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The Founding Feathers: the true ancestry of the domestic Barbary Dove

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Summary.—In 2008 the International Commission for Zoological Nomenclature (ICZN) ruled that the name *Streptopelia risoria* (Linnaeus, 1758) should have priority for both African Collared Dove and its domestic form, Barbary Dove, as it is senior to *S. roseogrisea* (Sundevall, 1857). Many ignored the ruling in the belief that the ancestry of Barbary Dove is still unproven. Given the lack of a name-bearing specimen and in anticipation of the ICZN decision, in 2008 a neotype was designated for *S. risoria*. To clarify the taxonomic status of *roseogrisea*, as its original type series was mixed, in 2018 a neotype was also designated for this junior synonym of African Collared Dove. As the species was assumed to be polytypic, synonymisation of *roseogrisea* with *risoria* at species level was questioned thereafter. The results of a whole genome-resequencing study now show that African Collared Dove is the principal ancestor of Barbary Dove, and that the species is monotypic.

'*risoria: C*[olumba] *supra lutescens, lunula cervicali nigraon.…Nobis communis Turtur*'
[dove with yellowish upperparts and black neck-ring.…Our common Turtle Dove]
(Linnaeus 1758)

The Barbary Dove, Ringed Dove or Ringneck Dove is the domestic form of African Collared Dove *Streptopelia risoria* (Linnaeus, 1758) and was already known in the 16th century, but details concerning its domestication are unclear. At the time Barbary Dove occurred in two varieties: a pale fawn-coloured form, and a near-white one. The original dark colour of the ancestral species was not then known to exist in captivity.

Long before the wild form was known to science, the pale fawn Barbary Dove had been described by Linnaeus (1758) as *Columba risoria* (Latin *risoris*: a laugher), presumably for its 'giggling' call. In his description, Linnaeus also listed *Turtur Indicus* of Aldrovandi (1600), Willughby (1678), Ray (1713) and Albin (1738) in its synonymy. He further stated that the bird was 'our common Turtle Dove' (nobis communis Turtur), which may suggest that it was commonly kept in Europe. It was later transferred, via the genus *Turtur* Selby, 1835, to *Streptopelia* Bonaparte, 1855. Its wild counterpart, African Collared Dove, was subsequently named *Streptopelia roseogrisea* (Sundevall, 1857) but, although the scientific name *S. risoria* is senior to *S. roseogrisea*, the latter was commonly accepted in ornithology and used as the valid name for both African Collared Dove and its domestic form until 2008.

Donegan (2007) applied to the International Commission for Zoological Nomenclature (ICZN) to conserve the junior name *roseogrisea* for the wild species but allow continued use of *risoria* for the domestic form, based on their previous approach to domestic mammals and their wild forms (ICZN 2003). However, the ICZN (2008) ruled that the valid name for both the wild and domestic forms is *Streptopelia risoria* (Linnaeus 1758). This change was not

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generally accepted, and many authorities, e.g. Dickinson & Remsen (2013), ignored the ruling in the belief that the ancestry of Barbary Dove is still unproven.

Donegan (2007, 2008) also argued that the nomenclature of *S. risoria* and *S. roseogrisea* is complicated by apparent reference to individuals of other species in the description of *Columba risoria*. This, however, is unlikely as was demonstrated by van Grouw (2018). As Donegan (2008) considered Linnaeus' name to be based on a mixed type series and, in connection with his application but prior to the ICZN's final decision, he established a neotype for *risoria*, based on a pale fawn-coloured specimen from captivity whose label indicated India as the specimen's origin (Fig. 1). The neotype designation for *S. risoria* (Linnaeus 1758) was justified, as no name-bearing specimen for *risoria* is believed to exist (and a type was necessary to define the taxon *risoria* objectively). Although Donegan (2008) argued that both Linnaeus and all other authors referred to in the latter's description, considered *risoria* to occur in India, Donegan ignored that the accounts on which Linnaeus was based include more details on the species as a captive bird in Europe. Captive birds were also the basis of the different illustrations (Fig. 2). A better choice therefore might have been a captive bird from Britain or elsewhere in Europe.

Figure 1. Neotype of *Streptopelia risoria*, NHMUK 2008.3.1 (Harry Taylor, © Natural History Museum, London)

The type series used by Sundevall (1857) to name African Collared Dove, however, certainly *was* mixed as the information concerning *risoria* [African Collared Dove] in Rüppell (1845), where he listed Le Vaillant's La Tourterelle blonde [= *Streptopelia capicola damarensis*] in synonymy, formed the basis for Sundevall's *roseogrisea* (van Grouw 2018). Given the conflict with *capicola*, van Grouw (2018) provided a neotype for *roseogrisea* to clarify its taxonomic status (Fig. 3). As two wild subspecies of African Collared Dove are currently recognised by most authorities, Donegan (2019) argued correctly that objective synonymisation of *roseogrisea* with *risoria* at species level might not be possible for several reasons. Firstly, Donegan (2019) questioned which subspecies is ancestor to the domestic form: the western population, nominate *roseogrisea* Sundevall, 1857, or eastern birds, *arabica* von Neumann, 1904. Further, as the neotype was collected in 'Abyssinia', which could refer to either modern-day Ethiopia or Eritrea, and both subspecies occur in parts of Ethiopia, it is unclear which subspecies the specimen represents. Lastly, if both subspecies have contributed to the domesticated form, and if domestic *risoria* has a mixed origin but is the senior name for the wild species then, according to Donegan (2019), subspecies taxonomy for wild populations would be impossible to unravel, and a further case to reverse the earlier decision (ICZN 2008) would prove necessary. Another possibility was not mentioned by Donegan; the species may be, in fact, monotypic. A molecular study of the history of African Collared Dove, its subspecies and

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Figure 2. 'The Turtle Dove from the East Indies' [Barbary Dove], pl. 45 in Albin (1738). Albin wrote that they are 'kept in cages by the curious' and that all plates were based on live birds. Based on its colour and because Eurasian Collared Dove *Streptopelia decaocto* did not occur in Europe at the time, the dove used for this plate must have been a caged Barbary Dove in England. Linnaeus' description of *Columba risoria* was in part based on Albin's plate (Harry Taylor, © Natural History Museum, London)

Figure 3. Adult male African Collared Dove *Streptopelia risoria* collected by Rüppell in Eritrea and the designated neotype for the junior synonym *roseogrisea* of Sundevall, SMF 22887 (Sven Tränkner, © Senckenberg Museum, Frankfurt am Main). The species name *albiventris* on the label is a mistake by Finsch & Hartlaub (1870), who thought the dove collected by Rüppell was the same species as *Turtur albiventris* G. R. Gray, 1844. The latter, however, is a synonym of Vinaceous Dove *Streptopelia vinacea* (J. F. Gmelin, 1789). In their account of '*Turtur albiventris*' Finsch & Hartlaub used this specimen to describe the plumage.

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the domestic form was necessary to unravel its internal taxonomy. The decision to do so was made shortly after van Grouw (2018) was published, and the results are presented herein.

