

S23-4 Species concepts and their application: insights from the genera *Seicercus* and *Phylloscopus*

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Abstract Using several examples from the Old World warbler genera *Seicercus* and *Phylloscopus*, I highlight difficulties in ranking allopatric taxa whatever the conceptual base for species delimitation. Given that related sympatric taxa are separate species whatever their conceptual base, the complexity of morphological, vocal and genetic characters makes ranking of allopatric taxa problematic. Under the Phylogenetic Species Concept, judgement of diagnosability becomes a core problem. If the Biological Species Concept is applied, the issue shifts to evaluation of the degree of reproductive isolation. And under the Monophyletic Species Concept, phylogenetic hypotheses are required.

Key words Species concepts, Sympatry, Allopatry, Morphology, Vocalizations, DNA

1 Introduction

The concept of species has been debated for decades, and a plethora of different species concepts have been formulated (reviews in Haffer, 1992; Zink and McKittrick, 1995; Mayden, 1997). Nearly all classifications of birds in the past 50 years are based on the Biological Species Concept (BSC) of Mayr (1942) and others, while the Phylogenetic Species Concept (PSC) of Cracraft (1989), Nixon and Wheeler (1990) and others forms the basis for some recent classifications, as in Hazevoet (1995) and Sangster et al. (1999). The Monophyletic Species Concept (MSC) of Mishler and Donoghue (1982) and Lidén and Oxelman (1989) is another that has been adopted in one recent taxonomic review (Alström et al., 2003).

Here I use examples from five well studied groups in the Old World warbler genera *Seicercus* and *Phylloscopus* (Table 1) to highlight difficulties in ranking allopatric (geographically disjunct) and parapatric (geographically abutting) taxa whatever the conceptual base for species delimitation.

2 The *Seicercus burkii* complex

This species complex, which comprises eight taxa (Table 1), has recently been revised by Alström and Olsson (1999, 2000) and Martens et al. (1999). Up to four taxa are syntopic (Fig. 1), although almost entirely segregated altitudinally. All taxa are diagnosably different in both morphology and vocalizations, except the parapatric *valentini-latouchei* and the disjunct *whistleri-nemorali*s groups, which only differ from each other in plumage, not in song. The disjunct *tephrocephalus-burkii* and, especially, *valentini-latouchei-whistleri-nemorali*s groups resemble

each other to a high degree in morphology and, particularly, song. According to mitochondrial DNA (mtDNA) sequence data, *S. burkii sensu lato* is non-monophyletic (Fig. 2; Olsson et al., 2004). mtDNA further reveals that *valentini-latouchei* and *whistleri-nemorali*s separated considerably later than other taxa (Fig. 2), yet are diagnosable by molecular markers (U. Olsson and P. Alström, unpublished).

The syntopic taxa are separate species whatever the conceptual base for species delimitation (Table 2), since they are diagnosably different and apparently reproductively isolated from each other. In contrast, the classification of recently diverged allopatric sister taxa only diagnosable by genetic markers (*valentini-latouchei*, *whistleri-nemorali*s) varies with the species concept adopted (Table 2). All of the disjunct taxa are treated as species under the PSC, while

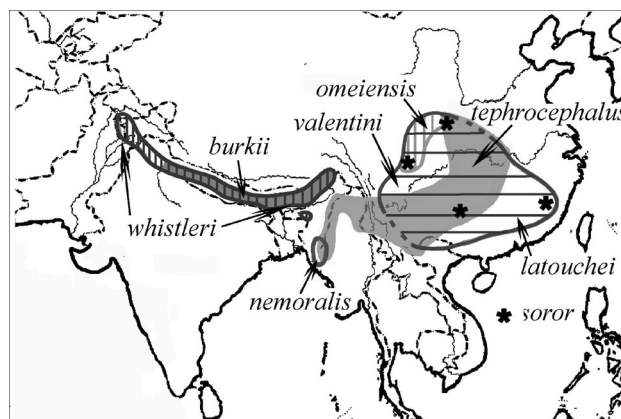


Fig. 1 Distribution of taxa in the *Seicercus burkii* complex. Based on Alström and Olsson (1999, 2000), Martens et al. (1999) and Olsson et al. (2004). The border between *valentini* and *latouchei* is uncertain and indicated by a dashed line.

