



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

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## 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. eminiibey* 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 eminiibey* 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 Palearctic 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*, *Pseudonigrita* 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 Jønsson 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).

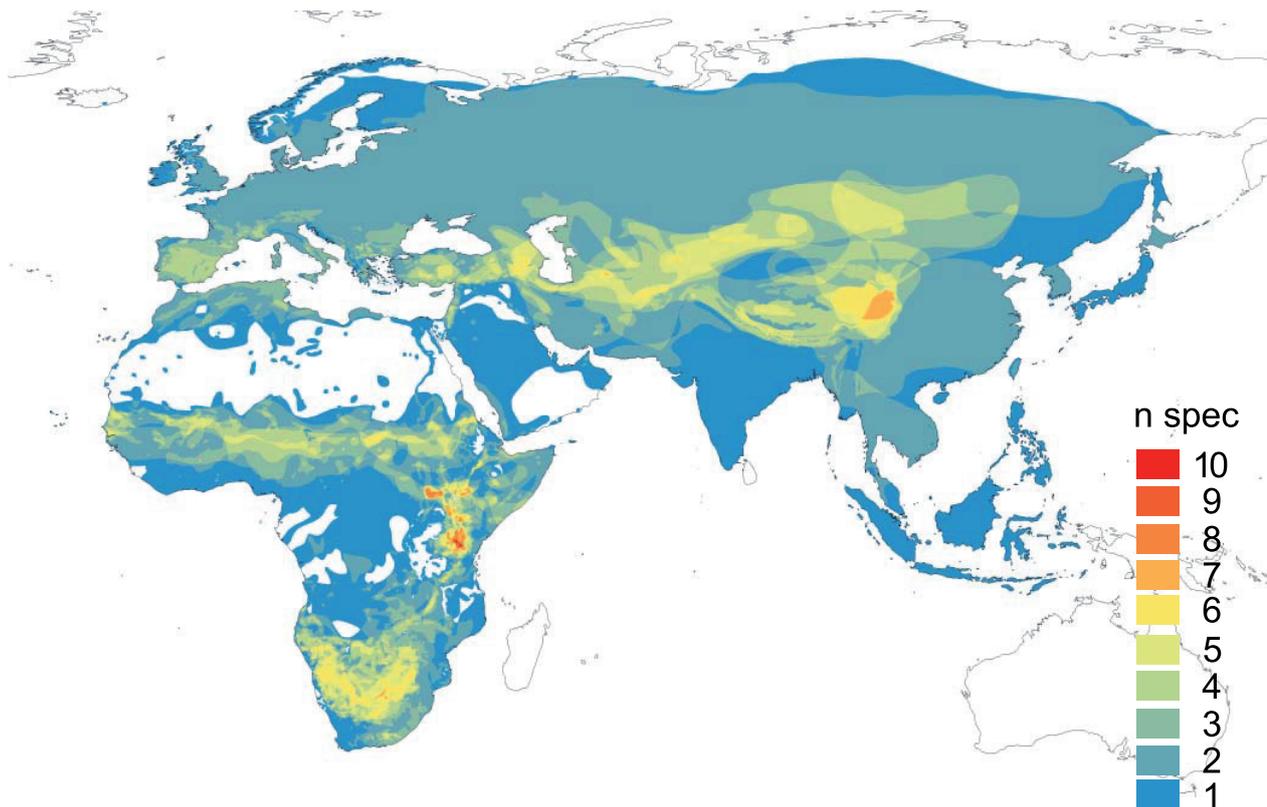
A first phylogenetic hypothesis for Passeridae was based on a single mitochondrial gene (Allende et al. 2001) and included only eleven species. Since then, a few molecular studies focused on the phylogenetic relationships of snowfinches (*Onychostruthus*, *Pyrgilauda*, *Montifringilla* [Fig. 2A]), a group of eight high alpine endemic species from the QTP and from other Palearctic 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 Palearctic 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	cytb	ND2	myo2	ODC
NRM 986044*	<i>Bombycilla garrulus</i>	Bombycillidae	Sweden	—	AY228049	DQ466855	AY228286	EU680709
NHMD135615*	<i>Amandava amandava</i>	Estrildidae	Captivity	—	KJ456191	KJ455319	KJ454750	KJ455720
ZMUC0785*	<i>Cryptospiza reichenovii</i>	Estrildidae	—	—	AY228056	GU816843	AY228293	EU680719
GenBank*	<i>Erythrura gouldiae</i>	Estrildidae	—	—	AY495403	AF407030	U40496	—
GenBank*	<i>Lonchura malacca</i>	Estrildidae	India	—	KJ456324	KJ455481	KJ454825	—
CAS:92755*	<i>Lonchura punctulata</i>	Estrildidae	China	—	KJ456325	KJ455482	KJ454826	KJ455824
ZMUC1425*	<i>Hypocryptadius cinnamomeus</i>	Passeridae	Philippines	Mindanao, Katanglad Volcano	—	FJ460769	GU816939	GU816916
MAR2212	<i>Montifringilla adamsi</i>	Passeridae	China	Qinghai, Huashixia	MN337349	MN337357	MN337368	MN337374
MAR2004	<i>Montifringilla henrici</i>	Passeridae	China	Qinghai, Nanshan	DQ244059	MN337360	MN337369	MN337376
MTD C64406	<i>Montifringilla nivalis nivalis</i>	Passeridae	Italy	Dolomites	KX109628	KX109703	KX109668	KX109742
MAR3111	<i>Montifringilla nivalis gromgrzimaili</i>	Passeridae	Mongolia	Bondoch Gol, Altai	MN337353	MN337362	MN337371	MN337378