Clarifying the status of African Collared Dove

Barbary Dove is widely considered to be the long-domesticated form of African Collared Dove. Shelley (1883) was probably first to recognise it as such, but thereafter many authors confirmed its ancestry based on evidence such as voice, behaviour and colour (Hartert 1916, Goodwin 1952, 1970, van Grouw 2018). Until now, there was no molecular confirmation of this, but based on more than ten years of personal observations on behaviour, voice and inheritance in Barbary, African Collared and Eurasian Collared Doves *S. decaocto* (van Grouw 1999), there appeared no doubt as to Barbary Dove's ancestry. Eurasian Collared and Barbary Doves readily hybridise, their offspring are fertile (van Grouw 1999) and, in places where both species occur, e.g. the Canary Islands, hybrid characters appear in both species (van Grouw 2022). However, for many reasons, e.g. voice, behaviour, range and colour, Eurasian Collared Dove is unlikely to have contributed to the domestic Barbary Dove. Also, Eurasian Collared Dove does not become tame in captivity, even after several generations, whereas wild-caught African Collared Doves quickly settle down in confinement (HvG pers. obs.).

Apart from its ancestry, nothing appears to be known of the early history of the domestic Barbary Dove. Aldrovandi (1600) received his live birds—a fawn male and white female—from Egypt and despite old common names like Indian Turtledove and, for the 'white' form, Java Dove (Swinhoe 1866; see Fig. 4), it is probable that the first domestication indeed occurred in Egypt (Sonnini de Manoncourt 1799).

Supposed differences between the two subspecies of African Collared Dove are marginal. Eastern *arabica*, in north-east Sudan, Eritrea, north-east Ethiopia, northern Somalia, and southern Arabia (Dickinson & Remsen 2013), is described as being slightly darker with more greyish underwings than nominate *risoria* (former *roseogrisea*) (Goodwin 1983, Gibbs *et al*. 2001), which ranges from Senegambia and Mauritania to central and southern Sudan and north-west Ethiopia (Dickinson & Remsen 2013). However, these characters occur throughout the species' range. Moreover, many 'nominate-like' features—paler coloured with whitish underwings—are also found in supposed *arabica* (HvG pers. obs.), making the hypothesis of two subspecies questionable. A third subspecies—*bornuensis*

Figure 4. Colombe Blanche *Columba alba* (= white form of Barbary Dove), pl. 46 in Temminck (1808) (Harry Taylor, © Natural History Museum, London)

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Figure 5. Holotype of *Streptopelia roseogrisea bornuensis* Bannerman, 1931, adult male, Maidugari, Bornu, northern Nigeria, 20 December 1922, NHMUK 1923.10.26.8 (Jonathan Jackson, © Natural History Museum, London)

Bannerman, 1931—from northern Nigeria (for the province of Bornu), was described also as darker than the nominate (Bannerman 1931, Fig. 5) but is no longer recognised due to this character not being consistent.

The following questions need to be addressed using genetic data if the taxonomy of *S. risoria* is to be resolved: (1) is African Collared Dove the sole ancestor of domestic Barbary Dove, or has Eurasian Collared Dove contributed?; (2) are the two currently recognised subspecies of African Collared Dove, *risoria* and *arabica*, genetically distinct or not?; (3) if African Collared Dove possesses two genetically differentiated subspecies, can it be determined which, *risoria* or *arabica*, was involved in the domestication of Barbary Dove?; and (4) is 'modern' Barbary Dove genetically identical to 'early' Barbary Dove prior to European invasion by Eurasian Collared Dove, or are they now 'polluted' with Eurasian Collared Dove genes?

To achieve this, we elected to generate and analyse whole genome-resequencing data from samples of the following (see Table 1): historic museum specimens of Eurasian Collared Dove from 'India' and 'Arabia'; historic museum specimens of both subspecies of African Collared Dove; historic museum specimens of Barbary Doves of different origin; and modern captive Barbary Doves of different origin.

Methods

DNA extraction and quantification.—A total of 26 *Streptopelia* samples were loaned from multiple museums (23 dry toe-pad samples) and one private collection (three dry feather quills). The samples date from between 1871 and 2019 (Table 1). For DNA extraction and preparation for sequencing, we treated not only the historic but also more recently collected quill samples as 'historic' due to the post-collection storage conditions of the latter, thus all

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TABLE 1
Specimens sampled by this study. Museum acronyms: NHMUK = Natural History Museum, Tring; NMW = Naturhistorisches Museum Wien; SNM = Statens Naturhistoriske Museum, Copenhagen; SAM = South Australian Museum, Adelaide.

Species	Locality	Collection date	Specimen number	Sample	Notes
Streptopelia decaocto	Rajasthan (Rajputana), India	07/05/1871	NHMUK 1889.2.2.1485	D1 (toe-pad)	
Streptopelia decaocto	Rajasthan (Rajputana), India	14/06/1875	NHMUK 1889.2.2.1407	D2 (toe-pad)	
Streptopelia decaocto	Punjab (Mughal Serai), India	12/01/1875	NHMUK 1889.2.2.1505	D3 (toe-pad)	
Streptopelia decaocto	Oman, east Arabia	21/11/1977	NHMUK 1977.25.4	D4 (toe-pad)	
Streptopelia decaocto	Rostaq, Oman, east Arabia	19/04/1975	NHMUK 1975.8.4	D5 (toe-pad)	
Streptopelia decaocto	Imhoff, Saudi Arabia	10/11/1978	NHMUK 1978.7.2	D6 (toe-pad)	
Streptopelia decaocto	Bir Salem, coastal Israel	24/11/1918	NHMUK 1965.M.4694	D22 (toe-pad)	
Streptopelia risoria (*roseogrisea*)	South-west of Maidugari, Bornu, north Nigeria	24/12/1922	NHMUK 1923.10.26.9	D7 (toe-pad)	'*S. r. bornuensis*' collected at same time and place as holotype of *bornuensis* (see Fig. 5)
Streptopelia risoria (*roseogrisea*)	Mali (French Sudan)	15/11/1931	NHMUK 1932.8.6.25	D8 (toe-pad)	'*S. r. bornuensis*'
Streptopelia risoria (*roseogrisea*)	Tibesti, north Chad	01/04/1953	NHMUK 1955.41.12	D9 (toe-pad)	
Streptopelia risoria (*roseogrisea*)	El Fasher, Darfur, Sudan	16/03/1920	NHMUK 1920.12.22.54	D23 (toe-pad)	Specimen appears to have *S. decaocto* features, see Fig.13
Streptopelia risoria (*arabica*)	Western Saudi Arabia	29/02/1948	NHMUK 1965.M.4702	D10 (toe-pad)	
Streptopelia risoria (*arabica*)	Aden, Yemen, Arabia	25/02/1922	NHMUK 1965.M.4705	D11 (toe-pad)	
Streptopelia risoria (*arabica*)	Jeddah, Saudi Arabia	16/04/1934	NHMUK 1934.9.20.89	D12 (toe-pad)	
Streptopelia risoria (domestic form)	Preston Hall Aviary (captive)	before 1881	NHMUK 1881.5.1.2776	D13 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Staffordshire (captive)	24/03/1891	NHMUK 1891.3.14.2	D14 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	India (captive)	before 1900	NHMUK 2008.3.1	D15 (toe-pad)	Fawn, neotype of *risoria*
Streptopelia risoria (domestic form)	Australia (feral)	1893	NMW 48.483	D16 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Europe (captive)	before 1900	NMW 37.875	D17 (toe-pad)	White
Streptopelia risoria (domestic form)	Adelaide, Australia (feral)	07/05/1992	SAM B46855	D18 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Copenhagen (captive)	09/01/1951	SNM 57.011	D19 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Copenhagen (captive)	04/10/1960	SNM 64.268	D20 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Europe (captive)	Before 1900	SNM 57.012	D21 (toe-pad)	White
Streptopelia risoria (domestic form)	Kuwait origin (captive)	2018	LDA (collection HvG)	D24 (feather quill)	Fawn and crested
Streptopelia risoria (domestic form)	Dutch origin (captive)	2018	LDB (collection HvG)	D25 (feather quill)	White
Streptopelia risoria (domestic form)	Belgium origin (captive)	2019	LDC (collection HvG)	D26 (feather quill)	White and silkie

