A revised multilocus phylogeny of Old World sparrows (Aves: Passeridae)

Martin Päckert1, Jens Hering2, Abdelkrim Ait Belkacem3, Yue-Hua Sun4, Sabine Hille5, Davaa Lkhagvasuren6, Safiqul Islam1, Jochen Martens7

1 Senckenberg Natural History Collections Dresden, Museum of Zoology, Königsbrücker Landstraße 159, 01109 Dresden, Germany
2 Verein Sächsischer Ornithologen e.V., 09212 Limbach-Oberfrohna, Germany
3 Laboratoire d’Exploration et de Valorisation des Écosystèmes Steppiques, Faculté des Sciences de la nature et de la vie, Université de Djelfa, Djelfa, Algeria
4 Key Laboratory of Animal Ecology and Conservation, Institute of Zoology, Chinese Academy of Sciences, Beijing, China
5 Institute of Wildlife Biology and Game Management (IWW), University of Natural Resources and Life Sciences, Gregor-Mendel-Straße 33, 1180 Vienna, Austria
6 Department of Biology, School of Arts and Sciences, National University of Mongolia, P.O.Box 464-546, Ulaanbaatar-210646, Mongolia
7 Institute of Organismic and Molecular Evolution (iomE), Johannes Gutenberg University, 55099 Mainz, Germany

http://zoobank.org/5C48BDBC-3761-4766-9E32-0C431F689992

Corresponding author: Martin Päckert (martin.paeckert@senckenberg.de)

Abstract

The Old World sparrows include some of the best-studied passerine species, such as the cosmopolitan human commensal, the house sparrow (Passer domesticus) as well as poorly studied narrow-range endemics like the Iago sparrow (P. iagoensis) from the Cape Verde Archipelago or specialists from extreme environments like the desert sparrow (P. simplex). It is therefore notable that to date the most complete phylogenetic hypothesis for the Old World sparrows comprised only ten of 43 currently accepted species. With this study we provide an updated phylogeny of Passeridae covering about two third of the family’s species richness. Though still being far from taxon-complete, this new phylogenetic hypothesis provides firm evidence to clarify some open taxonomic questions. All genus-level taxa were reciprocally monophyletic with strong support. Contrary to previous classifications, bush sparrows and rock sparrows were not sister taxa, and therefore their classification in separate genera Gymnoris and Petronia is justified. Plumage color traits like the yellow throat patch of the latter two genera or head color pattern in Passer species do not provide reliable phylogenetic information, except for the large-sized African grey-headed sparrows that resulted as a monophyletic group (P. diffusus, P. griseus, P. gongoensis). Unexpectedly, two small-sized species, P. eminibey and P. luteus that to date are regarded as close relatives were firmly nested in two separate clades of Passer sparrows. Therefore, their separate generic treatment under Sorella eminibey and Auripasser luteus (together with A. euchlorus) does not seem justified.

Keywords

bush sparrows, introns, mitochondrial DNA, snowfinches, systematics, taxonomy
Introduction

The Old World sparrows, Passeridae, are a speciose passerine family distributed all over the Afrotropics, the Paleartic and parts of the Oriental Region. Throughout the entire Old World, only the Australian Region and Madagascar are not inhabited by any species of the family – except the human-introduced house sparrow. Several species are highly adapted to extreme environments such as the snowfinches (Montifringilla, Pyrgilauda and Onychostruthus) from the high alpine ecosystems of Eurasian mountain systems (Lei et al. 2014; Päckert et al. 2020). Recent comparison of high-quality genomes provided evidence of divergent adaptation to local selective pressures in each of the three snowfinch genera (Qu et al. 2021). Also, the extremely hot and dry Sahara harbors suitable habitat for specialists like the Desert sparrow, Passer simplex. Areas of highest species richness are located in the African Rift Valley and at the eastern margin of the Qinghai-Tibet Plateau (QTP) (Fig. 1).

Though formerly included in Passeridae (e.g. Dickinson 2003), the sparrow-weavers (genera Plocepasser, Histurgops, Pseudonigriga and Philetarius) had often been affiliated to the Ploceidae based on morphological features like tongue musculature (Bock and Morony Jr 1978; Summers-Smith 2010). Recent phylogenies by de Silva et al. (2017, 2019) confirmed the inclusion of sparrow-weavers in Ploceidae (compare also Jonsson and Fjeldså 2006) in accordance with most taxonomic authorities (Dickinson and Christidis 2014; del Hoyo and Collar 2016; Clements et al. 2019; Gill et al. 2020). The Passeridae are characterized by several synapomorphies of tongue morphology, too (Bock and Morony Jr 1978) and representatives of major genera (Montifringilla, Passer and Petronia) belong to a monophyletic group that was consistent across several recently published phylogenies (e.g. Ericson and Johansson 2003; Zuccon et al. 2012).

To date, the Passeridae are generally classified into eight genera, four of them monotypic (Hypocryptadius, Carpospiza, Petronia and Onychostruthus), with a total number of 43 currently accepted species (according to the IOC World Bird List by Gill et al. 2020). Among these, Passer is the most diverse genus with 28 currently recognized species (del Hoyo and Collar 2016; Gill et al. 2020), of which the house sparrow, Passer domesticus (Fig. 2C), is probably one of the best studied species (reviews in Anderson 2006; Liebl et al. 2015), not least because as a commensal of human civilization it is fairly common all over its range (Sætre et al. 2012). Moreover, past and extant hybridization of the house sparrow with other conspecifics has been intensively studied on a genetic basis with respect to the stabilized hybrid form Passer italiae (Elgvin et al. 2011, 2017; Hermansen et al. 2011, 2014; Eroukhmanoff 2013, 2017; Sætre et al. 2017; Runemark et al. 2018), to distinct genetic lineages in Asia (Ravinet et al. 2018) and to the mosaic hybrid zone with the Spanish sparrow, P. hispaniolensis, in North Africa (Belkacem et al. 2016; Päckert et al. 2019).

In contrast, the phylogenetic relationships among genera and species of Passeridae are poorly studied to date, which is mainly due to a lack of data from the Afrotropics. Recently, it came out as a rather surprising finding, that the Philippine endemic cinnamon ibon, Hypocryptadius cinnamomeus, was sister to a clade of Passeridae species (Fjeldså et al. 2010). Previously, that Philippine endemic had been included in the white-eyes (Zosteropidae), however based on molecular phylogenetic evidence this species is included in Passeridae by several taxonomic authorities today (del Hoyo and Collar 2016; Gill et al. 2020).

A first phylogenetic hypothesis for Passeridae was based on a single mitochondrial gene (Allende et al. 2001) and included only eleven species. Since then, a few molecular studies focused on the phylogenetic relationships of snowfinches (Onychostruthus, Pyrgilauda, Montifringilla [Fig. 2A]), a group of eight high alpine endemic species from the QTP and from other Paleartic mountain systems (Qu et al. 2006; Gebauer et al. 2006; Lei et al. 2014; del Mar Delgado et al. 2019; Päckert et al. 2020). However, to date no multi-locus analysis has ever been performed for a broader taxon sampling across different genera of Passeridae. The most comprehensive phylogenetic hypothesis available for Passeridae by Jønsson and Fjeldså (2006; their Passeroidea clade 8) included 14 species from three genera.

As a contribution to the current discussion on phylogenetic relationships within Passeridae, we provide a new phylogenetic hypothesis for 18 species of Old World sparrows (Passer) and another 11 species of African bush-sparrows (Gymnoris), rock sparrows (Petronia, [Fig. 2B]) and snowfinches (Onychostruthus, Pyrgilauda, Montifringilla) from the Qinghai-Tibet Plateau and other Paleartic mountain systems.

