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On the taxonomic status of the Siberian Chiffchaff *Phylloscopus* [*collybita*] *tristis* (Phylloscopidae)

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The Common Chiffchaff *Phylloscopus collybita* is a common, widespread and polytypic species of the Palearctic comprising six recognised subspecies: *collybita* (Vieillot, 1817) breeding in most of western and central Europe and wintering in western and southwestern Europe; *abietinus* (Nilsson, 1819) breeding from Scandinavia and northwestern Russia to the Black Sea and wintering in southeastern Europe, the western part of the Middle East and northeastern Africa; *caucasicus* Loskot, 1991, breeding in the Caucasus and Iran; *menzbieri* Shestoperov, 1937, breeding in northeastern Iran and Turkmenistan; *brevirostris* (Strickland, 1837) breeding in northwestern Turkey; and *tristis* Blyth, 1843, breeding in most of Siberia from the western foothills of the Urals to the Kolyma River in eastern Siberia and wintering mostly in the Indian subcontinent and potentially marginally in the eastern part of the Middle East (Shirihai & Svensson 2018; Raković *et al.* 2019). The wintering grounds of *menzbieri, caucasicus* and *brevirostris* are much less well-known (Shirihai & Svensson 2018). The taxonomic status of the taxon *tristis*, widely known as the Siberian Chiffchaff, has always been hotly debated, some authors arguing that it deserves specific status based on morphological, acoustic and mitochondrial divergence, whereas others prefer to keep it as a subspecies of the Common Chiffchaff because of unclear levels of reproductive isolation in the contact zone (Helbig *et al.* 1996; Talla *et al.* 2017; Shirihai & Svensson 2018; Raković *et al.* 2019). Currently, only one of the four main global ornithological taxonomic authorities, the HBW & BirdLife Taxonomic Checklist (del Hoyo *et al.* 2016), considers the Siberian Chiffchaff as a valid species, whereas the IOC World Bird List (Gill *et al.* 2024), the Clements Checklist of the Bird of the World (Clements *et al.* 2023) and the Howard & Moore Complete Checklist of the Birds of the World (Dickinson & Christidis 2014) keep it as a subspecies of the Common Chiffchaff. The aim of this article is to review the published knowledge on phenotypic, acoustic, genetic, biogeographical and migratory divergence between the Siberian Chiffchaff and the Common Chiffchaff to allow a re-evaluation of species limits.

Plumage

Plumage divergence between *tristis* and the other Common Chiffchaff subspecies is well-studied and described in the field ornithological literature, as the taxon is a rare to scarce, mostly autumnal, vagrant to western Europe (Dean & Svensson 2005; Dean *et al.* 2010; van der Spek & de Knijff 2021). Outside contact zones in which intermediates birds occur (see Marova *et al.* 2009, 2017; Shipilina *et al.* 2017), most Siberian Chiffchaffs can be confidently separated from Common Chiffchaffs (while on the contrary *collybita* and *abietinus* are indistinguishable, Shirihai & Svensson 2018; van der Spek & de Knijff 2021) based on the plumage criteria summarized in Table 1.

Vocalizations

Oscine passerine calls, which are mostly innate (Marler 2004), and songs, which are most often learned (Päckert 2018), have proven to be useful in species delimitation by frequently reflecting deep genetic divergence and by yielding results congruent with other taxonomically useful datasets (e.g. Alström *et al.* 2021). The vocalisations of *tristis* are well-described in the ornithological literature and are often considered to be the most reliable identification criterion of the taxon (Dean & Svensson 2005; Van der Berg 2009; Dean *et al.* 2010).

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TABLE 1. Identification criteria between *Phylloscopus collybita* and *P.* [*c.*] *tristis* in bare parts and plumage coloration.