ISSN-2513-9894 (Online)

samples were processed in a PCR-free laboratory dedicated to handling ancient DNA. During DNA extraction, the toe-pads were digested whole, while for feathers the *c*.5 mm tip of each quill (containing dried blood residues) was used. A 'blank' negative control extraction was included to screen for potential cross-contamination. We followed the Campos & Gilbert (2012) method for extracting DNA from historic keratinous materials, as follows. To remove potential external contaminants, the dry tissue was washed by vortex with 0.5 ml of a 5% dilution of commercial-strength bleach solution, followed immediately by a 0.5 ml ethanol wash and rinsing with two rounds of molecular grade water to remove bleach residue. The cleaned tissue was then immersed in 300μL of digestion buffer and incubated overnight (minimum 20 hours) at 57°C with 350RPM agitation. Subsequently DNA was recovered from the digested material using a silica-based purification that utilises Monarch DNA clean-up columns (New England Biolabs). DNA was eluted in 42μL of EBT constituting a mixture of Buffer EB (Qiagen) and 0.05% TWEEN20 detergent (Sigma Aldrich) and was quantified using the Qubit 4.0 Fluorometer (Thermo Fisher Scientific, Inc) and the 5200 Fragment Analyzer system (Agilent Technologies).

Genomic library building and sequencing.—Extracted DNA plus additional extraction blanks were converted into BGISeq sequencing technology-compatible (see Supplementary Table 1) single-stranded shotgun libraries following the Santa-Cruz Reaction (SCR) method of Kapp *et al*. (2021). DNA input volume and amount were determined via the tier system presented with this method. Libraries were purified using MinElute reaction clean-up columns (Qiagen) and were subsequently eluted in 30μL of EBT. The number of PCR cycles for each sample was determined through a real-time quantitative PCR performed on the purified libraries. Per sample, 10μL DNA library template was used for a single reaction of PCR amplification per 50μL containing 2.5U PFU Turbo CX Polymerase, 1× PFU Turbo buffer, 0.4 mg ml^{-1} bovine serum albumin (BSA), 0.25 μM mixed dNTPs, 0.1 μM BGI forward primer, and 0.1 μM BGI reverse index-primer. Amplified libraries were purified using a 1.4X beads:library ratio of HiPrep PCR clean-up beads (Magbio Genomics), were eluted in 30μL of EBT, quantified using the Qubit 2.0 Fluorometer (Thermo Fisher Scientific, Inc) and 2100 BioAnalyzer (Agilent), and were sequenced across a total of ten DNBseq-G400 lanes using 100bp SE sequencing chemistry via BGI Europe's commercial service. The raw sequence data generated can be accessed at the ENA Project ID PRJEB58897.

Data processing.—Sequence reads were mapped to the *Streptopelia turtur* reference genome (bStrTur1.1, Dunn *et al*. 2021) using PALEOMIX v.1.2.13.4 BAM pipeline (Schubert *et al*. 2014). This pipeline includes the trimming of adapters using AdapterRemoval v.2.2.0 (Schubert *et al*. 2016) according to the default parameters, followed by alignment of sequences against the reference genome using BWA v.0.7.17 backtrack algorithm (Li & Durbin 2009). The next step removes PCR duplicates using Picard MarkDuplicates (http://broadinstitute.github.oi/picard/) and, finally, local realignment around indels was performed using GATK v.3.8.3 IndelRealigner module (McKenna *et al*. 2010).

Multidimensional scaling plot.—We created a pseudo-haploid SNP panel using the function -doHaploCall in ANGSD v.0.931 (Korneliussen *et al*. 2014), which randomly samples one read at each site and retains the base if it fulfills the used filtering parameters. Sampling was restricted to only those scaffolds with a length of >1 Mb. Transitions were removed to avoid aDNA damage that could be found in historic samples. Sites with base quality and mapping quality lower than 30 were discarded. The final SNP dataset consisted of 4,287,405 transversion sites. We then used the SNP dataset to generate a multi-dimensional scaling (MDS) plot by estimating the pairwise distances between samples using Plink 1.90 (Chang *et al*. 2015).

ISSN-2513-9894 (Online)

Nuclear genome phylogeny.—To estimate evolutionary relationships among *Streptopelia* individuals included in the dataset, a nuclear genome phylogeny was inferred. For this analysis, a Common Pheasant *Phasianus colchicus* (Liu *et al*. 2019) was included as the most external outgroup, as well as Band-tailed Pigeon *Patagioenas fasciata* (Murray *et al*. 2017). For each genome, ANGSD v.0.931 was implemented to generate genomic consensus sequences using *Streptopelia turtur* as reference genome ('-dofasta2' option). Then, 1,000 independent phylogenetic trees were estimated in RAxML-ng v.0.9.0 (Kozlov *et al*. 2019) under the GTR+G evolutionary model, using 1,000 random regions of 5,000 bp taken from the genomic consensus sequences previously created. Prior to the phylogenetic analysis, a quality check was implemented on the multiple sequence alignments using the function 'check' in RAxML-ng to search for format issues, including duplicate sequences. Later, all gene trees were concatenated to generate a species tree using ASTRAL-III (Zhang *et al*. 2018) which was visualised using the Interactive Tree Of Life (iTOL) v4 online tool (Letunic & Bork 2019).

Finally, a relative frequency analysis was implemented in DiscoVista (Sayyari *et al*. 2018) to measure discordance between the 1,000 individual gene tree topologies and the species tree generated with ASTRAL-III. This analysis evaluates the frequency of all gene tree topologies around internal branches of the inferred species tree.

Whole mitochondrial genome phylogeny.—A whole mitochondrial genome phylogeny was also estimated from the data. Sequence reads were mapped to the *Streptopelia decaocto* mitogenome (NC_037513.1) using PALEOMIX v.1.2.13.4 with the same parameters as described above. Consensus sequences were then generated using the '-dofasta2' function in ANGSD v.0.931. A mitochondrial genome sequence alignment was performed using the global pair iterative method as implemented in MAFFT v7.490 (Katoh & Standley 2013). A maximum likelihood phylogenetic tree was then estimated using RAxML-ng v.0.9.0 under the GTR+G evolutionary model.