Methods

We amplified and sequenced four molecular markers using 65 samples from 22 species of the Passeridae genera Passer, Petronia, Gymnoris, Montifringilla, Pyrgilauda and Onychostruthus. Based on previous evidence of intraspecific diversification from Päckert et al. (2020) we included some additional subspecific taxa of Montifringilla nivalis and Petronia petronia (Table 1), further samples from different island populations of the Cape Verde endemic Iago sparrow (Passer iagoensis; Fig. 2D) and from the range of overlap of two of the smaller snowfinch species (Pyrgilauda blanfordi and P. davidiana; further samples for intraspecific comparison, see supplementary Table S1).

We extracted DNA from frozen blood or tissue samples using the innuPREP DNA Mini Kit (for muscle tissue) or the innuPREP BloodDNA Mini Kit (for blood), respectively (both Analytik Jena AG, Germany) accord-
Figure 1. Diversity heat map of Old World sparrows (Passeridae) with two hotspots of diversity in the African Rift Valley and at the eastern margin of the Qinghai-Tibet Plateau; modified from Päckert et al. (2020).

Figure 2. Selected study species of Old World sparrows, Passeridae; A) white-winged snowfinch, *Montifringilla nivalis* (photo: DL, Gobi Altai, Mongolia); B) rock sparrow, *Petronia petronia*, at nesting hole (photo: MP, China Qinghai); C) house sparrow, *Passer domesticus* (photo: MP, Greece, Santorini); D) Iago sparrow, *Passer iagoensis*; (photo: SH, Cape Verde Islands).
Table 1. Samples and sequences used for phylogenetic reconstruction; collections who donated samples for this study: MTD = Senckenberg Natural History Collections Dresden (SNSD), Museum of Zoology, Germany (MAR = tissue sample collection J. Martens at SNSD); IPMB = Department of Biology, Institute of Pharmacy and Molecular Biotechnology, Heidelberg University, Heidelberg, Germany; ZMUC = Zoological Museum of the University of Copenhagen, Denmark (NHMD = Natural History Museum of Denmark); UWBM = Burke Museum of Natural History and Culture, Seattle, USA—further collection acronyms (GenBank sequences; sample numbers marked with an asterisk); NRM = Natural History Museum of Stockholm, Sweden; ANSP = The Academy of Natural Sciences of Drexel University, USA; FMNH = The Field Museum of Natural History, Chicago, USA, CAS = Chinese Academy of Sciences, Institute of Zoology, Beijing, China.

| sample no | species (Gill et al. 2020) | family | country | location | cyt | ND2 | myo2 | ODC |
|-----------|---------------------------|--------|---------|----------|-----|-----|-----|-----|
| NRM 986044* | Bombycilla garrulus | Bombycillidae | Sweden | — | | | | |
| NHDMD135615* | Amandava amandava | Estrildidae | Captivity | — | | | | |
| ZMUC0785* | Cryptospiza reichenowi | Estrildidae | — | | | | | |
| GenBank* | Erythura Gouldiae | Estrildidae | India | — | | | | |
| CAS/92755* | Lonchura melacca | Estrildidae | China | — | | | | |
| ZMUC117473 | Pyrgilauda blanfordi | Passeridae | Philippines | Mindanao, Katanglad Volcano | — | | | |
| MAR2212 | Montifringilla adamsi | Passeridae | China | Qinghai, Huashixia | MN337349 | MN337357 | MN337368 | MN337374 |
| MAR2004 | Montifringilla hirici | Passeridae | China | Qinghai, Nanshan | DQ244059 | MN337360 | MN337369 | MN337376 |
| MTD C64406 | Montifringilla nivalis nivalis | Passeridae | Italy | Dolomites | KX109628 | KX109703 | KX109668 | KX109742 |
| MAR3111 | Montifringilla nivalis grumgrzimali | Passeridae | Mongolia | Bondoco Gol, Altai | MN337353 | MN337362 | MN337371 | MN337372 |
| MAR1532 | Montifringilla nivalis alpica | Passeridae | Russia | Dagestan, Kunurah | MN337352 | MN337361 | MN337370 | MN337379 |
| MAR1775 | Pyrgilauda bianfoldi | Passeridae | China | Qinghai, highlands near Madai | MN337350 | MN337358 | MN337366 | — |
| MAR2093 | Pyrgilauda davidiana | Passeridae | China | Qinghai, Heimahe | MN337351 | MN337359 | MN337367 | MN337375 |
| NC 25915 | Pyrgilauda davidiana | Passeridae | China | — | NC 25915 | NC 25915 | — | — |
| MAR2206 | Pyrgilauda ruficollis | Passeridae | China | Qinghai, Heimahe | MN337354 | MN337363 | MN337372 | MN337380 |
| MAR8787 | Passer ammodendri | Passeridae | Mongolia | Gobi Altai, Echin Gol oasis | MT210107 | MT210145 | MT277434 | MT332606 |
| UWBM95153 | Passer domesticus | Passeridae | South Africa | Vorstershoop, 10 km W | MT210109 | MT210144 | MT277435 | MT332607 |
| MTD C64358 | Passer domestica | Passeridae | Germany | Saxony, Dresden | KX109629 | KX109704 | KX109669 | KX109743 |
| MTD 2012-202 | Passer eminibey | Passeridae | captivity | — | MT210111 | MT277436 | MT332608 | |
| GenBank | Passer flavus | Passeridae | Vietnam | — | AF230907 | — | — | — |
| ZMUC117473 | Passer gongensis | Passeridae | Kenya | Samburu Serena Lodge | MT210112 | MT210140 | MT277437 | MT332609 |
| GenBank* | Passer gracilis | Passeridae | Senegal | — | AF230908 | — | — | — |
| IPMB9505 | Passer hispaniolensis | Passeridae | Spain | Lanzarote | MT210113 | MN488960 | MT277438 | MT332610 |
| MAR4076 | Passer longipennis | Passeridae | Cape Verde | Sal, Buracona | MT210104 | MT210136 | MT277439 | MT332611 |
| SOC4* | Passer minimus | Passeridae | Yemen | Socotra | EU478434 | — | — | — |
| ITA1 | Passer rustrei | Passeridae | Italy | Piantella | MT210114 | KX370756 | MT277440 | MT332612 |
| NRM 20106041* | Passer tulliae | Passeridae | Nigeria | — | AF230934 | — | — | — |
| MAR7031 | Passer melanurus | Passeridae | Namibia | — | MT210106 | MT210142 | MT277441 | MT332613 |
| ISR237192* | Passer mozabicus | Passeridae | Israel | — | MF767302 | — | — | — |
| UWBM95160 | Passer motitensis | Passeridae | South Africa | Vorstershoop, 10 km W | MT210110 | MT210147 | MT277442 | MT332614 |
We amplified and sequenced the mitochondrial cytochrome-\(b\) (\(cyt-b\)) for all samples available for comparison with the \textit{Passer} phylogeny by Allende et al. (2001). For multi-locus reconstruction we sequenced one further mitochondrial gene, NADH-dehydrogenase subunit2 (ND2) and two nuclear introns, myoglobin-intron2 (myo) and ornithine-decarboxylase intron7 (ODC). Primers and PCR protocols are documented in Päckert et al. (2020). PCR products were purified using ExoSap-IT (GE Healthcare; adding 0.1 mL ExoSap-IT solution in 4 mL H2O to each sample; 37 °C for 30 min, 94 °C for 15 min). The sequencing of the PCR products was performed with BigDyeTM 3.1 Dye Terminator Cycle Sequencing Kits (Applied Biosystems), according to the manufacturers' instructions. Cycle sequencing products were purified by salt/ethanol precipitation or by using Sephadex (GE Healthcare, Munich, Germany), and sequenced in both directions on an ABI 3130xl DNA sequencer.

