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Type specimens matter: new insights on the systematics, taxonomy and nomenclature of the subalpine warbler (*Sylvia cantillans*) complex

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We revise the taxonomy of the *Sylvia cantillans* complex, a group of phenotypically distinct warblers with mainly parapatric distributions around a large part of the Mediterranean basin. We redefine the species limits using a combination of mitochondrial and nuclear markers and we objectively link available names to the genetically defined lineages by genotyping the surviving type specimens. In addition, the study of archival documents clarifies the exact

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composition of type series and provides further evidence for the identification of lost types. These results support the recognition of three species-level taxa: Moltoni's warbler, *Sylvia subalpina* (north-central Italy, Corsica, Sardinia and the Balearics); the western subalpine warbler, *S. iberiae* (North Africa, Iberia, southern France and extreme north-west Italy); and the eastern subalpine warbler, *S. cantillans*, with subspecies *S. cantillans cantillans* (southern Italy, Sicily) and *S. cantillans albistriata* (Balkans, Greece, western Turkey).

ADDITIONAL KEYWORDS: species limits – *Sylvia cantillans* – taxonomy – types.

INTRODUCTION

The subalpine warbler, *Sylvia cantillans* (Pallas, 1764), complex includes a number of phenotypically distinct forms with mainly parapatric distributions around a large part of the Mediterranean basin (Dickinson & Christidis, 2014; del Hoyo & Collar, 2016). Following the prevailing biological species concept (Mayr, 1942), a single species was generally recognized during the 20th century (Table 1). Using plumage characters, the different populations were separated into three subspecies: the nominate *Sylvia cantillans cantillans* from Portugal, Spain, France and Italy, including Sicily, Sardinia and Corsica; the subspecies *Sylvia cantillans inornata* Tschusi, 1906 for the North African populations; and the subspecies *Sylvia cantillans albistriata* (Brehm CL, 1855) restricted to the Balkans, Greece and the Aegean side of Turkey.

Although plumage characters among subspecies are subtle and often better appreciated when museum series are compared, field observations revealed that birds from Sardinia, Corsica and the Balearics shared a peculiar, markedly different contact call, unknown in mainland populations (Lemaire, 1973; Bergmann, 1976; Cody & Walter, 1976; Thibault, 1983; Gargallo, 1994). Moreover, Gargallo (1994) and Shirihai *et al.* (2001) pointed out that the populations in the central Mediterranean islands share a distinct moult strategy

Table 1. Taxonomic changes in the subalpine warbler *Sylvia cantillans* complex over the last century

Reference	Number of species	North Africa	Iberia–France	South Italy	North–central Italy	Central Mediterranean islands	Balkans–Greece–west Turkey
Hartert (1910)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. albistriata*
Vaurie (1959)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. albistriata*
Williamson (1976)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. albistriata*
Wolters (1980)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. albistriata*
Peters (1986)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. albistriata*
Glutz von Blotzheim & Bauer (1991)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. albistriata*
Cramp (1992)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. albistriata*
Shirihai *et al.* (2001)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. c. moltonii*	*S. c. albistriata*
Dickinson (2003)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. moltonii*?	*S. c. cantillans*	*S. c. moltonii*	*S. c. albistriata*
del Hoyo *et al.* (2006)	1	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. moltonii*	*S. c. moltonii*	*S. c. albistriata*
Brambilla *et al.* (2008c)	2	*S. c. inornata*	'Western' *S. cantillans*	'Southern' *S. cantillans*	*S. c. moltonii*	*S. c. moltonii*	*S. c. albistriata*
Svensson (2013a,b)	3	*S. i. inornata*	*S. i. iberiae*	*S. c. cantillans*	*S. subalpina*	*S. subalpina*	*S. c. albistriata*
Dickinson & Christidis (2014)	3	*S. i. inornata*	*S. i. iberiae*	*S. c. cantillans*	*S. subalpina*	*S. subalpina*	*S. c. albistriata*
Sangster *et al.* (2015)	2	*S. c. inornata*	*S. c. iberiae*	*S. c. cantillans*	*S. subalpina*	*S. subalpina*	*S. c. albistriata*
del Hoyo & Collar (2016)	2	*S. c. inornata*	*S. c. iberiae*	*S. c. cantillans*	*S. subalpina*	*S. subalpina*	*S. c. albistriata*
Clements (2018)	2	*S. c. inornata*	*S. c. cantillans*	*S. c. cantillans*	*S. c. cantillans*	*S. subalpina*	*S. c. albistriata*
Shirihai & Svensson (2018)	3	*S. i. inornata*	*S. i. iberiae*	*S. c. cantillans*	*S. subalpina*	*S. subalpina*	*S. c. albistriata*
Gill & Donsker (2019)	2	*S. c. inornata*	*S. c. iberiae*	*S. c. cantillans*	*S. moltonii*	*S. moltonii*	*S. c. albistriata*
This paper	3	*S. iberiae*	*S. iberiae*	*S. c. cantillans*	*S. subalpina*	*S. subalpina*	*S. c. albistriata*

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and pinkish male underparts, without any rusty, chestnut or orange shade. For these populations, they resurrected the subspecies *Sylvia cantillans moltonii* Orlando, 1937, previously subsumed in the synonymy of the nominate form, presumably under the influence of Vaurie (1954). The name *moltonii* was quickly accepted by Dickinson (2003) and the *Handbook of the Birds of the World* (del Hoyo *et al.*, 2006).

Further field observations by Festari *et al.* (2002) and a subsequent detailed survey across mainland Italy (Brambilla *et al.*, 2006) indicated that the same vocally distinct population occurs in both the central Mediterranean islands and in central-northern Italy, where it overlaps with the populations occurring both further south and in extreme north-west Italy, bordering France. The largely parapatric distribution, the distinct call types and the lack of mixed pairs at syntopic sites, in addition to the differences in the moult strategy and the differential response to a playback test to the same vs. other songs, strongly suggested that this distinctive population could be ranked as a separate species (Brambilla *et al.*, 2006, 2008b, c).

A phylogeographical analysis using a single mitochondrial locus demonstrated that the *Sylvia cantillans* complex consists of four deeply divergent, mostly parapatric lineages (Brambilla *et al.*, 2008c), with the most divergent lineage indeed uniting birds from north-central Italy with those from the central Mediterranean islands (Corsica, Sardinia and the Balearics). The southern Italian populations form a different clade, sister to the Balkan lineage, and a further group covers Spain and France. Although the four-clade phylogeographical structure is well supported, the number and limits of species to be recognized in the complex still remain to be clarified. In addition, the appropriate names for taxa within the complex are also contentious. On the one hand, multiple traits (see above), coupled with genetic distinctiveness, definitively identify the populations inhabiting central Mediterranean islands and central-northern Italy as a distinct species, Moltoni's warbler [*Sylvia subalpina* syn. *Sylvia moltonii*, according to Brambilla *et al.*, 2008b]. On the other hand, the same study stated that 'when more data are provided […] a further subdivision into two branches, i.e. southern *cantillans* and *albistriata* on the one side and western *cantillans* on the other, representing two different (allo)species, could be expected', which could be regarded as phylogenetic species (Brambilla *et al.*, 2008b). The two-species approach was then followed by most authors (see below), although a three-species split was already foreseen as likely on the basis of the complex phylogeography; eastern and western clades could be regarded as two allospecies, the names for which remained to be defined (Brambilla, 2013).

The split into three species was then proposed by Svensson (2013a, b), who combined available phenotypic and mitochondrial evidence (Gargallo, 1994; Shirihai *et al.*, 2001; Brambilla *et al.*, 2008b). He recognized three species in the complex: *Sylvia subalpina* (north-central Italy and central Mediterranean islands); *S. cantillans*, with subspecies *S. c. cantillans* (South Italy) and *S. c. albistriata* (Balkans, Greece and Turkey); and *S. inornata*, with subspecies *S. i inornata* (North Africa) and the newly described subspecies *Sylvia inornata iberiae* Svensson, 2013 (Portugal, Spain and France). Apart from the transfer of these taxa to the genus *Curruca* following the split of the genus *Sylvia*, the three-species approach was incorporated into the fourth edition of the *Howard & Moore Checklist* (Dickinson & Christidis, 2014). However, a more conservative two-species approach remains prevalent (Sangster *et al.*, 2015; del Hoyo & Collar, 2016; Clements *et al.*, 2018; Gill & Donsker, 2019), with a polytypic *S. cantillans* including three or four subspecies (i.e. *S. c. cantillans*, *S. c. albistriata*, *S. c. inornata* and *S. c. iberiae*) and a monotypic *S. subalpina*, although Clements *et al.* (2018) restricted *S. subalpina* to the central Mediterranean islands and maintained birds from central-northern Italy in *S. cantillans*. Furthermore, as stated above, the continuous recognition of the North African populations as distinct from the rest of the complex relies on no genetic evidence and thus needs to be tested.

The current nomenclatural treatment is even more controversial, at both the species and the subspecies level. Baccetti *et al.* (2007) provided a brief summary of species names available for the complex and recommended that *Sylvia cantillans moltonii* Orlando, 1937 should be synonymized with *Sylvia subalpina* Temminck, 1820. Further nomenclatural remarks were presented by Svensson (2013a), in connection with the designation of a neotype for *Motacilla cantillans* Pallas, 1764. However, the surviving type material has never been studied critically, and a number of statements concerning the type specimen of *Sylvia subalpina* Temminck, 1820 seem to be cited repeatedly from secondary sources (Baccetti *et al.*, 2007; Svensson, 2013a).

In the present contribution, we address some systematic, taxonomic and nomenclatural points to provide a robust revision of the *Sylvia cantillans* complex, starting from the examination of type material still available. Namely, we aim at: (1) expanding the phylogeographical analysis of Brambilla *et al.* (2008b) with more comprehensive sampling, including the Maghreb, thus covering the entire range of the complex; (2) inferring the species limits by integrating mitochondrial and nuclear data; (3) objectively linking available names to genetic lineages by genotyping the surviving historical types; and (4) studying original archival documents to provide further evidence for the identification of the lost types.

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MATERIAL AND METHODS

Sampling

We obtained fresh samples of tissue, blood or feathers for 91 individuals covering the entire range of the *Sylvia cantillans s.l.* complex (Table 2). We paid special attention to use samples obtained from breeding individuals. Breeding status was inferred directly for ringed birds, using behaviour (singing males trapped with playback) or examination of the cloacal protuberance in males and presence of a brood patch in females as proxies. We further assumed a breeding status for specimens sampled from mid May to the beginning of July, i.e. during the full breeding period and outside the known migration time for the taxa belonging to the complex. One of the specimens from which we obtained a tissue sample was selected as the neotype of *Sylvia subalpina* Temminck, 1820 (see Discussion). We supplemented the fresh sample dataset with toe-pad samples from four study skins to achieve better coverage for some key geographical areas.

In addition, we included toe-pad samples from surviving historical types: one syntype of *Sylvia leucopogon* Meyer, 1822, the lectotypes of *Curruca albistriata* Brehm, 1855 and *Sylvia subalpina inornata* Tschusi, 1906 and two syntypes and the supposed lectotype of *Sylvia cantillans moltonii* Orlando, 1937.

Museum acronyms are given in Table 2.

Laboratory work

Tissue samples were extracted using a Qiagen DNA Mini Kit, following the manufacturer's protocol or the modified protocol described by Zuccon & Ericson (2010) for the toe-pad samples. All extractions and the polymerase chain reaction (PCR) set-up for toe-pad specimens were carried out in separate spaces dedicated to handling archival DNA.

For the phylogeographical analysis, we amplified two mitochondrial genes, cytochrome *b* (*Cytb*) and cytochrome oxidase I (*COI*). *Cytb* was amplified either as a single fragment, using the primers 4L and 1137H, or in two fragments, using the internal primers 538L and 662H, following the protocol described by Brambilla *et al.* (2008c). The *COI* gene was amplified using the primers COI-ExtF and VerteR1, following the protocol of Johnsen *et al.* (2010). The toe-pad samples were amplified in a series of short, overlapping fragments of 150–300 bp, using a large set of internal primers, designed using GeneFisher2 (Giegerich *et al.*, 1996) and the alignment obtained from the fresh samples (Supporting Information, Table S1). For a subset of specimens (60 individuals) we also sequenced three nuclear introns, using published primers and amplification protocols: β-fibrinogen intron 5 (*bFib5*; Fuchs *et al.*, 2004), glyceraldehyde 3-phosphate dehydrogenase intron 11 (*GAPDH*; Fjeldså *et al.*, 2003) and adenylate kinase intron 5 (*AK1*; Shapiro & Dumbacher, 2001).

The PCR products were Sanger sequenced bidirectionally using an ABI 3130 sequencer (Applied Biosystems) and the sequences assembled using CodonCode Aligner (LI-COR, Inc., USA). To determine the allele phase of nuclear loci unambiguously, we resequenced the same products that showed more than one heterozygous position using an Ion Torrent PGM, following the protocol of Dettai *et al.* (2012).

Phylogenetic analyses

Selection and recombination

Before molecular analyses, we tested whether our datasets conformed to the hypothesis of neutral evolution and whether recombination events could be detected in the intron loci. Selection acting on the mitochondrial protein-coding genes was tested using the McDonald–Kreitman test (McDonald & Kreitman, 1991), with significance assessed using Fisher's exact test (threshold value of $\alpha = 0.05$), as implemented in DnaSP v.6.0 (Librado & Rozas, 2009). For the nuclear introns, we used the Hudson–Kreitman–Aguadé (HKA) test (Hudson *et al.*, 1987), in the version implemented in HKA software (https://bio.cst.temple.edu/~hey/hka_manual). We used the GARD (Genetic Algorithm for Recombination Detection) software, as implemented in HyPhy (Kosakovsky Pond *et al.*, 2005, 2006) to detect whether the nuclear loci were subject to recombination.