such ranking is arbitrary for some under the BSC (Table 2). The close similarity in vocalizations within *burkii- tephrocephalus* and, especially, *valentini/latouchei - whistleri/nemoralis* groups suggests, *a priori*, that they would interbreed if in contact. That, however, is contradicted by playback tests, even though only a few males have been tested (Alström and Olsson, 1999). Moreover, it is possible that non-vocal cues would act as reproductive isolating barriers between these taxa were they to meet. Under the MSC, there are alternative options for ranking the allopatric taxa (Table 2).

3 The *Seicercus affinis-poliogenys* complex

The four taxa in this complex (Table 1) have more southerly distributions than the *S. burkii* complex. The

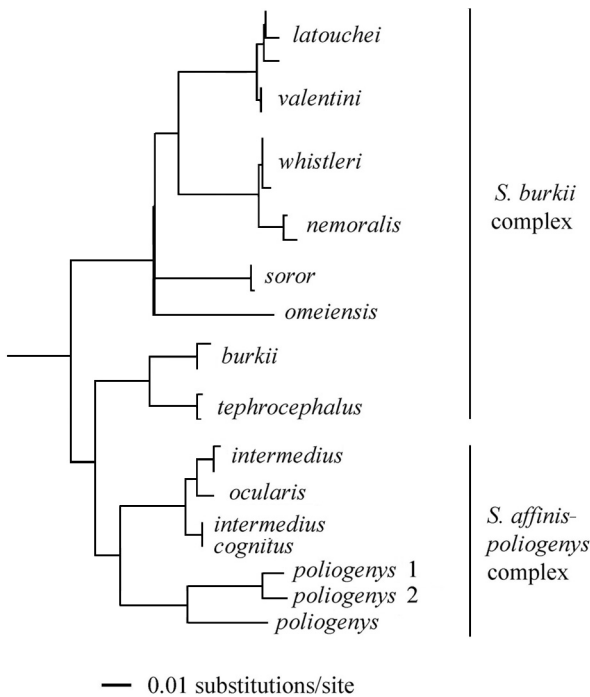


Fig. 2 mtDNA tree of the *Seicercus burkii* and *S. affinis-poliogenys* complexes

taxon *poliogenys* is sympatric with *affinis* and *ocularis*, while the distributions of the latter two, as well as *intermedius*, are disjunct; and all except *ocularis* are sympatric with two to five taxa in the “*S. burkii*” complex. Except for *ocularis*, which is usually synonymized with *affinis*, the taxa are diagnosable morphologically. Vocally, *poliogenys* differs from the others, which all have similar songs. According to mtDNA (Olsson et al., 2004: Fig. 2), *intermedius* is non-monophyletic, and different populations of *poliogenys* differ markedly from each other.