Trait	*P. collybita*	*P.* [*c.*] *tristis*
Bare parts (bill and legs) colour	Brown to dark brown	Usually more densely black
Eye-ring	Uniformly whitish to yellowish	White, often more marked on its lower half
Supercilium	Always tinged with yellow, often thin, not very clear and weakly marked behind the eye	Whitish to buff, thick, clearly marked, reaching the bill and far behind the eye
Head pattern	Often uniform except from the supercilium	Wide and more contrasting supercilium and sandy ear coverts
Upperparts	Variable from brown to greenish with yellow suffusion	Drab grey-brown to grey without yellow or green feathers
Underparts	Often brownish, always with yellow suffusion	Uniformly whitish to buff
Distribution of green colouration	Variable, often on most of the upperparts	Restricted to scapulars, edges of primaries and rectrices, sometimes on the rump
Distribution of yellow colouration	Variable, often on most of the body (breast, flanks, supercilium etc.)	Restricted to underwing coverts and axillaries

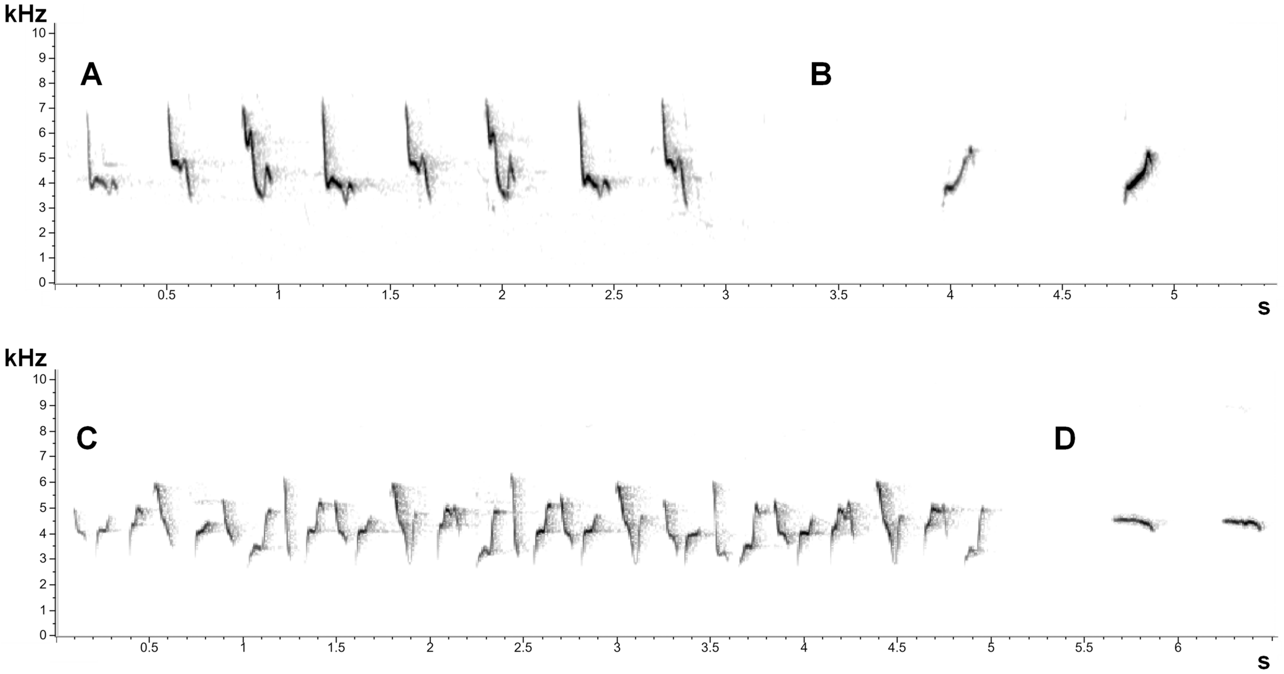

FIGURE 1. Sonagrams of typical songs and calls recordings retrieved from xeno-canto.org. A) *Phylloscopus collybita* (*abietinus*) song (XC718643; Pärnu, Estonia, Uku Paal); B) *Phylloscopus c.* (*abietinus*) calls (XC147829; Cheboksary, Russian Federation, Albert Lastukhin); C) *Phylloscopus* [*c.*] *tristis* song (XC486704; Parfenovka, Russian Federation, Stanislas Wroza); D) *Phylloscopus* [*c.*] *tristis* calls (XC750898; Novosibirsk, Russian Federation, Geoff Carey).