Phylogenetic trees

The *Cytb* and *COI* sequences were combined in a single mitochondrial dataset, analysed under the maximum likelihood criterion using RAxML v.8.2.12 (Stamatakis, 2006), implemented on the CIPRES portal (Miller *et al.*, 2010). We imposed a partitioned analysis, selecting the GTR+Γ+I substitution model and a random starting tree. Nodal support was estimated using 100 bootstrap replicates. The topology was rooted using six other *Sylvia* species (see Table 2) that are among the most closely related to *S. cantillans* in phylogenies of the genus by Shirihai *et al.* (2001) and Böhning-Gaese *et al.* (2003).

Allele networks

We built a separate minimum spanning network for each nuclear locus with PopART v.1.7 (Leigh & Bryant, 2015). We recoded indels as a single base pair mutation event, substituting the indel with a base different from the one occurring at that position in the remaining alleles.

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Table 2. Samples included in the phylogenetic analysis, with museum accession numbers and collection localities

Taxon	Mitochondrial clade	Sample number	Locality	Collection date	Status
S. cantillans albistriata	5	AMNH 455634	Egypt (no exact locality)	–	Lectotype *albistriata*
S. cantillans albistriata	5	ISPRA SCA065	Dalmatia, Croatia	April 2005	Dubious
S. cantillans albistriata	5	ISPRA SCA135	Kaminia, Lesvos, Greece	1 August 2006	Dubious
S. cantillans albistriata	5	ISPRA SCA136	Kaminia, Lesvos, Greece	1 August 2006	Dubious
S. cantillans albistriata	5	ISPRA SCA137	Kaminia, Lesvos, Greece	1 August 2006	Dubious
S. cantillans albistriata	5	ISPRA SCA138	Kaminia, Lesvos, Greece	1 August 2006	Dubious
S. cantillans albistriata	5	ISPRA SCA139	Kaminia, Lesvos, Greece	1 August 2006	Dubious
S. cantillans albistriata	5	ISPRA SCA140	Kaminia, Lesvos, Greece	1 August 2006	Dubious
S. cantillans albistriata	5	ISPRA SCA141	Kaminia, Lesvos, Greece	26 July 2006	Breeding
S. cantillans albistriata	5	ISPRA SCA142	Tsichliotas, Lesvos, Greece	26 July 2006	Breeding
S. cantillans albistriata	5	ISPRA SCA143	Tsichliotas, Lesvos, Greece	26 July 2006	Breeding
S. cantillans albistriata	5	MCCI 3146	Marettimo, Sicily, Italy	11 May 2008	Migrant
S. cantillans albistriata	5	NHMB B6157	Avas, Macedoni, Greece	3 May 2012	Breeding
S. cantillans albistriata	5	NHMB B6158	Avas, Macedoni, Greece	3 May 2012	Breeding
S. cantillans albistriata	5	NHMB B6159	Avas, Macedoni, Greece	3 May 2012	Breeding
S. cantillans albistriata	5	NHMB MR1424	Odoljen, Kotor, Montenegro	3 May 2013	Breeding
S. cantillans albistriata	5	NHMB MR1425	Odoljen, Kotor, Montenegro	3 May 2013	Breeding
S. cantillans albistriata	5	NHMB MR1426	Odoljen, Kotor, Montenegro	3 May 2013	Breeding
S. cantillans albistriata	5	NHMB MR1427	Odoljen, Kotor, Montenegro	3 May 2013	Breeding
S. cantillans albistriata	5	NHMB MR1428	Odoljen, Kotor, Montenegro	3 May 2013	Breeding
S. cantillans albistriata	5	NHMB MR1429	Odoljen, Kotor, Montenegro	19 April 2013	Dubious
S. cantillans cantillans	4	ISPRA SCA001	Veio, Lazio, Italy	27 May 2005	Breeding
S. cantillans cantillans	4	ISPRA SCA017	Castel di Guido, Lazio, Italy	8 June 2005	Breeding
S. cantillans cantillans	4	ISPRA SCA021	Castel di Guido, Lazio, Italy	2 August 2005	Dubious
S. cantillans cantillans	4	ISPRA SCA030	L'Aquila, Abruzzo, Italy	6 July 2005	Breeding
S. cantillans cantillans	4	ISPRA SCA073	Ventotene, Lazio, Italy	27 May 2006	Breeding
S. cantillans cantillans	4	ISPRA SCA075	Ventotene, Lazio, Italy	15 May 2006	Breeding
S. cantillans cantillans	4	ISPRA SCA077	Lumello, Lombardy, Italy	1 June 2006	Breeding
S. cantillans cantillans	4	ISPRA SCA079	Bocca di Serchio, Tuscany, Italy	12 June 2006	Breeding
S. cantillans cantillans	4	ISPRA SCA089	Alanno, Abruzzo, Italy	2 June 2006	Breeding
S. cantillans cantillans	4	ISPRA SCA093	Todi, Umbria, Italy	2006	Dubious
S. cantillans cantillans	4	ISPRA SCA112	Cà Budrio, Casola Valsenio, Emilia Romagna, Italy	3 July 2006	Breeding
S. cantillans cantillans	4	ISPRA SCA259	Contrada Pettinèo, Vicari, Sicily, Italy	19 August 2006	Dubious
S. cantillans cantillans	4	ISPRA SCA264	Ficuzza, Sicily, Italy	14 June 2006	Breeding
S. cantillans cantillans	4	ISPRA SCA265	Ficuzza, Sicily, Italy	14 June 2006	Breeding
S. cantillans cantillans	4	ISPRA SCA318	Calanchi Ripabianca, Jesi, Marche, Italy	27 June 2010	Breeding
S. cantillans cantillans	4	ISPRA SCA410	Monterenzio, Emilia-Romagna, Italy	18 May 2015	Breeding

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Table 2. Continued

Taxon	Mitochondrial clade	Sample number	Locality	Collection date	Status
S. cantillans cantillans	4	ISPRA SCA411	Oasi WWF, Conza, Campania, Italy	17 May 2015	Breeding
S. cantillans cantillans	4	ISPRA SCA412	L'Aquila, Abruzzo, Italy	14 May 2015	Breeding
S. cantillans cantillans	4	ISPRA SCA413	L'Aquila, Abruzzo, Italy	14 May 2015	Breeding
S. cantillans cantillans	4	MCCI 2981	Marettimo, Sicily, Italy	12 May 2008	Migrant
S. cantillans cantillans	4	MNHN 0516.01	Palmaria, Liguria, Italy	16 May 2003	Breeding
S. cantillans cantillans	4	MSNM Av5924	Sannicandro Garganico, Apulia, Italy	2 May 1959	Breeding
S. cantillans cantillans	4	NHMW 42230	Palermo, Sicily, Italy	Spring 1820	Syntype *leucopogon*
S. iberiae	3	ISPRA SCA044	Leon, Spain	July 2005	Breeding
S. iberiae	3	ISPRA SCA049	Leon, Spain	July 2005	Breeding
S. iberiae	3	ISPRA SCA050	Leon, Spain	July 2005	Breeding
S. iberiae	3	ISPRA SCA116	Apt, Villars, France	2006	Dubious
S. iberiae	3	ISPRA SCA118	Apt, Villars, France	2006	Dubious
S. iberiae	3	ISPRA SCA126	Vacarisses, Puigventòs, Barcelona, Spain	12 July 2006	Breeding
S. iberiae	3	ISPRA SCA133	Vacarisses, Puigventòs, Barcelona, Spain	12 July 2006	Breeding
S. iberiae	3	ISPRA SCA156	La Verdière, Var, France	2 July 2006	Breeding
S. iberiae	3	ISPRA SCA161	La Verdière, Var, France	2 July 2006	Breeding
S. iberiae	3	ISPRA SCA162	Cheval-Blanc, Vaucluse, France	11 June 2006	Breeding
S. iberiae	3	ISPRA SCA164	Cheval-Blanc, Vaucluse, France	1 June 2006	Breeding
S. iberiae	3	MCCI 3666	Mt Musiné, Piedmont, Italy	21 June 2012	Breeding
S. iberiae	3	MNHN JMP340	El Feija National Park, Tunisia	1 May 2012	Breeding
S. iberiae	3	MNHN JMP646	Leucate, Aude, France	27 August 2013	Dubious
S. iberiae	3	MNHN JMP647	Oasis of Tafilalet, Morocco	2 June 2013	Breeding
S. iberiae	3	MNHN JMP648	Oasis of Tafilalet, Morocco	2 June 2013	Breeding
S. iberiae	3	MNHN JMP649	Oasis of Tafilalet, Morocco	2 June 2013	Breeding
S. iberiae	3	MNHN JMP650	Oasis of Tafilalet, Morocco	2 June 2013	Breeding
S. iberiae	3	MNHN JMP651	Oasis of Tafilalet, Morocco	2 June 2013	Breeding
S. iberiae	3	ZSM 58.72	Linares de Riofrio, Salamanca, Spain	26 April 1958	Breeding
S. subalpina	1	ISPRA SCA056	Faeto, Tuscany, Italy	July 2005	Breeding
S. subalpina	1	ISPRA SCA060	Sarna, Tuscany, Italy	29 July 2005	Breeding
S. subalpina	1	ISPRA SCA069	Settefonti, Emilia Romagna, Italy	8 June 2006	Breeding
S. subalpina	1	ISPRA SCA072	Settefonti, Emilia Romagna, Italy	12 June 2006	Breeding
S. subalpina	1	ISPRA SCA076	Lumello, Lombardy, Italy	1 June 2006	Breeding
S. subalpina	1	ISPRA SCA078	Lumello, Lombardy, Italy	1 June 2006	Breeding
S. subalpina	1	ISPRA SCA081	Bocca di Serchio, Tuscany, Italy	12 June 2006	Breeding
S. subalpina	1	ISPRA SCA082	Bocca di Serchio, Tuscany, Italy	12 June 2006	Breeding
S. subalpina	1	ISPRA SCA084	San Rossore, Tuscany, Italy	11 June 2006	Breeding
S. subalpina	1	ISPRA SCA107	Cà Budrio, Casola Valsenio, Emilia Romagna, Italy	3 July 2006	Breeding

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Table 2. Continued

Taxon	Mitochondrial clade	Sample number	Locality	Collection date	Status
S. subalpina	1	ISPRA SCA114	Villalvernia, Piedmont, Italy	11 June 2001	Breeding
S. subalpina	2	ISPRA SCA119	Manso, Pirio, Corsica, France	11 June 2006	Breeding
S. subalpina	1	ISPRA SCA144	PFR Taro, Collecchio, Emilia Romagna, Italy	2006	Dubious
S. subalpina	2	ISPRA SCA271	San Rossore, Tuscany, Italy	25 June 2006	Breeding
S. subalpina	1	ISPRA SCA289	Giglio, Tuscany, Italy	22 July 2006	Breeding
S. subalpina	2	ISPRA SCA290	Bunyola, Mallorca, Spain	2 August 2006	Dubious
S. subalpina	2	ISPRA SCA291	Bunyola, Mallorca, Spain	11 August 2006	Dubious
S. subalpina	2	MCCI 3122	Marettimo, Sicily, Italy	10 May 2008	Migrant
S. subalpina	1	MCCI 3483	Malvicino, Piedmont, Italy	3 June 2011	Breeding
S. subalpina	1	MCCI 3484	Malvicino, Piedmont, Italy	3 June 2011	Breeding
S. subalpina	1	MCCI 3876	Alto, Piedmont, Italy	5 June 2013	Breeding
S. subalpina	2	MNHN 20.28	Corsica, France	July 1998	Breeding
S. subalpina	2	MNHN JMP199	Patrimonio, Corsica, France	5 June 2011	Breeding
S. subalpina	2	MNHN JMP200	Oletta, Corsica, France	18 June 2011	Breeding
S. subalpina	2	MNHN JMP433	San Colombanu, Corsica, France	26 June 2012	Breeding
S. subalpina	2	MNHN JMP495	Patrimonio, Corsica, France	25 August 2012	Dubious
S. subalpina	2	MNHN JMP500	Patrimonio, Corsica, France	3 August 2012	Dubious
S. subalpina	1	MNHN JMP583	Variante, Tuscany, Italy	18 May 2013	Breeding
S. subalpina	1	MNHN JMP593	Greve in Chianti, Tuscany, Italy	2 May 2013	Breeding
S. subalpina	2	MRT 1664	Lanusei, Sardinia, Italy	22 April 1937	'Lectotype' *moltonii*
S. subalpina	2	MRT 2819	Sardinia, Italy (no exact locality)	No date	Dubious
S. subalpina	1	MSNM Av37427	Pocapaglia, Piedmont, Italy	9 June 2018	Neotype *subalpina*
S. subalpina	2	MSNM Av5918	Lanusei, Sardinia, Italy	24 June 1930	Syntype *moltonii*
S. subalpina	2	MSNM Av5919	Lanusei, Sardinia, Italy	7 June 1930	Syntype *moltonii*
S. subalpina	2	MSNM Av5956	Monte Taré, Lanusei, Sardinia, Italy	14 June 1956	Breeding
S. subalpina	1	MSNM Av5987	Zavattarello, Lombardy, Italy	24 June 1964	Breeding
S. subalpina	2	ZSM 17.2694	Tunis, Tunisia	May 1906	Lectotype *inornata*
Outgroup					
S. communis		MNHN 1995.231			
S. conspicillata		from Genbank			
S. melanocephala		MNHN 0816.01			
S. melanothorax		from Genbank			
S. mystacea		from Genbank			
S. undata		MNHN 2000.1650			

The taxonomy follows the conclusions of this paper. Museum acronyms: AMNH, American Museum of Natural History, New York; ISPRA, Istituto Superiore per la Protezione e la Ricerca Ambientale, Bologna; MCCI, Museo Civico di Storia Naturale, Carmagnola; MNHN, Muséum National d'Histoire Naturelle, Paris; MRT, Museo Regionale di Terrasini, Terrasini; MSNM, Museo Civico di Storia Naturale, Milano; NHMB, Museum of Natural History, Belgrade; NHMW, Naturhistorische Museum, Vienna; ZSM, Zoologische Staatssammlung München, Munich.

