

## Graphical abstract

Phylogeny of Phylloscopidae based on the mitochondrial cytochrome *b* and nuclear ODC, [myoglobin](#) and [GAPDH introns](#) inferred by \*BEAST.

Traditional *Seicercus* species are highlighted in red. Photo by Craig Brelsford (14), James Eaton (2, 10, 18, 19), Göran Ekström (9, 15, 16, 22), Jocko Hammar (6), Jonathan Martinez (5, 7, 8, 11, 20), Yann Muzika (1), Frédéric Pelsy (12), Megan & Chris Perkins (3), Nick Robinson (4, 13, 17, 21).



## Complete species-level phylogeny of the leaf warbler (Aves: Phylloscopidae) radiation

Per Alström<sup>a,b,c,\*</sup>, Frank E. Rheindt<sup>d</sup>, Ruiying Zhang<sup>c</sup>, Min Zhao<sup>c</sup>, Jing Wang<sup>c</sup>, Xiaojia Zhu<sup>c</sup>, Chyi Yin Gwee<sup>d</sup>, Yan Hao<sup>c</sup>, Jan Ohlson<sup>e</sup>, Chenxi Jia<sup>c</sup>, Dewi M. Prawiradilaga<sup>f</sup>, Per G.P. Ericson<sup>e</sup>, Fumin Lei<sup>c</sup>, Urban Olsson<sup>g</sup>

<sup>a</sup> Department of Ecology and Genetics, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 752 36 Uppsala, Sweden

<sup>b</sup> Swedish Species Information Centre, Swedish University of Agricultural Sciences (SLU), Box 7007, Uppsala SE-750 07, Sweden

<sup>c</sup> Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

<sup>d</sup> Department of Biological Sciences, National University of Singapore, 16 Science Drive 4, 117558 Singapore, Singapore

<sup>e</sup> Department of Bioinformatics and Genetics, Swedish Museum of Natural History, Box 50007, Stockholm SE-10405, Sweden

<sup>f</sup> Research Centre for Biology, Indonesian Institute of Sciences (LIPI), Cibinong Science Centre, Jalan Raya Jakarta Bogor KM 46, Bogor 16911, Indonesia

<sup>g</sup> Department of Biology and Environmental Science, University of Gothenburg, Box 463, SE-405 30 Gothenburg, Sweden

### ARTICLE INFO

#### Keywords:

Species tree

Concatenation

Taxonomic revision

### ABSTRACT

The leaf warbler radiation (Aves: Phylloscopidae) has undergone a c. 50% increase in the number of recognised species over the last three decades, mainly as a result of analyses of vocalisations and DNA. Using a multilocus dataset for all of the species in this family, and multispecies coalescent-based as well as concatenation methods, we provide the first complete species-level phylogeny for this important group, as well as an estimate of the timing of diversification. The most recent common ancestor for the family was dated at 11.7 million years ago (mya) (95% highest posterior density 9.8–13.7 mya), and divergence times between sister species ranged from 0.5 mya (0.3–0.8 mya) to 6.1 mya (4.8–7.5 mya). Based on our results, we support synonymising *Seicercus* with *Phylloscopus*, which results in a monogeneric Phylloscopidae. We discuss the pros and cons of this treatment, and we argue against proliferation of taxonomic names, and conclude that a large monogeneric Phylloscopidae leads to the fewest taxonomic changes compared to traditional classifications.

We briefly discuss morphological evolution in the light of the phylogeny. The time calibrated phylogeny is a major improvement compared to previous studies based on a smaller number of species and loci and can provide a basis for future studies of other aspects of phylloscopid evolution.

### 1. Introduction

The systematics of the avian superfamily Sylvioidea have been the subject of multiple studies in the last two decades, both at the superfamily level (Alström et al., 2006; Fregin et al., 2012) and at the level of individual families (Cibois et al., 1999; Cibois, 2003; Cibois et al., 2001; Pasquet et al., 2001; Sheldon et al., 2005; Moyle and Marks, 2006; Johansson et al., 2007, 2016; Nguembock et al., 2007; Fregin et al., 2009; Gelang et al., 2009; Päckert et al., 2010; Alström et al., 2011a, 2011b, 2013a; Moyle et al., 2012; Olsson et al., 2013). This has led to major reclassifications at both these ranks (comprehensive review, also at lower levels, in Alström et al. (2013b)), and at family level in Winkler et al. (2015)).

One of the families in Sylvioidea is the Phylloscopidae, which has been recognised at the family level since 2006 (Alström et al., 2006).

This family comprises the Old World leaf warblers, which are small insectivorous birds renowned for often being difficult to identify by appearance but more easily distinguishable by song (Ticehurst, 1938; Williamson, 1967; Alström and Ranft, 2003; Bairlein et al., 2006). They are distributed throughout much of the Old World, with the highest number occurring in Asia. Up to 16 species occur along an elevational gradient in the eastern Himalayas and at least 20 species in the Qinling mountains in north central China. Northerly breeding species or populations are migratory, whereas more southern breeders are resident or short distance, often altitudinal, migrants (Bairlein et al., 2006). Some of the species are remarkable long-distance migrants. For example, the Willow Warbler *Phylloscopus trochilus* breeds across the northern Palearctic from western Europe to northeastern Siberia, and all populations winter in Sub-Saharan Africa, south to southern South Africa. The leaf warblers are very prominent members of many

\* Corresponding author at: Department of Ecology and Genetics, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 752 36 Uppsala, Sweden.  
E-mail address: [per.alstrom@ebc.uu.se](mailto:per.alstrom@ebc.uu.se) (P. Alström).

Table 1

Taxonomy according to five different sources. We support the genus classification by del Hoyo and Collar (2016). The sequence presented here is the one we advocate based on our phylogeny (see Section 2.4 for principles applied). References are to taxonomic revisions, including descriptions of new species. Names in bold refer to species new to science or species elevated from subspecies to species rank since Watson et al. (1986).