The calls of *tristis* are typically described as a flat, monosyllabic and melancholic *heeee*, which differs greatly from the higher-pitched, disyllabic *hu-it* calls of the Common Chiffchaff. Calls of *tristis* and the Common Chiffchaff are therefore easy to identify in the field or on sonograms (Figure 1). Calviño-Cancela *et al.* (2022), in their thorough call divergence analysis of all the taxa of the chiffchaff complex, showed that *tristis* has the most distinct calls of the complex, even more distinct than those of the Common Chiffchaff from the calls of other widely recognised species (*P. ibericus* Ticehurst, 1937; *P. canariensis* (Hartwig, 1886); *P. sindianus* Brooks, 1880). In contrast, the calls of the subspecies *collybita* and *abietinus* overlap to a large extent and appear to be indistinguishable in the field and on sonograms (Calviño-Cancela *et al.* 2022).

The song of *tristis* is also strikingly divergent from the song emitted by the Common Chiffchaff. The song of the western subspecies of the Common Chiffchaffs is fairly well described by its onomatopoeic English name ("chiff-chaff-chiff-chaff") and is composed of a simple succession of near-identical notes which appears as descending on sonagrams, whereas *tristis* emits a much faster, complex, lower pitched and varied song comprising several types of ascending and descending notes (Figure 1; Martens & Meincke 1989; Marova *et al.* 2017). Il'ina *et al.* (2021) measured various song parameters and analysed song divergence between *P. sindianus sindianus*, *P. s. lorenzii*, *P.* [*c.*] *tristis* and *P. c. caucasicus*. *Phylloscopus c. caucasicus* shows the same song structure as all the other western subspecies of Common Chiffchaff (Shirihai & Svensson 2018) making the comparison between songs of *caucasicus* and *tristis* pertinent for estimating song divergence between western Common Chiffchaff subspecies and *tristis*. The authors demonstrated that *tristis* shows the most divergent song of all analysed taxa and that the song of Common Chiffchaff is closer to that of another species, *P. sindianus*, than to that of *tristis*. However, mixed singers that give intermediate songs or alternate between *tristis* and *abietinus* song types have been recorded in the Ural foothills contact zone (Marova *et al.* 2009, 2017; Shipilina *et al.* 2017). Furthermore, while playback experiments in pure populations did not elicit a response to the song of allochthonous taxa, birds in the contact zone often responded to both types of song (Martens & Meincke 1989). This, as well as the presence of mixed singers, could result from mutual learning in parapatric areas and/or could result from ongoing hybridization (Helb *et al.* 1985; Martens & Meincke 1989; Bensch *et al.* 2002; Marova *et al.* 2017).

Biogeography and migratory strategy

The Siberian Chiffchaff and the western Common Chiffchaff subspecies are mostly allopatric and occupy different major biogeographic regions (Figure 2; Shirihai & Svensson 2018; Raković *et al.* 2019): The breeding distribution of the Siberian Chiffchaff is almost entirely within the eastern Palearctic region, as it only extends into the western Palearctic around the western foothills of the Urals. In contrast, the western Common Chiffchaff subspecies are mostly distributed in the western Palearctic (Figure 2). The wintering ranges of both groups also differ, as Common Chiffchaff subspecies mostly winter in the southern part of the western Palearctic, whereas *tristis* winters mostly in the Indian subcontinent (Figure 2; Shirihai & Svensson 2018; Raković *et al.* 2019). Given their current parapatric distributions and the general biogeographic patterns observed between Western and Eastern Palearctic sister taxa, these two taxa likely diverged in allopatry during distribution contractions imposed by Pleistocene glacial periods (Hewitt 2011; Shipilina *et al.* 2017; Talla *et al.* 2017). As often described in the Palearctic region fauna, the successive recolonization events from their distinct glacial refugia following retractation of the ice cap during interglacial periods probably allowed secondary contact between the two taxa and the formation of the current contact zone in the western foothills of the Urals (Hewitt 2011; Shipilina *et al.* 2017; Talla *et al.* 2017). The migratory strategies and orientations of the two groups strongly diverge. The subspecies *tristis* migrates in a mostly south (for populations breeding in the east of the range) to south-easterly (for the western Siberian populations) orientation to reach the Indian subcontinent. On the contrary, the western subspecies of the Common Chiffchaff mostly migrates in a south-westerly orientation to reach Southern Europe, the Levant or Northern Africa (Shirihai & Svensson 2018; Raković *et al.* 2019). Populations of both taxa that meet around the foothills of the Urals should thus migrate following different orientations. The existence of such strong migratory divide between population entering in contact is known to potentially act as a reproductive barrier as hybrids might take intermediate and/or unfavourable migratory routes and hence be selected against (Delmore & Irwin 2014; Turbek *et al.* 2022). Hybrid individuals produced in the contact zone between *abietinus* and *tristis* in the western foothills of the Urals could thus be counter-selected during their migration, which could participate in reproductive isolation between these taxa.