We aligned forward and reverse Sanger sequences for each gene by ClustalW using MEGA 5.1 (Tamura et al. 2011) and we cross-checked the respective electropherograms with Chromas v.2.6.5 (Technelysium Pty Ltd) for possible inaccuracies due to sequencing or reading errors. For each marker per sample, we manually combined sequences of both reading directions to a single consensus sequence. All sequences used for analysis were deposited at GenBank (Table 1).

Newly generated sequences were incorporated in a sequence alignment for Passeroidea from Päckert et al. (2016, 2020), including outgroup taxa from closely related families Ploceidae, Viduidae, Estrildidae and Urocynchramidae (Table 1). The final alignment comprised 3485 base pairs (\(cyt-b\): 1041 bp; ND2: 1041 bp; myo: 732 bp; ODC: 671 bp). We complemented our sequence data set for Passeridae with sequence data from GenBank for eight species missing from our sampling including the cinnamon ibon, \textit{Hypocryptadius cinnamonomus} (Table 1). Altogether, our final data set comprised 30 species of Passeridae among these 18 out of 28 currently recognized species from genus \textit{Passer} (del Hoyo and Collar 2016). These are more than two third of all species from this genus (see Table 1) and twice as many species-level taxa compared to the most recent phylogenetic hypothesis for Passeridae (Jonsson and Fjeldså 2006). For hierarchical outgroup rooting we used the waxwing, \textit{Bombycilla Garrulus} (compare Päckert et al. 2020).

We reconstructed multi-locus phylogenies using Bayesian inference of phylogeny BEAST vers. 1.8.1 (Drummond et al. 2012) and Maximum Likelihood (ML) using RAxML (Stamatakis 2006, 2014). We relied on the partitioning scheme applied to the Passeroidea data set by Päckert et al. (2020) who included Passeridae with 26 species. According to their estimates using PARTITIONFINDER (Lanfear et al. 2012) the best-fit partition scheme was a nine-partition scheme by gene and codon: ND2, 1041 bp, three partitions by codon position, \(GTR+\Gamma+I\) model; cytochrome-\(b\), 1041 bp, three partitions by codon position,
GTR +Γ+I model; myo, 730 bp, one partition, HKY+Γ model; ODC, 643 bp, one partition, GTR+Γ model.

For inference of divergence times estimates, we applied a molecular clock calibration using mean substitution rate estimates for the two mtDNA markers estimated by Lerner et al. (2011) for Hawaiian honeycreepers (Drepanidinae): cyt-b = 0.014; ND2 = 0.029 (both in in substitutions per site per lineage per million years). The cyt-b rate applied here ranges at a similar dimension like the empirical cyt-b rate of 0.0105 evaluated by Weir and Schluter (2008).

We performed three independent runs with BEAST for 30,000,000 generations (parameters were logged and trees sampled every 3,000 generations) under the uncorrelated lognormal clock model for all loci with the “auto-optimize” option activated and a birth-death process prior applied to the tree. We combined log files and tree files from independent BEAST runs with used LOG-COMBINER v.1.8.1 and checked the combined log file in TRACER v. 1.4 (Rambaut and Drummond 2007) to ensure adequate ESS files for all parameters (all ESS > 200). All obtained phylograms were edited in FIGTREE vers. 1.4.2 (Rambaut 2009).

For illustration of intra- and interspecific genetic variation and divergence of selected species, we reconstructed unrooted minimum parsimony networks with PopART (http://popart.otago.ac.nz) using the “tcs network” algorithm (Clement et al. 2000). We calculated uncorrected pairwise p-distances (based on cytochrome-b sequences) using MEGA 5.1.

Results

The Old World sparrows resulted as a strongly supported monophyletic group from all analyses and were sister to another well supported clade including weavers (Ploceidae), Przewalski’s finch (Urocynchramus pyczowi), estrildid finches and wydahs (Estrildidae and Viduidae; Fig. 3). The subclade of Passeridae is shown in Fig. 4. The basal split in Old World sparrows was dated to approximately 17.5 mya and separated the cinnamon ibon (Hypocrypta cinnamomeus) from all other Passeridae. These were divided into two major clades.

Clade I showed a deep split at about 10 mya between the rock sparrows (genus Petronia; clade Ia) and the snowfinches (Montifringilla, Pyrgilauda, Onychostruthus; clade Ib, Fig. 4). The latter three snowfinch genera started diversifying at about 6.9 mya, a sister-group relationship of the Southeast Asian plain-backed sparrow (Petronia) to that terminal clade received moderate and poor support, respectively. Another poorly supported Afro-Arabian clade of four sparrow species united the Saharan desert sparrow (P. simplex), the Sudan golden sparrow (P. luteus) from the Sahel Region, the Dead Sea sparrow (P. moabiticus) from the Near East and the Middle East and the Cape Verde endemic Iago sparrow (P. iagoensis). In the latter, no clear phylogeographic structure among island populations could be observed in the maximum parsimony network of five cyt-b haplotypes (Fig. 5C). Finally, a well-supported terminal clade united four closely related species that started diversifying in the early Pleistocene: the house sparrow (P. domesticus), the Spanish sparrow (P. hispaniolensis), the Italian sparrow (P. italicus) and the Socotra sparrow (P. insularis) (Fig. 4). The sister-group relationship of the Southeast Asian plain-backed sparrow (P. flaveolus) to that terminal clade received moderate support.

High intraspecific differentiation with split ages estimated at 2.3–2.7 Ma was found in two species of clade I: Both Petronia petronia and Montifringilla nivalis showed a deep split between European and Asian lineages (Fig. 4). Paraphyly of M. nivalis with respect to its Tibetan congener M. adamsi was only poorly supported. European and Asian populations of the white-winged snowfinch (M. nivalis) appeared as two distinct clusters in the cyt-b haplotype network separated by a minimum of 22 substitutions (Fig. 5A). Uncorrected pairwise distances between the European and the Asian mitochondrial lineage ranged between 4.9–5.1% (cyt-b) at the same p-distance level like interspecific comparison between M. nivalis and M. ad-
Figure 3. Phylogenetic relationships of Old World sparrows (Passeridae) and closely related outgroups weaverbirds (Ploceidae), estrildid finches (Estrildidae), indigobirds and wydahs (Viduidae) and Przewalski’s finch (Urocynchramidae, monotypic: *Urocynchramus pylzowi*); combined MCMC tree from three runs with BEAST 30 Million generations each, burning 3000 trees (of 30.000 sampled trees); node support: Bayesian posterior probabilities above nodes, thorough bootstrap from RAXML below nodes; full node support from both analyses (BI: 1.00, ML:100) indicated by an asterisk.