Watson et al. (1986)	Dickinson and Christidis (2014)	Boyd (2017)	Gill and Donsker (2017)	del Hoyo and Collar (2016)	References
<i>Phylloscopus sibilatrix</i>	<i>Rhadina sibilatrix</i>	<i>Rhadina sibilatrix</i>	<i>Phylloscopus sibilatrix</i>	<i>Phylloscopus sibilatrix</i>	
<i>Phylloscopus bonelli</i>	<i>Rhadina bonelli</i>	<i>Rhadina bonelli</i>	<i>Phylloscopus bonelli</i>	<i>Phylloscopus bonelli</i>	
<i>Phylloscopus bonelli orientalis</i>	<i>Rhadina orientalis</i>	<i>Rhadina orientalis</i>	<i>Phylloscopus orientalis</i>	<i>Phylloscopus orientalis</i>	Helbig et al. (1995)
<i>Phylloscopus maculipennis</i>	<i>Abornis maculipennis</i>	<i>Abornis maculipennis</i>	<i>Phylloscopus maculipennis</i>	<i>Phylloscopus maculipennis</i>	
<i>Phylloscopus pulcher</i>	<i>Abornis pulchra</i>	<i>Abornis pulcher</i>	<i>Phylloscopus pulcher</i>	<i>Phylloscopus pulcher</i>	
<i>Phylloscopus inornatus</i>	<i>Abornis inornata</i>	<i>Abornis inornata</i>	<i>Phylloscopus inornatus</i>	<i>Phylloscopus inornatus</i>	Irwin et al. (2001a)
<i>Phylloscopus inornatus humei</i>	<i>Abornis humei</i>	<i>Abornis humei</i>	<i>Phylloscopus humei</i>	<i>Phylloscopus humei</i>	
<i>Phylloscopus subviridis</i>	<i>Abornis subviridis</i>	<i>Abornis subviridis</i>	<i>Phylloscopus subviridis</i>	<i>Phylloscopus subviridis</i>	
<i>Phylloscopus proregulus<sup>a</sup></i>	<i>Abornis yunnanensis</i>	<i>Abornis yunnanensis</i>	<i>Phylloscopus yunnanensis</i>	<i>Phylloscopus yunnanensis</i>	Alström et al. (1990), Alström et al. (1992), Martens et al. (2004) <sup>b</sup>
<i>Phylloscopus proregulus proregulus<sup>d</sup></i>	<i>Abornis proregulus</i>	<i>Abornis proregulus</i>	<i>Phylloscopus proregulus</i>	<i>Phylloscopus proregulus</i>	
<i>Phylloscopus proregulus chloronotus<sup>d</sup></i>	<i>Abornis kansuensis</i>	<i>Abornis kansuensis</i>	<i>Phylloscopus kansuensis</i>	<i>Phylloscopus kansuensis</i>	Alström et al. (1997), Martens et al. (2004)
<i>Phylloscopus proregulus chloronotus<sup>c</sup></i>	<i>Abornis chloronotus</i>	<i>Abornis chloronotus</i>	<i>Phylloscopus chloronotus</i>	<i>Phylloscopus chloronotus</i>	Alström and Olsson (1990), Martens et al. (2004)
<i>Phylloscopus proregulus chloronotus<sup>c</sup></i>	<i>Abornis forresti</i>	<i>Abornis forresti</i>	<i>Phylloscopus forresti</i>	<i>Phylloscopus forresti</i>	Martens et al. (2004)
<i>Phylloscopus tyleri</i>	<i>Phylloscopus tyleri</i>	<i>Phylloscopus tyleri</i>	<i>Phylloscopus tyleri</i>	<i>Phylloscopus tyleri</i>	
<i>Phylloscopus armandii</i>	<i>Phylloscopus armandii</i>	<i>Phylloscopus armandii</i>	<i>Phylloscopus armandii</i>	<i>Phylloscopus armandii</i>	
<i>Phylloscopus schwarzi</i>	<i>Phylloscopus schwarzi</i>	<i>Phylloscopus schwarzi</i>	<i>Phylloscopus schwarzi</i>	<i>Phylloscopus schwarzi</i>	
<i>Phylloscopus griseolus</i>	<i>Phylloscopus griseolus</i>	<i>Phylloscopus griseolus</i>	<i>Phylloscopus griseolus</i>	<i>Phylloscopus griseolus</i>	
<i>Phylloscopus affinis</i>	<i>Phylloscopus affinis</i>	<i>Phylloscopus affinis</i>	<i>Phylloscopus affinis</i>	<i>Phylloscopus affinis</i>	
(not yet described)	<i>Phylloscopus occisensis</i>	<i>Phylloscopus occisensis</i>	<i>Phylloscopus occisensis</i>	<i>Phylloscopus affinis occisensis</i>	Martens et al. (2008)
<i>Phylloscopus fulgiventis<sup>f</sup></i>	<i>Phylloscopus fulgiventis</i>	<i>Phylloscopus fulgiventis</i>	<i>Phylloscopus fulgiventis</i>	<i>Phylloscopus fulgiventis</i>	
<i>Phylloscopus fuscatus<sup>f</sup></i>	<i>Phylloscopus fuscatus</i>	<i>Phylloscopus fuscatus</i>	<i>Phylloscopus fuscatus</i>	<i>Phylloscopus fuscatus</i>	
<i>Phylloscopus neglectus</i>	<i>Phylloscopus neglectus</i>	<i>Phylloscopus neglectus</i>	<i>Phylloscopus neglectus</i>	<i>Phylloscopus neglectus</i>	
<i>Phylloscopus affinis subaffinis</i>	<i>Phylloscopus subaffinis</i>	<i>Phylloscopus subaffinis</i>	<i>Phylloscopus subaffinis</i>	<i>Phylloscopus subaffinis</i>	Alström and Olsson (1992), Alström et al. (1993)
<i>Phylloscopus trochilus</i>	<i>Phylloscopus trochilus</i>	<i>Phylloscopus trochilus</i>	<i>Phylloscopus trochilus</i>	<i>Phylloscopus trochilus</i>	
<i>Phylloscopus sibilatrix</i>	<i>Phylloscopus sibilatrix</i>	<i>Phylloscopus sibilatrix</i>	<i>Phylloscopus sibilatrix</i>	<i>Phylloscopus sibilatrix</i>	
<i>Phylloscopus sibilatrix lorenzii</i>	<i>Phylloscopus lorenzii</i>	<i>Phylloscopus lorenzii</i>	<i>Phylloscopus sibilatrix lorenzii</i>	<i>Phylloscopus sibilatrix lorenzii</i>	
<i>Phylloscopus sibilatrix canariensis</i>	<i>Phylloscopus canariensis</i>	<i>Phylloscopus canariensis</i>	<i>Phylloscopus canariensis</i>	<i>Phylloscopus canariensis</i>	
<i>Phylloscopus collybita</i>	<i>Phylloscopus collybita</i>	<i>Phylloscopus collybita</i>	<i>Phylloscopus collybita</i>	<i>Phylloscopus collybita</i>	Helbig et al. (1996)
<i>Phylloscopus collybita tristis</i>	<i>Phylloscopus collybita tristis</i>	<i>Phylloscopus collybita tristis</i>	<i>Phylloscopus collybita tristis</i>	<i>Phylloscopus collybita tristis</i>	
<i>Phylloscopus collybita brehmii<sup>g</sup></i>	<i>Phylloscopus ibericus</i>	<i>Phylloscopus ibericus</i>	<i>Phylloscopus ibericus</i>	<i>Phylloscopus ibericus</i>	Shpilina et al. (2017)
<i>Phylloscopus cebuensis</i>	<i>Seicercus cebuensis</i>	<i>“Pycnosphyrys” cebuensis</i>	<i>Phylloscopus cebuensis</i>	<i>Phylloscopus cebuensis</i>	Salomon 1989, Helbig et al. (1996), Helbig et al. (2001)
<i>Phylloscopus olivaceus</i>	<i>Seicercus olivaceus</i>	<i>“Pycnosphyrys” olivaceus</i>	<i>Phylloscopus olivaceus</i>	<i>Phylloscopus olivaceus</i>	
<i>Phylloscopus coronatus</i>	<i>Seicercus coronatus</i>	<i>“Pycnosphyrys” coronatus</i>	<i>Phylloscopus coronatus</i>	<i>Phylloscopus coronatus</i>	
<i>Phylloscopus ijimae</i>	<i>Seicercus ijimae</i>	<i>“Pycnosphyrys” ijimae</i>	<i>Phylloscopus ijimae</i>	<i>Phylloscopus ijimae</i>	
<i>Phylloscopus ruficapilla</i>	<i>Seicercus ruficapilla</i>	<i>Pindulus ruficapilla</i>	<i>Phylloscopus ruficapilla</i>	<i>Phylloscopus ruficapilla</i>	
<i>Phylloscopus umbrovirens</i>	<i>Seicercus umbrovirens</i>	<i>Pindulus umbrovirens</i>	<i>Phylloscopus umbrovirens</i>	<i>Phylloscopus umbrovirens</i>	
<i>Phylloscopus laetus</i>	<i>Seicercus laetus</i>	<i>Pindulus laetus</i>	<i>Phylloscopus laetus</i>	<i>Phylloscopus laetus</i>	