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The nuclear loci were combined in a multilocus network using POFAD v.1.07 (Joly & Bruneau, 2006) and SplitsTree v.4.0 (Huson & Bryant, 2006), selecting uncorrected pairwise (p) distances for POFAD and using the standardized matrix for the network reconstruction.

Population genetics analyses

We used ARLEQUIN v.3.5 (Excoffier & Lischer, 2010) to calculate standard diversity indices and perform population genetics analyses. We calculated population pairwise F_{ST} to estimate population differentiation attributable to genetic structure within the three main lineages recovered by phylogenetic analyses. We used Fu's F_S and Tajima's D tests (1000 replicates) to detect signatures of population expansion. Tajima's D and Fu's F_S tests have been shown to be especially sensitive to departure from population equilibrium in the event of a population expansion or selection (Excoffier & Lischer, 2010). Given that we did not detect any signature of selection in our dataset using the McDonald–Kreitman test (McDonald & Kreitman, 1991), we here interpret the significant negative values of Tajima's D and Fu's F_S tests as resulting from population expansion.

Reassessment of type material

We assembled a full list of names applied to the *Sylvia cantillans* complex over time. For each, we studied the original description, tried to locate the associated type material and, when relevant, we consulted archival documents to find additional information that could help to clarify the origin, identification and whereabouts of types.

RESULTS

Phylogenetics

The *Cytb* and *COI* sequences showed no unusual mutation patterns, indels or stop codons, suggesting that they were of mitochondrial origin. Evidence of selection was detected in neither the mitochondrial genes (MK test: *Cytb*, $P = 1.000$ and *COI*, $P = 0.342$) nor the nuclear introns (HKA test, sum of deviations: 1.4162, d.f. = 2, $P = 0.49257$), and no recombination hotspots were identified in the introns by the GARD algorithm.

Mitochondrial DNA phylogenetic tree

We obtained 1090 bp of *Cytb* and 648 bp of *COI* genes for 97 individuals (91 fresh and six study skin specimens, including the neotype of *Sylvia subalpina* Temminck, 1820 and two syntypes of *Sylvia cantillans moltonii* Orlando, 1937). Owing to specimen age and the low quality of the DNA extracted, we recovered only partial mitochondrial sequences from the other type specimens: 232 bp (*Cytb*) for the syntype of *Sylvia leucopogon* Meyer, 1822; 242 bp (*Cytb*) for the lectotype of *Curruca albistriata* Brehm, 1855; 769 bp (*Cytb*) for the supposed lectotype of *Sylvia cantillans moltonii* Orlando, 1937; and 857 bp (*Cytb*) and 456 bp (*COI*) for the lectotype of *Sylvia subalpina inornata* Tschusi, 1906. All new sequences are deposited in Genbank, with the accession numbers MN642106–MN642549 (Supporting Information Table S2).

Mitochondrial data defined five major, well-supported clades in the maximum likelihood tree: clade 1, central-northern Italy; clade 2, the western Mediterranean islands (Corsica, Sardinia and Balearics); clade 3, North Africa, Spain, France and the westernmost end of Italy; clade 4, central-southern and southern Italy (including Sicily), with scattered occurrences in northern Italy; and clade 5, the Balkans and Greece (Figs 1, 2). Clades 1 and 2 on the one side, and clades 4 and 5 on the other, were sister groups, and these nodes received high bootstrap support, but the branching order of the three major lineages departing from the basal nodes remained unsupported in the mitochondrial tree. We observed little genetic intraclade variability (mean uncorrected p-distance 0.08–0.22 and 0.06–0.30% for *Cytb* and *COI*, respectively; Table 3) and no clear geographical structure except within clade 3, where North African haplotypes did not mix with their European counterparts (see population genetics results). Within clade 5, three individuals formed a paraphyletic lineage, basal to the other individuals.

Position of the types in phylogenetic trees

The phylogenetic reconstruction unambiguously allocated the neotype of *Sylvia subalpina* Temminck, 1820 to clade 1, the types of *Sylvia cantillans moltonii* Orlando, 1937 (syntypes and supposed lectotype) and *Sylvia subalpina inornata* Tschusi, 1906 to clade 2, the syntype of *Sylvia leucopogon* Meyer, 1822 to clade 4 and the lectotype of *Curruca albistriata* Brehm, 1855 to clade 5.

Nuclear allele networks and population genetics

For 60 individuals, selected from all clades identified above, we obtained 547 and 275 bp for the *GAPDH* and *bFib5* introns, respectively. The allele networks of both genes were strongly structured. The central part of the *GAPDH* network was formed by alleles recovered in individuals belonging to the mitochondrial clades 4 and 5 (Fig. 3B). These were almost completely separated from those obtained from individuals in clades 1 and

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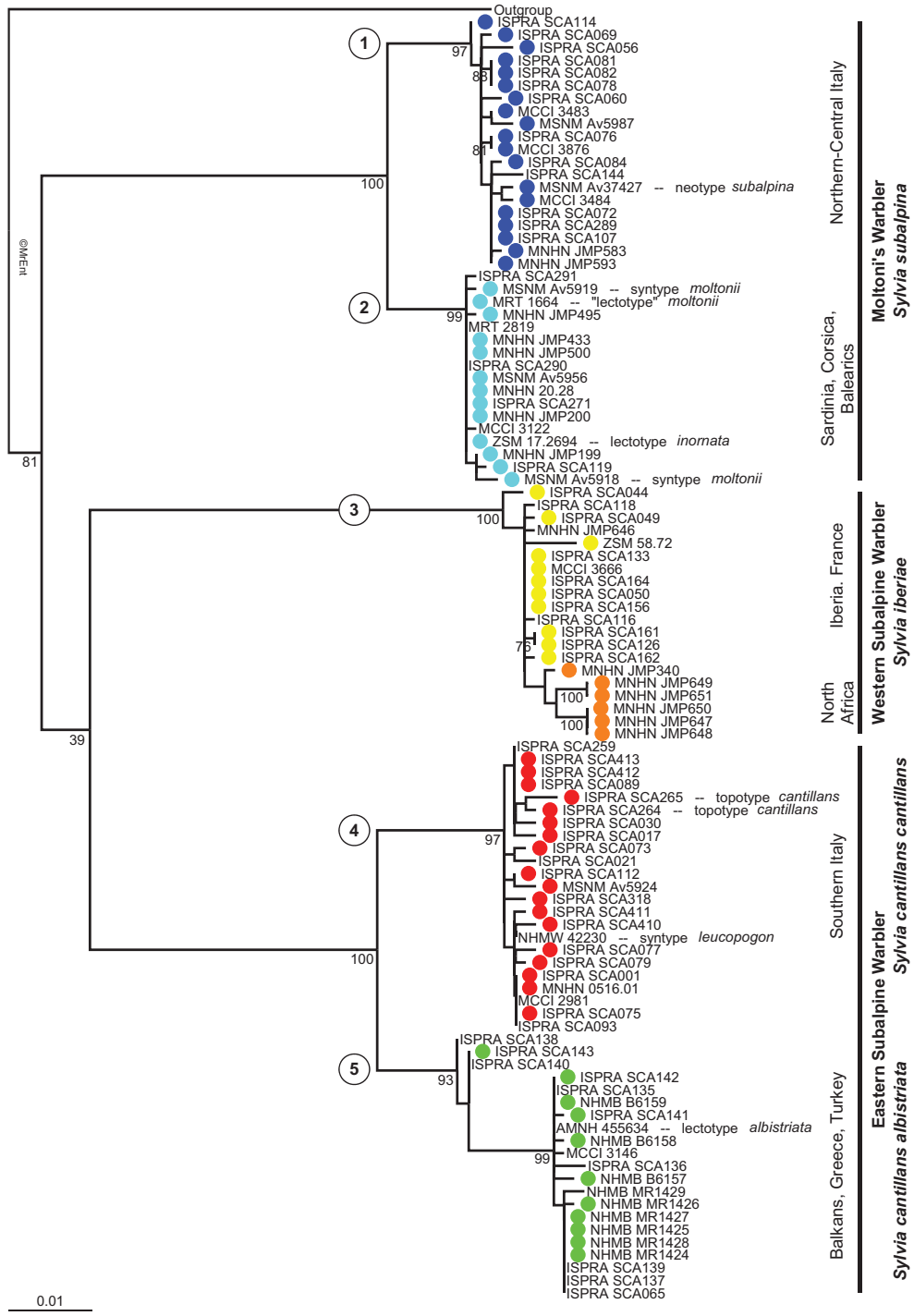

Figure 1. The maximum likelihood tree obtained from the mitochondrial dataset (*Cytb* + *COI*). The bootstrap support values are indicated at the nodes. Numbers on branches refer to the clades discussed in the text. Samples obtained from breeding specimens are highlighted with coloured dots, matching the clade coding in the map (Fig. 2). Clade distribution and proposed taxonomy are on the right. The tree has been edited in MrEnt v.2.5 (Zuccon & Zuccon, 2014).

2 on one side and from clade 3 on the other. A similar network structuring was observed for the *bFib5* gene (Fig. 3A). Except for the second most common allele recovered, which was shared by all mitochondrial clades, the individuals from clade 1 + 2, 3 and 4 + 5 occupied different portions of the network.

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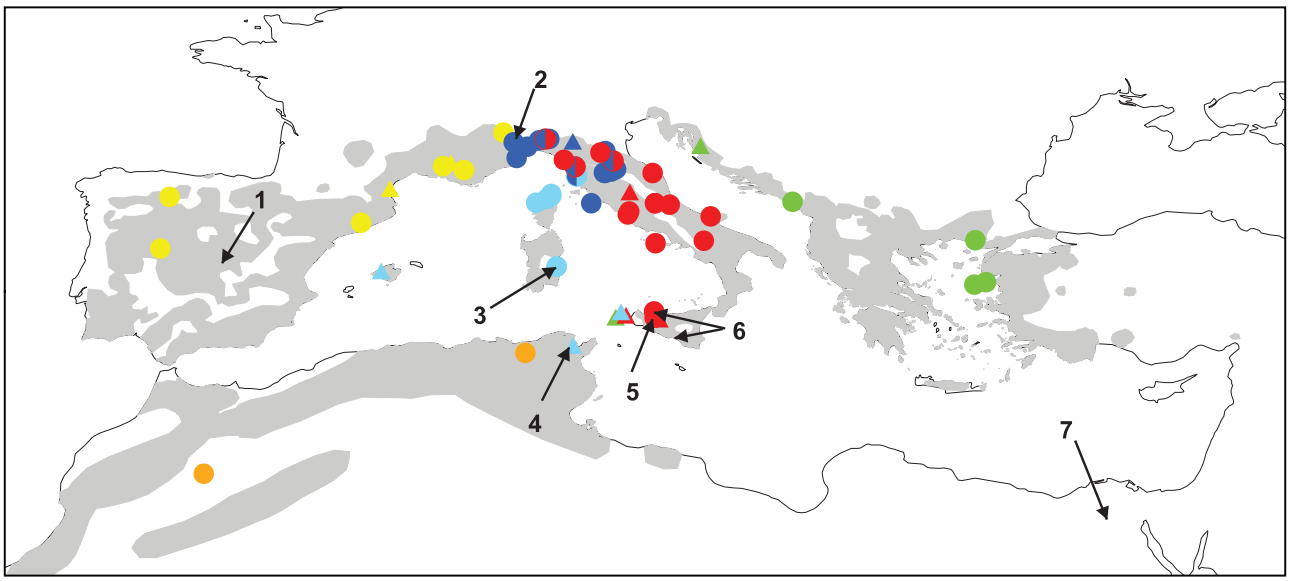

Figure 2. Breeding range of the subalpine warbler *Sylvia cantillans* complex and origin of samples used in the phylogenetic analysis. The colour code matches the clades recovered in the mitochondrial tree (dots, breeding specimens; triangles, status unknown or migrants; bicoloured dots, localities where specimens of two clades were recorded in syntopy). Collection localities of types are indicated by arrows and numbers: 1, *Sylvia inornata iberiae*; 2, *Sylvia subalpina*; 3, *Sylvia cantillans moltonii*; 4, *Sylvia subalpina inornata*; 5, *Motacilla cantillans*; 6, *Sylvia leucopogon*; 7, *Curruca albistriata* (approximate). The species range shapefile has been supplied by BirdLife International and Handbook of the Birds of the World (2018).

Table 3. Mitochondrial *p*-distances between clades (below the diagonal) and within clades (along the diagonal, in italic text) for the the cytochrome *b* and *COI* genes

Gene		Clade 1	Clade 2	Clade 3	Clade 4	Clade 5
Cytb						
	Clade 1	*0.19073*				
	Clade 2	0.96361	*0.08038*			
	Clade 3	4.05734	3.81162	*0.22211*		
	Clade 4	4.70475	4.38894	3.63053	*0.16641*	
	Clade 5	4.11009	3.79969	3.30734	1.60175	*0.2197*
COI		Clade 1	Clade 2	Clade 3	Clade 4	Clade 5
	Clade 1	*0.13239*				
	Clade 2	1.16512	*0.06173*			
	Clade 3	4.30556	4.79167	*0.29646*		
	Clade 4	3.5094	3.34877	4.36378	*0.22513*	
	Clade 5	4.28241	4.16667	5.17747	1.35066	*0.22742*

The neat geographical separation of haplotypes observed in the mitochondrial clade 1 and 2 (Fig. 1), for which the F_{ST} value was highly significant (Table 4), was not matched by the nuclear loci, which showed full admixture (Fig. 3A, B). Accordingly, the nuclear F_{ST} values between these two clades were low and not significant (Table 4). The most common alleles observed in clades 1 and 2 were equally shared by the two mitochondrial clades in both networks, with only 18–21% of alleles private to either lineage.

