

# Specific status of taxa within the Greenish Warbler complex

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**ABSTRACT** The taxonomic status of six subspecies of Greenish Warbler *Phylloscopus trochiloides* was re-examined in the light of fresh evidence about their identification characters and biological relationships. Although *P. t. viridanus* and *P. t. plumbeitarsus* ('Two-barred Greenish Warbler') behave as distinct species in their zone of overlap, the five subspecies *viridanus*, *ludlowi*, *trochiloides*, *obscuratus* and *plumbeitarsus* form a cline within which it is not possible to define species boundaries. There is currently insufficient evidence to recognise 'Two-barred Greenish Warbler' or the allopatric taxon *P. t. nitidus* ('Green Warbler') as separate species. Consequently, no changes to their classification are recommended.

Six subspecies of Greenish Warbler *Phylloscopus trochiloides* are currently recognised (Irwin 2000): *viridanus*, *ludlowi*, *trochiloides*, *obscuratus* (collectively known as Greenish Warbler), along with the more distinctive *plumbeitarsus* ('Two-barred Greenish

Warbler') and *nitidus* ('Green Warbler'). Of these, *viridanus*, *nitidus* and *plumbeitarsus* have occurred in Britain (Dean 1985; Bradshaw 2001). Several recent publications have provided new information about species limits within *P. trochiloides* (Helbig *et al.* 1995; Irwin

2000; Irwin *et al.* 2001a,c), prompting this taxonomic review. Some of the evidence has been summarised previously by Collinson (2001) and in recent reviews by Irwin *et al.* (2001b) and Irwin & Irwin (2002).

#### The specific status of Greenish Warbler taxa

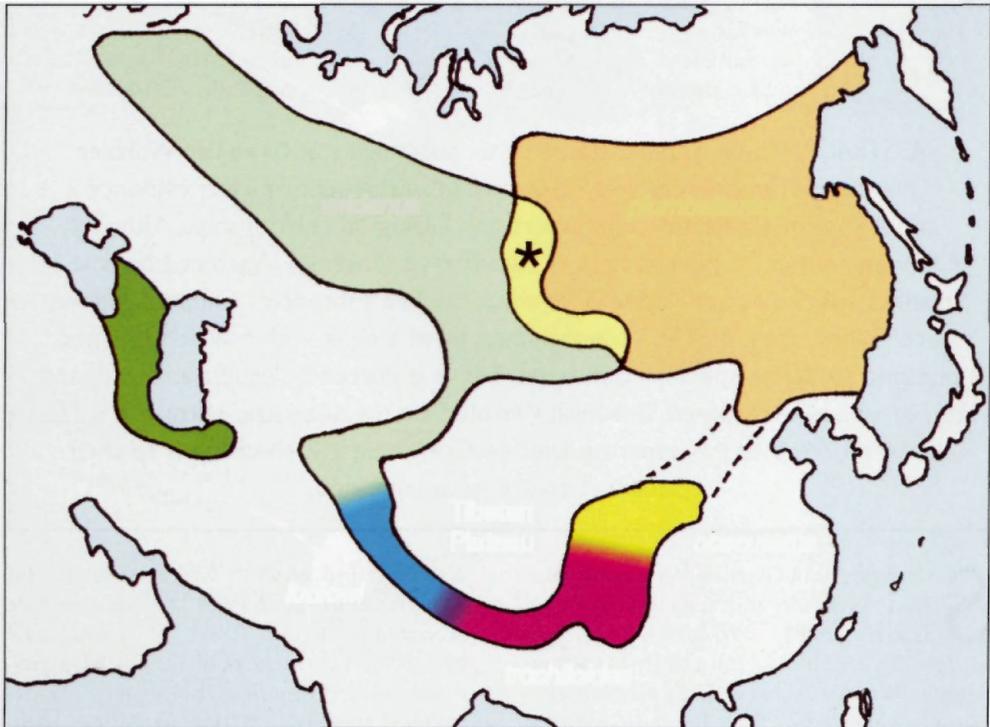
The five subspecies *viridanus*, *ludlowi*, *trochiloides*, *obscuratus* and *plumbeitarsus* have been described as a 'ring species' (Ticehurst 1938; Mayr 1942; Irwin *et al.* 2001a,b). Two of the taxa, *viridanus* and *plumbeitarsus*, coexist in central Siberia without interbreeding (they are reproductively isolated), but are connected by a chain of intermediate, interbreeding populations which change progressively in morphology around the southern borders of the Tibetan plateau (Irwin 2000; Irwin *et al.* 2001a). If *viridanus* and *plumbeitarsus* were the only taxa to be considered, they would be regarded as different species under any species concept,

and would follow the Species Guidelines developed by the BOURC Taxonomic Sub-committee (Helbig *et al.* 2002). They are partly sympatric (there is a 500-km overlap between the two); diagnosable with respect to each other on the basis of several independent morphological and genetic criteria; and no hybridisation or gene flow has been detected either by observation or genetic analysis.