Genetics

Studies based on mitochondrial DNA (mtDNA) have recovered five of the six Common Chiffchaff subspecies (*collybita*, *abietinus*, *brevirostris/caucasicus* and *menzbieri*) as monophyletic groups within one larger western clade, and a basal and most divergent group only comprising *tristis,* which exhibited divergent private haplotypes in all mtDNA studies (Marova *et al.* 2017; Shipilina *et al.* 2017; Talla *et al.* 2017; Raković *et al.* 2019). The taxon *tristis* is in parapatric contact with *abietinus* in the western foothills of the Urals in a narrow, approximately 10 km wide, broadly north-south contact zone (Figure 2; Marova *et al.* 2009; 2017). This contact zone was first analysed using mtDNA, suggesting past and ongoing hybridization because of mismatches between phenotypes (morphology and song) and mtDNA haplotypes (Marova *et al.* 2009, 2017). Such secondary contact or so-called hybrid zones between diverging taxa have proven useful to study for species delimitation as they allow measurement of the strength of reproductive isolation between taxa and therefore estimation of the "stage of speciation" of the taxa entering in contact (reviewed in Talla *et al.* 2017). Due to the importance of studying such contact zones, the *tristis*-*abietinus* hybrid zone was studied at its southern and northern ends using complete genome sequencing (Shipilina *et al.* 2017; Talla *et al.* 2017). This approach confirmed the existence of a secondary contact between *tristis* and *abietinus* in the western foothills of the Urals. Population genomics analysis showed the existence of a narrow hybrid zone with substantial introgression and confirmed the existence of mismatches between phenotypes and dominant genotypes based on genome-wide markers (Shipilina *et al.* 2017; Talla *et al.* 2017). Genome-wide differentiation between taxa was found to be lowered in the contact zone, but distinct differentiation peaks or islands of genomic divergence were found to resist introgression across the genomes of both taxa (Talla *et al.* 2017). Despite the existence of hybridization, pure and nearly pure individuals were sampled in and relatively close to the contact zone, showing that introgression is limited to a narrow bimodal hybrid zone (restricted to the western foothills of the Urals) and has not spread further east or west, showing that these taxa have reached an advanced stage of speciation (see Gay *et al.* 2008 for a review of hybrid zone modalities; Shipilina *et al.* 2017; Talla *et al.* 2017). The outlined characteristics of the *tristis*-*abietinus* contact zone therefore support the recognition of *tristis* as a separate species (Gay *et al.* 2008; Shipilina *et al.* 2017; Talla *et al.* 2017). It should also be noted that the occurrence of hybridization, including also of mixed singers, in the contact zone does not preclude the recognition of taxa as separate species, as a similar contact zone dynamic has long been known between two undoubtedly valid species: *P. collybita* and *P. ibericus* (Bensch *et al.* 2002; Shirihai & Svensson 2018).