For alleles recovered from individuals in mitochondrial clades 4 and 5 there was some overlap, with the common alleles shared by individuals belonging to the two clades. However, a larger proportion of alleles were private to either clade (25% in *GAPDH* and 58% in *bFib5*), and F_{ST} values were

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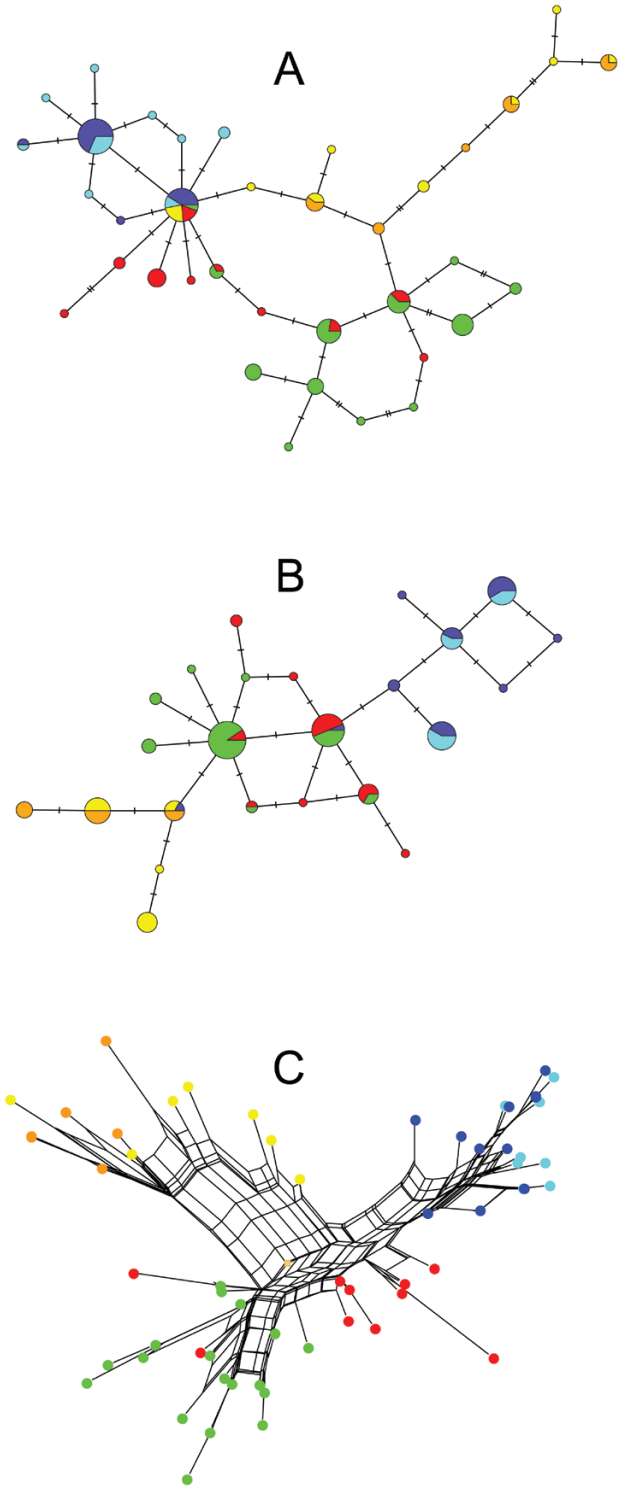

Figure 3. A, B, minimum spanning networks showing relationships among *GAPDH* (A) and *bFib5* (B) alleles for the subalpine warbler *Sylvia cantillans* complex. The colour code matches the clades recovered in the mitochondrial tree; circle size is proportional to the allele frequency. C, multilocus networks obtained using standardized genetic distances of the two nuclear loci (*GAPDH* and *bFib5*). The colour code matches the clades recovered in the mitochondrial tree.

highly significant (Table 4), again suggesting that the evolutionary trajectory of these mitochondrial groups was mostly independent from each other.

Although the genetic distance within the mitochondrial clade 3 was low (mean uncorrected *p*-distance 0.2%), we found a significant population differentiation for the mitochondrial DNA and the nuclear intron *GAPDH* between the North African and the European populations (Table 4), suggesting a modest level of gene flow between the two sides of the western Mediterranean basin. The mitochondrial genetic distance between clades 1 and 2 (~1%) was slightly lower than that measured between clades 4 and 5 (Table 3).

The multilocus network based on the two nuclear introns showed a strong structure, in part matching the mitochondrial tree (Fig. 3C). The individuals from mitochondrial clades 1 and 2 intermixed without structure in a single group apart from the other specimens. Those in clades 4 and 5 appeared to be closely related, with specimens from each clade clustering on distinct sides of the same network branch with limited admixture. Only two specimens from clade 4 appeared to be closer to those of the other clade than to their own. All F_{ST} values between clades 4 and 5 were highly significant (Table 4). Clearly distinct from all others were the specimens from clade 3.

Haplotype diversity was high for the five mitochondrial clades. Nucleotide diversity values reached moderate and similar values for all clades (Table 5).

For a reduced number of individuals (32 specimens), and focusing on clades 4 and 5, we obtained 570 bp for the *AK1* intron 5. The strong network structure confirmed the segregation of specimens from clade 3 on one side, placing those from clades 1 and 2 together without any separation, and those from clades 4 and 5 together, showing a significant allele sharing, with only 25% of private alleles (Fig. 4A). Likewise, the multilocus network based on the three alleles confirmed a three-way partition. Although the specimens in clades 4 and 5 clustered on opposite sides of the same branch, their genetic distance overall was reduced, and some individuals from both clades appeared closer to those of the opposite group (Fig. 4B).

Population expansion

Our results strongly suggested a pattern of population expansion for all mitochondrial clades but one. No signs of population expansion were detected for the North African population in clade 3 (Table 6).

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Table 4. F_{ST} values between mitochondrial clades within the tree main lineages calculated for two nuclear introns (*bFib5* and *GAPDH*) and the combined mitochondrial data set (cytochrome *b* and *COI*, 1738 bp)

Clades	*bFib5*	*GAPDH*	Mitochondrial DNA
Clades 1/2	$F_{ST} = -0.01$	$F_{ST} = -0.01$	$F_{ST} = 0.87$
(North Italy/Islands)	$P = 0.54$, NS	$P = 0.48$, NS	$P < 0.001$, S
Clade 3	$F_{ST} = 0.10$	$F_{ST} = 0.24$	$F_{ST} = 0.58$
(Europe/Maghreb)	$P = 0.10$, NS	$P < 0.001$, S	$P < 0.001$, S
Clades 4/5	$F_{ST} = 0.32$	$F_{ST} = 0.27$	$F_{ST} = 0.87$
(South Italy/Balkans)	$P < 0.001$, S	$P < 0.001$, S	$P < 0.001$, S

Abbreviations: NS, non-significant; S, significant.

Table 5. Genetic diversity indices of the combined mitochondrial dataset (1738 bp, *Cytb* + *COI*)

Index	Clade 1	Clade 2	Clade 3 (Europe)	Clade 3M (Maghreb)	Clade 4	Clade 5
Number of gene copies	20	15	15	6	23	21
Number of substitutions	18	27	15	8	20	21
Mean number of pairwise differences	2.8	1.3	2.1	4.1	3.2	3.7
Haplotype diversity	0.94	0.84	0.85	0.73	0.92	0.85
Nucleotide diversity	0.002	0.002	0.001	0.002	0.002	0.002

We acknowledge that larger sample sizes would be required to confirm this last result.

Reassessment of available names in the *Sylvia cantillans* complex

Motacilla (cantillans) *[Pallas], 1764,* Adumbratiunculae*, p. 4, in: [Vosmaer], 1764.* Beredeneerde catalogus, van eene, by uitstek fraaye en weergaalooze verzameling, zoo van inlandsche als uitheemsche vogelen, viervoetige en gekorvene dieren

Type locality: 'Uit Italie' [i.e. from Italy, no further information]; restricted to 'Sicily' by Svensson (2013a).

Type: Syntypes presumed lost; neotype NHMUK 1909.11.18.50, first summer male, collected at Ficuzza, Sicily, on 23 May 1906, by Alphonse Robert; designated by Svensson (2013a). A picture of the neotype is available in the paper by Svensson (2013a).

Notes: The species was based on two mounted syntypes, male and female, formerly in the private Vroeg collection and sold at auction on 6 October 1764 (Vosmaer, 1764; Sherborn, 1905; Rookmaaker & Pieters, 2000). According to handwritten notes on a copy of the sale catalogue (Vosmaer, 1764) kept at the Koninklijke Bibliotheek (Den Haag, The Netherlands), the lot comprising the two syntypes was bougth by Vosmaer for *f* 5.12, and it is likely that the specimens were entered into the natural history cabinet of Stadtholder William V, where Vosmaer was curator at the time. After the invasion of The Netherlands by the French revolutionary army in 1795, the Stadholder's cabinet was dispersed. The whereabouts of the royal collection is rather complex. The largest part was looted and transferred to the MNHN, where the specimens were integrated into the museum collections, further dispersed or returned to The Netherlands after 1815. A part of the collection was apparently hidden locally and later incorporated into several smaller Dutch collections, from where the specimens were further dispersed or reached the museums in Leiden, Groningen, Utrecht and Amsterdam (Boseman, 1970; Boyer, 1971; Pieters, 1980). At present, the whereabouts of the syntypes is unknown. They are not present at the MNHN nor at Naturalis Biodiversity Center, Leiden, and in all evidence they are lost.

Assuming that the syntypes originated from Italy, it is most likely that they belong to the populations from the southern part of Italy because of the brick-coloured breast ('subtus testacea') mentioned in the original description. The neotype designation (Svensson, 2013a) links this name objectively to clade 4.

Sylvia rhodogastra *Rafinesque, 1810,* Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia*, p. 7*

Type locality: Not explicitly stated, but Sicily by inference.

Type: Not explicitly stated.

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Notes: The description lacks diagnostic characters and it could apply to several *Sylvia* warblers ('Bigia scura al disopra, rosastra al disotto, rostro, ale e coda fosche, le penne esterne della coda terminate di bianco, piedi fulvini.' [Warbler dark above, pinkish below, bill, wing and tail dark, outer tail feathers ending white, feet tawny.]). It is not clear whether the name was based on specimens or observations, but the entire collection assembled by Rafinesque during his residence in Sicily is lost. In part, it was lost at sea with the shipwreck of the 'Union' during Rafinesque's voyage to the USA in 1815, in part abandoned in Palermo and subsequently dispersed (Lentini, 2012). Although Hartert & Steinbacher (1932–1938: 278) included the name *rhodogastra* in the synonymy of *Sylvia cantillans*, we concur with Salvadori (1872) that the name is not clearly identifiable, and we treat it as a *nomen dubium*. However, it remains available for nomenclatural purposes, *contra* Baccetti *et al.* (2007).

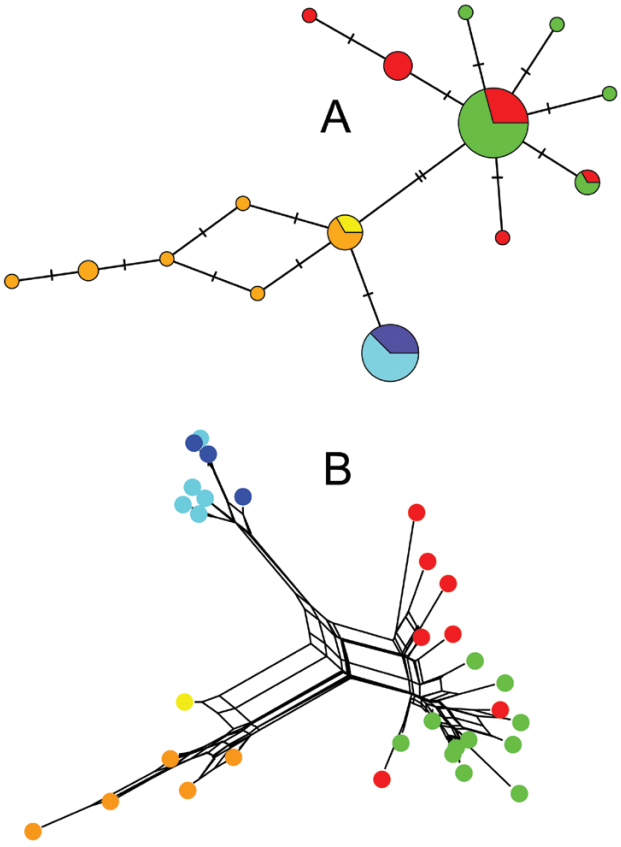

Figure 4. A, minimum spanning network showing relationships among *AK1* alleles. B, multilocus networks obtained using standardized genetic distances of the three nuclear loci (*AK1*, *GAPDH* and *bFib5*). The colour code matches the clades recovered in the mitochondrial tree.

Sylvia turdella *Rafinesque, 1810,* Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia*, p. 7*

Type locality: Not explicitly stated, but Sicily by inference.

Type: Not explicitly stated.

Notes: With an even shorter description ('Bigia rossiccia scura, biancastra al disotto, rostro e piedi foschi.' [Dark reddish warbler, whitish below, dusky bill and feet.]), this name could also apply to several *Sylvia* warblers. Although identified as a senior synonym of *Sylvia subalpina* by Trischitta (1922), we concur with Salvadori (1872) in considering *turdella* a *nomen dubium*. Also in this case, it is not clear whether the name was based on specimens or observations, and all evidence as to whether a type ever existed is now lost (Lentini, 2012). The name *turdella* remains available for nomenclatural purposes.

Sylvia subalpina *Temminck, 1820,* Planches Coloriées*, livraison I, pl. 6*

Type locality: 'Près de la ville de Turin' [i.e. near the town of Turin, north-west Italy], from the subsequent description in Temminck (1820b: I p. 214).

Type: Holotype Regio Museo di Zoologia, Turin, no. 1977, male, collected near Turin on 6 September

Table 6. Tajima's *D* and Fu's F_S statistics of population expansion obtained for each mitochondrial clade based on the combined mitochondrial dataset (cytochrome *b* and *COI*, 1738 bp)

	Clade 1	Clade 2	Clade 3 (Europe)	Clade 3M (Maghreb)	Clade 4	Clade5
Tajima's *D* test	−1.70	−2.25	−2.16	0.95	−1.53	−1.37
P-value	0.032	0.002	0.003	0.82	0.049	0.069
Fu's F_S test	−7.53	−1.95	−4.24	2.47	−8.45	−2.68
P-value	0.001	0.13	0.003	0.89	0.001	0.091

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1819; disposed of in 1827 owing to insect damage. A neotype is here designated (see below).