Four taxa (*viridanus*, *ludlowi*, *trochiloides* and *obscuratus*) are connected by a series of interbreeding populations, so that, theoretically, gene flow is possible between all these taxa. Statistically diagnosable populations joined by a cline are treated as subspecies on the British List maintained by the BOURC (Helbig *et al.* 2002). The contiguous distribution and clinal variation in biometrics, plumage and song (Irwin 2000; Irwin *et al.* 2001a) among *viridanus*, *ludlowi*, *trochiloides* and *obscuratus* show that these four taxa should be treated as subspecies

Fig. 1. Distribution of the races of Greenish Warbler *Phylloscopus trochiloides*.

Racial variation is clinal through the intergradation of the subspecies *viridanus* (eastern Europe to western Asia and Afghanistan), *ludlowi* (southeast Afghanistan to Kumaon), *trochiloides* (central and eastern Himalayas), *obscuratus* (central China) and *plumbeitarsus* (eastern Russia); the dotted lines indicate a gap in the distribution due to deforestation. The 'Green Warbler' *P. t. nitidus* is fully allopatric, and is not considered further. All other subspecies interbreed with adjacent subspecies with the exception of *viridanus* and *plumbeitarsus*, which show no apparent intergradation in the zone where their distributions overlap (indicated by \*). 'Two-barred Green Warbler' *P. t. plumbeitarsus* was regarded as a separate species, *P. plumbeitarsus*, by Cramp (1992).



of *P. trochiloides*. The east Siberian breeding form, *plumbeitarsus*, is geographically separate from *obscuratus* (see fig. 1) by a gap of unsuitable habitat up to about 1,000 km wide. Irwin (2000) suggested that the habitat gap may be comparatively recent, and reported that the populations on either side of the divide are very similar, supporting a recent common ancestry.

Analyses based upon c. 1200 bases of the mitochondrial-DNA control region have been used to examine the phylogeny of Greenish Warblers (Irwin *et al.* 2001a). The sequences form two major groups (see fig. 3 in Collinson 2001, based on Irwin *et al.* 2001a): a western clade containing individuals of *nitidus*, *viridanus* and western *ludlowi*, and an eastern clade containing individuals of eastern *ludlowi*, *trochiloides*, *obscuratus* and *plumbeitarsus*. Within the range of *ludlowi*, birds carrying eastern- and western-clade DNA are otherwise indistinguishable and respond strongly to each other's songs, suggesting that DNA differences alone cannot be used to define species boundaries in these taxa. Nevertheless, both *plumbeitarsus* and *nitidus* are diagnosably distinct genetically from all other Greenish Warbler taxa on the basis of these data (as indeed is *obscuratus*).

Thus, where *viridanus* and *plumbeitarsus* coexist in central Siberia, they are markedly (diagnosably) different in mtDNA sequence, supporting the acoustic and morphological evidence for reproductive isolation of these taxa, and thus their specific status. Therefore, if *obscuratus* and *plumbeitarsus* could also be shown to be specifically distinct, then *plumbeitarsus* could clearly be split from the remaining taxa in the *viridanus-obscuratus* cline. A key comparison is thus *obscuratus* with *plumbeitarsus*: for the purposes of a taxonomic assessment these are treated below as allopatric taxa and assessed against the Species Guidelines. The main criteria are diagnosability and the degree of differentiation compared with sympatric taxa of very close taxonomic affinity (Helbig *et al.* 2002).