D-statistics.—We used D-statistics, as implemented in ADMIXTOOLS (Patterson *et al*. 2012), to test the obtained topology in the species tree, as well as to explore the possibility of admixture among Eurasian Collared Dove (ECD), African Collared Dove (ACD) and domestic Barbary Dove (DBD). The previously generated dataset of SNPs was used for this analysis, and *Patagioenas fasciata* was used as outgroup in all of the tests described below. First, to understand the position of sample *S. risoria* D09 from Chad in the obtained tree, which appears in an intermediate position between the two *S. risoria* subspecies clades, a test was done in the form D(Outgroup, ACD-D09; ACD-*risoria*, ACD-*arabica*). A second set of tests was implemented to explore the possibility of admixture between ECD and DBD, using each DBD to be compared in the form D(Outgroup, ECD; DBD, ACD). A third set of tests aimed to clarify possible gene flow between ECD and ACD (*arabica* subspecies), comparing ECD against ACD samples of the *risoria* and *arabica* subspecies. Then, to explore in more detail the admixture patterns obtained in the last two tests, we implemented another D statistics analysis in form D(Outgroup, ACD/DBD; ECD, ECD) expecting to find the populations involved in the admixture process. Finally, with the intension to describe the different levels of ECD admixture in our DBD samples a set of tests was implemented in form D(Outgroup, ECD; DBD, DBD).

For any D-statistics analyses in the form D(Outgroup, A; B, C), any deviation of the result from 0 suggests possible shared ancestry or gene flow between the tested populations. If D <0, A and B share a higher level of genetic drift than expected, indicating possible gene flow; If D >0, it indicates possible gene flow between A and C. Deviation from 0 was considered statistically significant when the Z-score was below –3 or above +3. The significance of the test was estimated using a weighted block jack-knife procedure over 1 Mb blocks.

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Results

We generated between *c*.86 and 278 million sequencing reads for each of the 26 sequenced specimens. Average read length ranged from 44 to 81 bp, and 22–59% of these reads could be mapped to the *Streptopelia turtur* reference nuclear genome, yielding final depths of coverages spanning *c*.1.23–8.48×. For full details see Supplementary Table 2. Both the MDS and whole-genome phylogeny show clear structure (Figs. 6–7), in particular separating the samples into three general groups. At a broad level, the MDS identifies the three groups as consisting of *S. decaocto*; domesticated Barbary Doves (*S. r. domestica*); and both putative subspecies of African Collared Dove (*S. r. risoria* and *S. r. arabica*) (Fig. 6). While this general separation into three groups is confirmed in the phylogeny based on 1,000 concatenated trees, it provides additional insights relevant to the initial questions raised. Firstly, rather than being reciprocally monophyletic, at face value our data reveal that *arabica* may be derived from *risoria*, given the relative placement of *risoria* sample D09 from Chad as more closely related to *arabica* samples than the other *risoria*. Secondly, domestic Barbary Dove derives principally from *arabica* African Collared Dove. We undertook several steps to explore these findings further. Firstly, we performed a relative-frequency analysis using DiscoVista to query the robustness of the species tree structure (Fig. 7B). These results confirm both high support for the separation of *S. decaocto* from other *Streptopelia* samples analysed (branch 6, Fig. 7B), and that *S. r. arabica* is more closely related to domestic Barbary Doves than to *S. r. risoria* (branch 8, Fig. 7B). However these results also revealed that the observed frequencies obtained for branches 7 and 9 (relating to the placement of *risoria* sample D09 and *arabica* D12, respectively) show high levels of discordance. This could potentially be caused by lack of resolution, hybridisation, or gene-tree estimation errors (Sayyari *et al*. 2018). The whole mitochondrial genome phylogeny estimated was also found to be generally consistent with the structure recovered for the whole-genome phylogeny, although small differences were observed (Fig. S1). Specifically, most of the domestic Barbary Doves were placed in the African Collared Dove clade, with the

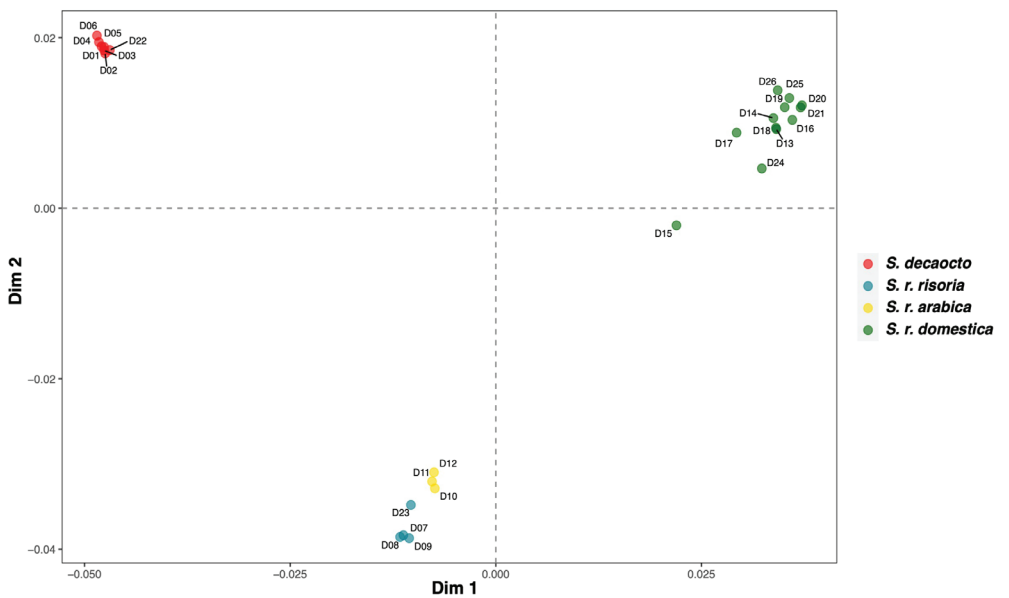

Figure 6. Multi-dimensional scaling (MDS) plot of all *Streptopelia* samples included in this study, using 4,287,405 random SNP variants from genomic data.