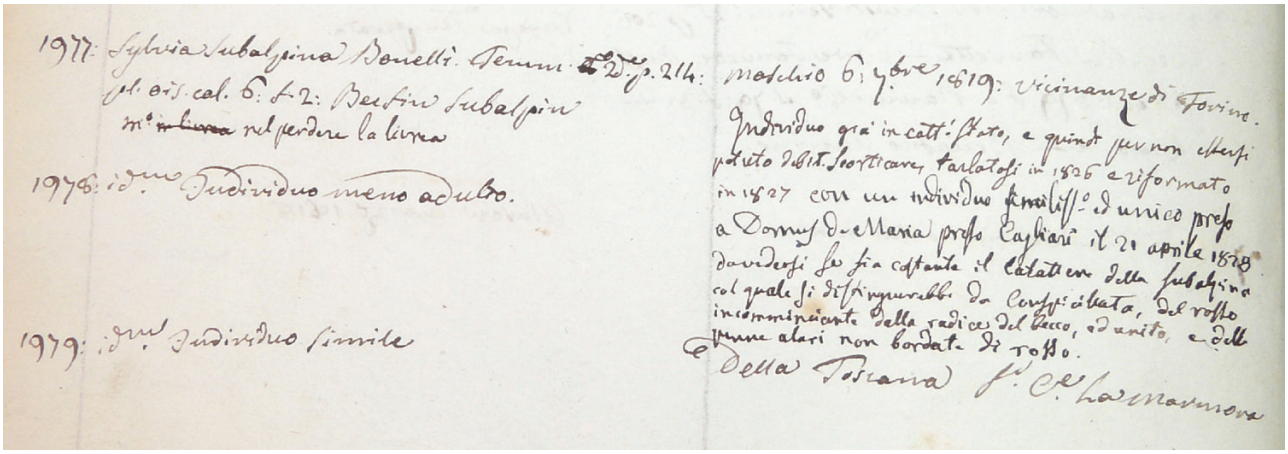
Notes: The name is invariably cited from Temminck's second edition of *Manuel d'Ornithologie* (Temminck, 1820b: I p. 214). However, the *Manuel* was published only in October 1820, as indicated on the title page and by its inclusion among the newly published books in the 21 October 1820 issue of the *Bibliographie de la France* (Anonymous, 1820). The name was first made available in the first livraison of the *Planches Coloriées* (Temminck, 1820a), published in August 1820 (for the publication date, see Dickinson, 2001; for the name spelling, see Dickinson, 2012).

Bonelli sent the holotype to Temminck, and it was clearly the model used by Prètre, the artist, for the plate ('Cette espèce du midi de l'Europe m'a été communiquée par M. Bonelli, qui me fit l'amitié de m'envoyer à Paris l'individu unique qu'il possédait, pour en publier la description dans le *Manuel d'Ornithologie*, et le figurer dans nos planches coloriées.' [This species from southern Europe has been passed on by Mr Bonelli, who did me the kindness of sending to Paris the only specimen he owned, to publish the description in the *Manuel d'Ornithologie*, and figure it in our coloured plates.]; Temminck, 1823), *contra* Baccetti *et al.* (2007).

The text accompanying the plates of the first 20 livraisons of the *Planches Coloriées* was issued well after the plates, with the text of plate 6 distributed only in June 1823 (Dickinson, 2001). This explains the apparent contradiction in the text, where Temminck indicated that a single female specimen was available for the illustration, but at the same time he also described the male plumage and refered to additional specimens obtained since.

In the first published description, Temminck (1820b) reiterated that the specimen is an adult female collected in spring ('La vieille femelle au printemps … On ne connait point encore la livrée du male; l'individu tué dans les environs de Turin est une femelle.' [The old female in spring … the male plumage is not known, the specimen killed near Turin is a female.]), but this contradicts Bonelli's entry in the museum catalogue. The '*Catalogo numerico degli Animali Vertebrati del R. Museo*' [Numerical catalogue of vertebrate animals of the Royal Museum] was started by Bonelli in 1820, and it is still present in the archive of the Biblioteca del Dipartimento di Scienze della Vita e Biologia dei Sistemi (University of Turin). In the entry for the type specimen, Bonelli indicated that it was a male collected near Turin on 6 September 1819 and subsequently disposed of owing to insect damage (Fig. 5). According to Salvadori (1916), the specimen was supplied by Alason, a regular correspondent of Bonelli.

At the meeting of the Reale Accademia delle Scienze of Turin on 27 February 1820, Bonelli read the first



1977. Sylvia Subalpina Bonelli Temm. ed. 2e p. 214
pl.ois.col. 6: f.2: Becfin Subalpin
m. ~~in livrea~~ nel perdere la livrea

[m. ~~in summer plumage~~ losing the summer plumage]

maschio 6. 7bre 1819: vicinanze di Torino.
Individuo già in catt. stato, e questo per non essersi potuto debit. scorticare, tarlatosi in 1826 e riformato in 1827 con un individuo similiss.o ed unico preso a Domus de Maria presso Cagliari il 21 aprile 1828.

[male 6 september 1819: near Turin.
Specimen already in poor conditions, and this for not having been properly skinned, moth damaged in 1826 and disposed of in 1827 with a very similar and unique specimen, taken at Domus de Maria, near Cagliari on 21 April 1828]

Figure 5. Bonelli's catalogue entry for the type specimen of *Sylvia subalpina* Temminck, 1820, in *Catalogo numerico degli Animali Vertebrati del R. Museo* [Numerical catalogue of vertebrate animals of the Royal Museum].

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part of a contribution on new bird species observed in Piedmont since 1811 that also included the description of *S. subalpina* (Archives of the Accademia delle Scienze, Turin; Gené, 1834). For unknown reasons, the rest of the manuscript was never presented at the Academy meetings, and it was never published. Although the manuscript survived after Bonelli's death in 1830 and was examined by Gené (1834), the present whereabouts are unknown, and it might have been lost (P. Passerin d'Entrèves, personal communication). It is not present in any of the libraries or archives holding Bonelli's material (Archive of the Accademia delle Scienze, Turin; Biblioteca Reale, Turin; Biblioteca Nazionale Universitaria, Turin; Biblioteca del Dipartimento di Scienze della Vita e Biologia dei Sistemi, University of Turin).

Sylv.[ia] leucopogon *'Heckeli' Schinz, 1821,* Das Thierreich I, *p. 556*

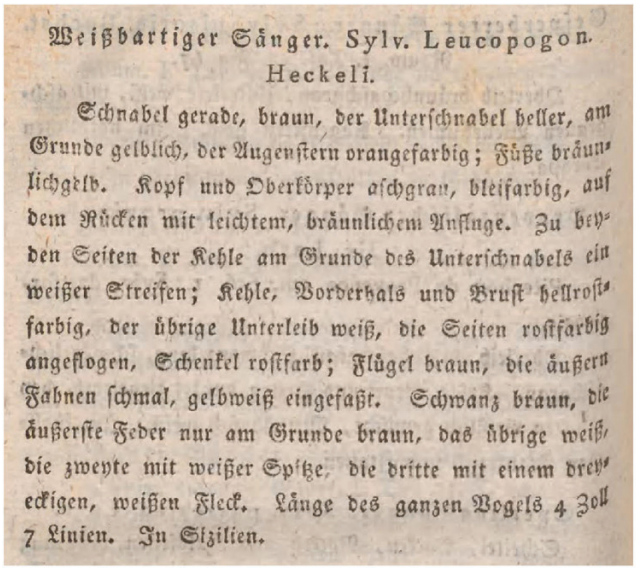
Type locality: 'Sizilien' [Sicily].

Type: Not explicitly stated, but apparently based on the same type series as *Sylvia leucopogon* Meyer, 1822 (see next section).

Notes: The name *Sylvia leucopogon* has always been attributed to Meyer (see below). Although systematically omitted from all checked synonymies, the name published by Schniz in his translation of Cuvier's *Règne Animal* is perfectly valid and pre-dates Meyer's name. Like Meyer, Schinz credited Heckel for the authorship of the new species and used the name selected by Heckel himself (it is under '*Sylvia leucopogon*' that, in 1821, Heckel's specimens were entered into the collection register of the NHMW; see next section).

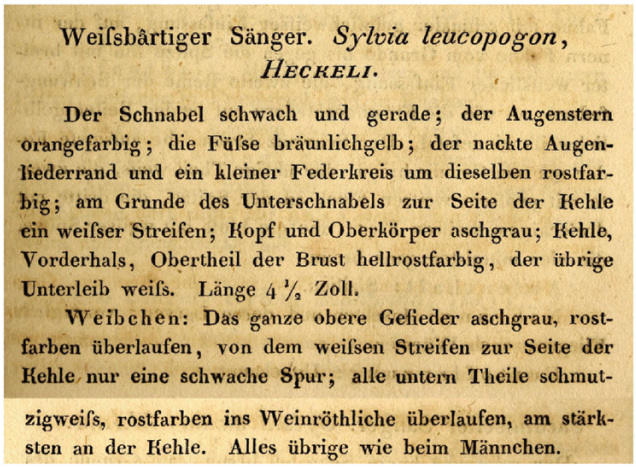
Schinz was secretary of the Naturforschenden Gesellschaft in Zurich and curator of the zoological collection. The newly established Zoologische Museum at Zurich University bought the zoological collection in 1837, together with a handwritten catalogue ('*Verzeichniss der zoologischen Sammlung*' [Register of the zoological collection]) that still exists in the museum archives. One specimen is listed in the catalogue under the name *Sylvia leucopogon*, indicating that Schinz likely received at least one specimen from Heckel. However, that specimen is no longer extant in the collection (D. Hansen, M. Schenkel, personal communication).

Schinz's description is surprisingly similar in the word choice and has almost the same sentence order as the one of Meyer (1822) (Fig. 6). Moreover,



Weißbartiger Sänger. Sylv. Leucopogon. Heckeli.

Schnabel gerade, braun, der Unterschnabel heller, am Grunde gelblich, der Augenstern orangefarbig; Füße bräunlichgelb. Kopf und Oberkörper aschgrau, bleifarbig, auf dem Rücken mit leichtem, bräunlichem Anfluge. Zu beyden Seiten der Kehle am Grunde des Unterschnabels ein weißer Streifen; Kehle, Vorderhals und Brust hellrostfarbig, der übrige Unterleib weiß, die Seiten rostfarbig angeflogen, Schenkel rostfarb; Flügel braun, die äußern Fahnen schmal, gelbweiß eingefaßt. Schwanz braun, die äußerste Feder nur am Grunde braun, das übrige weiß, die zweyte mit weißer Spitze, die dritte mit einem dreyeckigen, weißen Fleck. Länge des ganzen Vogels 4 Zoll 7 Linien. In Sizilien.



Weifsbärtiger Sänger. *Sylvia leucopogon*, Heckeli.

Der Schnabel schwach und gerade; der Augenstern orangefarbig; die Füfse bräunlichgelb; der nackte Augenliederrand und ein kleiner Federkreis um dieselben rostfarbig; am Grunde des Unterschnabels zur Seite der Kehle ein weifser Streifen; Kopf und Oberkörper aschgrau; Kehle, Vorderhals, Obertheil der Brust hellrostfarbig, der übrige Unterleib weifs. Länge 4 ½ Zoll.

Weibchen: Das ganze obere Gefieder aschgrau, rostfarben überlaufen, von dem weifsen Streifen zur Seite der Kehle nur eine schwache Spur; alle untern Theile schmutzigweifs, rostfarben ins Weinröthliche überlaufen, am stärksten an der Kehle. Alles übrige wie beim Männchen.

Schnabel gerade, braun, der Unterschnabel heller, am grunde gelblich, der Augenstern orangefarbig; Füße bräunlichgelb. Kopf und Oberkörper aschgrau, bleifarbig, auf dem Kücken mit leichtem, bräunlichen Anfluge. Zu bey den Seiten der Kehle am Grunde des Unterschnabels ein weißer Streifen; Kehle, Vorderhals und Brust hellrostfarbig, der übrige Unterleib weiß, die Seiten roßtfarbig angeflogen, Schenkel rostfarb; Flügen braun, die äußern Fahnen schmal, gelbweiß eingefaßt. Schwanz braun, die dußerste Feber nur am Grunde braun, das ubrige weiß, die zwente mit weißer Spike, die dritte mit einem brenedigen, weißen Flech. Länge des ganzen Vogels 4 Zoll 7 Linien. In Sizilien.

Der Schnabel schwach und gerade; der Augenstern orangefarbig; die Füfse bräunlichgelb; der nackte Augenliederrand und ein kleiner Federkreis um dieselben rostfarbig; am Grunde des Unterschnabels zur Seite der Kehle ein weifser Streifen; Kopf und Oberkörper aschgrau; Kehle, Vorderhals, Obertheil der Brust hellrostfarbig, der übrige Unterleib weifs. Länge 4 ½ Zoll. Weibchen: Das ganze obere Gefieder aschgrau, rostfarben überlaufen, von dem weifsen Streifen zur Seite der Kehle nur eine schwache Spur; alle untern Theile schmutzigweifs, rostfarben ins Weinröthliche überlaufen, am stärksten an der Kehle. Alles übrige wie beim Männchen.

Figure 6. Comparison between Schinz's and Meyer's descriptions of *Sylvia leucopogon* (left and right, respectively). Word groups identical in both texts are highlighted in colour. Images from the Biodiversity Heritage Library. Digitized by Naturalis Biodiversity Center (Schinz) and Smithsonian Libraries (Meyer). www.biodiversitylibrary.org

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the description mentions the eye colour, a character not observable in a skin. It is highly probable that Heckel supplied a description, perhaps the same to both Schinz and Meyer, and Schinz used it as draft to prepare his own text. In this case, in accordance with Articles 72.1.1, 72.4.1 and 72.4.1.1 (ICZN, 1999), all specimens collected by Heckel must form the type series of Schinz's name (see also next section).