Figure 4. Inter- and intrageneric phylogenetic relationships of Passeridae; zoom on the Old World sparrow clade of the combined MCMC tree from three runs with BEAST 30 Million generations each, burning 3000 trees (of 30.000 sampled trees); node support: Bayesian posterior probabilities above nodes, thorough bootstrap from RAXML below nodes; full node support from both analyses (BI: 1.00, ML:100) indicated by an asterisk; conflicting topology in the RAXML tree indicated by “-”; # = poor node support values below 0.5 (BI) and 50 (ML); bars with numbers indicate indels of nuclear introns shared by all members of the respective clade (grey= myoglobin; white= ODC; + = insertion; - = deletion); variation of two male plumage color traits indicated at tip clades for species of *Passer, Petronia* and *Gymnoris*; head pattern according to Stephan (2000) who classified the grey-headed *P. simplex* and the Sudan golden sparrow (*P. luteus*) as ancestral forms of brown-headed sparrows.
Discussion

To date, there is no comprehensive phylogeny of Old World sparrows (Passeridae) available except for a single-locus tree covering about 40% of the currently accepted species (Allende et al. 2001) and a Passeridae clade from a supertree by Jonsson and Fjeldså (2006) which was largely based on the same sequence information (see below). Though our new phylogeny still misses ten out of 28 Passer species we are covering 30 of 43 currently accepted species of Passeridae (about 70%) and several clear conclusions can be drawn from this new (though still incomplete) phylogenetic hypothesis. Most importantly, our results confirm the monophyly of the genera Gymnoris, Passer, Montifringilla and Pyrgilauda (the remaining genera are monotypic). This is particularly relevant with respect to the taxonomic treatment of bush sparrows and rock sparrows.

Bush sparrows and rock sparrows

Bush sparrows (Gymnoris) have long been merged in one genus Petronia together with rock sparrows (Wolters 1952; Vaurie 1956; Stephan 2000; Summers-Smith 2010: fig. 113). In their Illustrated Checklist of the Birds of the World del Hoyo and Collar (2016) classified bush sparrows in a separate genus Gymnoris but added a side remark that these species were “often merged into Petronia”. Until recently, congeneric treatment of these species was even reflected by vernacular names, such as “bush petronia” and “rock petronia” (P. dentata and P. petronia, in Clements et al. 2017, 2019, with reference to Rasmussen and Anderton 2005 and to Praveen et al. 2016). A distinctive yellow throat patch that is shared by bush sparrows and rock sparrows might have been the major common trait to mislead taxonomists and to treat those species under the same genus name (Fig. 4). However, Roselaar (1995) suggested a recognition of Gymnoris as a genus of its own for major differences from Petronia petronia in other plumage traits, habitat preferences and behavior (see also Summers-Smith 2010). This recommendation was discussed by the Taxonomic Advisory Committee of the Association of European Records and Rarities (AERC TAC 2003), however, they stressed the need of a reliable phylogenetic framework and postponed a decision on this “pending category”. Despite this lack of evidence from phylogenetic studies, several taxonomic authorities later restricted Petronia to the type species (the rock sparrow, P. petronia) and subsumed bush sparrows under Gymnoris (del Hoyo and Collar 2016; Gill et al. 2020). Jonsson and Fjeldså (2006) who to date provided the most complete phylogenetic hypothesis for Passeridae [their Passe- roidea clade 8] could not show the paraphyly of Petronia sensu lato because their tree included only two species from this group, Petronia petronia and Gymnoris pyrgita. These two formed a monophyletic group of the Passeroidea tree (Jonsson and Fjeldså, 2008) which might be an effect of incomplete taxon sampling. Density of taxon

amsi (4.5–4.8%; cyt-b). Similarly, uncorrected p-distances between rock sparrow populations from Spain (P. p. brevirostris) and from China (P. p. brevirostris) were as high as 4.8% (cyt-b; compare the deep split in Fig. 4). In the small-sized species of genus Pyrgilauda, one specimen of Père David’s snowfinch, P. davidiana, was sister to a syntopic P. blanfordi specimen instead to a conspecific specimen from the northern allopatric part of the breeding range (Fig. 4; however this grouping was not supported in the RAXML tree that united both P. davidiana sequences in a poorly supported clade). The haplotype network for a larger set of Pyrgilauda samples showed that regardless of phenotypic species identification all specimens from the region of sympathy at Koko Nor in northern Qinhai belonged to one haplotype cluster that was separated from another distantly related P. davidiana haplotype (shared by two specimens of unknown origin) by 37 substitutions (Fig. 5B). The Koko Nor cluster had a star-like structure with eight tip haplotypes and a central haplotype shared by eleven individuals of both species (P. davidiana and P. blanfordi).
sampling has been repeatedly evaluated as one of the crucial factors affecting the accuracy of phylogenetic analyses and the resulting topologies (Zwickl and Hillis 2002; Heath et al. 2008; Albert et al. 2009; Nabhan and Sarkar 2011; Wiens and Tiu 2012; Tplitsch et al. 2017). Though important for our phylogeny we still failed to include the yellow-spotted bush sparrow (G. pyrgita) from the Sahel Region, however, our tree topology clearly rejects a sister group relationship of the three remaining Gymnoris species and Petronia petronia and therefore supports their taxonomic treatment in different genera. Jönsson and Fjeldså (2006) had apparently included G. pyrgita as the sole bush sparrow species in their supertree (see above), however, the source of sequence information could not be inferred from the documentation in their paper. To date, there is no sequence data available for this species at Genbank.

Rock sparrows (Petronia) were consistently revealed as sister to snowfinches (Montifringilla and allies) and are therefore part of a trans-Eurasian alpine radiation (Päckert et al. 2020; this study) whereas bush sparrows (Gymnoris) represent a subtropical/tropical radiation across the Afrotropics, the Middle East and southern Asia (this study).

Snowfinches

Snowfinches were shown to represent a monophyletic group in previous phylogenetic studies (Qu et al. 2006; Lei et al. 2014; both based on cyt-b and myoglobin intron 2). Like the previous studies, our four-gene phylogeny did not fully resolve their interfertic relationships and provided only poor support of a sister-group relationship of Pyrgilauda and Montifringilla. Future studies based on genome-wide SNPs may shed light on this. All snowfinch species except M. nivalis are endemics of the Qinghai-Tibet Plateau with a large area of sympatry at its eastern margin (Fig. 1). In this region, in the vicinity of Qinghai Lake we found indications of mitochondrial introgression of P. blanfordi haplotypes into phenotypic P. davidiana. Though this conclusion certainly needs further support from population genetic analyses based on nuclear markers, introgression and gene flow was documented for several regions where two sparrow species come into secondary contact (Elgvin et al. 2011; Hermansen et al. 2011, 2014; Belkacem et al. 2015; Gedeon et al. 2015; Päckert et al. 2019).

Since long, there is firm evidence from previous phylogenies of a placement of snowfinches in sparrows (Passeridae) rather than in finches (Fringillidae) – unlike for example other high-alpine specialists from the same region, the mountain finches (Leucosticte). These are indeed members of Fringillidae (Zuccon et al. 2010) and represent a recent radiation of East Asian faunal elements to the Nearctic (Päckert et al. 2020). Despite many recent changes of vernacular names, Gebauer et al. (2006) were the only authorities who used the names “mountain-steppe sparrows” (for Pyrgilauda) and “snow sparrows” (for Montifringilla), which is in good accordance with their sister clade, the rock sparrows (for Petronia). However, since the terms “sparrows” and “finches” in particular are in use for completely different bird families without any closer relationships (e.g. New World sparrows, Passerellidae, are indeed the closest relatives to buntings, Emberizidae, and were previously included in this family), a correction of vernacular names for snowfinches might not be recommendable.