(continued on next page)

Table 1 (continued)

Watson et al. (1986)	Dickinson and Christidis (2014)	Boyd (2017)	Gill and Donsker (2017)	del Hoyo and Collar (2016)	References
<i>Phylloscopus laurae</i> <i>Phylloscopus budongoensis</i> <i>Phylloscopus herberti</i> <i>Seiurus affinis</i> <i>Seiurus poliopteryx</i> <i>Seiurus burkii</i> <sup>†</sup>	<i>Seiurus laurae</i> <i>Seiurus budongoensis</i> <i>Seiurus herberti</i> <i>Seiurus affinis</i> <i>Seiurus poliopteryx</i> <i>Seiurus burkii</i>	<i>Pindulus laurae</i> <i>Pindulus budongoensis</i> <i>Pindulus herberti</i> <i>Seiurus affinis</i> <i>Seiurus poliopteryx</i> <i>Seiurus burkii</i>	<i>Phylloscopus laurae</i> <i>Phylloscopus budongoensis</i> <i>Phylloscopus herberti</i> <i>Seiurus affinis</i> <i>Seiurus poliopteryx</i> <i>Seiurus burkii</i>	<i>Phylloscopus laurae</i> <i>Phylloscopus budongoensis</i> <i>Phylloscopus herberti</i> <i>Phylloscopus intermedius</i> <sup>†</sup> <i>Phylloscopus poliopteryx</i> <i>Phylloscopus burkii</i>	Alström and Olsson (1999), Alström and Olsson (2000), Martens et al. (1999), Olsson et al. (2004), Päckert et al. (2004)
<i>Seiurus burkii</i> <sup>†</sup> <i>Seiurus burkii</i> <sup>†</sup> <i>Seiurus burkii</i> <sup>†</sup> (not yet described) (not yet described) <i>Phylloscopus nitidus</i> <i>Phylloscopus plumbeitarsus</i> <i>Phylloscopus trochiloides</i>	<b><i>Seiurus tephrocephalus</i></b> <i>Seiurus valentini</i> <i>Seiurus whistleri</i> <i>Seiurus omeiensis</i> <i>Seiurus soror</i> <i>Seiurus nitidus</i> <i>Seiurus plumbeitarsus</i> <i>Seiurus trochiloides</i>	<i>Seiurus tephrocephalus</i> <i>Seiurus valentini</i> <i>Seiurus whistleri</i> <i>Seiurus omeiensis</i> <i>Seiurus soror</i> <i>Acanthopneuste nitidus</i> <i>Acanthopneuste plumbeitarsus</i> <i>Acanthopneuste trochiloides</i>	<b><i>Seiurus tephrocephalus</i></b> <i>Seiurus valentini</i> <i>Seiurus whistleri</i> <i>Seiurus omeiensis</i> <i>Seiurus soror</i> <i>Phylloscopus nitidus</i> <i>Phylloscopus plumbeitarsus</i> <i>Phylloscopus trochiloides</i>	<b><i>Phylloscopus tephrocephalus</i></b> <i>Phylloscopus valentini</i> <i>Phylloscopus whistleri</i> <i>Phylloscopus omeiensis</i> <i>Phylloscopus soror</i> <i>Phylloscopus nitidus</i> <i>Phylloscopus plumbeitarsus</i> <i>Phylloscopus trochiloides</i>	See S. burkii See S. burkii See S. burkii See S. burkii See S. burkii See P. trochiloides See P. trochiloides Irwin (2000), Irwin et al. (2001b), Irwin et al. (2005), Irwin et al. (2008), Alcáide et al. (2014)
<i>Phylloscopus trochiloides viridanus</i> <i>Phylloscopus trochiloides obscuratus</i> (not yet described) <i>Phylloscopus magnirostris</i> <i>Phylloscopus tenellipes</i> <i>Phylloscopus tenellipes</i> <sup>†</sup> <i>Phylloscopus borealis xanthodryas</i> <i>Phylloscopus borealis</i> <sup>k</sup>	<i>Seiurus trochiloides viridanus</i> <i>Seiurus trochiloides obscuratus</i> <i>Seiurus emeiensis</i> <i>Seiurus magnirostris</i> <i>Seiurus tenellipes</i> <i>Seiurus borealoides</i> <i>Seiurus xanthodryas</i> <i>Seiurus borealis</i>	<i>Acanthopneuste viridanus</i> <i>Acanthopneuste obscuratus</i> <i>Acanthopneuste emeiensis</i> <i>Acanthopneuste magnirostris</i> <i>Acanthopneuste tenellipes</i> <i>Acanthopneuste borealoides</i> <i>Acanthopneuste xanthodryas</i> <i>Acanthopneuste borealis</i>	<i>Phylloscopus trochiloides viridanus</i> <i>Phylloscopus trochiloides obscuratus</i> <b><i>Phylloscopus emeiensis</i></b> <i>Phylloscopus magnirostris</i> <i>Phylloscopus tenellipes</i> <b><i>Phylloscopus borealoides</i></b> <b><i>Phylloscopus xanthodryas</i></b> <i>Phylloscopus borealis</i>	<i>Phylloscopus trochiloides viridanus</i> <i>Phylloscopus trochiloides obscuratus</i> <b><i>Phylloscopus emeiensis</i></b> <i>Phylloscopus magnirostris</i> <i>Phylloscopus tenellipes</i> <b><i>Phylloscopus borealoides</i></b> <b><i>Phylloscopus xanthodryas</i></b> <i>Phylloscopus borealis</i>	See P. trochiloides See P. trochiloides Alström and Olsson (1995) Martens (1988) See P. borealis Saitoh et al. (2006), Reeves et al. (2008), Saitoh et al. (2010), Martens, (2010), Alström et al. (2011c), Withrow et al. (2016) See P. borealis
<i>Phylloscopus borealis xanthodryas</i> <i>Seiurus castaneiceps</i> <i>Seiurus grammiceps</i> <i>Seiurus grammiceps sumatrensis</i> <i>Seiurus montis</i> (not yet described) <i>Phylloscopus cantator</i> <i>Phylloscopus ricketti</i> <sup>m</sup> <i>Phylloscopus occipitalis</i> <i>Phylloscopus reguloides</i> <sup>n</sup> <i>Phylloscopus reguloides claudiae</i>	<b><i>Seiurus examinandus</i></b> <i>Seiurus castaneiceps</i> <i>Seiurus grammiceps</i> <i>Seiurus grammiceps sumatrensis</i> <i>Seiurus montis</i> <i>Seiurus calcitatis</i> <i>Seiurus cantator</i> <i>Seiurus ricketti</i> <i>Seiurus occipitalis</i> <i>Seiurus reguloides</i> <i>Seiurus claudiae</i>	<b><i>Acanthopneuste examinandus</i></b> <i>Pycnosphyus castaneiceps</i> <i>Pycnosphyus grammiceps</i> <i>Pycnosphyus grammiceps sumatrensis</i> <sup>n</sup> <i>Pycnosphyus montis</i> <i>Cryptigata calcitatis</i> <i>Cryptigata cantator</i> <i>Cryptigata ricketti</i> <i>Cryptigata occipitalis</i> <i>Cryptigata reguloides</i> <i>Cryptigata claudiae</i>	<b><i>Phylloscopus examinandus</i></b> <i>Seiurus castaneiceps</i> <i>Seiurus grammiceps</i> <i>Seiurus grammiceps sumatrensis</i> <i>Seiurus montis</i> <b><i>Phylloscopus calcitatis</i></b> <i>Phylloscopus cantator</i> <i>Phylloscopus ricketti</i> <i>Phylloscopus occipitalis</i> <i>Phylloscopus reguloides</i> <b><i>Phylloscopus claudiae</i></b>	<b><i>Phylloscopus examinandus</i></b> <i>Phylloscopus castaneiceps</i> <i>Phylloscopus grammiceps</i> <i>Phylloscopus sumatrensis</i> <i>Phylloscopus montis</i> <b><i>Phylloscopus calcitatis</i></b> <i>Phylloscopus cantator</i> <i>Phylloscopus ricketti</i> <i>Phylloscopus occipitalis</i> <i>Phylloscopus reguloides</i> <b><i>Phylloscopus claudiae</i></b>	Alström et al. (2010) Olsson et al. (2005), Päckert et al. (2009)