The sympatric taxa are species under any species con-

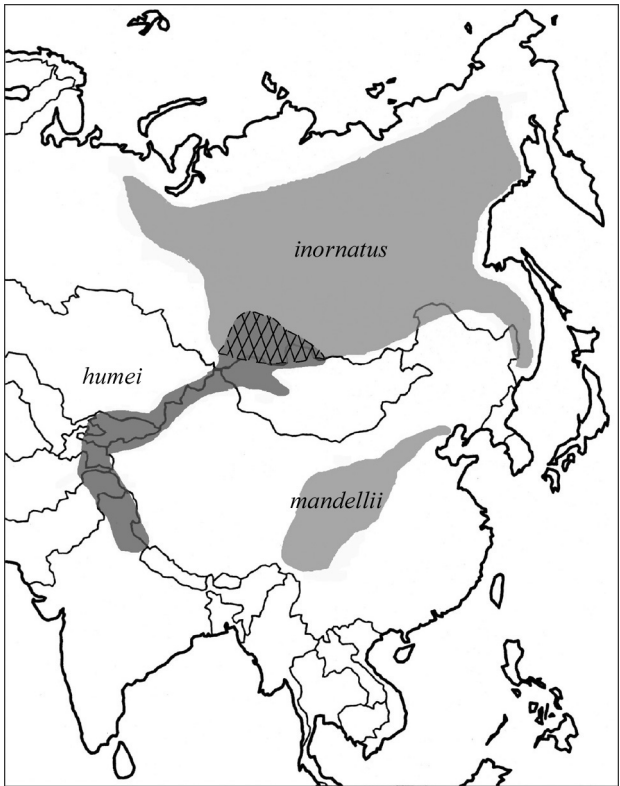


Fig. 3 Distribution of taxa in the *Phylloscopus inornatus* complex
Based on Irwin et al. (2001a). The cross-barred area represents sympatry between *inornatus* and *humei*.

Table 1 Species complexes discussed in this paper

<i>Seicercus burkii</i> complex	<i>Seicercus affinis - poliogenys</i> complex	<i>Phylloscopus inornatus</i> complex	<i>Phylloscopus proregulus</i> complex	<i>Phylloscopus trochiloides</i> complex
<i>burkii</i>	<i>affinis</i>	<i>inornatus</i>	<i>proregulus</i>	<i>trochiloides</i>
<i>tephrocephalus</i>	<i>ocularis</i> ¹	<i>humei</i>	<i>kansuensis</i>	<i>obscuratus</i>
<i>omeiensis</i>	<i>intermedius</i> ²	<i>mandellii</i>	<i>chloronotus</i>	<i>plumbeitarsus</i>
<i>soror</i>	<i>poliogenys</i>		<i>simlaensis</i>	<i>viridanus</i> ³
<i>valentini</i>				<i>nitidus</i>
<i>latouchei</i>				
<i>whistleri</i>				
<i>nemoralis</i>				

¹Usually synonymized with *affinis*. ²*cognitus* treated as a color morph. ³*ludlowi* synonymized with *viridanus*.

cept (Table 3), because they are diagnosably different and reproductively isolated from each other. The disjunct *ocularis*, *intermedius* and different populations of *S. poliogenys* are all separate species under the PSC (Table 3), because they are diagnosable genetically (*affinis* not studied). In contrast, they are treated as subspecies or are unrecognized under the BSC (Table 3) since, owing to their morphological and vocal similarities, they can be assumed to interbreed freely should they meet. Under the MSC, there are alternative options for ranking these taxa (Table 3).

4 The *Phylloscopus inornatus* complex

This complex comprises the partly sympatric *inornatus* and *humei* and the disjunct *mandellii* (Table 1, Fig. 3). Although there are morphological differences between all three taxa, it is doubtful that they are diagnosable by morphology because of much overlap. Vocally, *inornatus* differs markedly from the other two, while *humei* and *mandellii* differ only in call, not in song (Irwin et al., 2001a). mtDNA suggests that *humei* and *mandellii* are sister taxa, which have been separated a long time (Irwin et al., 2001a: Fig. 4).

The sympatric taxa are treated as separate species

under all species concepts (Table 4), since they are diagnosably different and reproductively isolated. The ranking of the geographically isolated *mandellii* differs between the BSC and the PSC, while any of the alternatives canvassed is possible under the MSC (Table 4).

5 The *Phylloscopus proregulus* complex

The four taxa in this complex (Table 1) have disjunct or parapatric distributions (Fig. 5). The taxa *proregulus*, *chloronotus* and *simlaensis* differ in plumage, but at least the two latter, at least, are doubtfully diagnosable; *kansuensis* is indistinguishable morphologically from *chloronotus* (Alström and Olsson, 1990; Alström et al., 1997). Vocally, the parapatric *simlaensis* and *chloronotus* are similar, while the other two are very distinct (Alström and Olsson, 1990; Alström et al., 1997). Hence, there is no correspondence between morphological and vocal differentiation. Based on mtDNA, all taxa are diagnosably different (U. Olsson and P. Alström, unpublished).