Although paraphyletic of the white-winged snowfinch, Montifringilla nivalis, did not receive strong support, divergence times between the nominate form M. n. nivalis and Asian subspecies (M. n. alpicola and M. n. grousmezimali) equal (and even exceed) those between several currently accepted Passer species. In fact, there has been a long debate on species-level taxa in Montifringilla: Both the black-winged snowfinch and the Tibetan snowfinch have been previously included in M. nivalis at the subspecies level (M. n. adamsi: Cramp and Perrins 1994; M. n. henrici: Vaurie 1956; Moreau and Greenway Jr 1962; Portenko and Viténghoff-Scheel 1974; Cheng 1987). A closer relationship among M. nivalis and M. adamsi than among M. henrici and each of the latter two was already suggested based on morphological traits (Eck 1996; Martens and Eck 1995) and was confirmed by our phylogeny. Based on the criterion of diagnosability (Sangster 2014) with respect to phenotypes (del Hoyo and Collar 2016), vocalizations and ecology (Gebauer and Kaiser 1994; Gebauer et al. 2006) and mitochondrial lineages (Qu et al. 2006; Lei et al. 2014; Päckert et al. 2020) the three currently accepted Montifringilla species are currently separated at the species-level (e.g. Gill et al. 2020).

For the time being, we refrain from making any taxonomic recommendations for M. nivalis until further evidence for another species-level split can be inferred from population genetic studies based on a range-wide sampling (including missing M. n. leucura from the Near East, M. n. gaddi from Iran, M. n. tianshanica from the Central Asian mountains and M. n. kwenhuensis from the Kunlun Shan in southwestern China; del Hoyo and Collar 2016).

Old World sparrows – the genus Passer

To date, phylogenetic relationships among members of the most diverse genus of Passeridae are insufficiently resolved and our study can only be considered another step further towards a taxon-complete Passer sparrow tree. The Passeridea tree by Jönsson and Fjeldså (2006) is a supertree inferred from sequence data from 99 independent studies of which Allende et al. (2001) provided single-locus data (cytochrome-b) for all ten Passer species included in the final supertree. Thus, the phylogenetic hypothesis by Jönsson and Fjeldså (2006) is largely based on the cytochrome-b-based tree by Allende et al. (2001), and since node support values were not provided for their supertree, these phylogenetic relationships have to be interpreted with maximum caution. Except for the grey-headed sparrows, none of the major superspecific
classifications in *Passer* based on phenotypic traits is reflected by monophyletic groups in our phylogeny, neither the “grey-crested” nor the “brown-headed” sparrows, two groups classified by Stephan (2000: “Grauscheitel- sperlinge” and “Braunkopfsperlinge”). His classification was based on a combination of plumage color traits (i.e. 10 traits of the facial color pattern and 17 gradually varying color patterns of single contour feathers; Figs 1, 2 and 3 in Stephan 2000). Based on this combination of traits Stephan (2000) came to some rather striking conclusions, e.g. he classified the grey-headed *P. simplex* and the entirely yellow-headed “golden-sparrows” (*P. luteus* and *P. euchlorus*) as ancestral forms of his “brown-headed sparrows” (Fig. 4). However, our phylogeny does not support Stephan’s (2000) classification: Members of “brown-headed sparrows” and “grey-crested sparrows” are scattered across the two major subclades of the *Passer* clade, thus this phenotypic trait is not really informative as concerns phylogenetic relationships – as could have been expected due to a low phylogenetic signal of many morphological traits compared for example to behavioral traits, such as bird song (Cicero et al. 2020).

According to our multi-locus phylogeny, two major radiations of Old World sparrows started during the late Miocene at about 6 Mya. Six species united in a monophyletic group represent a Sub-Saharan radiation south of the equator. The large-sized grey-headed sparrows (*P. griseus, P. diffusus, P. gongoensis*) were often lumped in one species, Wolters (1979), however even placed them in a separate genus Pyrgitopsis, whereas Summers-Smith (2010) united them in one superspecies (Amadon 1964).

Dickinson and Christidis (2014) treated gongoensis as a subspecies of the northern grey-headed sparrow, *P. griseus*, and separated *P. diffusus* at the species level (compare Dickinson 2003). However, because in our tree *P. gongoensis* was sister to the southern grey-headed sparrow, *P. diffusus*, with strong support (Fig. 4), our phylogenetic hypothesis does not support this classification.

The sister clade of the grey-headed sparrows united two representatives of the Cape fauna, *P. motitensis* and *P. melanurus*, with a small-sized East-African species, the chestnut sparrow, *P. eminibey*. This grouping is instantly surprising, because the latter species was regularly affiliated with two other small-sized ‘golden sparrows’, *P. luteus* and *P. euchlorus*. These three have long been regarded as rather ancient lineages of Old World sparrows without any closer relationships to other *Passer* species (Summers-Smith 2010). Our tree topology does neither support a placement of *P. eminibey* and *P. luteus* outside *Passer* nor a placement of the chestnut sparrow in a monotypic genus Sorella Hartlaub, 1880 (Wolters 1979). The great sparrow, *P. motitensis*, from the Cape Region was traditionally affiliated with further Sub-Saharan sparrow taxa. Summers-Smith (2010) distinguished “five allopatric populations” of *P. motitensis*, Dickinson and Christidis (2014) included three of them in *P. motitensis: P. m. chordofanicus, P. m. shelleyi* and *P. m. ryfocinctus*. Today, they are all separated at the species-level (del Hoyo and Collar 2016; Gill et al. 2020) and their phylogenetic relationships will remain subject to future studies.

The second major clade including twelve *Passer* species represents a larger radiation across the Palearctic and the Oriental Region with an early Pliocene onset at about 5.5. Mya. The East Asian russet sparrow as the earliest offshoot from this clade was traditionally known under the scientific name *Passer rutilans* (as such included in the phylogenies by Allende et al. 2001 and by Jonsson and Fjeldså 2006; see also Clements et al. 2017). However, a recent debate on the correct dates of two competing original descriptions by C. J. Temminck and J. Gould ended up in a broad consent on the priority of the name *Passer cinnamomeus* Gould, 1835 (based on Milkovský 2011). Except that basal split, the position of the tree sparrow, *P. montanus*, as the second oldest offshoot and further phylogenetic relationships in this Eurasian/Oriental clade are poorly to moderately supported or even conflicting between the Bayesian and the maximum likelihood tree. For the Cape Verde endemic, *P. iagoensis*, a close relationship with Afrotropical species (*P. motitensis* and *P. melanurus*) was previously assumed (Stephan 2000), conspecific classification with *P. motitensis* was even advocated by Wolters (1979) and by Summers-Smith (2010). Our phylogenetic hypothesis clearly rejects any closer relationship of *P. iagoensis* with these two representatives of the Cape fauna, but suggests a closer relationship with *P. moabiticus* from the eastern Mediterranean and the Middle East and two Afrotropical species: *P. simplex*, a desert-dwelling specialist from the Sahara and *P. luteus* from the Sahel Region (however with poor node support). The firm placement of the latter in the *Passer* clade is as unexpected as that of *P. eminibey* (see above), and does not support a classification of golden sparrows in a separate genus Auripasser (Wolters 1979; Summers-Smith 2010). Contrary to the traditional classification, our tree topology clearly rejected a closer relationship of *P. eminibey* with the Sudan golden sparrow, *P. luteus*, whereas phylogenetic relationships of the Arabian golden sparrow, *P. euchlorus*, remain an open question due to data deficiency (Summers-Smith 2010 included it in the Sudan golden sparrow as subspecies *P. l. euchlorus*). A zone of sympatry in western Sudan without evidence of interbreeding between *P. eminibey* and *P. luteus* also justifies their treatment as separate species (Summers-Smith 2010).