ISSN-2513-9894 (Online)

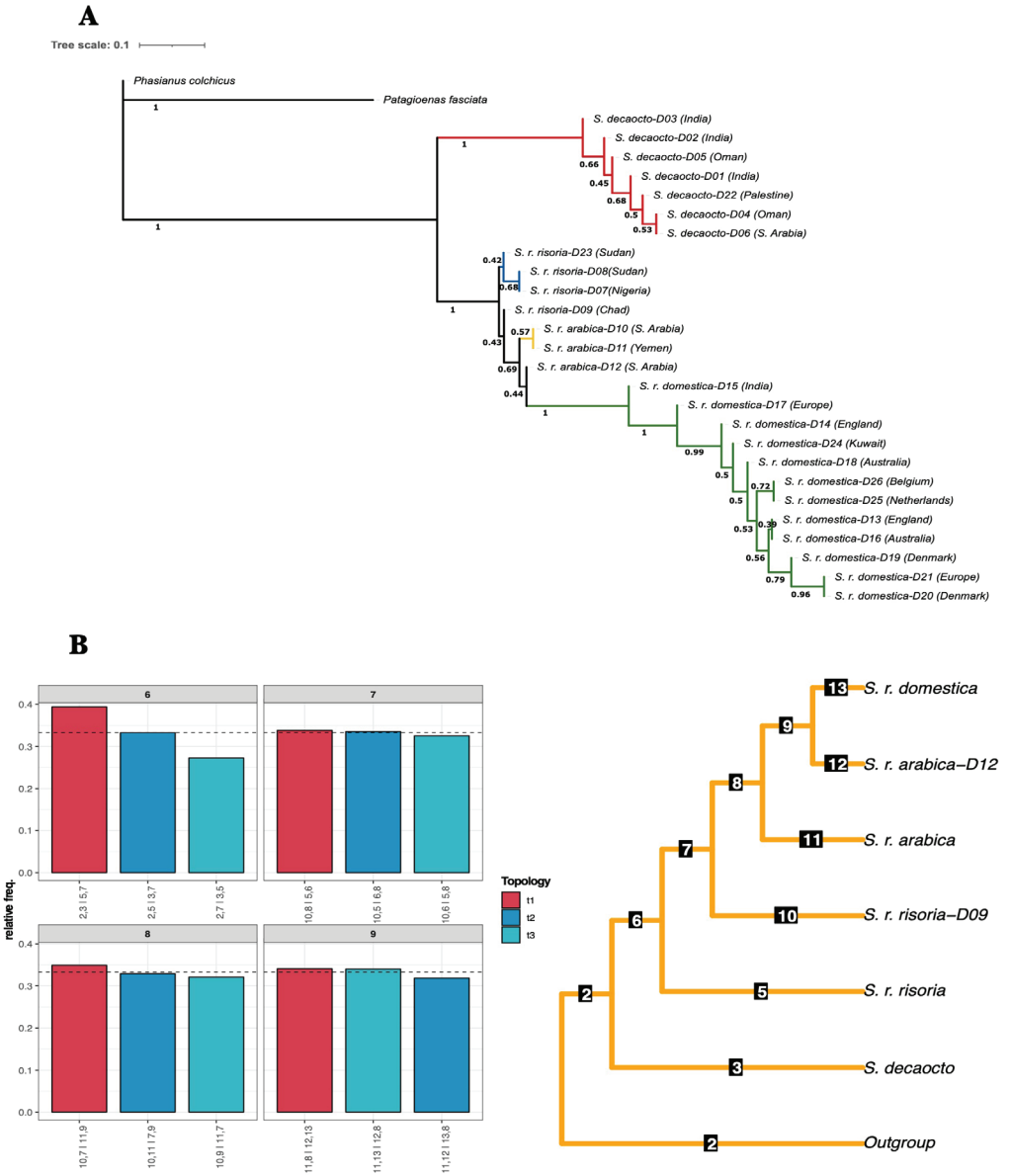

Figure 7. Concatenated nuclear genome phylogeny and relative frequency analysis of the concatenated species tree. (A) Maximum likelihood phylogenetic tree generated with ASTRAL-III using 1,000 genomic regions. The tree was rooted on Common Pheasant *Phasianus colchicus*. Bootstrap values are shown at the base of each internal node. Branch clade colour patterns match the colours used in the MDS plot in Fig. 6. (B) DiscoVista relative-frequency analysis. The tree at the left represents the species tree estimated by ASTRAL-III with monophyletic clades collapsed, where numbers are used to label the different branches of the tree. At the right, the frequencies of three possible configurations around focal internal branches are presented. Each box title refers to an internal branch on the left-hand tree. The first topology in red is the main topology followed by the other two alternatives in blue. On the Y-axes the relative frequency is indicated and the dashed lines represent the 1⁄3 threshold. On the X-axis each quartet topology is shown using neighbouring branch labels.

exception of four that were placed among Eurasian Collared Dove (samples D15, D16, D24 and D25). This could suggest possible admixture for those samples. Furthermore, we observed

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that *risoria* D09 from Chad was placed among the *arabica* samples, adding to the possibility that this sample or its lineage contains admixture with populations of the latter.

With respect to the question as to whether *arabica* and *risoria* are reciprocally monophyletic, we used D-statistics to explore the intermediate position of the *S. r. risoria* sample from Chad, D09, that places it as ancestor to the *arabica* clade (Fig. 8). Specifically, we compared this sample with all other *risoria* and *arabica* samples, finding that while in general D09 seems more closely related to other *risoria* than to *arabica* samples, one exception is its relationship to *arabica* D10, from Saudi Arabia, which may suggest a history of gene flow between the ancestors of D09 and *S. r. arabica* populations. Thus could explain the high discordance observed in branch 7 of the relative-frequency analysis (Fig. 7A).

D-statistics (Fig. 9) reveal a clear signal of admixture between Eurasian Collared and domestic Barbary Doves. When subspecies *arabica* was used in these tests, the signal is less strong and in some cases non-statistically significative (see Figs. S2–S3), which could be explained by a close relationship between *S. r. arabica* and domestic Barbary Doves, or be due to some degree of gene flow between Eurasian Collared and African Collared Doves in Arabia. To explore further for gene flow between Eurasian Collared and *arabica* African Collared Doves, we implemented another D-statistics analysis comparing each Eurasian Collared Dove against African Collared Dove samples of both subspecies (Fig. 10). The results showed that *S. decaocto* samples share a higher number of alleles than expected with the samples of *S. r. arabica*, suggesting possible gene flow between them. All tests showed a similar pattern (Fig. S4) except sample D09 from Chad which had less negative or even non-statistically significant D-values in line with our other results (Figs. 7–8) indicating that it is an admixed individual of the two *S. risoria* subspecies.

To identify which Eurasian Collared Dove populations were involved in the admixture processes, we performed additional D-statistics analyses that compared each domestic Barbary Dove, and each *arabica* African Collared Dove, against all Eurasian Collared Doves (Fig. 11). All tests revealed a similar pattern, in which all historic domestic Barbary Doves or *arabica* African Collared Doves share significantly more alleles with European Collared Doves