MAR1532	<i>Montifringilla nivalis alpicola</i>	Passeridae	Russia	Dagestan, Kurush	MN337352	MN337361	MN337370	MN337377
MAR1775	<i>Pyrgilauda blanfordi</i>	Passeridae	China	Qinghai, highlands near Madoi	MN337350	MN337358	MN337366	—
MAR2093	<i>Pyrgilauda davidiana</i>	Passeridae	China	Qinghai, Heimaha	MN337351	MN337359	MN337367	MN337375
NC_25915	<i>Pyrgilauda davidiana</i>	Passeridae	China	—	NC_25915	NC_25915	—	—
MAR2206	<i>Pyrgilauda ruficollis</i>	Passeridae	China	Qinghai, Heimaha	MN337354	MN337363	AY228306	GU816915
MAR426	<i>Onychostruthus taczanowskii</i>	Passeridae	China	Qinghai, Heimaha	MN337355	MN337364	MN337372	MN337380
MAR8787	<i>Passer ammodendri</i>	Passeridae	Mongolia	Gobi Altai, Echin Gol oasis	MT210107	MT210145	MT277434	MT336206
UWBM95153	<i>Passer diffusus</i>	Passeridae	South Africa	Vorstershooop, 10 km W	MT210109	MT210144	MT277435	MT336207
MTD C64358	<i>Passer domesticus</i>	Passeridae	Germany	Saxony, Dresden	KX109629	KX109704	KX109669	KX109743
MTD 2012-202	<i>Passer emiteibey</i>	Passeridae	captivity	—	MT210111	—	MT277436	MT336208
GenBank*	<i>Passer flaveolus</i>	Passeridae	Vietnam	—	AF230907	—	—	—
ZMUC117473	<i>Passer gongoensis</i>	Passeridae	Kenya	Samburu Serena Lodge	MT210112	MT210140	MT277437	MT336209
GenBank*	<i>Passer griseus</i>	Passeridae	Senegal	—	AF230908	—	—	—
IPMB9505	<i>Passer hispaniolensis</i>	Passeridae	Spain	Lanzarote	MT210113	MN488960	MT277438	MT336210
MAR4076	<i>Passer iagouensis</i>	Passeridae	Cape Verde	Sal, Buracona	MT210104	MT210136	MT277439	MT336211
SOC4*	<i>Passer insularis</i>	Passeridae	Yemen	Socotra	EU478434	—	—	—
ITA 1	<i>Passer italiae</i>	Passeridae	Italy	Pantelleria	MT210114	KX370756	MT277440	MT336212
NRM20106041*	<i>Passer luteus</i>	Passeridae	Nigeria	—	AY495394	GU816846	GU816938	GU816913
MAR7031	<i>Passer melanurus</i>	Passeridae	Namibia	Sossusvlei-Namtip	MT210106	MT210142	MT277441	MT336213
ISR237192*	<i>Passer moabiticus</i>	Passeridae	Israel	—	MF767302	—	—	—
UWBM95160	<i>Passer motitensis</i>	Passeridae	South Africa	Vorstershooop, 10 km W	MT210110	MT210147	MT277442	MT336214