(continued on next page)



Table 1 (continued)

Watson et al. (1986)	Dickinson and Christidis (2014)	Boyd (2017)	Gill and Donsker (2017)	del Hoyo and Collar (2016)	References
<i>Phylloscopus reguloides folioides</i> + <i>P. ricketti</i> <i>goodsoni</i>	<b><i>Seicercus goodsoni</i></b>	<b><i>Cryptigata goodsoni</i></b>	<b><i>Phylloscopus goodsoni</i></b>	<b><i>Phylloscopus goodsoni</i></b>	Alström et al. (1995), Olsson et al. (2005), Päckert et al. (2009)
<i>Phylloscopus davisoni</i>	<i>Seicercus klossi</i> <sup>f</sup>	<i>Cryptigata davisoni</i>	<i>Phylloscopus davisoni</i>	<i>Phylloscopus intensior</i> <sup>l</sup>	Olsson et al. (2005), Päckert et al. (2009)
<i>Seicercus xanthoschistos</i>	<i>Seicercus xanthoschistos</i>	<i>Cryptigata xanthoschistos</i>	<i>Phylloscopus xanthoschistos</i>	<i>Phylloscopus xanthoschistos</i>	Olsson et al. (2005)
(not yet described)	<b><i>Seicercus hainanus</i></b>	<b><i>Cryptigata hainanus</i></b>	<b><i>Phylloscopus hainanus</i></b>	<b><i>Phylloscopus hainanus</i></b>	Olsson et al. (1993)
<i>Phylloscopus davisoni ogilviegranti</i>	<b><i>Seicercus ogilviegranti</i></b> <sup>4</sup>	<b><i>Cryptigata ogilviegranti</i></b>	<b><i>Phylloscopus ogilviegranti</i></b>	<b><i>Phylloscopus ogilviegranti</i></b>	Olsson et al. (2005), Päckert et al. (2009)
<i>Phylloscopus trivirgatus</i>	<i>Seicercus trivirgatus</i>	<i>Cryptigata trivirgata</i>	<i>Phylloscopus trivirgatus</i> <sup>o</sup>	<i>Phylloscopus trivirgatus</i>	
<i>Phylloscopus trivirgatus nigrorum</i>	<i>Seicercus trivirgatus nigrorum</i>	<i>Cryptigata nigrorum</i>	<i>Phylloscopus nigrorum</i>	<i>Phylloscopus trivirgatus nigrorum</i>	
<i>Phylloscopus presbytes</i>	<i>Seicercus presbytes</i>	<i>Cryptigata presbytes</i>	<i>Phylloscopus presbytes</i>	<i>Phylloscopus presbytes</i>	
<i>Phylloscopus makirensis</i>	<i>Seicercus makirensis</i>	<i>Cryptigata makirensis</i>	<i>Phylloscopus makirensis</i>	<i>Phylloscopus poliocephalus makirensis</i>	
<i>Phylloscopus sarasinorum</i>	<i>Seicercus sarasinorum</i>	<i>Cryptigata sarasinorum</i>	<i>Phylloscopus sarasinorum</i>	<i>Phylloscopus sarasinorum</i>	
<i>Phylloscopus amoenus</i>	<i>Seicercus amoenus</i>	<i>Cryptigata amoena</i>	<i>Phylloscopus amoenus</i>	<i>Phylloscopus amoenus</i>	
<i>Phylloscopus poliocephalus</i> <sup>p</sup>	<i>Seicercus majorensis</i> <sup>p</sup>	<i>Cryptigata majorensis</i> <sup>p</sup>	<i>Phylloscopus majorensis</i> <sup>p</sup>	<i>Phylloscopus poliocephalus</i> <sup>p</sup>	
<i>Phylloscopus poliocephalus</i> <sup>p</sup>	<i>Seicercus majorensis</i> <sup>p</sup>	<i>Cryptigata majorensis</i> <sup>p</sup>	<i>Phylloscopus majorensis</i> <sup>p</sup>	<i>Phylloscopus majorensis</i> <sup>p</sup>	
<i>Phylloscopus poliocephalus misortensis</i>	<i>Seicercus majorensis misortensis</i>	?	<i>Phylloscopus majorensis misortensis</i>	<i>Phylloscopus misortensis</i>	