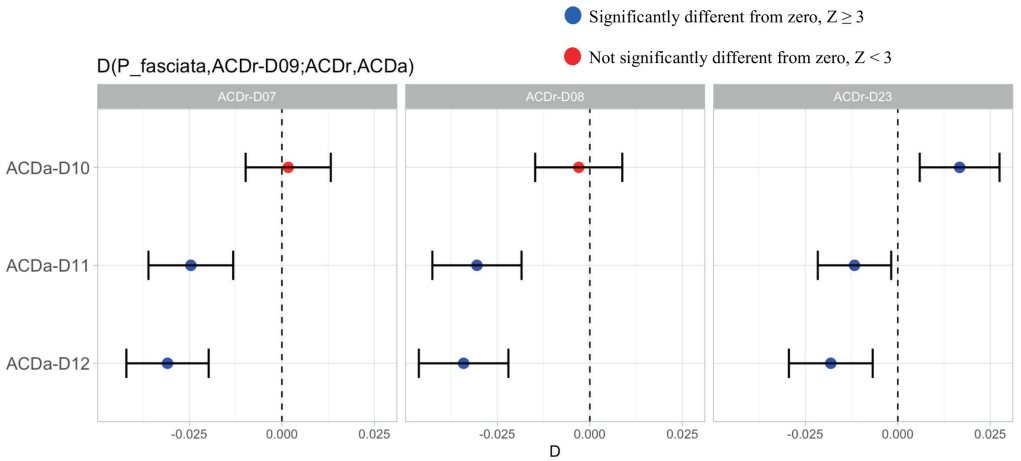

Figure 8. D-statistics analysis testing the species tree topology in Fig. 7 to confirm the intermediate position of *S. r. risoria* sample D09 between the *S. r. risoria* and *S. r. arabica* clades. The sample was compared with those of *risoria* (ACDr) and *arabica* (ACDa). D09 seems closer related to other *S. r. risoria* than to *S. r. arabica*, except sample D10, confirming its placement in the species tree and suggesting possible gene flow between *S. r. risoria* sample D09 and *S. r. arabica*. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup.

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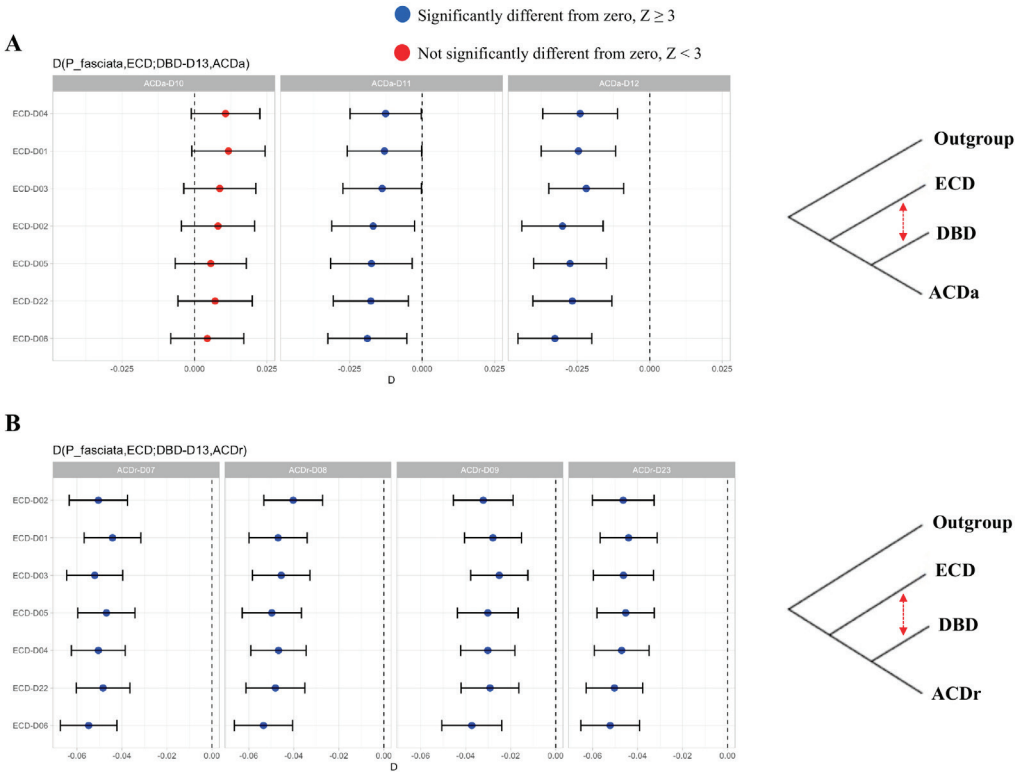

Figure 9. D-statistics analyses testing possible admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD). Results indicate gene flow between them. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. For this analysis each DBD was tested, obtaining a similar pattern. The plots shown were chosen as examples of the results: (A) when samples labelled *S. r. arabica* (ACDa) were used; and (B) samples labelled *S. r. risoria* (ACDr). ACDr samples show higher admixture signals than ACDa samples. The trees at the right represent the structure for each D-statistics test and the red arrows the gene-flow patterns obtained.

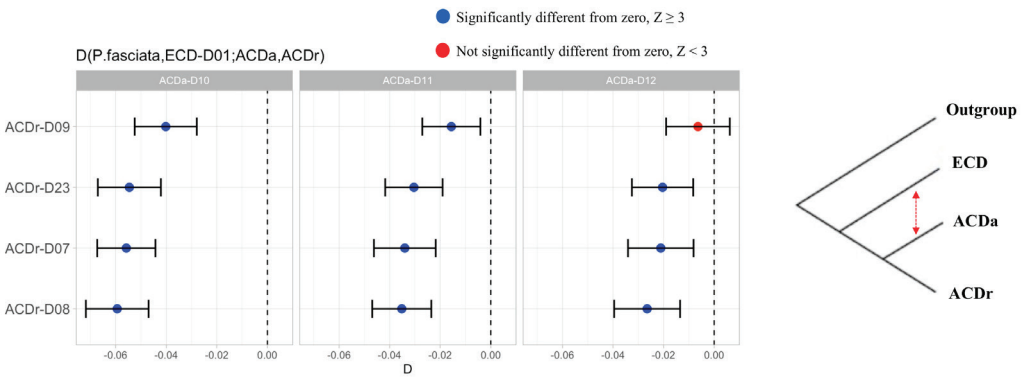

Figure 10. D-statistics analyses to test the possibility of admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and samples of *S. r. arabica* (ACDa). ACDr represents samples of *S. r. risoria*. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. An independent test was performed using each ECD sample in our dataset. The plot shown is used as an example of the results, which suggest admixture between ECD and ACDa. The tree at the right represents the structure for the D-statistics test and the red arrows the gene-flow pattern obtained.