#### Diagnosability of *obscuratus* with respect to *plumbeitarsus*

The taxon *obscuratus* is considered to be intermediate in plumage between *trochiloides* and *plumbeitarsus* (Cramp 1992; Irwin 2000). It is darker grey-green above than nominate *trochiloides* with a whiter supercilium and an

increased tendency to show a median-covert wing-bar (Svensson 1992). The 'average' *obscuratus* probably differs in upperpart coloration from the 'average' *plumbeitarsus*, but it is not clear that this has ever been quantified and it would be expected that many individuals cannot be ascribed to either taxon on this character alone. Irwin *et al.* (2001a) suggested that the two are, however, diagnosably different (but not with respect to other Greenish Warbler taxa) on body size alone (combining tarsus, wing and tail length, and bill length, depth and width measurements). Body size is not always taxonomically informative for allopatric taxa, however, as it can vary in response to latitude (Helbig *et al.* 2002). Since this is one of the clinal features by which Greenish Warbler taxa differ (Irwin *et al.* 2001a), this difference in body size is not a strong argument for splitting *obscuratus* and *plumbeitarsus*.

The greater-covert wing-bar increases in size clinally from *viridanus* through the southern subspecies to *plumbeitarsus* (Irwin *et al.* 2001a; van der Vliet *et al.* 2001). The proportion of birds with a median-covert wing-bar in fresh plumage also increases, presumably being developmentally linked to the size of the greater-covert wing-bar. Many *obscuratus* are, therefore, 'two-barred'. Irwin *et al.* (2001a) showed that the width of the greater-covert wing-bar is identical in *obscuratus* and *plumbeitarsus*, but apparently significantly wider in these two than in all other Greenish Warbler taxa (although *nitidus* was not analysed). Consequently, the number and characteristics of the wing-bars cannot be used to differentiate between the two taxa.

The analysis presented in Irwin *et al.* (2001a) indicates that the songs of *plumbeitarsus* and *obscuratus* are close to being diagnosably distinct. These differences may not, however, be biologically significant, since the birds appear not to differentiate between them: *plumbeitarsus* in eastern Siberia responded strongly to *obscuratus* songs recorded in central China. Such playback experiments may provide useful background information for taxonomists looking at allopatric species, but they do not provide conclusive proof one way or the other.

Irwin *et al.* (2001a) established that considerable genetic variation exists within *plumbeitarsus*. Furthermore, *obscuratus* and *plumbeitarsus* were found to be diagnosably different from each other on the basis of the mito-

chondrial control-region DNA, although only a small sample of *obscuratus* was analysed, and no *plumbeitarsus* from the southern edge of their range were sampled.

In summary, *obscuratus* is at best diagnosably different from *plumbeitarsus* on the basis of a combination of four parameters: body size, mtDNA, upperpart coloration and song. These differences are slight and/or not taxonomically informative. Predictions about possible reproductive isolation between allopatric taxa which differ only slightly (e.g. in size or darkness of plumage) are very uncertain. There are no described differences between *obscuratus* and *plumbeitarsus* which fulfil the species-defining criteria set out in Helbig *et al.* (2002). They should, therefore, be treated as subspecies of a single species, *P. trochiloides*.

We recognise that the decision to maintain a single species containing two taxa, *viridanus* and *plumbeitarsus*, which are apparently specifically distinct, is problematic. If they were, however, to be split, current evidence does not allow anything but an arbitrary decision with respect to the inclusion of *obscuratus*, *trochiloides* and *ludlowi* in either proposed species. Until further information is published, no change of classification is recommended.

#### *The taxonomic status of nitidus with respect to other Greenish Warblers*

The taxon *nitidus* was assessed against the Guidelines (Helbig *et al.* 2002), in the light of research by Helbig *et al.* (1995) and Irwin *et al.* (2001a,c), as it is allopatric in relation to other Greenish Warblers. DNA evidence shows that *nitidus* is most closely related to *viridanus*, although the two taxa are clearly distinct with 2.5–3.1% divergence in their mitochondrial cytochrome-*b* gene (Helbig *et al.* 1995; Irwin *et al.* 2001a).