<sup>a</sup> Not included, not even as a synonym, despite having been described in 1922.

<sup>b</sup> Described as a new species, *Phylloscopus sichuanensis*, by Alström et al. (1992).

<sup>c</sup> Synonymised with *Phylloscopus proregulus chloronotus*.

<sup>d</sup> Synonymised with *Phylloscopus proregulus proregulus*.

<sup>e</sup> Includes *P. proregulus* (sensu stricto), *P. kansuensis*, *P. chloronotus* and *P. forresti*.

<sup>f</sup> The taxon *weigoldi* is treated as a subspecies of *P. fuscatus* by Watson et al. (1986), but as a subspecies of *P. fuligiventer* by other authors.

<sup>g</sup> The name *ibericus* has priority over *brehmii*, as noted by later authors.

<sup>h</sup> No subspecies included, so this is inferential.

<sup>i</sup> See del Hoyo and Collar (2016) for explanation.

<sup>j</sup> Includes *S. burkii* (sensu stricto), *S. tephrocephalus*, *S. valentini* and *S. whistleri* (*S. soror* and *S. omeiensis* not yet described).

<sup>k</sup> Includes *P. examinandus* and *P. xanthodryas*.

<sup>l</sup> Synonymised with *P. tenellipes* (monotypic).

<sup>m</sup> Includes *P. goodsoni*.

<sup>n</sup> Includes *P. claudiae* and *P. goodsoni*.

<sup>o</sup> Circumscription differs from other authors.

<sup>p</sup> Circumscription varies somewhat among authors.

<sup>q</sup> Treated as monotypic based on misinterpretation of results by Olsson et al. (2005) and Päckert et al. (2009).

<sup>r</sup> This is a mistake based on misinterpretation of results by Olsson et al. (2005) and Päckert et al. (2009).

ecosystems; e.g., they comprise up to 40% of all birds at some localities in the western Himalayas (Price et al., 2003), and *P. trochilus* has the largest population of all Swedish birds (Ottosson and Ottvall, 2012).

The leaf warblers are usually placed in the genera *Phylloscopus* (“classic leaf warblers”) and *Seicercus* (“spectacled warblers”) (Watson et al., 1986; Sibley and Monroe, 1990; Dickinson, 2003; Bairlein et al., 2006). The taxonomy has undergone dramatic change in the past three decades, with the number of recognised species rising from 52 in the mid-1980s (Watson et al., 1986) to 77–78 at present (Dickinson and Christidis, 2014; del Hoyo and Collar, 2016; Gill and Donsker, 2017; Table 1). Six new species have been described (Table 1), and Eaton et al. (2016) have proposed six further splits and documented three new species from Indonesia. This sharp increase in the number of species is mainly the result of studies of vocalisations and DNA, which have elevated multiple subspecies to species rank and also been of importance in the discovery of the new species (Table 1; see reviews in Rheindt (2006); Martens (2010) and Alström et al. (2013b)).

Several phylogenetic studies have been undertaken based on a variable number of species and a small number of loci (Richman and Price, 1992; Martens et al., 2004; Päckert et al., 2004; Olsson et al., 2004, 2005; Johansson et al., 2007; Martens et al., 2008; Päckert et al., 2009). The most comprehensive analysis, which only utilised published sequences from two mitochondrial genes and one nuclear intron, included 69 species (Alström et al., 2013b). These studies have suggested that the traditional *Seicercus* is nested within *Phylloscopus*, and also that *Seicercus* is separated into two non-sister clades. These analyses have instigated others to propose taxonomic changes. Dickinson and Christidis (2014) split *Phylloscopus* into *Rhadina*, *Abrornis* and *Phylloscopus sensu stricto*, and expanded *Seicercus* to also include many of the traditional *Phylloscopus*. In contrast, del Hoyo and Collar (2016) synonymised *Seicercus* with *Phylloscopus* to create a monogeneric family. At the other extreme, Boyd (2017) recognised no fewer than nine genera (Table 1).

Leaf warblers have been used as model organisms in studies of evolution of, e.g., breeding distributions (Price et al., 1997; Johansson et al., 2007), ecological differentiation (Richman and Price, 1992; Richman, 1996; Price, 2010), vocalisations (Badyaev and Leaf, 1997; Irwin, 2000; Irwin et al., 2008; Mahler and Gil, 2009; Singh and Price, 2015; Tietze et al., 2015), eco-morphological adaptations (Marchetti, 1993; Marchetti et al., 1995; Marchetti, 1998; Forstmeier and Keßler, 2001; Forstmeier et al., 2001b), migration (Bensch et al., 1999, 2006a,b; Chamberlain et al., 2000), and ring species (Irwin et al., 2001b, 2005; Alcaide et al., 2014).

Until now, no complete species level phylogeny has been available for the family, and divergence time estimates have only been carried out for a subset of species (Price, 2010; Päckert et al., 2012; Price et al., 2014). Here, we present the first time-calibrated phylogeny of all currently recognised species of Phylloscopidae, using mitochondrial and nuclear markers. We also discuss the genus-level taxonomy based on our results.

## 2. Material and methods

### 2.1. Study group

We studied all 76 species unanimously treated as separate species by Dickinson and Christidis (2014), del Hoyo and Collar (2016) and Gill & Donsker (2017), plus *P. occisnensis* (treated as a subspecies of *P. affinis* by del Hoyo and Collar, 2016). We aimed to include three samples per species, but for 18 species we could not obtain that number; in total, 198 individuals were analysed (Supplementary Table S1). As outgroups, we used *Cettia cetti* and *Aegithalos caudatus*, based on Fregin et al. (2012).