sample no	species (Gill et al. 2020)	family	country	location	cytb	ND2	myo2	ODC
NRM976359*	<i>Passer montanus</i>	Passeridae	Sweden	—	AY228073	GU816845	AY228311	DQ785937
MAR6957	<i>Passer cinnamomeus</i>	Passeridae	China	Sichuan, Mamize Nat. Res.	MT210105	MT210143	MT277443	MT336215
PS3	<i>Passer simplex</i>	Passeridae	Algeria	—	MZ005607	MZ005629	MZ054179	MZ054180
UWBM66486	<i>Petronia petronia brevirostris</i>	Passeridae	Russia	Mongun-Tajiginskiy Kozhuun	MT210108	MT210141	MN337373	MN337381
GenBank*	<i>Petronia petronia petronia</i>	Passeridae	Spain	Madrid	AF230914	—	—	—
ANSP-25010*	<i>Gymnoris superciliosus</i>	Passeridae	—	—	KJ456382	KJ455547	KJ454861	KJ455859
AV20*	<i>Gymnoris xanthocollis</i>	Passeridae	India	—	KF289836	—	—	—
GenBank*	<i>Gymnoris dentata</i>	Passeridae	Ghana	Gbele Resource Reserve	—	KY120916	KY201280	—
NRM20076168*	<i>Dinemellia dinemelli</i>	Ploceidae	—	—	—	GU816840	GU816935	GU816908
ZMUC 01706*	<i>Euplectes ardens</i>	Ploceidae	—	—	—	GU816841	KY201263	GU816909
GenBank*	<i>Euplectes prognus</i>	Ploceidae	—	—	AY228061	—	AY228299	—
FMNH357374*	<i>Ploceus cucullatus</i>	Ploceidae	DR Congo	—	AF290141	AF290104	EU740022	—
NHMD 118547*	<i>Ploceus manyar</i>	Ploceidae	—	—	KJ456410	KJ455581	KJ454869	KJ455877
UWBM83556*	<i>Ploceus philippinus</i>	Ploceidae	Singapore	Pasir Ris, 1 km NW	KJ456411	KJ455583	KJ454870	KJ455878
MTD C64770	<i>Urocynchramus pylzowi</i>	Urocynchramidae	China	Qinghai, near Heimaha	KX109639	KX109715	KX109682	KX109758
GenBank*	<i>Vidua chalybeata</i>	Viduidae	—	—	NC_000880	NC_000880	EU740058	—
NRM20026168*	<i>Vidua macroura</i>	Viduidae	—	—	DQ270405	GU816842	GU816936	GU816910

ing to the manufacturer's instructions except for overnight incubation of tissue with proteinase K (instead of one hour).

We amplified and sequenced the mitochondrial cytochrome-*b* (*cyt-b*) for all samples available for comparison with the *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 H<sub>2</sub>O to each sample; 37 °C for 30 min, 94 °C for 15 min). The sequencing of the PCR products was performed with BigDye™ 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, *Hypocryptadius cinnamomeus* (Table 1). Altogether, our final data set comprised 30 species of Passeridae among these 18 out of 28 currently recognized species from genus *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 (Jønsson and Fjeldså 2006). For hierarchical outgroup rooting we used the waxwing, *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 + $\Gamma$ +I model; myo, 730 bp, one partition, HKY+ $\Gamma$  model; ODC, 643 bp, one partition, GTR+ $\Gamma$  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 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 LOGCOMBINER 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 pylzowi*), 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 (*Hypocryptadius cinnamomeus*) from all other Passeridae. These were divided into two major clades.