Sylvia leucopogon *'Heckeli' Meyer B, 1822,* Zusätze und Berichtigungen zu Meyers und Wolfs Taschenbuch der deutschen Vögelkunde*, p. 91*

Type locality: 'Sizilien' [Sicily].

Type: Surviving syntypes NHMW 42230 (old number 1821.LXXV.13a), adult male; NHMW 43687 (old number 1821.LXXV.13), adult male; NHMW 60134 (old number 1821.LXXV.13c), adult female; NHMW 35603 (old number 1821.LXXV.13d) adult female (Supporting Information, Fig. S1). All four were obtained in 1820 by Johann Jakob Heckel in Sicily, the males in Palermo and the females in Terranova (today Gela). The specimen SMF 78882 (Italy) in the Senckenberg Naturmuseum (Frankfurt am Main) might represent a fifth surviving syntype, but its status remains questionable (Supporting Information, Fig. S2). The specimens RMNH 171709 and RMNH 171711 in the Naturalis Biodiversity Center (NBC, Leiden) bear identical Temminck-style labels, and one of the two should be another syntype (Supporting Information, Fig. S3). Other lost syntypes include one female formerly in the Naturalis Biodiversity Center (Leiden) and at least one specimen formerly in the Zoologische Museum (Zurich University).

Notes: In the original description, Meyer stated that a male collected in Sicily was sent by Heckel from Vienna to Frankfurt. This specimen is described in detail. However, the authorship is attributed to Heckel ('Heckeli'); the text also contains a shorter description with slightly different wording for the female in addition to the male, and the eye colour, a character obviously not observable in a skin, is mentioned. Also, as remarked above, the word choice and sentence order are surprisingly similar in Meyer's and Schinz's descriptions (Fig. 6). All this strongly suggests that Heckel supplied Meyer not only with one specimen, but also with a written description and that he selected the name *leucopogon* (already used in 1821 in the collection registers of the NHMW). We conclude that the description by Meyer is based on his own study of the male specimen sent to Frankfurt, combined with information supplied by Heckel, who in turn based his diagnosis on all specimens collected by him during his Italian journey in 1820. In agreement with Articles 72.1.1, 72.4.1 and 72.4.1.1, we assume that all specimens collected by Heckel form the type series of *Sylvia leucopogon* Meyer, 1822.

The precise number of specimens collected by Heckel is not known, and at present the archives in the NHMW have no notebooks or documents relative to his Italian journey. However, apparently no less than eight specimens were collected. The male specimen sent to Frankfurt could not be located unambiguously, although one male specimen from Italy (SMF 78882) in the Senckenberg Naturmuseum (Frankfurt am Main) belongs to the old collection, and it might be the specimen received by Meyer. Unfortunately, the lack of original labels or other archival evidence casts doubts on its type status (G. Mayr, personal communication). The specimen sent to Schinz in Zurich is apparently lost (see above). According to the museum register, six specimens were bought by the NHMW in October 1821 from Heckel (original numbers 1821.LXXV.13–1821.LXXV.13e). A subsequent annotation in the catalogue indicates that the male 1821.LXXV.13b and the female 1821.LXXV.13e were sent to Leiden at an unknown date, but obviously before 1824, because these specimens are those figured and described by Temminck (1824) in the *Planches Coloriées*, pl. 251 fig. 2–3 and accompanying text. The whereabouts of the female is unknown; it is no longer present in the NBC collection and is presumably lost. There are two mounted adult male specimens, RMNH 171709 and RMNH 171711, with identical Temminck-style labels, both referring to pl. 251 f. 2, and both collected in Italy. Unfortunately, the preparation style appears to be similar if not identical in both specimens, and both match well the illustration in pl. 251. It is likely that the two specimens received the same label in error, but at present it is not possible to identify the syntype unambiguously. The other four specimens are still present in the NHMW collection (Pelzeln & Lorenz, 1887). Of these, NHMW 43687 is mounted, whereas the other three are relaxed round skins, all retaining an old label. The exact collection date is not given, but Heckel returned to Vienna during the summer of 1820 to be appointed taxidermist at the NHMW in August (Svojtka *et al.*, 2012), suggesting that the specimens were obtained during spring or early summer of the same year. Although the specimens are partly discoloured, clearly suffering from exposure to light and dust when mounted, it is still possible to appreciate the brick-red throat and breast in males contrasting with the paler flanks and belly. The colour agrees well with the known plumage variability in populations breeding in central-southern Italy.

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Curruca albistriata Brehm CL, 1855, Vogelfang*, p. 229*

Type locality: 'In Egypten, wahrscheinlich auch in Südosteuropa' [in Egypt, probably also in south-eastern Europe].

Type: Lectotype AMNH 455634, adult male, collected in Egypt; lectotype designation by Hartert (1918: 33) (Supporting Information Fig. S4).

Notes: Originally in the Brehm Collection, the type was acquired by Rothschild in 1900 and entered into his collection, from where it reached the AMNH in 1932 (Hartert, 1918). The lectotype status was provisionally accepted by LeCroy (2008: 74). This specimen label bears three names: '*Curruca albigularis*' and '*albistriata*' on one label side, both crossed out, and '*Curruca leucopogon orientalis*' on the other side (Supporting Information, Fig. S4). In the original reference, there is no indication of the number of specimens involved. However, in the catalogue of the Brehm Collection published by Alfred Brehm (1866) after his father's death, a single specimen is listed under the name '*Curruca leucopogon orientalis*'. The specimen could thus have the status of holotype, making Hartert's selection (1918) irrelevant.

Curruca leucopogon major *Brehm AE, 1866,* Verzeichniss der nachgelassenen Sammlung*, p. 6*

Curruca leucopogon minor *Brehm AE, 1866,* Verzeichniss der nachgelassenen Sammlung*, p. 6*

Curruca leucopogon orientalis *Brehm AE, 1866,* Verzeichniss der nachgelassenen Sammlung*, p. 6.*

Notes: These three names are used in the published list of specimens in the Brehm Collection. All three lack any description or reference, making them *nomina nuda*, as indicated by Hartert (1910). See above for the use of the name *Curruca leucopogon orientalis*.

Sylvia subalpina inornata *Tschusi, 1906,* Ornithologische Jahrbuch 17(3–4)*, p. 141*

Type locality: 'Tunis'.

Type: Lectotype ZSM 17.2694, originally no. 636 in the second Tschusi Collection, adult male collected at Tunis, in May 1906; lectotype designation by Tschusi (1906b: 108) (Supporting Information, Fig. S5).

Notes: The use of the plural ('Grasmücken' [warblers]) and a wing length range are clear indications that the new taxon was based on more than one specimen (Tschusi, 1906a). The type series was originally in the second Tschusi Collection. Despite its inclusion in the published list of Tschusi types deposited in the NHMW (Tschusi, 1906b), the type series, together with other 1600 Tschusi specimens, passed into Alfred Laubmann's private collection at an unknown time, but probably around 1912. Eventually, the Laubmann Collection was, in turn, incorporated into the Zoologische Staatssammlung München in 1916 (Gengler, 1924; Hellmayr, 1928).

The ZSM collection holds four specimens with original Tschusi labels. The specimen with number no. 694 (Tunis, May 1911, now ZSM 17.2695) must be excluded from the type series because of a collection date later than the original description. Of the remaining three, the adult male no. 636 (Tunis, May 1906, now ZSM 17.2694) is the lectotype after Tschusi's designation (1906) (Article 74.5), and the adult female no. 637 (Tunis, May 1906, now ZSM 17.2696) is, from all evidence, a paralectotype. The last specimen, adult male no. 1052 (Tunis, May 1906, now ZSM 17.2697) most probably does not belong to the type series. Although its collection locality and date are compatible with the original description, the label bears a much higher registration number. The Tschusi catalogue of his second collection has not been located, but it is likely that it passed first into Laubmann's possession together with the bird collection and then transferred to the ZSM, whose archives were lost during World War II (Fittkau, 1992). However, an examination of other Tschusi catalogues in Vienna, and in particular the collection dates and registration order, strongly suggests that he registered the new specimens as they arrived, indicating that specimen no. 1052 was probably received much later than the others, and thus should not be included in the original type series. This is further supported when considering that all specimens were supplied by Marius Blanc, a French dealer of natural history specimens based in Tunis (Mars, 1969). A perusal of Tschusi catalogues in NHMW indicates that Blanc supplied specimens from Tunisia from at least 1895 up to 1915, and that they could be entered into the catalogues at dates considerably later than the collection date.

Sylvia cantillans moltonii *Orlando, 1937,* Rivista Italiana di Ornitologia (n.s.) 7*, p. 213*

Type locality: 'Nidifica in Sardegna (e Corsica?)' [nesting in Sardinia (and Corsica?)].

Type: Syntypes MSNM Av5916 (adult male, collected at Tortolì, Sardinia, on 10 April 1931), MSNM Av5917 (adult male, collected at Tortolì, Sardinia, on 10 April 1931), MSNM Av5918 (adult male, collected at Lanusei, Sardinia, on 24 June 1930), MSNM Av5919 (adult male, collected at Lanusei, Sardinia, on 7 June

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1930), MSNM Av5943 (collected at Cagliari, Sardinia, on 16 May 1924), MSNM Av5952 (adult male, collected at Lanusei, Sardinia, on 10 August 1914, old number 23031), MSNM Av5954 (adult male, collected at Arbatax, Sardinia, on 7 July 1915, old number 23030), MSNM Av5960 (adult female, collected at Lanusei, Sardinia, on 29 July 1927), MSNM Av5962 (adult female, collected at Ilbono, Sardinia, on 15 April 1928), MSNM Av5963 (adult male, collected at Tortolì, Sardinia, no date), MSNM Av5966 (collected at Quartu S. Elena, Sardinia, on 25 October 1925), MSNM Av5967 (collected at Quartu S. Elena, Sardinia, on 23 September 1925) (Supporting Information, Fig. S6).

Notes: In the short, original description, no information was provided concerning the number of specimens examined (Orlando, 1937). Subsequently, in a longer article Orlando (1939) stated that he examined 16 specimens in his collection and another eight in the MSNM, all considered to represent the new taxon. He designed specimen no. 1664 (now MRT 1664) as type (i.e. a lectotype according to Article 74.5), and the other 15 specimens in his collection (now MRT 1665–1679) as paratypes (i.e. paralectotypes). The type status of these specimens has been accepted by Arnone & Orlando (1990). However, after examining the correspondence between Orlando and Moltoni (then bird curator at the MSNM), which is kept in Moltoni's archive in the MSNM library, the situation appears much more complex. The original description was published in the July issue of *Rivista Italiana di Ornitologia*, and the short note is dated April 1937. A date no later than April is compatible with the time required for typesetting and printing the July issue and further confirmed by a letter from Orlando to Moltoni (9 March 1937: ' … al mio desiderio di pubblicare un lavoro che ha carattere di urgenza. Soltan- [sic] chiarisco che intendevo alludere al 3° fascicolo del corrente anno che, a quanto ho creduto di comprendere nella Sua precedente, sarà pubblicato fra due mesi e prima della sua assenza' [… my wish to publish a work with urgency. I would only clarify that I was suggesting the 3rd issue of the current year that, as I understood from your previous [letter], it will be published in two months and before your departure]).

In the same letter, Orlando affirms, 'Io ne ho esaminato della Sardegna, ma in piccolissimo numero … Però non ne ho nessuna di questa provenienza nella mia raccolta ed ho già scritto per procurarmene.' [I have examined some from Sardinia, but in a small number … However, I have none of this provenance in my collection and I already wrote to obtain some.]. Indeed, the 16 specimens in the Orlando collection were supplied by Amalia Mameli Meloni, a dealer in natural history specimens based in Lanusei (Sardinia). The collection dates span from 18 April to 22 May 1937. When taking into account the time needed to prepare and ship the specimens, none of these could have been available to Orlando at the time of writing his 1937 note, and we conclude that none of them has a type status.

According to other letters, on 26 February 1937 Moltoni sent 19 specimens from the MSNM to Orlando, who acknowledged receipt on 3 March. Among these specimens, 12 are from Sardinia, and they were returned to Moltoni on 3 January 1938 (the other seven specimens are from Lybia, Apulia, Dalmatia and Sahara). We verified in the MSNM catalogues that the museum indeed acquired 12 specimens from Sardinia before 1937, and all of them are still extant. All these must be considered syntypes. We assume that the reference to eight instead of 12 specimens from MSNM by Orlando (1939) is in error.

Both in letters and in the 1939 publication, Orlando refers several times to specimens examined in different museums and collections. However, the wording is usually ambiguous, and it is not clear if, in addition to those from MSNM, Orlando ever examined any other Sardinian specimens. The two other collections mentioned are the 'R. Museo' (i.e. Museo di Zoologia, University of Palermo) and the Whitaker Collection (at that time in Palermo and now split between the National Museums Northern Ireland and the National Museums Scotland). However, none of these museums has any specimens from Sardinia that could be included in the type series (Lo Valvo & Massa, 2000; B. McGowen, A. Ross, Z. Timmons and D. Tosh, personal communications).

Sylvia inornata iberiae *Svensson, 2013,* Bulletin of the British Ornithologists' Club 113*, p. 244*

Type locality: 'El Pardo, Madrid, Spain'.

Type: Holotype NHMUK 1934.1.1.249, adult male, collected at El Pardo, Madrid, Spain, on 24 May 1931. A picture of the holotype is available in the paper by Svensson (2013a).

Notes: This new taxon was proposed to differentiate the populations from Spain, southern France and north-west Italy from those in North Africa. Although we did not genotype the holotype, a breeding individual, our specimens from mainland Spain were all collected during the breeding season and all belong to clade 3, making the name *iberiae* unquestionably available for this clade.