Under the PSC, all four taxa are separate species, since they are at least diagnosable genetically (Table 5). In contrast, *chloronotus* and *simlaensis* are best considered conspecific under the BSC, because they intergrade where

Table 2 Three alternative classifications of the *Seicercus burkii* complex

1. BSC 1/MS 1	2. BSC 2/MS 2	3. PSC/MS 3
<i>S. burkii</i>	<i>S. burkii</i>	<i>S. burkii</i>
<i>S. tephrocephalus</i>	<i>S. b. burkii</i>	<i>S. tephrocephalus</i>
<i>S. omeiensis</i>	<i>S. b. tephrocephalus</i>	<i>S. omeiensis</i>
<i>S. soror</i>	<i>S. omeiensis</i>	<i>S. soror</i>
<i>S. valentini</i>	<i>S. soror</i>	<i>S. valentini</i>
<i>S. v. valentini</i>	<i>S. valentini</i>	<i>S. latouchei</i> ¹
<i>S. v. latouchei</i>	<i>S. v. valentini</i>	<i>S. whistleri</i>
<i>S. whistleri</i>	<i>S. v. latouchei</i>	<i>S. nemoralis</i> ²
<i>S. w. whistleri</i>	<i>S. v. whistleri</i>	
<i>S. w. nemoralis</i>	<i>S. v. nemoralis</i>	

BSC = Biological Species Concept; MSC = Monophyletic Species Concept; PSC = Phylogenetic Species concept. ¹Only diagnosably different from *valentini* by mtDNA. ²Only diagnosably different from *whistleri* by mtDNA.

Table 3 Three alternative classifications of the *Seicercus affinis-poliogenys* complex

1. BSC 1 ¹	2. PSC/MS 1	3. MSC 2
<i>S. affinis</i>	<i>S. affinis</i>	<i>S. affinis</i>
<i>S. a. affinis</i> ²	(<i>S. ocularis</i> ³)	<i>S. a. affinis</i>
<i>S. a. intermedius</i>	<i>S. intermedius</i>	<i>S. a. ocularis</i>
<i>S. poliogenys</i>	<i>S. sp. 1</i> ⁴ ("intermedius")	<i>S. a. intermedius</i>
	<i>S. poliogenys</i>	<i>S. a. ssp. 4</i> ("intermedius")
	<i>S. sp. 2</i> ⁴ ("poliogenys 1")	<i>S. poliogenys</i>
	<i>S. sp. 3</i> ⁴ ("poliogenys 2")	<i>S. sp. 4</i>
		<i>S. sp. ssp. 1</i> ⁴ ("poliogenys 1")
		<i>S. sp. ssp. 2</i> ⁴ ("poliogenys 2")

BSC = Biological Species Complex; PSC = Phylogenetic Species Concept; MSC = Monophyletic Species Concept.

¹It is not common practice under the BSC to recognize taxa based only on molecular characters, hence the small number of taxa. ²*ocularis* is usually synonymized with *affinis*. ³It is not known whether *ocularis* is diagnosably different from *affinis*. ⁴Unnamed: only diagnosable genetically.

they meet, suggesting gene flow. Ranking of the others is arbitrary under the BSC (Table 5), since their ranges do not overlap, although it seems likely that the striking differences in songs would act as reproductive isolating barriers were they to meet. Under the MSC, options are open for ranking taxa (Table 5).

6 The *Phylloscopus trochiloides* complex

This complex comprises five taxa (Table 1), four of which occur in a parapatric chain around the Tibetan plateau; one additional taxon is geographically isolated from the others (Fig. 6). There is somewhat continuous variation in morphology and song around the “chain”, except for a sharp transition in central Siberia where the ranges of *viridanus* and *plumbeitarsus* overlap (Irwin, 2000; Irwin et al., 2001b). The taxa comprise two main clades (Fig. 7; Irwin et al., 2001b).

Under the PSC, at least four of the taxa would be treated as separate species, since they are diagnosable, at least genetically (Table 6). Ranking is very problematic under the BSC. The taxa *viridanus* and *plumbeitarsus*, which are marginally sympatric and apparently reproductively isolated (Irwin, 2000; Irwin et al., 2001b), should be treated as separate species. These two taxa, however, are connected to *trochiloides* through intermediate populations, and there is evidence of past or present gene flow between *viridanus* and *trochiloides* (Irwin, 2000; Irwin et al., 2001b). The classification in Table 6 might be the most sensible outcome under the BSC, although it should be noted that it conflicts with the phylogeny. Polytypic species that are paraphyletic

are not acceptable under the MSC (Table 6).

