 2 (Lanfear et al. 2016).

Bayesian analysis (BA) and maximum-likelihood (ML) inference approaches were applied to both concatenated and single-gene data sets. BA was conducted using Markov Chain Monte Carlo (MCMC) tree searches implemented in MrBayes ver. 3.2.6 (Ronquist et al. 2012). The analysis consisted of two independent runs of 2×10^8 generations and 4 Markov chains, each of which was sampled every 20 000 generations. Convergence parameters and posterior probabilities were evaluated using Tracer 1.6 (Rambaut et al. 2014). In addition, average standard deviation of split frequencies

Table 1. Taxonomic sampling, gene availability, and Genbank accession numbers used in this study.

Taxon	Genbank accession		
	Cytb	ND2	βFib7
<i>Cecropis abyssinica</i>	AY825975	AY826034	–
<i>Cecropis cucullata</i>	AY825974	AY826033	–
<i>Cecropis daurica</i>	AY825977	AY826036	–
<i>Cecropis domicella</i>	AY825978	–	–
<i>Cecropis semirufa</i>	AY825976	AY826035	–
<i>Cecropis striolata</i>	AY825979	–	–
<i>Cheramoeca leucosternus</i>	AY825956	AY826013	AY827428
<i>Delichon dasyopus</i>	AY825986	AY826044	AY827450
<i>Delichon nipalensis</i>	AY825987	AY826045	–
<i>Delichon urbica</i>	AF074592	AY826043	AY827449
<i>Hirundo aethiopica</i>	AY825964	AY826023	AY827433
<i>Hirundo albigularis</i>	AY825966	AY826025	AY827437
<i>Hirundo angolensis</i>	AY825965	AY826024	AY827434
<i>Hirundo atrocaerulea</i>	AY825971	AY826030	AY827438
<i>Hirundo dimidiata</i>	AY825973	AY826032	–
<i>Hirundo leucosoma</i>	AY825972	AY826031	–
<i>Hirundo lucida</i>	AY825963	AY826022	–
<i>Hirundo neoxena</i>	AY825968	AY826027	AY827436
<i>Hirundo nigrata</i>	AY825970	–	–
<i>Hirundo rustica</i>	AY825962	AY52475	AY827432
<i>Hirundo smithii</i>	AY825969	AY826028	AY827439
<i>Hirundo tahitica</i>	AY825967	AY826026	AY827435
<i>Notiochelidon pileata</i>	AY825953	AY826005	AY827425
<i>Petrochelidon ariel</i>	AY825985	AY826042	AY827447
<i>Petrochelidon fluvicola</i>	AY825984	–	–
<i>Petrochelidon fuliginosa1</i>	MH049600	MH049597	MH049603
<i>Petrochelidon fuliginosa2</i>	MH049601	MH049598	MH049604
<i>Petrochelidon fuliginosa3</i>	MH049602	MH049599	MH049605
<i>Petrochelidon fulva</i>	AF182389	–	–
<i>Petrochelidon nigricans</i>	AY825983	AY826041	AY827448
<i>Petrochelidon preussi</i>	AY825981	AY826037	AY827444
<i>Petrochelidon pyrrhonota</i>	AF074591	AY826039	–
<i>Petrochelidon rufigula</i>	AY825982	–	–
<i>Petrochelidon rufocollaris</i>	AF182381	AY826040	–
<i>Petrochelidon spilodera</i>	AF074582	AY826038	AY827446
<i>Phedina borbonica</i>	AY825958	AY826018	AY827404
<i>Progne subis</i>	AY825996	AY825996	AY827413
<i>Psalidoprocne albiceps</i>	AY825990	–	–
<i>Psalidoprocne fuliginosa</i>	AY825989	AY826046	AY827431
<i>Psalidoprocne holomelas</i>	AF074587	AY826048	AY827430
<i>Psalidoprocne nitens</i>	AY825988	–	–
<i>Psalidoprocne obscura</i>	AY825993	–	–
<i>Psalidoprocne orientalis</i>	AY825992	–	–
<i>Psalidoprocne petiti</i>	AY825991	AY826047	–
<i>Pseudhirundo griseopyga</i>	AF074579	AY826014	AY827429
<i>Pseudochelidon eurystomina</i>	AY825944	AY826050	–
<i>Pseudochelidon sirintarae</i>	–	AY826049	–
<i>Ptyonoprocne concolor</i>	AY825961	–	–
<i>Ptyonoprocne fuligula</i>	AF074581	AY826021	AY827451
<i>Ptyonoprocne rupestris</i>	AY825960	AY826020	–
<i>Riparia riparia</i>	AF074578	AY826015	AY827423
<i>Stelgidopteryx serripennis</i>	AY825955	AY826011	AY827410
<i>Tachycineta albilinea</i>	AY052445	AY52468	AY827408