### 2.2. Lab work

DNA was extracted from fresh material (muscle, blood or feathers) and from toepad samples (two samples from two species) using the Qiagen DNA Mini Kit and following the manufacturer's protocol, but with 30 µl DTT added to the initial incubation step for the extraction from feathers and toepads. We sequenced the mitochondrial cytochrome *b* (*cytb*) gene and three nuclear regions: myoglobin intron 2 (*myo*), ornithine decarboxylase (mainly) introns 6–7 (*ODC*) and glyceraldehyde-3-phosphodehydrogenase intron 11 (*GAPDH*). Amplification and sequencing of the fresh samples followed the protocols described in Fregin et al. (2012). The toepads were sequenced in short (150–300 bp) segments with specifically designed primers and specific amplification profiles (Supplementary Table S2). Not all loci were obtained for all species (Supplementary Table S1). All sequences have been deposited in GenBank (Supplementary Table S1).

Authenticity of sequences obtained from toepad samples is supported by several lines of evidence. (1) When independent samples from the same species were included, the sequences were always highly similar. (2) Phylogenetic relationships based on individual PCR amplicons were the same as those using full contigs. (3) No fragment was identical to any other species included in this study. (4) Overlapping forward and reverse sequence fragments were identical. (5) The mitochondrial sequences showed no double signal in the electropherograms or stop codons, insertions or deletions, and a vast majority of nucleotide substitutions were found in the 3rd codon position and resulted in few amino acid substitutions (of which a majority also was found in sequences obtained from the fresh samples). The mitochondrial sequences from fresh samples were also validated in the same way.

### 2.3. Phylogenetic analyses

Sequences were aligned and checked using Geneious 7.1.9 (Biomatters Ltd.). For the nuclear loci, heterozygous sites were coded as ambiguous. Substitution models were selected based on the Akaike Information Criterion calculated in jModeltest 2.1.7 (Darriba et al., 2012). The GTR +  $\Gamma$  + I model was selected for *cytb*, and GTR +  $\Gamma$  for the other loci. Trees were estimated by Bayesian inference using BEAST 1.8.4 (Drummond et al., 2012). Xml files were generated in the BEAST utility program BEAUti version 1.8.4. Different data partitioning schemes were applied: (1) all loci were analysed separately (single-locus analyses) under the best-fit models and both (i) a strict clock and (ii) an uncorrelated lognormal distributed relaxed clock. (2) All sequences were concatenated and partitioned by locus. The best-fit models and a “birth-death incomplete sampling” tree prior with a normal distribution with mean 2.0 and standard deviation 1.0 were used. Because the strict clock was found to have higher posterior than the relaxed clock in the single-locus analyses (Supplementary Fig. S1), the strict clock was applied. Substitution and clock models were unlinked. (3) As in (2), but the GTR +  $\Gamma$  model was used also for *cytb* (cf. Weir and Schluter, 2008), and a strict clock with a mean rate of 2.1%/million years (Weir and Schluter, 2008) and a normal prior distribution with standard deviation 0.001 was applied to *cytb*. All analyses were run for 100–150 million generations and sampled every 1000 generations. Good mixing of the MCMC and reproducibility was established by multiple runs from independent starting points.

Integrative species tree estimation was performed using \*BEAST (Heled & Drummond, 2010) in BEAST 1.8.4, with gene trees and species trees estimated simultaneously. We ran analyses under the best-fit models, and a strict clock prior with the rate fixed to 1 (as per default). A piecewise linear population size model with a constant root was used as a prior for the multispecies coalescent and “birth-death incomplete sampling” as prior on divergence times. Default settings were used for the priors, except for the “birth-death mean growth rate”, for which a normal prior with initial value 1.0, mean 2.0 and Stdev. 1.0 was applied. 100–150 million generations were run in different runs, sampled

every 1000 generations; the analysis was repeated multiple times.

In all BEAST and \*BEAST analyses, convergence to the stationary distribution of the single chains was inspected in Tracer 1.6 (Rambaut et al., 2014). The effective sample sizes (ESS) for the joint likelihood and other parameter values were > 1000, representing good mixing of the MCMC, except in the \*BEAST analyses, where ESSs for at least the posterior were < 100. We also examined convergence and reproducibility by running each analysis at least twice (4 times for \*BEAST), with random starting points. In all analyses, including the \*BEAST analyses with low ESSs, the topologies (including relative branch lengths) and posterior probabilities (PPs) were similar across different runs. In most analyses the first 25% of generations were discarded as “burn-in”, and the PPs were calculated from the remaining samples; in the \*BEAST analyses where parameter convergence was not reached, the series of trees with the lowest posterior values were discarded (these were not only within the first 25% of the sampled trees). Trees were summarized using TreeAnnotator version 1.8.4 (included in BEAST package), choosing “Maximum clade credibility tree” and “Mean heights”, and displayed in FigTree version 1.4.3 (Rambaut, 2012). The trees from all \*BEAST analyses were combined using LogCombiner 1.8.4. Xml files for all analyses and a tree file in Newick format for the \*BEAST tree are available as Supplementary Material S1.

Analyses were also run using MrBayes 3.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Sequences were concatenated and partitioned by locus, and the best-fit models were applied. Default priors were used. Four Metropolis-coupled MCMC chains were run for 5 million generations and sampled every 1000 generations. Convergence was checked as for the BEAST analyses, as well as by the average standard deviation of split frequencies passing below 0.01 and the potential scale reduction factor (PSRF) being close to 1.00 for all parameters.

## 2.4. Principles for linear taxonomic sequence

There are a large number of alternative ways in which a phylogeny can be presented as a linear sequence. The sequence in which the species are listed in Table 1 is based on our phylogeny, and on the following simple principles. For each bifurcation in the tree, starting from the most basal one, we first list members of the smallest daughter lineage, or in the case of equal-size clades, the daughter lineage that contains the oldest bifurcation. This essentially conforms to listing the species in the order from the bottom to the top in Fig. 1 (because all clades are ordered in an “increasing” order). Sister species are listed either alphabetically or, in the case of species that have previously been treated as conspecific, with the oldest name first (e.g., *P. inornatus* before *P. humei*, because the latter was previously treated as a subspecies of the former).