7 Discussion

Because speciation is a gradual process in time, different populations are in different stages of divergence. Some lineages have split recently and only just started to differentiate, whereas others have evolved multitudinous differences and are reproductively isolated from their nearest relatives. Furthermore, divergence rates vary considerably, both among lineages and in the traits affected, whether morphological, vocal, behavioral or genetic. As is evident in examples above, plumage differentiation can be very slow compared to vocal or mtDNA differentiation. Such phenomena seriously hamper attempts to sort observed variation in nature.

Least-inclusive nominal taxa are usually delimited using morphological characters. The PSC is unique among the species concepts addressed here in explicitly stating how least-inclusive taxa should be delimited: “smallest diagnosable clusters” (Cracraft, 1989; Nixon and Wheeler, 1990). Such principles could equally well be adopted by proponents of the BSC and MSC, in which case the same taxa would, theoretically, be recognized unanimously. As is evident from disagreements among taxonomists, the delimitation of allopatric taxa — especially those recently diverged — is highly subjective. Molecular markers are unlikely to solve the problem, and few ornithologists would endorse taxa that are only identifiable genetically. Even so, use of DNA sequencing may uncover previously overlooked “cryptic” taxa, opening their existence to confirmation by

Table 4 Two alternative classifications of the *Phylloscopus inornatus* complex

1. BSC/MS 1	2. PSC/MS 2
<i>P. inornatus</i>	<i>P. inornatus</i>
<i>P. humei</i>	<i>P. humei</i>
<i>P. h. humei</i>	<i>P. mandellii</i>
<i>P. h. mandellii</i>	

BSC = Biological Species Concept; MSC = Monophyletic Species Concept; PSC = Phylogenetic Species Concept.

Table 5 Two alternative classifications of the *Phylloscopus proregulus* complex

1. BSC	2. PSC/MS
<i>P. proregulus</i>	<i>P. proregulus</i>
<i>P. kansuensis</i>	<i>P. kansuensis</i>
<i>P. chloronotus</i>	<i>P. chloronotus</i>
<i>P. c. chloronotus</i>	<i>P. simlaensis</i> ¹
<i>P. c. simlaensis</i>	

BSC = Biological Species Concept; PSC = Phylogenetic Species Concept; MSC = Monophyletic Species Concept. ¹ Only diagnosably different from *chloronotus* by mtDNA.

Table 6 Three alternative classifications of the *Phylloscopus trochiloides* complex

1. BSC	2. PSC/MS 1	3. MSC 2
<i>P. trochiloides</i>	<i>P. trochiloides</i>	<i>P. trochiloides</i>
<i>P. t. trochiloides</i>	<i>P. obscuratus</i>	<i>P. t. trochiloides</i>
<i>P. t. obscuratus</i>	<i>P. viridanus</i>	<i>P. t. obscuratus</i>
<i>P. t. viridanus</i>	<i>P. nitidus</i>	<i>P. t. plumbeitarsus</i>
<i>P. t. nitidus</i>	<i>P. plumbeitarsus</i>	<i>P. viridanus</i>
<i>P. plumbeitarsus</i>		<i>P. v. viridanus</i>
		<i>P. v. nitidus</i>

BSC = Biological Species Complex; PSC = Phylogenetic Species Complex; MSC = Monophyletic Species Complex. Ranking is problematic under the BSC.