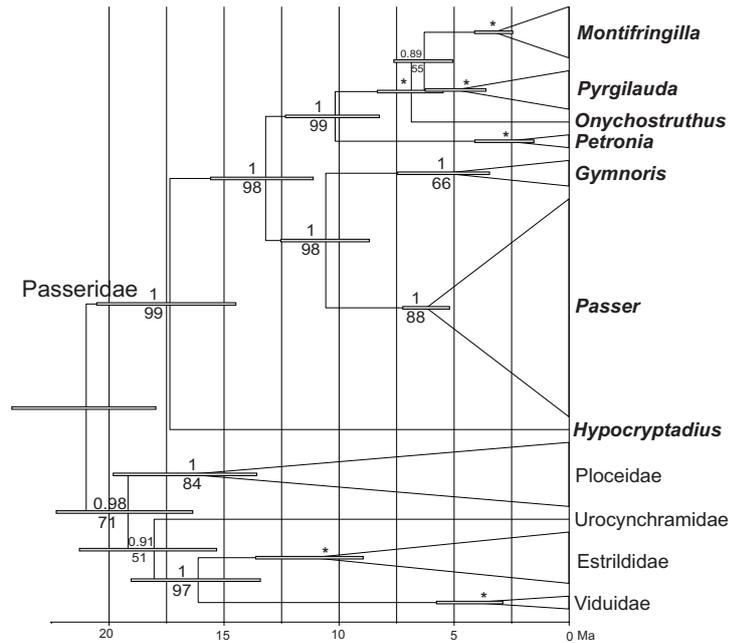
Clade I showed a deep split at about 10 mya between the rock sparrows (genus *Petronia*; clade Ia) and the snowfinches (*Montifringilla*, *Pyrgilauda*, *Onychostruthus*; clade Ib, Fig. 4). The latter three snowfinch genera started diversifying at about 6.9 mya, a sister-group relationship between *Montifringilla* and *Pyrgilauda* (with *Onychostruthus* as the earliest offshoot) received only poor support (Fig. 4; clade Ib). However, the clade uniting *Montifringilla* and *Pyrgilauda* was characterized by a shared 3-bp deletion in myoglobin intron 2, whereas the *Pyrgilauda* clade was characterized by another 4-bp insertion in the same intron marker (Fig. 4).

Clade II includes the sister genera *Passer* (IIa) and *Gymnoris* (IIb) and each of them with strong node sup-