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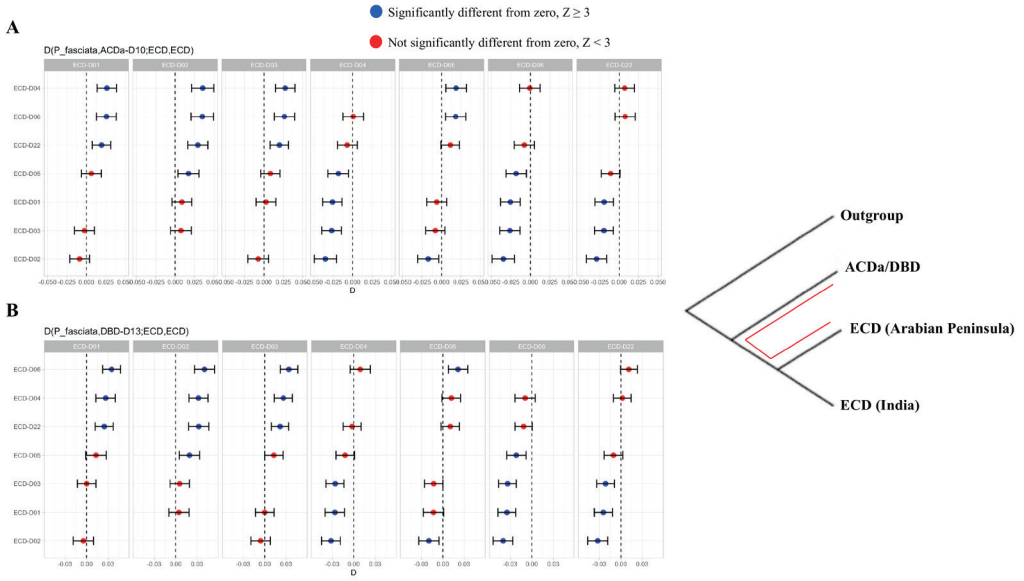

Figure 11. D-statistics analyses to identify Eurasian Collared Dove *Streptopelia decaocto* (ECD) populations involved in admixture with domestic Barbary Dove (DBD) and African Collared Dove *S. r. arabica* (ACDa). Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. ECD samples on the Y-axes represent the second ECD population tested in the D-statistics structure at the top of each plot. All DBD and ACDa samples were tested. The plots shown are used as example of the results. All tests show a similar pattern in which DBD or ACDa significantly share more alleles with ECD from Arabia (mainly D06, D04 and D22) than to ECD from India (D01, D02 and D03), independent of age or geographical origin. The tree at the right represents the structure of the D-statistics analyses implemented and the red line shows the shorter branch in the analyses between ACDa/DBD and ECD. (A) Plot showing the results for ACD samples. (B) Plot showing the results for DBD samples.

from Arabia (mainly D06, D04 and D22) than to birds from India (D01, D02 and D03). This was consistent irrespective of the age or geographical origin of the DBD sample (Figs. S5–S6). These results therefore imply that admixture has occurred between the two species in the Arabian Peninsula.

Lastly, we used D-statistics to explore the different levels of Eurasian Collared Dove admixture in our domestic Barbary Dove samples (Fig. 12). The results revealed a consistent pattern, in which the most modern samples (D25 and D26 from 2018 and 2019) show the strongest signals of admixture with Eurasian Collared Doves (Fig. S7). In contrast, the pre-1900 samples (in particular D15 and D17) show much lower signals of admixture. This result appears to be in accordance with prior results for samples D15 and D17 (Fig. 7A, Fig. S2–S3).

Conclusions and Discussion

Considering these results, how can we answer the four questions we originally posed?

(1) *Is African Collared Dove the sole ancestor of domestic Barbary Dove, or has Eurasian Collared Dove also contributed?* Although our genomic data provide strong evidence that African Collared Dove is the principal ancestor of Barbary Dove, there is evidence of some admixture with Eurasian Collared Dove. Naturally, we caveat that given our limited sample size, we cannot fully describe the geographic extent over which admixture has occurred. However, in light of the facts that (i) our evidence suggests that *S. r. arabica* is the ancestor of the domestic form, and (ii) the admixture signal is similar in all historic domestic Barbary

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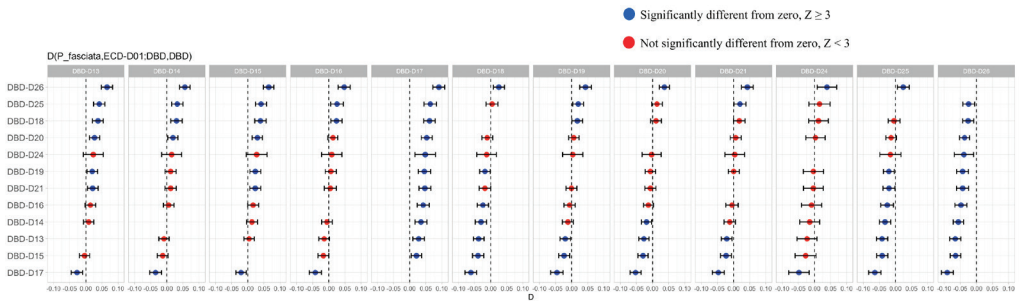

Figure 12. D-statistics analyses exploring the level of admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD). Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup. DBD samples on the Y-axes represent the second DBD population tested in the D-statistics structure at the top of the plot. The same analysis was implemented for each ECD sample in our dataset. All results showed a similar admixture. The plot shown was chosen as an example of the results. The most modern samples (DBD-D25 and DBD-D26) show stronger signals of admixture with ECD, whereas DBD-D15 and DBD-D17 had the lowest levels of admixture.

Doves analysed irrespective of geographic origin, this provides strong evidence that admixture occurred early in the domestication process, hence allowing Eurasian Collared Dove genetic material from Arabia to spread across the domestic Barbary Dove range.

Theoretically only a single cross can release 'foreign' genes into a population which, we stress, is categorically *not* the same as having multiple ancestors. Red Junglefowl *Gallus gallus*, for example, is still recognised as the major ancestor of the domestic chicken, but this does not preclude participation by other species (Lawal *et al*. 2020). The admixture with Eurasian Collared Dove happened very early in the domestication, and most likely even before, as the admixture is also seen in African Collared Doves from Arabia (see Results above). Further, Barbary Dove has all the morphological and behavioural characters of African Collared Dove, therefore we consider the latter to be the principal ancestral species.

(2) *Are the two subspecies of African Collared Dove genetically distinct or the same?* Our results suggest the species can be considered monotypic, given the very limited genomic divergence between proposed subspecies and because *S. r. risoria* appears paraphyletic with the placement of Chad sample D09 as sister to *S. r. arabica*. One possibility is that the subspecies instead represent natural morphological and genetic structure arising across the species' range, which analysis of a denser sample spanning the full geographical range could address.

Minor morphological differences in a species are often individual rather than taxonomic, and in this case earlier intermixing with Eurasian Collared Dove may also play a role (see Fig. 13). All but one of the described subspecies of Eurasian Collared Dove is now a considered synonym of the nominate because the supposed morphological differences are marginal and not consistent (van Grouw 2022). As the voice and behaviour of Barbary and African Collared Doves are similar (HvG pers. obs.), and differences in colour between African Collared Dove populations are minor and inconsistent, monotypy would be unsurprising.

(3) *If African Collared Dove has two genetically different subspecies, which is involved in the domestic Barbary Dove?* Irrespective of whether African Collared Dove should be considered polytypic, it is clear that domestic Barbary Dove derives from individuals assigned to *arabica*. This, combined with the evidence of early admixture with Arabian Peninsula Eurasian Collared Doves, may provide strong evidence for domestication having occurred in the region around the Red Sea, in line with earlier suggestions that domestication originated in Egypt (Sonnini de Manoncourt 1799).

