Molecular Phylogenetics and Evolution 125 (2018) 116–126

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Contrasting patterns of diversification in two sister species of martins (Aves: Hirundinidae): The Sand Martin *Riparia riparia* and the Pale Martin *R. diluta*

Manuel Schweizer[a], Yang Liu[b,*], Urban Olsson[c], Hadoram Shirihai[d], Qin Huang[b], Paul J. Leader[e], José Luis Copete[f], Guy M. Kirwan[g], Guoling Chen[b], Lars Svensson[h]

[a] *Manuel Schweizer, Naturhistorisches Museum der Burgergemeinde Bern, Bernastrasse 15, CH-3005 Bern, Switzerland*
[b] *State Key Laboratory of Biocontrol, Department of Ecology, School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, PR China*
[c] *University of Gothenburg, Department of Biology and Environmental Sciences, Systematics and Biodiversity, Box 463, SE-405 30 Göteborg, Sweden*
[d] *c/o Ausserdorfstrasse 6, CH 8052 Zürich, Switzerland*
[e] *AEC Ltd., 127 Commercial Centre, Palm Springs, Hong Kong, PR China*
[f] *Handbook of the Birds of the World Alive, Lynx Edicions, Montseny 8, 08193 Bellaterra, Spain*
[g] *Field Museum of Natural History, 1400 South Lakeshore Drive, Chicago, IL 60605, USA*
[h] *S:ta Toras väg 28, SE-269 77 Torekov, Sweden*

ARTICLE INFO

Keywords:
Molecular phylogeny
Taxonomy
Hirundinidae
Riparia
Phylogeography
Pleistocene

ABSTRACT

Species not only responded idiosyncratically to past climate changes, there were also regionally contrasting effects on spatio-temporal diversification patterns. Studies of closely related species appear to be a particularly promising comparative approach to disentangle such regionally differential impacts. In this study, we undertook a comprehensive geographic sampling to investigate the evolutionary history of the Holarctic Sand Martin *Riparia riparia* and the chiefly Central and East Asian Pale Martin *R. diluta*. Previous phylogenetic studies using only a limited geographic sampling, particularly for the latter, revealed the two to be genetically distinct, with the former showing only a shallow genetic structure in mitochondrial DNA. Based on one mitochondrial, one autosomal and one Z-linked nuclear marker, we confirmed the shallow genetic structure in *R. riparia* even when including the morphologically relatively distinct subspecies *R. r. shelleyi* from the Nile Valley in Egypt and probably the Middle East. On the other hand the different subspecies of *R. diluta*, i.e. *R. d. diluta* from Central Asia, *R. d. indica* from the northwestern Indian Subcontinent, *R. d. tibetana* from the Tibetan Plateau and *R. d. fohkienensis* from southeastern China, were found to be genetically distinct. Their diversification started before the Early to Middle Pleistocene Transition, which was followed by a pronounced succession of glacial and interglacial periods. These rather old divergence events contrast with the lack of any strong phylogeographic structure in *R. riparia*. Strongly structured populations and regional diversification have been reported in different forest passerine families of South-East Asia. Here we demonstrate, however, that species characteristic of open-country habitats such as *R. diluta* might display a similar pattern. Morphometric analyses of 120 individuals revealed no clear differences between the different subspecies of *R. diluta*. Given their similarity also in plumage features, we refrain from proposing any splits despite their marked genetic differentiation, pending further studies and particularly the discovery of potential secondary contact zones.

1. Introduction

Pliocene and particularly Pleistocene climate fluctuations have strongly influenced current biodiversity patterns on Earth by promoting speciation and population diversification, as well as by altering distributions (Head and Gibbard, 2005; Hewitt, 2004; Lovette, 2005). There is ample evidence that species respond idiosyncratically to climate change; moreover, as different regions were affected heterogeneously especially by Pleistocene glacial cycles, regional differences in spatio-temporal diversification patterns are also evident (Lovette, 2005; Qu et al., 2014; Weir and Schluter, 2004). Studies of closely related species or species complexes with a broad distribution across different biogeographic realms appear to be a particularly promising comparative approach to disentangle the regionally differential impacts of past climatic change on diversification patterns (e.g. Wang et al., 2017).

The Sand Martin *Riparia riparia* and Pale Martin *Riparia diluta* are now generally treated as two different sibling species after Gavrilov &

---

[*] Corresponding author.
E-mail address: liuy353@mail.sysu.edu.cn (Y. Liu).

https://doi.org/10.1016/j.ympev.2018.02.026
Received 29 August 2017; Received in revised form 25 January 2018; Accepted 27 February 2018

Table 1
Qualitative description of main morphological differences between treated taxa. x indicates that a character is present, while (x) means that there is some variation in the presence of this character. The table is giving a general overview and helps to discriminate the taxa, however, it presents facts in an oversimplified way and is potentially misleading, e.g. natural variation has many shades of grey, and there is some overlap in almost every aspect if a large enough sample is examined.