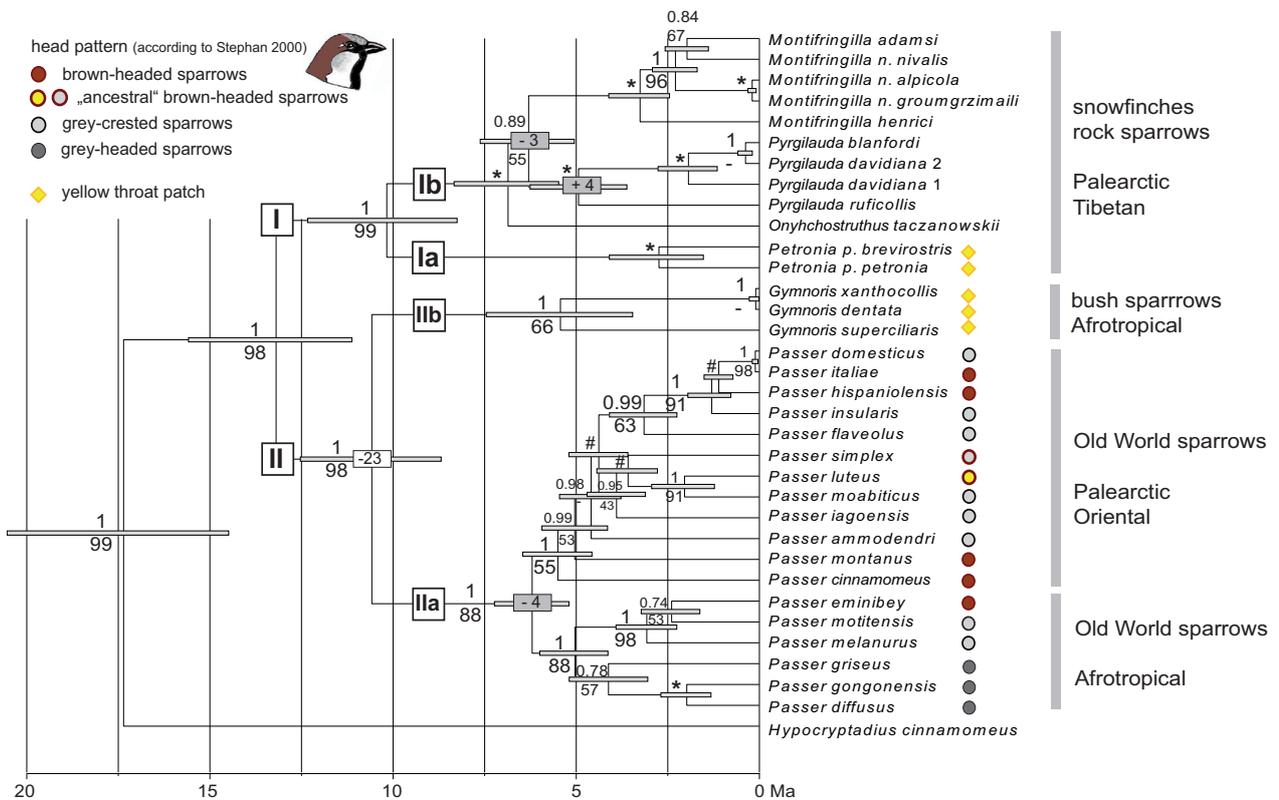
port. Members of Clade II shared a 23-bp deletion in ODC intron 7 (Fig. 4) and all members of *Passer* shared another 4-bp deletion in myo intron 2 (Fig. 4). Contrary to traditional systematic classification, the yellow-throated species of bush sparrows (*Gymnoris*) and rock sparrows (*Petronia*) were not closest relatives in the Passeridae phylogeny (Fig. 4).

Old World sparrows of genus *Passer* were also divided into two strongly supported clades. One entirely Afrotropical clade included seven species from Sub-Saharan Africa. One Sub-Saharan subclade included three species of grey-headed sparrows (Fig. 4: *P. griseus*, *P. diffusus* and *P. gongoensis*). Except for that monophyletic group of grey-headed sparrows, head color pattern does not reflect monophyletic units in the *Passer* clade (Fig. 4), which is once more in contrast to previous superspecific classifications. The second subclade united two species from South Africa (*P. melanurus*, *P. motitensis*) with the small-sized chestnut sparrow (*P. eminiibey*) from East Africa. The Afrotropical *Passer* clade was sister to a second moderately supported clade that comprised 12 species from the Palearctic and the Oriental Region that started diversifying at about 5.5 mya (Fig. 4). Phylogenetic relationships among members of that clade were ambiguous because of poor support values for many nodes. A basal split separated the Asian russet sparrow (*P. cinnamomeus*) from the remaining *Passer* species. Two further ancient offshoots of the Palearctic/Oriental clade, the widespread tree sparrow (*P. montanus*) and the Central Asian Saxaul sparrow (*P. ammodendri*) 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*) (Fig. 4). 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. italiae*) 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.