## 3. Results

### 3.1. Phylogeny

The species tree (\*BEAST) and concatenation (BEAST, MrBayes) analyses are summarised in Fig. 1. There are some topological incongruences between the species tree and concatenation trees, but none of them have PP  $\geq 0.95$  for alternative reconstructions in both the \*BEAST and concatenation trees (cf. Supplementary Figs. S2–S3). Two primary clades were recovered ( $\alpha$ ,  $\beta$ ; Fig. 1), although clade  $\beta$  was only strongly supported in the concatenation trees (Supplementary Figs. S2–S3). Within clade  $\alpha$ , there was strong support in all analyses (posterior probability, PP,  $\geq 0.95$ ) for seven main clades (E, F, I, J, M, N, O) and a single species (*Phylloscopus emeiensis*) with uncertain relationships. Within clade  $\beta$ , three main clades were consistently strongly supported (U, W, X). Five of the deep nodes (G, L, K, R, Y) received low support in the \*BEAST phylogeny, but strong support in the concatenation analyses, whereas clade P had high PP in all but the MrBayes

analysis. Neither *Phylloscopus* nor *Seicercus* were supported as monophyletic. Several smaller subclades were recovered within the main clades, with support varying among these subclades as well as among analyses. Fifteen of the nodes had PP 0.36–0.89 (median 0.66) in the \*BEAST but  $\geq 0.95$  in one or both of the concatenation analyses (highlighted in orange in Fig. 1). In contrast, in three cases \*BEAST reported PP  $\geq 0.95$ , whereas concatenation produced considerably lower support (highlighted in blue in Fig. 1). Single-locus analyses varied in resolution and support, with *cytb* fully resolved and with generally well supported relationships, and with the nuclear loci, especially GAPDH, showing much evidence of incomplete lineage sorting, but no strongly supported incongruences (Supplementary Fig. S4).

### 3.2. Dating

The most basal split, between clades  $\alpha$  and  $\beta$ , was dated to 11.7 million years ago (mya) (95% highest posterior density [HPD] 9.8–13.7 mya) (Fig. 2). Divergence times between the three youngest pairs of sister species were 0.5 mya (95% HPD 0.3–0.8 mya: *S. grammiceps*–*S. montis*), 0.8 mya (0.5–1.1 mya: *P. maforensis*–*P. amoenus*) and 1.1 mya (0.8–1.5 mya: *P. hainanus*–*P. ogilviegranti*); and between the three oldest strongly supported sister pairs 4.1 mya (3.1–5.1 mya: *P. fuscatus*–*P. fulgiventris*), 4.1 mya (3.2–5.1 mya: *P. humei*–*P. inornatus*) and 6.1 mya (4.8–7.5 mya: *P. pulcher*–*P. maculipennis*). *Phylloscopus emeiensis*, *P. neglectus* and *P. tyleri* are the oldest single-species lineages, with divergences from their closest relatives between c. 7.3–8.3 mya. Deep intraspecific divergence was suggested within especially *P. bonelli*.

## 4. Discussion

### 4.1. Phylogeny

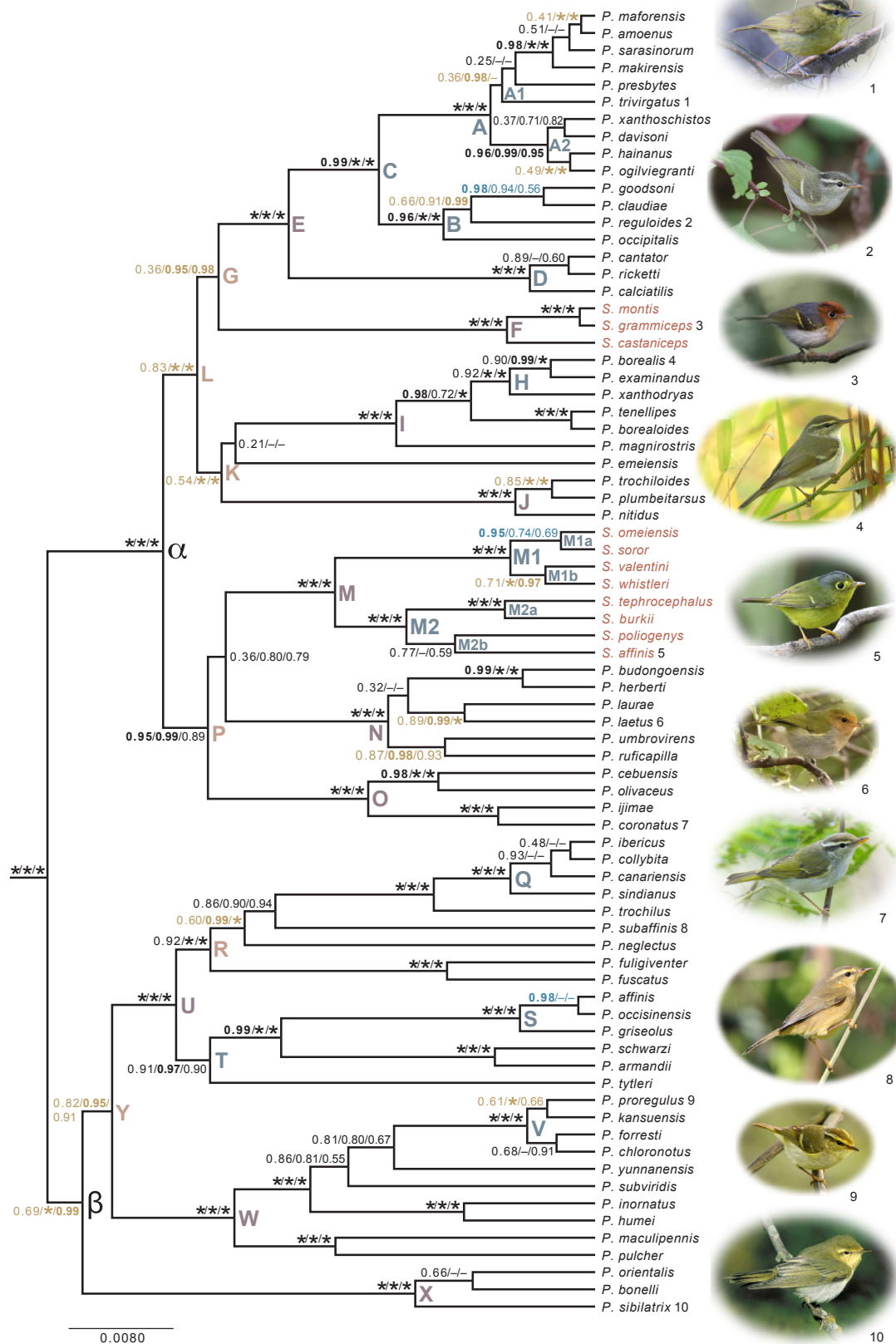
#### 4.1.1. Relationships among clades

The phylogeny is overall well resolved and well supported, and is a major improvement compared to previous studies based on a smaller number of species and loci (e.g. Alström et al., 2013a,b). The non-monophyly of both *Phylloscopus* and *Seicercus* suggested in previous analyses (Olsson et al., 2004, 2005; Päckert et al., 2009; Martens et al., 2008; Alström et al., 2013a,b) was well supported.