	R. d. diluta	*R. d. indica*	*R. d. tibetana*	*R. d. fohkienensis*	*R. r. riparia*	*R. r. ijimae*	*R. r. shelleyi*
Upperparts rather dark brown			x		x	x	(x)
Upperparts medium to pale grey-brown	x	x		x			(x)
Cheek patch dark, contrasting with white head-side				x	x	x	x
Cheek patch pale, grading into white head-side	x	x	x				
Breast-band dark and contrasting					x	x	x
Breast-band pale with diffuse borders	x	x	x	x			(x)
Wing < 100 mm		x					x
Wing *c.* 95–108 mm	x			x			
Wing 100–115 mm			x		x	x	
Tail-fork very shallow (*c.* 2–6 mm)		x	x	x			
Tail-fork rather shallow (*c.* 4–9 mm)	x		x				x
Tail-fork well-marked (*c.* 7–14 mm)					x	x	
Feathered tarsi (> 1/2 or rear edge)	x	x	x	x	(x)		x
Unfeathered tarsi, or nearly so					x	x	
Chin and upper throat uniformly pale	x	x	x	x	x	x	
Chin and upper throat finely spotted dark					(juv = x)		x (some)
Rather dark brown head thus dark eye-surround is less obvious			x		x	x	
Rather pale brown head making dark eye-surround more obvious ('sunglasses effect')	x	x		x			x

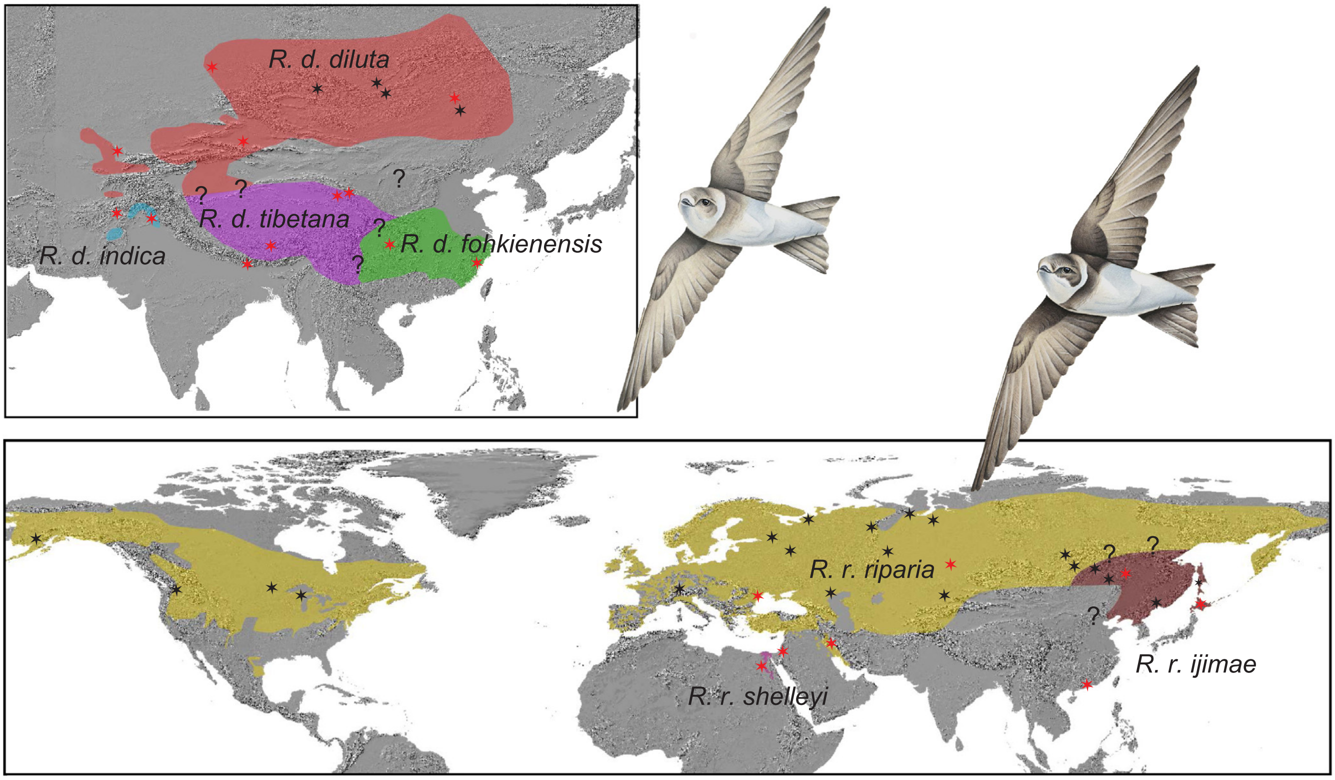

Fig. 1. Breeding distribution of the different subspecies of the Pale Martin *Riparia diluta* (top) and the Sand Martin *Riparia riparia* (bottom) modified from Bird Life International and Handbook of the Birds of the World (2016). Black stars show sample locations for sequences taken from Pavlova et al. (2008), while red stars represent new sample locations for this study. Hypothetical subspecies boundaries or potental breeding areas are indicated in question marks. Paintings by M. Schweizer. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Savchenko (1991) and Goroshko (1993) demonstrated a wide zone of overlap, as well as morphological and vocal differences between the two (cf. del Hoyo and Collar, 2016; Dickinson and Christidis, 2014; Table 1). While *R. diluta* breeds from east Iran to southwest Siberia and Mongolia, as well as on the Qinghai-Tibetan Plateau and in central and southeastern China, *R. riparia* is widespread across the entire Holarctic including the Middle East and the Nile Valley in Egypt (Turner, 2004) (Fig. 1). Their distinctiveness was subsequently confirmed by the discovery of mixed colonies without evidence of interbreeding in Kazakhstan (LS and others; pers. obs.), Russia (Buryatiya; Pavlova et al., 2008, and Novosibirsk; PJL pers. obs.) and China (north Xinjiang, PR China; YL pers. obs.). Moreover, they differ in mitochondrial and nuclear DNA loci, and appear to have diverged between the late Pliocene and middle Pleistocene (Pavlova et al., 2008).

A surprisingly low genetic diversity in mitochondrial DNA (mtDNA) was revealed in *R. riparia* over its entire Holarctic breeding area, indicating a recent population expansion (Pavlova et al., 2008). In contrast, relatively deep intraspecific genetic differences were found