(ASDSF) and potential scale reduction factor (PSRF) were assessed as measures of convergence between runs (Whidden and Matsen IV 2015). As initial burn-in, the first 25% of

MCMC generations were discarded; a majority-rule consensus tree was obtained by summarizing the remaining generations. ML analyses were conducted in RaxML 7.0.2 (Stamatakis 2006); the GTRGAMMA model was used to obtain 100 tree searches and 1000 bootstrap replicates.

Results

Swallow phylogeny and *Petrochelidon fuliginosa*

The forest swallow was placed firmly within the ‘mud nester’ clade, but outside of the clade corresponding to *Petrochelidon* (Fig. 2). Specifically, it linked to *Delichon* in our concatenated analysis with strong support in both Bayesian and ML analyses (1.0 PP; 100% bootstrap), outside of the well-supported *Petrochelidon* + *Cecropis* clade. Although our Cyt *b* gene tree placed the focal species, *Cecropis*, and *Petrochelidon*, together in a clade, the focal species was sister to *Petrochelidon* + *Cecropis*, such that its placement in the current concept of *Petrochelidon* is not appropriate (Supplementary material Appendix 1 Fig. A2). The Fib7 gene tree could not resolve relevant relationships since no *Cecropis* sequences were available, owing to the confusions relating to Genbank accession numbers mentioned above. Quite interestingly, similar to results presented by Sheldon et al. (2005), the *Petrochelidon* + *Cecropis* linkage was deep, not at all reflecting a recent derivation of these two lineages.

Our phylogenetic results (Fig. 3) showed that the forest swallow: 1) is not part of either the *Petrochelidon* or the *Petrochelidon* + *Cecropis* clades; 2) is likely sister to *Delichon*; and 3) is not closely related to any other swallow lineage. What is more, it is quite distinct phenotypically from other mud-nester lineages (Fig. 3). Taxonomically, three generic arrangements are therefore possible: 1) merge *Petrochelidon fuliginosa* into *Delichon*; 2) create a much more inclusive *Petrochelidon* to include all of *Delichon*, *Cecropis*, *Petrochelidon*, and *Petrochelidon fuliginosa*; or 3) recognize *Petrochelidon fuliginosa* as a new genus. We explored and discarded options 1) and 2), in light of the deep nature of the splits represented by the nodes linking *Delichon* and *Petrochelidon fuliginosa* to *Petrochelidon* and *Cecropis*, and also considering the plumage and morphological diversity that would be manifested within the more inclusive concepts (i.e. *Delichon* larger in size, with distinct black and white coloration; forest swallow small with uniform dark brown coloration; *Petrochelidon* and *Cecropis* large, with contrasting dark, brown, and light coloration).

As a consequence, we propose to recognize the distinctiveness of this taxon at the generic level. This species was originally described in the genus *Lecythoplastes* (Chapin 1925) with Preuss’s cliff swallow *Petrochelidon preussi*. *Lecythoplastes* had been proposed originally based on *preussi* as a type species by Reichenow (1898), and *preussi* falls firmly within *Petrochelidon* in all of our phylogenetic analyses. As such, *Lecythoplastes* must remain submerged in *Petrochelidon*; to our knowledge, then, no generic name is available for the forest swallow lineage. We therefore erect.