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Figure 13. The outer web of the outer tail feathers of Eurasian Collared Dove *Streptopelia decaocto* (left, NHMUK1889.2.2.1407, sample D2) is coloured and the coloured part extends beyond that on the inner web. The outer web of the outer rectrices of African Collared Dove *S. risoria* is usually not coloured (right, NHMUK1934.9.20.89, sample D12). First-generation hybrids (F1) between the two species have the outer web coloured, extending slightly beyond the coloured part of the inner web. The middle tail (NHMUK1920.12.22.54, sample D23), however, looks like a F1 hybrid based on morphological characteristics, but genetic analyses show it is a pure African Collared Dove; morphological differences within a species are often individual, rather than taxonomic characters (Jonathan Jackson, © Natural History Museum, London)

(4) *Are 'early' and 'modern' Barbary Dove genetically identical, or is the latter now 'polluted' by Eurasian Collared Dove genes?* Comparing the phylogenetic and admixture profiles of our Barbary Dove samples, we find neither evidence for major differences in origin nor admixture with Eurasian Collared Doves in the historic samples. Additionally, Barbary Dove has maintained similar genetic proportions of Eurasian Collared Dove through time, but modern samples D25 and D26 showed a much stronger admixture due to the fact that these samples are from after the invasion of Eurasian Collared Dove into western Europe. Since then, knowingly and unknowingly, breeders have crossed Barbary Doves with the now common Eurasian Collared Dove. Interestingly, the third modern sample, D24, did not show stronger admixture. Although the individual was received by HvG as a live bird in 1997 (died 2020) from Kuwait, according to the breeder the alleged origin of its ancestors was the Philippines. Eurasian Collared Dove does not (yet) occur in the Philippines, which may well explain its genetic make-up. The same applies to other more modern samples D18 (1992), D19 (1951) and D20 (1960), which are from countries where Eurasian Collared Dove does not occur or did not at the time. In sum, it appears that, other than in countries where Eurasian Collared Dove has invaded, over the last 100 years the domestic Barbary Dove has been genetically stable.

As indicated in earlier publications (e.g., Shelley 1883, Hartert 1916, van Grouw 1999, 2018) and now confirmed by genetic analysis, Eurasian Collared Dove has not contributed significantly to the domestic Barbary Dove, and African Collared Dove is the latter's principal ancestor. Despite being usually divided into two subspecies, African Collared Dove can be considered monotypic, and the domestic form (Barbary Dove) probably derived from the Arabian population.

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Figure 14. Possible syntypes at the American Museum of Natural History, New York, of *Peristera ridens* Brehm & Brehm 1855, collected by A. E. Brehm at Khartoum, Sudan in April–June 1851, from left to right, juvenile male, AMNH 613796; male, AMNH 613797; male, AMNH 613798; male, AMNH 613799; female, AMNH 613800. The name *ridens* (Latin *ridere*: to laugh) for the species given by Brehm & Brehm, 1855, is also senior to Sundevall's *roseogrisea*, but was never commonly used (Tom Trombone, © American Museum of Natural History, New York)

Furthermore, given that our data indicate that African Collared Dove is monotypic, the earlier assignment of a neotype for *roseogrisea* Sundevall, 1857, to clarify the status of this junior synonym (van Grouw 2018), is valid. The taxonomy of African Collared Dove is therefore as follows: *Streptopelia risoria* (Linnaeus, 1758), neotype at the Natural History Museum, Tring, NHMUK 2008.3.1 (Fig. 1), based on Donegan (2008). Synonyms: *Columba alba* Temminck, 1808, pl. 46 (see van Grouw 2018; Fig. 4), type specimen whereabouts unknown; *Peristera ridens* Brehm & Brehm, 1855, five possible syntypes at the American Museum of Natural History in New York (AMNH 613796–613800; Fig. 14); *Columba roseogrisea* Sundevall, 1857, neotype at the Senckenberg Museum, Frankfurt am Main, SMF 22887 (Fig. 3), based on van Grouw (2018); *Turtur fallax* Schlegel, 1873, holotype at Naturalis Biodiversity Center, Leiden, RMNH.AVES.87889; *Turtur roseogriseus arabicus* von Neumann, 1904, type specimen whereabouts unknown; *Streptopelia roseogrisea bornuensis* Bannerman, 1931, holotype in Tring, NHMUK 1923.10.26.8 (Fig. 5).

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Supplementary Materials

Figure S1. Maximum likelihood whole-mitochondrial genome phylogeny. Oriental Turtle Dove *Streptopelia orientalis* was used as outgroup. Bootstrap values are shown at the base of each internal node. The four different taxa are labelled as follows: Eurasian Collared Dove *S. decaocto* (red), African Collared Dove *S. r. risoria* (blue), *S. r. arabica* (yellow) and Barbary Dove *S. r. domestica* (green).

Figure S2. D-statistics analyses testing possible admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD) or African Collared Dove *S. r. arabica* (ACDa). Above each set of plots the analysis structure is shown. Each set of plots presents the results for each DBD in our dataset, excluding D13 which is shown in Fig. 4A. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3. The results for the domestic Barbary Doves D15 and D17 show distinct admixture patterns, suggesting that these samples present lower admixture with ECD, as also indicated by the results of other analyses (Fig. 7A and Fig 12).

Figure S3. D-statistics analyses testing possible admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD) or African Collared Dove *S. r. risoria* (ACDr). Above each set of plots the analysis structure is shown. Each set of plots presents the results for each DBD in our dataset, excluding D13 which is shown in Fig. 4B. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3. As in Fig. S2, domestic Barbary Dove sample D17 seems to exhibit the lowest admixture signals with ECD.

Figure S4. D-statistics analyses testing the possibility of admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and African Collared Dove *S. r. arabica* (ACDa). Each ECD sample in our dataset was tested. Each set of plots represents the performed analysis. All tests are presented here except the analysis for sample D01

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which is shown in Fig. 5. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3.

Figure S5. D-statistics analyses were performed to identify the Eurasian Collared Dove *Streptopelia decaocto* (ECD) populations involved in the admixture with African Collared Dove subspecies *arabica* (ACDa). ECD samples at the Y axes represent the second ECD population tested in the D-statistics structure shown at the top of each plot. All ACDa samples were tested. The set of plots corresponding to sample D10 can be found in Fig. 6A. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was under or above 3.

Figure S6. D-statistics analyses to identify the Eurasian Collared Dove *Streptopelia decaocto* (ECD) populations involved in admixture with domestic Barbary Dove (DBD). ECD samples on Y-axes represent the second ECD population tested in the D-statistics structure above each plot. All DBD samples were tested. The set of plots corresponding to sample D13 are shown in Fig. 6B. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3.

Figure S7. D-statistics analyses to explore different levels of admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD). DBD samples on Y-axes represent the second DBD population tested in the D-statistics structure shown above the plot. Each ECD sample in our dataset was tested. All results are shown except those for sample D01 shown in Fig. 7. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3.

Table S1. BGI sequencing technology-compatible adapter and splint sequences. BGI_AD1 adapter and splint are homologous to the Illumina P7 adapter and splint and BGI_AD2 adapter and splint are homologous to the Illumina P5 adapter and splint defined in Kapp *et al*. (2021).

Table S2. Sequencing data generated for all the *Streptopelia* samples used in this study. [1] Final reads used in the analyses after removing PCR duplicates and quality filtering.

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