DISCUSSION

SYSTEMATICS AND PHYLOGEOGRAPHY

The subalpine warbler complex represents a nice example of ongoing divergence among geographically

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structured populations showing varying degrees of divergence, suggesting that the lineages in the complex have reached different stages in the speciation process.

A geographically more complete sampling confirms the strong structuring of the *S. cantillans* complex reported in a previous phylogeographical study (Brambilla *et al.*, 2008b) and sheds further light on the relationships between the five clades identified in the complex. In short, our work based on combined mitochondrial and nuclear evidence supports three species in the *S. cantillans* complex. This treatment was already hypothesized by Brambilla (2013) and suggested by Svensson (2013a, b), but our arrangement includes important differences at the subspecific level and in the nomenclatural rearrangement, following a critical evaluation of available types.

Clade 3: western subalpine warbler

At the high end of genetic divergence, clade 3 is isolated from all other lineages in both mitochondrial and nuclear markers. Mitochondrial distances from the other clades are high (3.3–4.1 and 4.4–5.2% for *Cytb* and *COI* genes, respectively) and comparable to those observed between full species (Helbig *et al.*, 1995; Hebert *et al.*, 2004; Pons *et al.*, 2016). The substantial lack of shared nuclear alleles is evident in the single intron and in the multilocus networks, and the inferred lack of gene flow with the other lineages supports the recognition of clade 3 as a full species-level group.

Genetic analyses of our small North African sample size (one breeding bird from Tunisia and five breeding birds from Morocco) suggest that the populations from the entire Maghreb belong to the same lineage, which is closely related to western European populations from Portugal, Spain, France and north-west Italy. Gene flow between European and North African populations probably followed a western route across the Strait of Gibraltar rather than the Strait of Sicily. This interesting result would need to be confirmed using more individuals. Many species belonging to diverse zoological groups occur on both sides of the Strait of Gibraltar, whereas Italian–North African endemics shared across the Strait of Sicily are much rarer (Husemann *et al.*, 2014). Considering birds, the biogeographical importance of the Strait of Gibraltar as a link between Europe and North Africa has been pointed out by several studies dealing with different species [e.g. *Galerida cristata* (Linnaeus, 1758), Guillaumet *et al.*, 2008; *Muscicapa striata* (Pallas, 1764), Pons *et al.*, 2016]. Unlike the European population, we did not detect any sign of population expansion for the North African population. Such a difference suggests that these populations do not share the same demographic history. From a biogeographical perspective, it would be interesting to test whether the Maghreb could have played a role as a glacial refugium for the western subalpine warbler.

Clades 1 and 2: Moltoni's warbler

At the opposite end, only a shallow distance separates clades 1 and 2 (1.0 and 1.2% in *Cytb* and *COI*, respectively). The two mitochondrial lineages are geographically well separated, and only a few breeding birds observed along the Tuscany coast proved to belong to the island clade 2 (Brambilla *et al.*, 2008c). Nonetheless, the two clades began to diverge recently and still constitute a single nuclear genetic pool, as indicated by the lack of structure in the single intron and in the multilocus networks. Jointly, clades 1 and 2 are here recognized as a second species-level group.

Clades 1 and 2 are well differentiated from the rest of the species complex not only genetically, but also according to phenotypic traits. These populations have a distinct contact call and song, different moult strategy and later spring migration time, and males can be separated by their pinkish ventral coloration (Gargallo, 1994; Shirihai *et al.*, 2001; Svensson, 2013a, b). In addition, they occur sympatrically with clade 4 in central-northern Italy and show a different reaction to conspecific and heterospecific songs (Brambilla *et al.*, 2008b, c).

The neat mitochondrial separation between island and mainland populations might represent different evolutionary lineages, although no morphological differences and no nuclear genetic differences are known at present between the two groups. However, alternative hypotheses could not be excluded as explanation for this mitochondrial pattern (reviewed by Toews & Brelsford, 2012). The same phylogeographical structure could be a simple by-product of a sex-specific dispersal strategy, with highly philopatric females and nuclear gene flow assured by more dispersive males (even if, in general, the opposite pattern is more common in passerine birds; Greenwood, 1982). Alternatively, retention of nuclear ancestral polymorphism owing to a recent divergence event (Zink & Barrowclough, 2008) might also explain the mitonuclear discrepancy. Until more evidence becomes available, we favour a conservative approach and suggest that these populations should be treated as a single, monotypic species.

Clades 4 and 5: eastern subalpine warbler

Clades 4 and 5, representing eastern populations (from central Italy eastwards), display an intermediate case of population divergence. Mitochondrial clades 4 and 5 are clearly separate, with divergence values slightly higher (1.4 and 1.6% in *Cytb* and *COI*, respectively) than those obtained for insular vs. mainland Moltoni's

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warblers. Although some intron alleles are shared by the two mitochondrial lineages, a significant proportion of private alleles suggests a reduced gene flow between the two groups and a well-advanced lineage sorting. The multilocus networks clearly show that the two clades are closely related, but most individuals segregate on different sides of the network branch. Although we recognize that the two populations are close to the speciation threshold, weighting the molecular data, the difficult diagnosability of these two groups (Brambilla *et al.*, 2010) and the fact that the two interbreed where they meet at different sites of the Adriatic region (Brambilla *et al.*, 2008b; our unpublished data), we prefer a more conservative approach, and we assign clades 4 and 5 to a polytypic species-level taxon. Further molecular and bioacoustic data might shift the balance to a different taxonomy (e.g. they could be semispecies *sensu* Helbig *et al.*, 2002).

We remark also that in clade 5 three specimens collected in Lesvos (Greece) are basal and distinct from the rest of the clade, including six other individuals obtained on the same island, at the same time. Owing to the small sample, we are not able to discuss this pattern further, but we are confident that it is not an artefact attributable to the inclusion of nuclear pseudogenes, because both mitochondrial genes support the same signal, the sequences from these specimens align perfectly with the rest of the dataset, and all mutations are synonymous substitutions, mostly restricted to the third codon position. To determine whether these three specimens are indicative of a geographical structuring in the easternmost populations of the clade or the result of the co-occurence of distinct mitochondrial haplogroups requires more inclusive sampling.

Taxonomic and nomenclatural issues

The reappraisal of all original descriptions of names applied to the *Sylvia cantillans* complex, the study and genotyping of surviving type specimens and the use of archival documents provided a sound framework to revise the nomenclature of this complex.

From the original catalogue written by Bonelli, we have been able to ascertain that the type specimen of *Sylvia subalpina* Temminck, 1820 was collected near Turin on 6 September 1819 and disposed of in 1827 owing to insect damage. However, although Bonelli affirmed that the specimen was a male, Temminck (1820a, b) stated that it was a female in spring plumage.

The collection date indicates that the holotype was collected during the migratory period, and Turin lies between the ranges of Moltoni's and western subalpine warblers. In addition, the eastern subalpine warbler also occurs in Piedmont as a vagrant (Pavia & Boano, 2009). All these factors complicate the identification of the lost type.

We assume that Bonelli, a skilled ornithologist who examined the specimen in the flesh, was able to identify the sex correctly as male. The colour description and the plate published by Temminck (1820a,b) are more congruent with the male plumage, in particular the dorsal ('Sommet de la tête, joues, nuque, dos et scapulaires d'un joli cendré pur' [crown, cheeks, neck, back and scapulars of a pure ash colour]) and ventral colour ('gorge, devant du cou, poitrine, flancs et abdomen d'une belle couleur vineuse' [throat, front of the neck, chest, flanks and abdomen of a nice vinaceous colour]), whereas they would be too saturated for a female.

The vinaceous colour suggests that the lost type was more likely to have been a Moltoni's warbler (clades 1 and 2), excluding males of both eastern and western subalpine warblers, where the ventral side is invariably described as red brick (Svensson, 2013a, b). However, the molecular results indicate that Moltoni's warbler comprises two mitochondrial lineages for which no morphological differences have been identified, and Brambilla *et al.* (2012) demonstrated that the subalpine warblers *s.l.* have a complex migration pattern, with different lineages migrating together and co-occurring at the same stop-over site.

In agreement with Article 75, in order to stabilize the nomenclature and objectively link the name *subalpina* to the mainland populations of Moltoni's warbler, we here designate the specimen MSNM Av37427 as the neotype of *Sylvia subalpina* Temminck, 1820 (zoobank urn:lsid:zoobank.org:pub:8C077808-E903-4E40-82A1-E365F6630D30). It is a road-killed adult male found by G.B. and Gary Voelker on 9 June 2018 at Pocapaglia (44°43′N, 7°53′E), in the central hills of Piedmont, 40 km south-east of Turin. It has been prepared as a study skin by G.B. (field number GB 1365; Fig. 7). This bird was certainly breeding, considering the date and the gonad development (testis 6.5 mm × 5 mm), and the species is a rather common breeding bird in the area (Mingozzi *et al.*, 1988).

All conditions mandated by Article 75.3 are here met, in particular: the mitochondrial sequences obtained from the neotype (Genbank accession numbers MN642448 and MN642344) confirm that it belongs to clade 1, and the uniform vinaceous shade extending from throat to flanks is diagnostic of Moltoni's warbler, excluding the other species in the complex (Article 75.3.2); the neotype plumage colours match the plate published by Temminck (1820b) (Article 75.3.5); it comes from the Turin area (Article 75.3.6); it has been deposited in the Museo Civico di Storia Naturale, Milan, with the number MSNM Av37427, and a tissue sample preserved in

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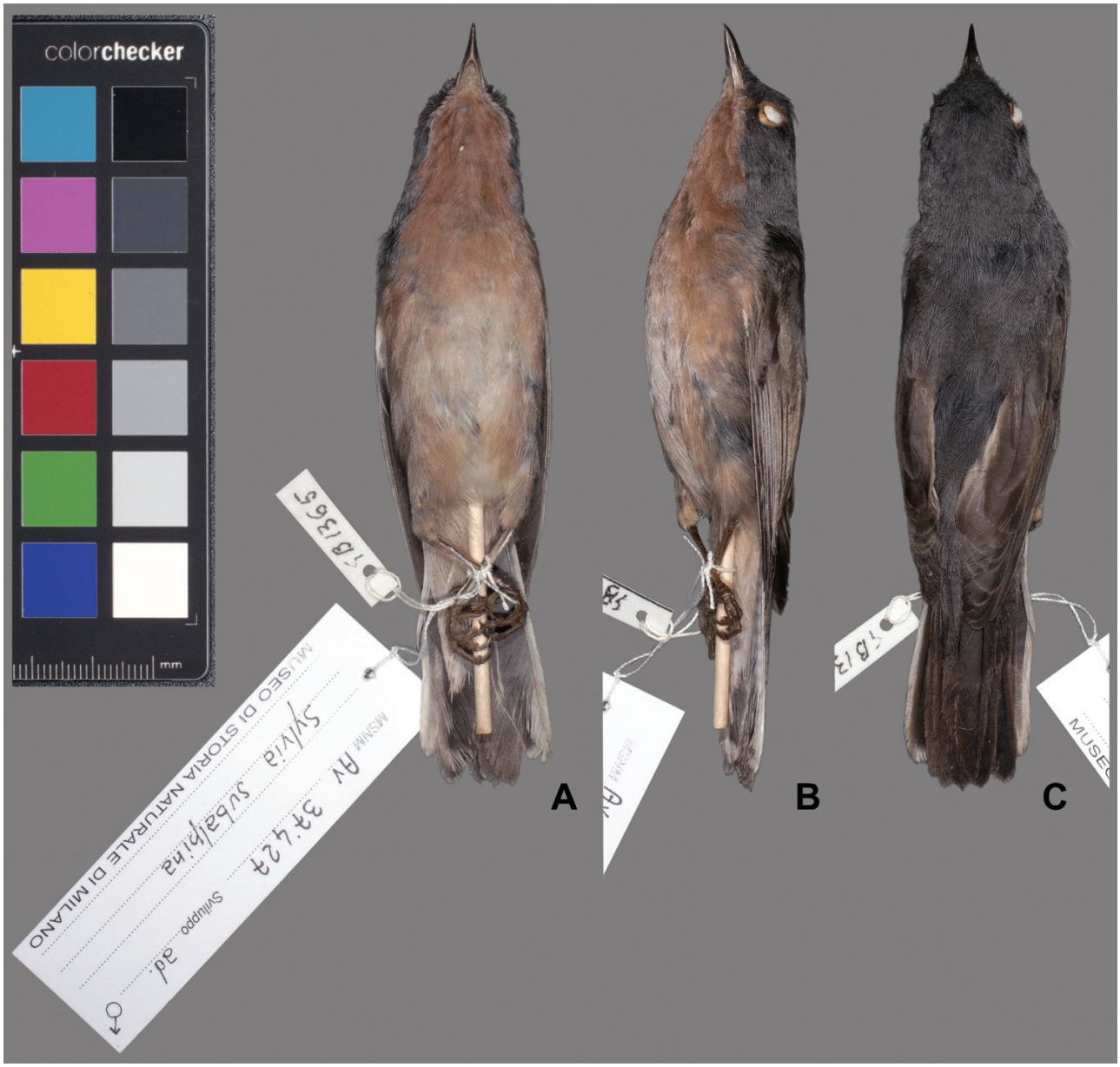

Figure 7. Neotype of *Sylvia subalpina* Temminck, 1820, MSNM Av37427, ventral (A), lateral (B) and dorsal (C) views. The images were calibrated with the Xrite ColorChecker.

ethanol is kept in the ornithological collection of the Museo Civico di Storia Naturale, Carmagnola, with number MCCI 5150 (Article 75.3.7).

Description of the neotype (capitalized colour names follow Ridgway, 1912): it has a Medium Dark Plumbeous front, Dark Greysh Brown head, nape and mantle, narrow Russet-Vinaceous orbital ring, White submoustachial stripe narrow, throat and breast between Vinaceous and Avellaneous, and this colour extends to lower flanks, fading in the central whitish belly. The wings are Olive Brown fringed Buffy Brown, the rectrices being Dusky Brown with large white portions on the outermost feather and a whitish rounded spot on the tip of the inner web of the penultimate feather. The pointed bill has a paler base. Legs pale. Wing length (max. chord) 63 mm, tail length 54 mm, tarsus 19 mm, weight 9.1 g.