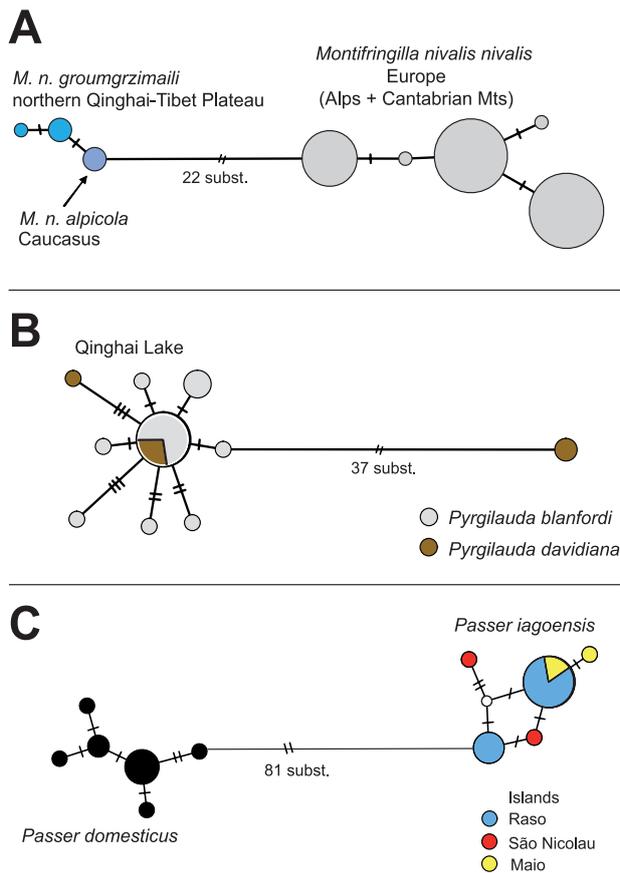
High intraspecific differentiation with split ages estimated at 2.3–2.7 Ma was found in two species of clade I: Both *Petronia petronia* and *Montifringilla nivalis* showed a deep split between European and Asian lineages (Fig. 4). Paraphyly of *M. nivalis* with respect to its Tibetan congener *M. adamsi* 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 intragenetic 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.



**Figure 5.** Haplotype networks showing intra- and interspecific variation of A) the white-winged snowfinch, *Montifringilla nivalis* (including the sequence data set by Resano-Mayor et al. 2016) based on 341 bp cytochrome-*b* ( $n=87$ ); B) Blanford's snowfinch and Père David's snowfinch (*Pyrgilauda blanfordi*, *P. davidiana*), based on 819 bp cytochrome-*b* ( $n=23$ ); C) the Cape Verde endemic Iago sparrow (*Passer iagoensis*) compared to the house sparrow (*P. domesticus*; population from eastern Germany from Päckert et al. 2019) based on 773 bp ND2 ( $n=29$ ).

*amsi* (4.5–4.8%; *cyt-b*). Similarly, uncorrected p-distances between rock sparrow populations from Spain (*P. p. petronia*) 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 sympatry at Koko Nor in northern Qinghai 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*).

## 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 Jönsson 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). Jönsson and Fjeldså (2006) who to date provided the most complete phylogenetic hypothesis for Passeridae [their Passeroidea 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 (Jönsson and Fjeldså, 2008) which might be an effect of incomplete taxon sampling. Density of taxon

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; Tritsch 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. Jønsson 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 intergeneric 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 paraphyly 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. gromgrzimaili*) 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. nivalis adamsi*: Cramp and Perrins 1994; *M. nivalis henrici*: Vaurie 1956; Moreau and Greenway Jr 1962; Portenko and Vietinghoff-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. kwenluensis* 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 Passeroidea tree by Jønsson 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 Jønsson 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. eminiibey*. 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. eminiibey* 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. rufocinctus*. 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 Jönsson 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 Mlíkovský 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. eminiibey* (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. eminiibey* 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. eminiibey* 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. italiae* 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 *Auripasser*. 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. chordinganicus*, *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).

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## Supplementary material

### File 1

**Authors:** Päckert, M, Hering J, Belkacem AA, Sun Y-H, Hille S, Lkhagvasuren 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*).

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### File 2

**Authors:** Päckert, M, Hering J, Belkacem AA, Sun Y-H, Hille S, Lkhagvasuren D, Islam S, Martens J (2021)

**Data type:** .docx

**Explanation note:** Gazetteer for collection sites with information on localities and/or coordinates.

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