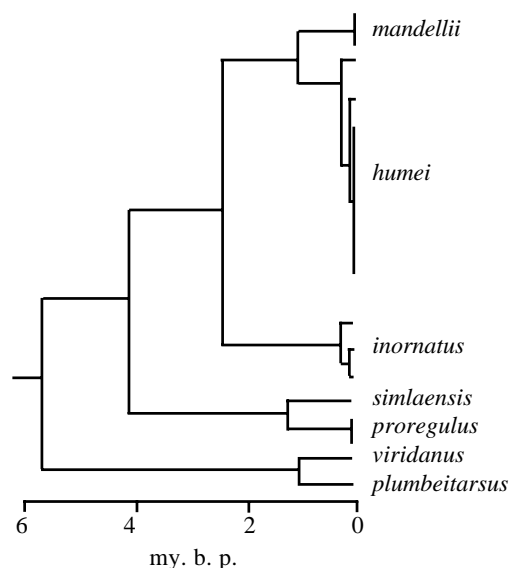


Fig. 4 mtDNA tree of the *Phylloscopus inornatus* complex. Based on Irwin et al. (2001a).

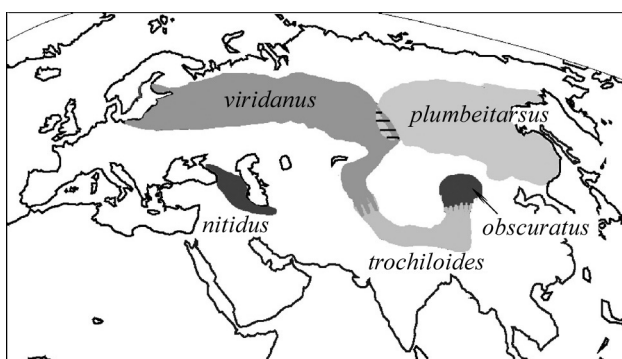


Fig. 6 Distribution of taxa in the *Phylloscopus trochiloides* complex. Based on Irwin et al. (2000, 2001b). The hatched area represents sympatry between *viridanus* and *plumbeitarsus*.

fine but genetically significant differences in morphology and voice, as in the *Seicercus affinis* - *S. poliogenys* complex.

The main operational discrepancy between different species concepts involves the principles by which least-inclusive taxa are ranked. Under the BSC and MSC, they are ranked either as monotypic species or as subspecies of polytypic species, while all valid taxa are species under the PSC *sensu* Cracraft (1989). Under the BSC, inferring the degree of reproductive isolation between taxa poses the main problem; under the PSC, the issue is one of simple diagnosability; and under the MSC, resolution turns on whether replacement taxa are monophyletic. As is evident from Tables 2–6, classifications based on different species concepts disagree in the treatment of allopatric (disjunct) or parapatric taxa.

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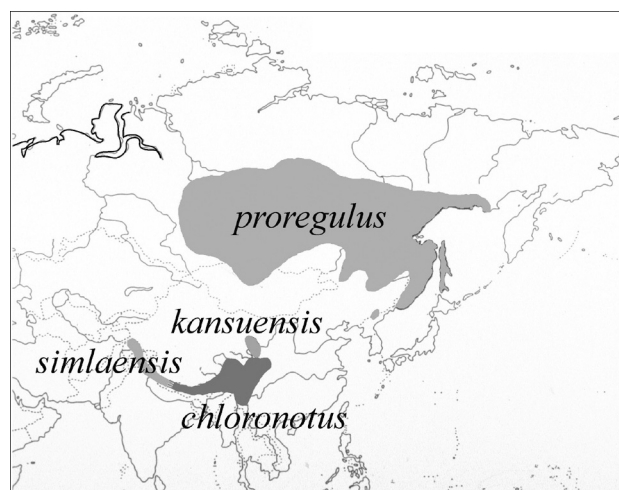


Fig. 5 Distribution of taxa in the *Phylloscopus proregulus* complex.

Based on Alström and Olsson (1990) and Alström et al. (1997).

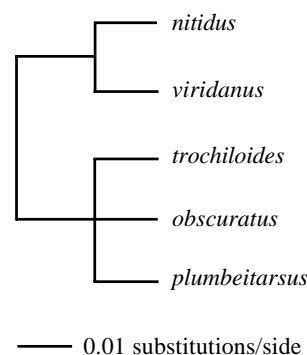


Fig. 7 mtDNA tree of the *Phylloscopus trochiloides* complex. Based on Irwin et al. (2001b).

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