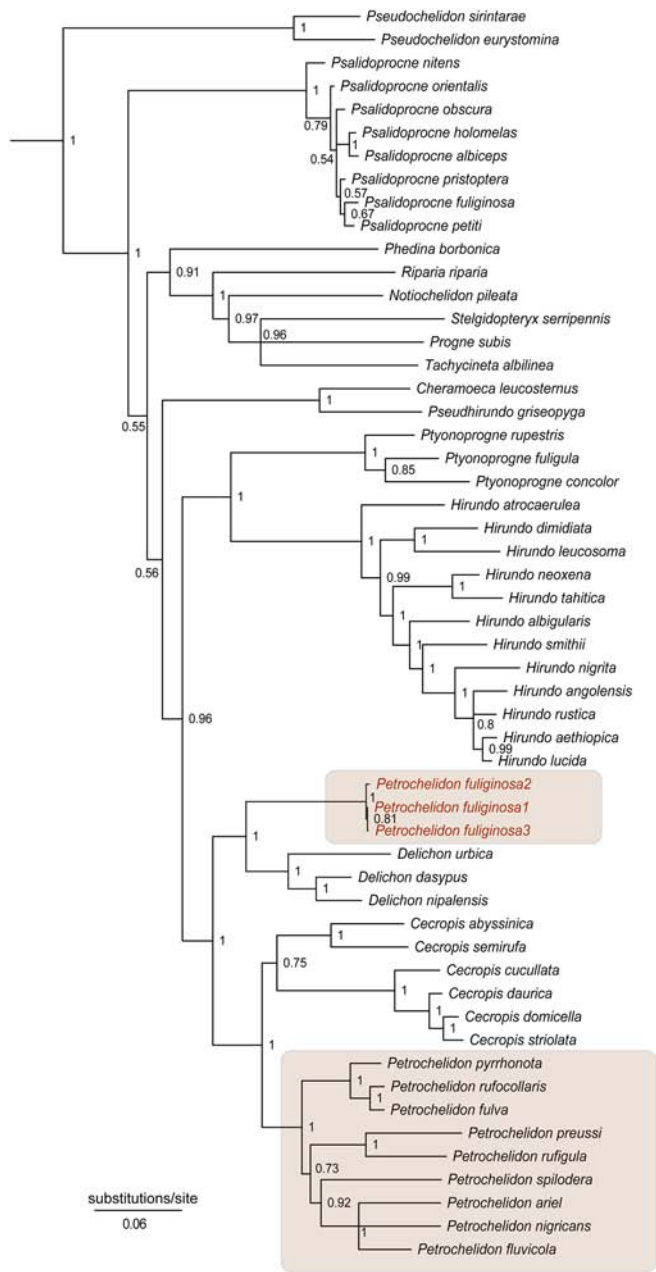


Figure 2. Multilocus phylogeny of swallows (Hirundinidae) outlining the placement of forest swallow *Petrochelidon fuliginosa*. The Bayesian majority-rule consensus tree of the concatenated, partitioned three-gene (Cytb, ND2, Fib7) dataset, with support values (posterior probability) listed at respective nodes.

Atronanus, new genus.

Type species – *Lecythoplastes fuliginosus* Chapin 1925.

Referred species – none.

Etymology – by combining two descriptors, we emphasize the small size and dusky black plumage of the only species referred to this genus. We combine the adjective *atro*, which means black, with the masculine noun *nanus*, which means dwarf. The combination is thus masculine in gender.