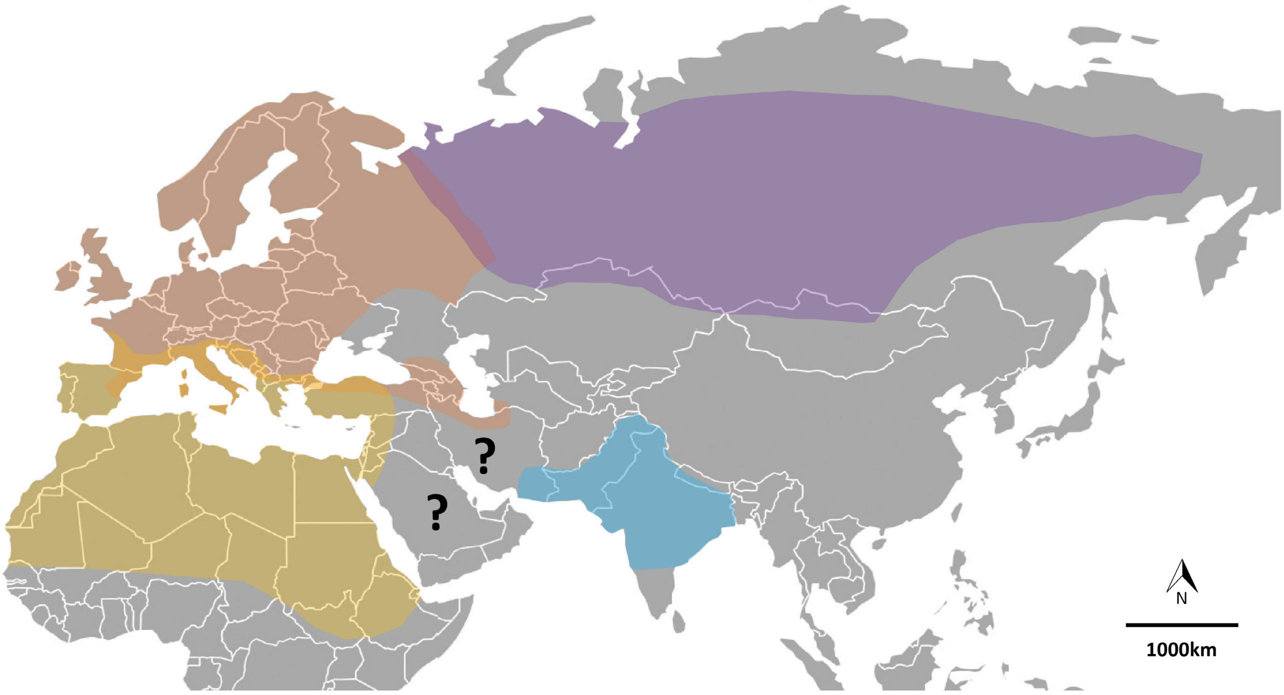

FIGURE 2. Distribution of the Common Chiffchaff, including *P. collybita collybita*, *abietinus*, *caucasicus, menzbieri* and *brevirostris*, with orange indicating breeding and yellow wintering ranges. Distribution of the Siberian Chiffchaff *P.* [*c.*] *tristis*, with purple indicating breeding and blue wintering ranges. The narrow (10km wide) contact zone between *P. c. abietinus* and *P.* [*c.*] *tristis* in the western Ural foothills is broadly located at the overlap between Common Chiffchaff and Siberian Chiffchaff distributions. The identity of populations wintering in the Middle East is unclear (Shirihai & Svensson 2018; Raković *et al.* 2019).

Taxonomic recommendation

The combination of various sources of evidence including plumage, vocalizations, population genomics, biogeography and migratory strategy reviewed here demonstrates the strong divergence between *tristis* and the western Common Chiffchaff subspecies as well as the existence of substantial intrinsic reproductive barriers at least between the taxa that enter into contact during the breeding period (*tristis* and *abietinus*). The Biological Species Concept (BSC; Mayr 1942) postulates that divergent populations which are able to coexist in close geographic proximity (i.e. in sympatry or parapatry) and to maintain their integrity, i.e. that have evolved intrinsic reproductive barriers, should be treated as separate species. Following the evidence outlined above, the case of the Common and Siberian Chiffchaffs matches the requirements of the BSC, and the Siberian Chiffchaff should therefore be considered as a separate species from the Common Chiffchaff. The same conclusion would apply following the General Lineage Concept (de Queiroz 2007) or the framework of integrative taxonomy (Padial *et al.* 2010). This split would result in the recognition of the monotypic Siberian Chiffchaff *Phylloscopus tristis,* as Shipilina *et al.* (2017) showed that the previously described morphologically intermediate subspecies "*fulvescens"* and *"riphaeus"* do not represent valid subspecies and probably correspond to hybrid or introgressed birds from the contact zone, and the polytypic Common Chiffchaff *Phylloscopus collybita* comprising *P. c. collybita*, *abietinus*, *brevirostris*, *caucasicus* and *menzbieri*. Both species show large distributions and, even though an accurate estimation of their population size is impossible, they do not seem to match any of the IUCN threat criteria, so they should be retained under the Least Concern IUCN status. This work and the long debated taxonomic debate it addresses underline the importance of taxonomic summaries of relevant data in advancing recommendations for revising species boundaries to enable taxonomic progress, which is vital for conservation, citizen science and biological research.

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