As expected, the phylogenetic analysis confirmed that the name *Sylvia cantillans moltonii* Orlando, 1937 belongs to the insular populations of Moltoni's warbler, with both genotyped syntypes falling in clade 2, together with the other specimens from Sardinia and Corsica. However, we demonstrated that

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the name itself was established on a totally different group of syntypes (12 specimens in MSNM) and that none of those indicated by Orlando (1939) could claim a type status.

Instead, the reidentification of *Sylvia cantillans inornata* Tschusi, 1906, is a totally unexpected result, with deep nomenclatural implications. Although accepted as valid and consistently applied to North African populations (Table 1), the name *inornata* also applies to clade 2, as indicated by the lectotype haplotype.

The ventral colour of specimens from North African populations is invariably described as red, orange or brick, at least since Hartert (1910: 'Kehle und Korperseiten mehr rotbraun, fast zimtrot' [throat and body sides more reddish brown, almost cinnamon red]) and Vaurie (1959: 'Male somewhat more brick red below, less pinkish'). However, in the original description, Tschusi (1906a) stated clearly, 'Kinn und Kehle sehr schwach weinrötlich' [Chin and throat pale wine red], a colour description that matches well with the 'belle couleur vineuse' [nice vinaceous colour] in Temminck's description of *subalpina*. When one of us (D.Z.) examined the type series of *inornata* at the ZSM, he was immediately surprised by the ventral colour. Although no other specimens from North Africa were available for direct comparison in the ZSM, the genotyping of the *inornata* lectotype confirmed that it did not belong to the North African populations, as traditionally assumed, but matched phenotypically similar birds in clade 2. The type series was collected in May (no day specified), and migrating Moltoni's warblers can be found throughout May (our data). It is thus clear that those collected in Tunis were migrants and not breeding locally, that the types have never been re-examined since and that the name *inornata* was applied relying merely on the collection locality.

With the recognition of the Moltoni's warbler as a monotypic species, the names *Sylvia subalpina inornata* Tschusi, 1906 and *Sylvia cantillans moltonii* Orlando, 1937 are here treated as junior synonyms of *Sylvia subalpina* Temminck, 1820. If island and mainland populations should be deemed to represent distinct taxonomic units, the name *inornata* will take precedence for the island populations.

However, we remark here that despite its continuous use for the North African populations, Tschusi's name is, in fact, preoccupied by a much older senior homonym, *Sylvia inornata* Latham, 1801 (Latham, 1801a: I p. liv). This is based on Latham's 'Terrene Warbler' (Latham, 1801b: p. 248 no. 30), in turn based on the Watling drawing no. 161 (Mathews & Iredale, 1923), an unidentified meliphagid, possibly referable to an Australian *Melithreptes* honeyeater (Gray, 1843). Latham's name has been used only occasionally as a valid name by a few early 19th century authors (e.g. Stephens, 1817: 696; Vieillot in Deterville, 1817: 600; Vieillot, 1821: 409; Drapiez in Bory de Saint-Vincent, 1822: 293) and subsequently forgotten. In contrast, the continuous use of *Sylvia subalpina inornata* Tschusi, 1906 meets the requirements of Articles 23.9.1.1 and 23.9.1.2 of the ICZN (1999), i.e. used as a valid name in ≥ 25 works by at least ten authors in the last 50 years over a span of ≥ 10 years. Under these circumstances, if a distinct subspecific rank is granted to the island populations of Moltoni's warbler, Tschusi's name should be declared a *nomen protectum*, taking precedence over *Sylvia inornata* Latham, 1801, a *nomen oblitum*.

The species corresponding to clade 3, the western subalpine warbler, has a continuous distribution around the western side of the Mediterranean basin, from Tunisia to Morocco, Spain to the westernmost end of Italy. Although the intraclade genetic distance is low (0.2%), our population genetics results suggest that a significant population structure separates African vs. European specimens. With the transfer of the name *inornata* to a different clade, *Sylvia inornata iberiae* Svensson, 2013 remains the only available name. Although the *iberiae* holotype has not been genotyped, its breeding status is indicated by a remark on the label ('Breeding by the river'), and all our Spanish specimens fall into clade 3 in the phylogeographical analysis. This name was introduced to differentiate the Iberian–French population in comparison to North African birds (Svensson, 2013a).

The description of *Sylvia inornata* iberiae Svensson, 2013 complies with the Code, and this name is nomenclaturally available. It thus becomes the valid name for clade 3 as a whole. However, owing to lack of morphological divergence and low genetic distinctiveness, we express doubts that North African and European populations should be recognized as distinct taxonomic units at the subspecies level and, at present, a new name seems unwarranted for the North African birds. The purported differences between North African and European specimens indicated by Svensson (2013a) appear to be extremely weak: (1) the main stated difference is the colour ('being less yellow-tinged above and below, which difference is particularly obvious in series'), but no quantitative analysis is presented, and a colour gradient has been suggested, with southern Spanish individuals becoming increasingly similar to African breeders (Shirihai *et al.*, 2001); (2) morphometric differences are vaguely stated without a proper statistical comparison and are apparently minute ('*iberiae* is on average slightly smaller, although differences are miniscule and unhelpful for identification'); and (3) the new taxon is based on the study of 58 and 57 specimens of *iberiae* and *inornata sensu* Svensson (2013a), respectively (see also Svensson, 2013b: table 1). However, the majority of these were collected during the migration period (Table 7). The species group has a complex migration

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Table 7. Number of specimens examined by Svensson (2013a, b) from North Africa (‘*S. i. inornata*’ *sensu* Svensson, 2013a) vs. Iberia–France (‘*S. i. iberiae*’ *sensu* Svensson, 2013a) and number of specimens collected outside the migration period (16 May–31 July)

Museum	‘*S. i. inornata*’	‘*S. i. iberiae*’	Breeding ‘*S. i. inornata*’	Breeding ‘*S. i. iberiae*’
NHMUK	19	31	5 ♂, 2 ♀*	6 ♂
AMNH	19	6	1 ♂, 2 ♀	–
MNHN	12	10	–	1 ♂
NRM	3	1	1 ♂	–
RMNH	1	7	–	1 ♂
ZFMK	2	–	?	–
ZMUC	1	1	?	?
Total	57	56	11 (7 ♂, 4 ♀)	8 (8 ♂)

Acronomys: AMNH, American Museum of Natural History, New York, NY, USA; MNHN, Muséum National d’Histoire Naturelle, Paris, France; NHMUK, The Natural History Museum, Tring, UK; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; RMNH, Naturalis Biodiversity Center, Leiden, The Netherlands; ZFMK, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMUC, Zoological Museum, University of Copenhagen, Copenhagen, Denmark.
*Includes a female collected on 10 May with large ovary drawing on the label.

pattern, with birds belonging to different clades migrating together and being captured at the same sites (Brambilla *et al.*, 2012). In addition, the phenotypic identification of individual specimens in the complex remains challenging, with 9% of genotyped birds misidentified and 19% considered as intermediate/doubtful when ringed individuals are examined in hand (Brambilla *et al.*, 2010). The difficulties in separating individual specimens between the two subspecies is acknowledged by Svensson (2013a) himself (‘at least 75% differ diagnosably, probably many more’). It seems to us that the only specimens available for a reliable comparison among those listed in table 1 of Svensson (2013b) should be those collected during the breeding period and well outside the migration. When specimens collected before 15 May and after 31 July are excluded, only 11 North African and eight European breeding birds remain, representing a much smaller sample than stated by Svensson (2013b) (Table 7). Attributing any other individual to the North African or the European breeding population seems to us either circular reasoning, if based on the supposed colour differences between the two groups, or totally unwarranted, if based on capture locality alone. For these reasons, until more robust analyses on breeding birds only are provided, we reject the recognition of any subspecies in clade 3, which will thus become a monotypic species named *Sylvia iberiae*.

Although the neotype of *Motacilla cantillans* Pallas, 1764 has not been genotyped, two breeding individuals obtained at the restricted type locality (Ficuzza, Sicily) are included in our phylogenetic reconstruction, and all evidence indicates that the name *cantillans* applies unquestionably to clade 4. We refer to the same clade the junior synonyms *Sylvia leucopogon* Schinz, 1821 and *Sylvia leucopogon* Meyer, 1822. By re-examining the original descriptions and from archival records, we conclude that the two names are not only absolute homonyms, but also absolute synonyms, both being based on the same series of specimens from Sicily obtained by Heckel in 1820.

The lectotype of *Curruca albistriata* Brehm, 1855 was collected in Egypt, and it must have been a migrant, because the species does not breed there. In plumage, it agrees well with the birds from the Balkans. The genotyping confirms its attribution to clade 5.

The clades 4 and 5 clearly represent an intermediate stage in the speciation process, forming distinct mitochondrial lineages, with some nuclear gene flow as indicated by the nuclear networks. Morphologically, most individuals in the two groups are fairly well identifiable, differing in size and plumage colour, especially in males, which are typically darker and with a more contrasting white belly in eastern birds (*albistriata*) than in Italian breeders (*cantillans*) (Shirihai *et al.*, 2001). However, a few individuals show more nuanced plumage coloration and can be misidentified even when examined in hand (Brambilla *et al.*, 2010), and nearly all measurements show a certain degree of overlap. Although differences exist in song and, especially, in calls, no quantitative comparisons or playback experiments have been carried out to test whether any acoustic isolation might exist. We consider that the evidence available at present is conflicting, and we recommend following a conservative approach, treating the two clades as a single species, *Sylvia cantillans*, with the subspecies *S. c. cantillans* and *S. c. albistriata*, but we recognize that according to other approaches or criteria for species delimitation, the arrangement of these two taxa might be different.

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CONCLUSION

The subalpine warbler complex illustrates how divergence took place even over relatively limited geographical extents, further confirming the importance of the Mediterranean basin as a biodiversity hotspot in Europe (Marchese, 2015) and its role in shaping the European avifauna (e.g. Perktaş *et al.*, 2019). The pattern of divergence and geographical structuring in the *Sylvia cantillans* complex shows some remarkable similarities with those reported for other complexes of avian species in the Mediterranean region and, in particular, the role of glacial refugia played by the western Mediterranean islands (Corsica, Sardinia and the Balearics) [e.g. *Certhia familiaris* Linnaeus, 1758, Pons *et al.*, 2015; *Muscicapa striata*, Pons *et al.*, 2016; *Periparus ater* (Linnaeus, 1758), Tritsch *et al.*, 2018].

Our study has been made possible by the integration of modern molecular analyses with the nomenclatural framework supplied by natural history collections and archives, highlighting once more the crucial role played by museums in modern biodiversity investigation. We also emphasize the importance of referring to type specimens in taxonomic revisions, even for species belonging to apparently well-known regions, such as Europe.

In conclusion, we recommend the recognition of three species in this complex:

Sylvia subalpina Temminck, 1820 (Moltoni's warbler), monotypic
north-central Italy, Corsica, Sardinia, Balearics
Synonyms: *Sylvia subalpina* Temminck, 1820
Sylvia subalpina inornata Tschusi, 1906
Sylvia cantillans moltonii Orlando, 1937

Sylvia iberiae Svensson, 2013 (western subalpine warbler), monotypic
North Africa, from Tunisia to Morocco, Iberia, southern France, extreme north-west Italy
Synonyms: *Sylvia inornata iberiae* Svensson, 2013

Sylvia cantillans (Pallas, 1764) (eastern subalpine warbler), polytypic
Sylvia cantillans cantillans (Pallas, 1764)
southern Italy, Sicily
Synonyms: *Motacilla cantillans* Pallas, 1764
Sylvia leucopogon 'Heckeli' Schinz, 1821
Sylvia leucopogon 'Heckeli' Meyer B, 1822
Sylvia cantillans albistriata (Brehm CL, 1855)
extreme north-east Italy, Balkans, Greece, western Turkey
Synonyms: *Curruca albistriata* Brehm CL, 1855

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Internal *Cytb* and *COI* primers used for the amplification and sequencing of the toe-pad samples.
Table S2. Sequences included in the phylogenetic analysis. See Table 1 for the museum acronyms. The taxonomy follows the conclusions of this paper.
Fig. S1. Confirmed syntypes of *Sylvia leucopogon* Schinz, 1821 and *Sylvia leucopogon* Meyer, 1832. A, NHMW 43687 (mounted), 35603, 60134 and 42230 (round skins, left to right). B–D, ventral, dorsal and lateral views of NHMW 42230, the genotyped syntype (photographs: Alice Schumacher, NHMW).
Fig. S2. Possible syntype of *Sylvia leucopogon* Schinz, 1821 and *Sylvia leucopogon* Meyer, 1832: SMF 78882 (photograph: Gerald Mayr, SMF).
Fig. S3. The two male specimens with identical Temminck labels in the Naturalis Biodiversity Center (RMNH 171709 and 171711). One of them should be a syntype of *Sylvia leucopogon* Schinz, 1821 and *Sylvia leucopogon* Meyer, 1832 (photograph: Dario Zuccon, courtesy of Naturalis Biodiversity Center, Leiden).
Fig. S4. Lectotype of *Curruca albistriata* Brehm CL, 1855: AMNH 455634 (photographs: Paul Sweet, AMNH).
Fig. S5. Lectotype (ZSM 17.2694), paralectotype (ZSM 17.2696) and possible paralectotype (ZSM 17.2697) of *Sylvia subalpina inornata* Tschusi, 1906. Ventral, dorsal and lateral views (photographs: Markus Unsöld, ZSM).
Fig. S6. Syntypes of *Sylvia cantillans moltonii* Orlando, 1937: MSNM Av5916, Av5917, Av5918, Av5919, Av5943 and Av5952 (left column), Av5954, Av5960, Av5962, Av5963, Av5966 and Av5967 (right column) (photographs: Giorgio Bardelli, MSNM).

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