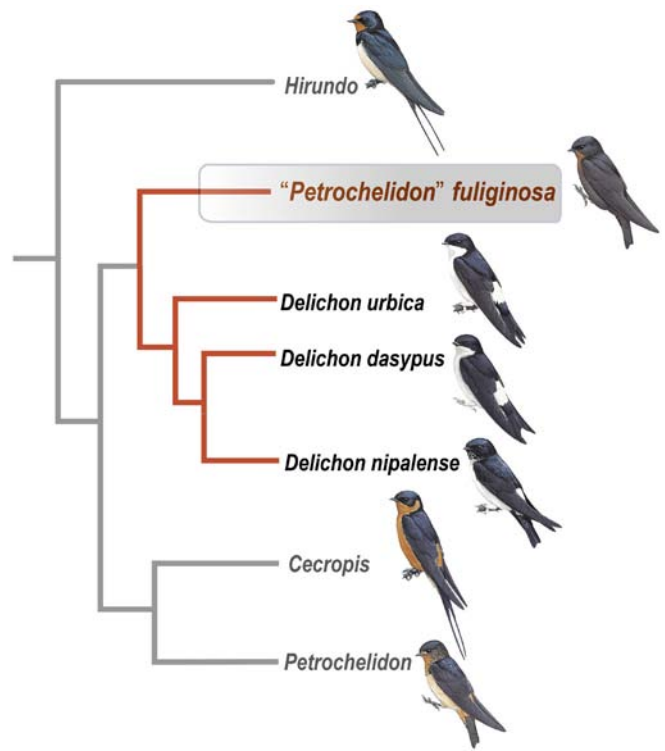


Figure 3. Summary phylogenetic tree for the ‘mud-nester’ clade of swallows (Hirundinidae), showing the placement of the key lineage in question (*Petrochelidon fuliginosa*), and external phenotype of each major lineage.

Diagnosis – the forest swallow is allocated to this genus based on a combination of molecular genetic results and distinctive morphological characters: 1) small size and 2) dark brown and relatively uniform plumage coloration with chin and throat rusty brown (Fig. 1). Superficially, the forest swallow is reminiscent of swiftlets (*Collocalia*, Apodidae), but is also strikingly similar to the smaller-bodied members of *Psalidoprocne* (e.g. *P. nitens*), albeit without the primary feather modifications that define *Psalidoprocne*. Its placement within the ‘mud nester’ clade is based on sequence data from multiple genes.

Discussion

As the species’ English name suggests, our Korup National Park experience with this swallow was limited to the forest interior; additional observations by JCC have placed it in forest-edge situations as well. Our specimens were captured, along with the similarly plumaged square-tailed saw-wing *Psalidoprocne nitens*, in mist nets set across a small forest stream (2–3 m wide). Based on gonadal data and presence of brood patches, both the forest swallows and *Psalidoprocne* were breeding. Earlé (1987) noted forest swallow breeding during the months of January, April–June and November. This species is a solitary retort-nester, a rare exception to the more common combination of coloniality and retort-nesting

in swallows (Winkler and Sheldon 1993). Interestingly, forest swallow eggs are white, like all three *Delichon* species, whereas *Petrochelidon* eggs are heavily spotted (Turner and Rose 1989).

This contribution documents and describes formally a distinct, generic-level lineage of swallows endemic to the Lower Guinean forest region of the ‘bend’ of Africa, a transition region between easternmost west Africa and northwestern central Africa. This region is part of the ‘West African Forests’ biodiversity hotspot (Myers et al. 2000), and holds isolated montane areas with extremely high endemism (Cameroon Mountains endemic bird area, ~30 endemic species) (BirdLife International 2016). Adjacent lowland regions also hold significant endemism (Cameroon and Gabon Lowlands endemic bird area, 6 endemic species; BirdLife International 2017). The distribution of *Atronanus fuliginosus* is remarkably similar to those of *Picathartes oreas* and *Malimbus racheliae* (Borrow and Demey 2014). Although elevating one already-endemic taxon to generic status does not change numbers of endemic species, it does underline the older and deeper nature of the lineages involved.

Acknowledgements – We thank our Cameroonian colleagues, Sainge N. Moses, for their assistance in all phases of the logistics and execution of this project. We thank Rob Moyle and Fred Sheldon for discussion of swallow relationships.

Funding – JRS Biodiversity Fund.

Author contributions – The first, second and sixth authors contributed to laboratory work, analysis, figures and writing of this paper. The third, fourth, and fifth authors were involved in the study design, field studies, and collections.

Permits – Official permission for scientific collecting in Cameroon was given by the Ministère de la Recherche Scientifique et Technique et de l’Innovation and the Ministère des Forêts et de la Faune.

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Supplementary material (Appendix JAV-01698 at <www.avianbiology.org/appendix/jav-01698>). Appendix 1.