Finally, a well-supported terminal clade represents a very recent circum-Mediterranean/Eurasian radiation of the house sparrow, *P. domesticus*, the Spanish sparrow, *P. hispaniolensis*, the stabilized hybrid form *P. italicæ* and the Socotran endemic, *P. insularis*. According to our divergence time estimates, this radiation started during the mid-Pleistocene and according to population genetic analyses lineage separation went along with multiple independent events of horizontal gene flow between the house sparrow and the Spanish sparrow that gave rise to several hybrid lineages in the Mediterranean of different age and origin (Runemark et al. 2018; Päckert et al. 2019). A sister-group relationship of the Southeast Asian *P. flaveolus* with the latter circum-Mediterranean quartet was only poorly supported. A putative closer relationship of *P. insularis* and *P. motitensis* as suggested by Summers-Smith (2010) could be rejected by our phylogeny.
Conclusions and perspectives

Despite from being far from taxon-complete, this updated phylogeny contributed further evidence for clarification of taxonomic controversy, e.g. the status of Petronia and Gymnoris as separate genera, the monophyly of grey-headed sparrows (but not of all grey-crested Passer species) or a lack of phylogenetic justification for recognizing the genera Sorella and Auiripasser. We failed to include the enigmatic pale rock sparrow, Carpospiza brachydactyla, from the Middle East and Central Asia that was long regarded as a member of Fringillidae. Based on shared traits of tongue morphology inclusion in Passeridae was recommended by Bock (2004), generally Carpospiza has been affiliated with Petronia sensu lato (including Gymnoris), however, it lacks the yellow throat patch (being a rather uninformative trait as shown in our phylogeny). Also, phylogenetic relationships of missing Passer species from India (P. pyrrhonotus), Central Asia (P. zarudnyi), the Socotra archipelago (P. hemileucus) and East Africa (P. chordofanicus, P. euchlorus, P. rufocinctus, P. shelleyi, P. suahelicus, P. swainsoni, P. castanopterus) will remain unresolved so far. Recently, the narrow-range endemic Somali sparrow, P. castanopterus, has attracted ornithologists’ attention for its putative hybridization with the house sparrow, P. domesticus, in the areas of range overlap in Somalia (Summers-Smith 2020), Ethiopia (Gedeon et al. 2015), Kenya (Turner 2016) and Djibouti (Cohen et al. 2011; Hering et al. 2020).

Acknowledgements

The phylogeny was reconstructed within the framework of a project on the evolutionary history of alpine and montane birds of the Qinghai-Tibet Plateau funded by Deutsche Forschungsgemeinschaft (DFG), grant number PA1818/3-1 (to M.P.). Field trips by J.M. received regular financial support by Feldbausch-Stiftung and Wagner-Stiftung at Johannes Gutenberg-Universität Mainz what is greatly acknowledged. We are grateful to the University of Djelfa, Algeria, who granted travel funding for A.A.B. to perform laboratory and collection work at Senckenberg Natural History Collections Dresden. For sample loans we thank F. Houle-Tibet Plateau funded by Deutsche Forschungsgemeinschaft (DFG), generally Carpospiza has been affiliated with Petronia sensu lato (including Gymnoris), however, it lacks the yellow throat patch (being a rather uninformative trait as shown in our phylogeny). Also, phylogenetic relationships of missing Passer species from India (P. pyrrhonotus), Central Asia (P. zarudnyi), the Socotra archipelago (P. hemileucus) and East Africa (P. chordofanicus, P. euchlorus, P. rufocinctus, P. shelleyi, P. suahelicus, P. swainsoni, P. castanopterus) will remain unresolved so far. Recently, the narrow-range endemic Somali sparrow, P. castanopterus, has attracted ornithologists’ attention for its putative hybridization with the house sparrow, P. domesticus, in the areas of range overlap in Somalia (Summers-Smith 2020), Ethiopia (Gedeon et al. 2015), Kenya (Turner 2016) and Djibouti (Cohen et al. 2011; Hering et al. 2020).

References

AECRTAC (2003) Association of European Records and Rarities Committees TAC’s Taxonomic Recommendations 1st December 2003. Online version under http://www.aerc.eu/tac.html
Albert EM, San Mauro D, García-Paris M, Rüther L, Zardoya R (2009) Effect of taxon sampling on recovering the phylogeny of squamate reptiles based on complete mitochondrial genome and nuclear gene sequence data. Gene 441: 12–21. https://doi.org/10.1016/j.gene.2008.05.014
Allende LM, Rubio I, Ruiz-del-Valle V, Guillén J, Martínez-Laso J, Lowy E, Varela P, Zamora J, Arnáiz-Villena A (2001) The Old World sparrows (Genus Passer). Phylology and their relative abundance of nuclear mtDNA pseudogenes. Journal of Molecular Evolution 53: 144–154. https://doi.org/10.1007/s002390010202
Amadon D (1966) The superspecies concept. Systematic Biology 15(3): 245–249. https://doi.org/10.2307/sysbio/15.3.245
Anderson T (2006) Biology of the Ubiquitous House Sparrow: From Genes to Populations. Oxford University Press, 560 pp. https://doi.org/10.1093/acprof:oso/9780195304114.001.0001
Belkacem AA, Gast O, Stuckas H, Canal D, Lo Valvo M, Giacalone G, Päckert M (2016) North African hybrid sparrows (Passer domesticus, P. hispaniolensis) back from oblivion – ecological segregation and asymmetric mitochondrial introgression between parental species. Ecology and Evolution 6: 5190–5206. https://doi.org/10.1002/ ece3.2274
Bock W (2004) Affinities of Carpospiza brachydactyla (Passeriiformes; Passeridae). Journal of Ornithology 145(3): 223–226. https://doi.org/10.1007/s10336-004-0034-9
Bock W, Morony Jr JJ (1978) Relationships of the passerine finches. Bonner Zoologische Beiträge 29: 122–147.
Cheng TH (1987) A synopsis of the avifauna of China. Paul Parey, Hamburg Berlin, 1223 pp.
Cicerò C, Mason NA, Benedict L, Rising JD (2020) Behavioral, morphological, and ecological trait evolution in two clades of New World Sparrows (Amphipita and Pecanaca, Passerellidae). PeerJ 8: e9249. https://doi.org/10.7717/peerj.9249
Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. Molecular Ecology. 9:1657–1659. https://doi.org/10.1046/j.1365-294x.2000.01020.x
Clements JF, Schulenberg TS, Liljef MA, Roberson D, Fredericks DTA, Sullivan BL, Wood CL (2017) The eBird/Clements checklist of birds of the world: v2017. Downloaded from http://www.birds.cornell.edu/clementschecklist/download (last accessed on 25.07.2018).
Clements JF, Schulenberg TS, Liljef MA, Billerman SM, Fredericks DTA, Sullivan BL, Wood CL (2019) The eBird/Clements Checklist of Birds of the World: v2019. Downloaded from https://www.birds.cornell.edu/clementschecklist/download (last accessed on 30.12.2020).
Cohen C, Mills M, Francis J (2011) Endemic and special birds of Somalia. Bulletin of the African Bird Club 18: 86–92.
Cramp S, Perrins CM (1994) Handbook of the birds of Europe the Middle East and North Africa – the birds of the Western Palearctic volume VIII – Crows to Finches. Oxford University Press, Oxford, New York, 956 pp.
Del Hoyo J, Collar NJ (Eds) (2016). Illustrated checklist of the birds of the world. Volume 2 Passerines. Lynx Edicions, Barcelona, 903 pp.
Del Mar Delgado M, Bettega C, Martens J, Päckert M (2019) Phylogenetic relationships of weaverbirds (Aves: Ploceidae): A first robust phylogeny based on mitochondrial and nuclear markers. Molecular Phylogenetics and Evolution, 109: 21–32. https://doi.org/10.1002/mol.3.2274
De Silva TN, Peterson AT, Bates JM, Fernando SW, Girard MG (2017) Robust phylogeny based on mitochondrial and nuclear markers. Molecular Phylogenetics and Evolution, 109: 21–32. https://doi.org/10.1002/mol.3.2274
De Silva TN, Peterson AT, Perktas U (2019) An extensive molecular phylogeny of weaverbirds (Aves: Ploceidae) unveils broad non-monophyly of traditional genera and new relationships. The Auk 136(3): ukz041. https://doi.org/10.1093/auk/ukz041
Dickinson EC (Ed.) (2003). The Howard and Moore complete checklist of the birds of the world. 3rd edition. Princeton University Press, Princeton and Oxford, 883 pp.