There is considerable overlap between *nitidus* and *viridanus* in all biometric measurements presented in both Cramp (1992) and Svensson (1992). The bill of *nitidus* is larger, on average, than in other Greenish Warbler taxa. Wing formula is similar to that of *viridanus*, although there are differences at the population level (Svensson 1992; van der Vliet *et al.* 2001). The primary projection of *nitidus* is longer, on average, than in the other taxa, but there is overlap. For example, plate 208 in van der Vliet *et al.* (2001) shows an individual of *nitidus* with the primary projection identical to that of a

typical *viridanus*. Width and depth of the greater-covert wing-bar are intermediate between those of *viridanus* and *plumbeitarsus* (van der Vliet *et al.* 2001), while *nitidus* may have a hint of median-covert wing-bar in fresh plumage (Cramp 1992; Svensson 1992). In fresh plumage, at all ages, *nitidus* usually has a lemon-yellow wash to the sides of the head and neck, a yellow supercilium and throat, and 'minty' green upperparts, a colour that probably never occurs in other taxa. There is, however, variation within *nitidus*, and western birds do not show such obvious yellow tones, which in any case are prone to fade and disappear with wear (Albrecht 1984; Dean 1985; van der Have 1987; van der Vliet *et al.* 2001). The supercilia of *nitidus* tend not to meet above the bill. This is atypical, although not unknown, in *viridanus*, and similar to typical *plumbeitarsus* (van der Vliet *et al.* 2001).

The call of *nitidus* is similar to that of *plumbeitarsus* and different from that of typical *viridanus*, although within *viridanus* itself it is certainly variable. The song is like that of *viridanus* in many respects, but differences have been described (Albrecht 1984; Cramp 1992). Further research into this aspect of the ecology of *nitidus* is required, but song length and frequency range appear similar to those of *viridanus* (Cramp 1992). In addition, *nitidus* is reported to react strongly to the song of *viridanus* (Mild, in Helbig *et al.* 1995), although details of the playback protocol were not published, and these can be crucial for the biological and taxonomic interpretation of such results (e.g. Kroodsmma 1989). The taxonomic merits of the reported song recognition are thus unclear.

Most individuals of *nitidus* are probably identifiable, at least in the hand, on the basis of the colour of their upperparts and underparts, wing formula, the dimensions and appearance of the wing-bar(s), and supercilium pattern (Dean 1985). Nonetheless, no single combination of features has been proposed to establish identity safely, and there are certainly difficult individuals, e.g. a bird trapped on Heligoland, Germany, in June 1987 and shown in plate 216 in van der Vliet *et al.* (2001). Absolute diagnosability probably requires an analysis of mtDNA.

The Guidelines set by Helbig *et al.* (2002) require that all, or almost all, individuals in a species be distinguishable from individuals in all other species. Variation within both *nitidus* and the other Greenish Warbler taxa makes the

diagnosability of 'Green Warbler' uncertain. The yellow colour of the supercilium, and sides of head and neck, would probably fulfil diagnosability criteria if this character was present in all individuals, yet this has been shown not to be the case. With further research, it might possibly be shown that, in addition to the molecular differences, *viridanus* and *nitidus* are 100% diagnosable on the basis of a combination of plumage and biometric characteristics. In the absence of this evidence, we have to conclude that *nitidus* is still best regarded as a subspecies of *P. trochiloides* at present.

### Conclusion

Although *P. t. plumbeitarsus* and *P. t. viridanus* behave as different species, the clinal nature of variation across the whole Greenish Warbler complex makes it impossible to draw biologically meaningful dividing lines between the subspecies. The relationship between the components of the 'ring species' is best regarded as speciation in process. Any split of the ring into two species would be entirely arbitrary, and as such cannot be supported at this time. Further evidence regarding the diagnosability (or otherwise) of *obscuratus* and *plumbeitarsus*, or gene flow across the distributional gap between these two taxa, may allow reassessment of these conclusions.

Irwin *et al.* (2001b) pointed out that ring species do not fall easily into traditional taxonomic hierarchies of species and subspecies. Previous taxonomic treatments of the five Greenish Warbler taxa in the proposed ring have either lumped them all as one species (the position maintained here) or have split *plumbeitarsus*. Neither taxonomic treatment yields all the relevant information about variation and inter-taxon relationships within the complex.

The relationship of *nitidus* to other taxa is complicated by its allopatric distribution and the phenotypic variation within the Greenish Warbler complex. Having reviewed current evidence, it cannot be shown that *nitidus* fulfils

formal requirements for diagnosability under the Guidelines (Helbig *et al.* 2002), and it is therefore retained as a subspecies of *P. trochiloides*. The evidence which has been central to the analysis of the other Greenish Warbler taxa, male-male song recognition, supports this conclusion. It seems likely, however, that further analysis of the variation within the Greenish Warbler complex will provide alternative, and better defined, diagnostic characters.

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