Dickinson EC, Christidis L (Eds) (2014) The Howard and Moore complete checklist of the birds of the world. 4th edition, Volume 2: Passerines. Aves Press, Eastbourne, 804 pp.

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution 29: 1969–1973. https://doi.org/10.1093/molbev/mss075

Eck S (1996) Die Paläarktischen Vogel – Geospizien und Biospezies. Zoologische Abhandlungen des Museums für Tierkunde Dresden 40 (suppl.): 1–103.

Elgvin TO, Hermansen JS, Fijarczyk A, Bonnet T, Borgé T, Stein S, Sæther SA, Voje KL, Sætre GP (2011) Hybrid speciation in sparrows II: a role for sex chromosomes? Molecular Ecology 20: 3823–3837. https://doi.org/10.1111/j.1365-294X.2011.05182.x

Elgvin TO, Trier CN, Torrøsen OK, Hagen UJ, Lien S, Nederbragt AJ, Ravenet M, Jensen H, Sætre GP (2017) The genomic mosaicism of hybrid speciation. Science Advances 3: e1602996. https://doi.org/10.1126/sciadv.1602996

Ericson PGP, Johansson US (2003) Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. Molecular Phylogenetics and Evolution 29: 126–138. https://doi.org/10.1016/S1055-7903(03)00067-8

Eroukhmanoff F, Hermansen JS, Bailey RI, Sæther SA, Sætre GP (2013) Local adaptation within a hybrid species. Heredity 111: 286–292. https://doi.org/10.1038/hdy.2013.47

Eroukhmanoff F, Bailey RI, Elgvin TO, Hermansen JS, Runemark A, Trier CN, Sætre GP (2017) Resolution of conflict between parental genomes in a hybrid species. BioRxiv. https://doi.org/10.1101/102970

Fjeldså J, Irestedt M, Ericson PGP, Zuccon D (2010) The Cinnamon Bzin Hypocryptadius cinnamomeus is a forest canopy sparrow. Ibis 152(4): 747–760. https://doi.org/10.1111/j.1474-919X.2010.01053.x

Gebauer A, Kaiser M (1994) Biologie und Verhalten zentralasiatischer Schneefinken (Montifringilla) und Erdspelinge (Pyrgilauda). Journal für Ornithologie 135: 55–71. https://doi.org/10.1007/BF01640275

Gebauer A, Eck S, Kaiser M, Lei FM, Martens J (2006) The Qinghai-Tibet Plateau: center of evolution for snow sparrows (Montifringilla s. str.) and mountain-steppe sparrows (Onychorhynchus, Pyrgilauda). Acta Zoologica Sinica 52 (suppl.): 305–309.

Gedeon K, Cauldwell A, Ewnetu M, Regasa F, Schönbrodt R, Töpfer T, Gebauer A, Kaiser M, Strutzenberger P (2019) Out of Tibet and out of the most ancient Tibetan endemic passerine known to date. Ibis, 158: 530–540. https://doi.org/10.1111/ibi.12382

Gill F, Donsker D, Rasmussen P (Eds) (2020) IOC World Bird List (v10.1). https://doi.org/10.14344/IOC.ML.10.1 (last accessed on 20.04.2020).

Heath TA, Hedtke SM, Hillis DM (2008) Taxon sampling and the accuracy of phylogenetic analyses. Journal of Systematics and Evolution 46: 239–257. DOI: 10.3724/SPJ3.1002.2008.08016

Hermansen JS, Sæther SA, Elgvin TO, Borgé T, Jhelle E, Sætre GP (2011) Hybrid speciation in sparrows I: phenotypic intermediary, genetic admixture and barriers to gene flow. Molecular Ecology 20: 3812–3822. https://doi.org/10.1111/j.1365-294X.2011.05183.x

Hermansen JS, Haas F, Trier CN, Bailey RI, Nederbragt AJ, Marziali A, Sætre GP (2014) Hybrid speciation through sorting of parental incompatibilities in Italian sparrows. Molecular Ecology 23: 5831–5842. https://doi.org/10.1111/mec.12910

Hering J, Mädlov W, Geiter O, Siegmund A, Elits HJ, Fuchs E, Müller K, Müller R, Rayaleh H, Vohwinkel R (2020) Untersuchungen zur Avifauna der Mangrovenwälder Deschutis sowie zur Klärung taxonomischer Fragestellungen bei Buntandraul Ptilya melba sowie Hausasperling Passer domesticus und Somalisperling Passer castanopterus – erste Ergebnisse. Vogelwarte 58: 349–362.

Jønsson KA, Fjeldså J (2006) A phylogenetic supertree of oscine passerine birds (Aves: Passeri). Zoologica Scripta 35(2): 149–86. https://doi.org/10.1111/j.1463-6409.2006.00221.x

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701. https://doi.org/10.1093/molbev/mss020

Lei F, Qu Y, Song G (2014) Species diversification and phylogeographical patterns of birds in response to the uplift of the Qinghai-Tibet Plateau and Quaternary glaciations. Current Zoology 60: 149–161. https://doi.org/10.1093/czoolo/60.2.149

Lerner HRL, Meyer M, James HF, Hofreiter M, Fleischer RC (2011) Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. Current Biology 21: 1–7. https://doi.org/10.1016/j.cub.2011.09.039

Liebl A, Schrey A, Andrew SC, Sheldon EL, Griffith SC (2015) Invasion genetics: Lessons from a ubiquitous bird, the house sparrow Passer domesticus. Current Zoology 61: 465–476. https://doi.org/10.1093/czoolo/61.3.465

Martens J, Eck S (1995) Towards an ornithology of the Himalayas. Systematics, ecology and vocalizations of Nepal birds. Bonner Zoologische Monographien 38: 1–454.

Mikolovský J (2011) Correct name for the Asian Russet Sparrow. Chinese Birds 2: 109–110. https://doi.org/10.5122/chbds.2011.0016

Moreau RE, Greenway Jr JC (1962) Family Ploceidae, Weaverbirds. In: Mayr E, Greenway Jr JC (eds) Check-List of the Birds of the World. Volume XV. Museum of Comparative Zoology, Cambridge Massachusetts, USA, 327 pp.

Nabhan AG, Sarkar IN (2011) The impact of taxon sampling on phylogenetic inference: a review of two decades of controversy. Briefings in Bioinformatics 13: 122–134. https://doi.org/10.1093/bib/bbr014

Päckert M, Martens J, Sun YH, Strutzenberger P (2016) The phylogenetic relationships of Przevalski's Finch Urocynchramus pylzowi, the most ancient Tibetan endemic passerine known to date. Ibis, 158: 530–540. https://doi.org/10.1111/ibi.12382

Päckert M, Belkacem AA, Wollfgramm H, Gast O, Canal D, Giacalone G, Lo Valvo M, Vamberger M, Wink M, Martens J, Stuckas H (2019) Genetic admixture despite ecological segregation in a North African sparrow hybrid zone (Aves, Passeriformes, Passer domesticus x Passer hispaniolensis). Ecology and Evolution 9: 12710–12726. https://doi.org/10.1002/ece3.5744

Päckert M, Favre A, Schnitzler J, Martens J, Sun YH, Tietze DT, Haller F, Michalak I, Strutzenberger P (2020) Out of Tibet and out of Himalayas: centers of origin and diversification of passerine birds in the Qinghai-Tibet Plateau region. Ecology and Evolution 10: 9283–9300. https://doi.org/10.1002/ece3.6615

Portenko LA, van Vieringhoff-Scheel E (1974) Montifringilla nivalis (L.). In: Stresemann E, Portenko LA, Dathe H, Mauersberger G (Eds) Atlas der Verbreitung Palaearktischer Vögel. 4. Lieferung. Akademie Verlag, Berlin.

Praveen J, Jayapal R, Pittie A (2016) A checklist of the birds of India. Praveen J, Jayapal R, Pittie A (2016) A checklist of the birds of India. Indian Birds 11: 113–170.

Qu Y, Ericson PGP, Lei F, Gebauer A, Kaiser M, Helbig A (2006) Molecular phylogenetic relationship of snow finch complex (genera Pyrgilauda and Onychostruthus) and hybrids with Somali Sparrow Passer domesticus. Molecular Phylogenetics and Evolution 38: 1–454.
Montifringilla, Pyrgilauda, and Onychostruthus) from the Tibetan plateau. Molecular Phylogenetics and Evolution 40: 218–226. https://doi.org/10.1016/j.ympev.2006.02.020
Qu Y, Chen C, Chen X, Hao Y, She H, Wang H, Ericson PGP, Lin H, Cai T, Song G, Jia C, Chen C, Zhang H, Li J, Liang L, Wu T, Zhao J, Gao Q, Zhang G, Zhai W, Zhang C, Zang YE, Lei F (2021) The evolution of ancestral and species-specific adaptations in snowfinches at the Qinghai–Tibet Plateau. PNAS 118: e2012398118. https://doi.org/10.1073/pnas.2012398118
Rambaut A (2009) FigTree version 1.2.2 - Computer program distributed by the author, website: http://tree.bio.ed.ac.uk (last accessed on 29.11.2010).
Rambaut A, Drummond AJ (2007) TRACER v1.4. http://beast.bio.ed.ac.uk/Tracer
Rasmussen PC, Anderton JC (2005) Birds of South Asia: the Ripley guide. Lynx, Barcelona, 1067 pp.
Ravinet M, Elgvin TO, Trier CN, Aliabadian M, Gavrilov A, Sætre GP (2018) Variation and constraints in hybrid genome formation. Nature Ecology and Evolution 2: 549–543.
Resano-Mayor J, Fernández-Martín Á, Hernández-Gómez S, Toranzo I, España A, Gil JA, de Gabriel M, Roa-Álvarez I, Strinella E, Hobson KA, Heckel G, Arletta R (2016) Integrating genetic and stable isotope analyses to infer the population structure of the White-winged Snowfinch Montifringilla nivalis in Western Europe. Journal of Ornithology 158: 395–405. https://doi.org/10.1007/s10336-016-1413-8
Roselaar CS (1995) Songbirds of Turkey. An atlas of biodiversity of Turkish passerine birds. GMB, Haarlem, 240 pp.
Runemark A, Trier CN, Eroukhmanoff F, Hermansen JS, Matschiner M, Ravinet M, Elgvin TO, Sætre GP (2018) Variation and constraints in hybrid genome formation. Nature Ecology and Evolution 2: 549–556. https://doi.org/10.1038/s41559-017-0437-7
Sætre GP, Cuevas A, Hermansen JS, Elgvin TO, Piñero-Fernández L, Sarther SA, Lo Cascio Sarther C, Eroukhmanoff F (2017) Rapid polygenic response to secondary contact in a hybrid species. Proceedings of the Royal Society B, 284(1853): 20170365. https://doi.org/10.1098/rspb.2017.0365
Sangster G (2014) The application of species criteria in avian taxonomy and its implications for debate over species concepts. Biological Reviews 89: 199–214. https://doi.org/10.1111/brv.12051
Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690. https://doi.org/10.1093/bioinformatics/btl446
Stamatakis A (2014) RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. Bioinformatics 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033
Stephan B (2000) Die Arten der Familie Passeridae (Gattungen Montifringilla, Petronia, Passer) und ihre phylogenetischen Beziehungen. Bonner Zoologische Beiträge 49: 39–70.
Summers-Smith JD (2010) The sparrows. T. & A.D. Poyser, Calton, 342 pp.
Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28: 2731–2739. https://doi.org/10.1093/molbev/msr121
Tritsch C, Martens J, Sun YH, Heim W, Strutzenberger P, P äckert M (2017) Improved sampling at the subspecies level solves a taxonomic dilemma – A case study of two enigmatic Chinese tit species (Aves, Passeriformes, Paridae, Poecile). Molecular Phylogenetics and Evolution 107: 538–550. https://doi.org/10.1016/j.ympev.2016.12.014
Turner DA (2016) Range expansion in the Somali Sparrow Passer castanopterus in east and northeast Africa. Scopus 36: 47–49.
Vaurie C (1956) Systematic notes on Palearctic birds. No 24 Ploceidae: the genera Petronia, Petronia and Montifringilla. American Museum Novitates 1814: 1–27.
Weir JT, Schluter D (2008) Calibrating the avian molecular clock. Molecular Ecology 17: 2321–2328. https://doi.org/10.1111/j.1365-294X.2008.03742.x
Wiens JJ, Tiu J (2012) Highly incomplete taxa can rescue phylogenetic analyses from the negative impacts of limited taxon sampling. PLoS ONE 8: e42925. https://doi.org/10.1371/journal.pone.0042925
Wolters HE (1952) Die Gattungen der westpaläarktischen Sperlingsvögel (Ord. Passeriformes, Paridae). Hamburg und Berlin, 746 pp.
Wolters HE (1979) Die Vögelarten der Erde. 1.-4. Lieferung. Paul Parey, Hamburg und Berlin, 746 pp.
Supplementary material

File 1

Authors: Päckert, M, Hering J, Belkacem AA, Sun Y-H, Hille S, Lkhagyasuren D, Islam S, Martens J (2021)
Data type: .docx
Explanation note: Additional samples and sequence data used for analysis of inter- and intraspecific variation of the cytochrome-b gene (Montifringilla, Pyrgilauda and Petronia) and the ND2 gene (Passer).
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/vz.71.e65952.suppl1

File 2

Authors: Päckert, M, Hering J, Belkacem AA, Sun Y-H, Hille S, Lkhagyasuren D, Islam S, Martens J (2021)
Data type: .docx
Explanation note: Gazetteer for collection sites with information on localities and/or coordinates.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/vz.71.e65952.suppl2