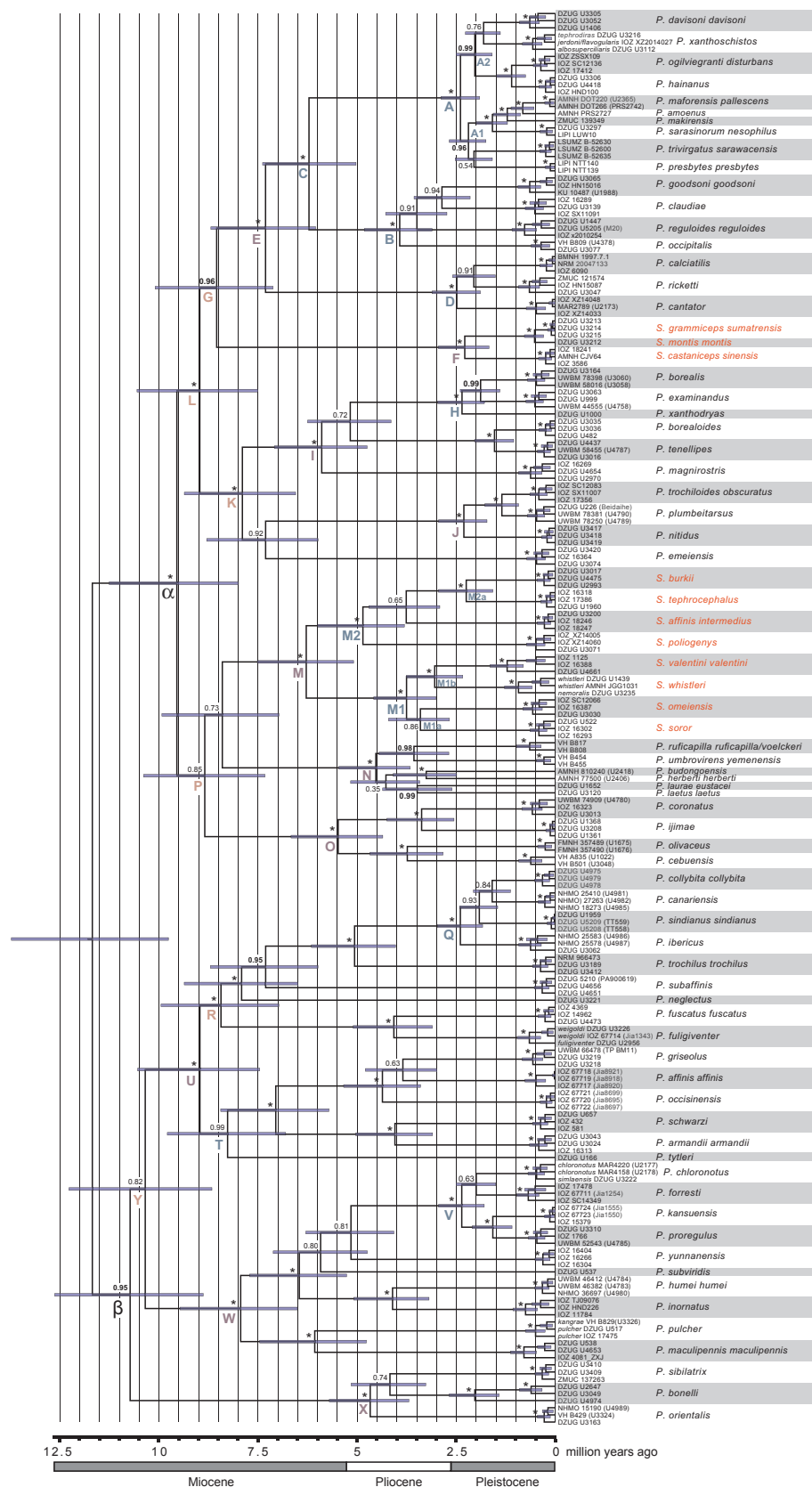
Except for a few poorly supported nodes, there was good topological congruence between the \*BEAST and concatenation trees. However, nodal support was generally lower in the \*BEAST than in the concatenation trees. This is expected, because \*BEAST accounts for gene tree heterogeneity (Heled and Drummond, 2010). \*BEAST should therefore provide more realistic support than concatenation for clades with incongruence among loci or cases where all or most of the signal comes from a single locus. All of the instances where concatenation reported much higher support than \*BEAST concern short branches – in fact, all but two of these branches are considerably shorter than any of those with higher support in the \*BEAST than in the concatenation analyses. This pattern indicates poor or conflicting signal in the data, and a more credible support provided by \*BEAST. However, as argued below, some of these cases are further corroborated by non-molecular data. With respect to the three nodes in which \*BEAST reported higher support than concatenation, the coalescent species tree approach might have lent additional signal that was not so strong in any of the individual single-gene or concatenation analyses, as has been shown in some other studies (Edwards et al., 2007; Brumfield et al., 2008; Liu et al., 2008; Liu and Edwards, 2009; Edwards, 2009).

The deeper nodes are generally less strongly supported than more terminal ones. Clade  $\alpha$ , which includes both traditional *Phylloscopus* and *Seicercus* warblers, was strongly supported in all analyses. Clade  $\beta$ , which contains only traditional *Phylloscopus*, was only strongly supported by concatenation. Within clade  $\alpha$ , none of the early splits into clades G, L, K and P received unanimously strong support across all





**Fig. 1.** Phylogeny of Phylloscopidae based on the mitochondrial cytochrome *b* and nuclear ODC, myoglobin and GAPDH introns inferred by \*BEAST. Traditional *Seicercus* species are highlighted in red. Values at nodes indicate posterior probabilities (PP) in the order \*BEAST/BEAST concatenated/MrBayes concatenated; \* indicates PP  $\geq 0.95$ . Nodes with PP  $< 0.90$  in \*BEAST but  $\geq 0.95$  in one or both concatenation trees are highlighted in orange, and nodes with PP  $\geq 0.95$  in \*BEAST but lower PP in the concatenation trees are highlighted in blue. – indicates alternative topology in concatenation analysis (see Supplementary Figs. S2–S3). Nodes referred to in the text are labelled with letters. Photos by Craig Brelsford (7), James Eaton (2), Göran Ekström (10), Jonathan Martinez (4, 5, 9), Yann Muzika (1, 3), Frédéric Pelsy (6), Nick Robinson (8). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** Chronogram for Phylloscopidae based on same data as in Fig. 1, inferred by BEAST and a 2.1%/million year molecular clock for cytochrome *b*. *Seicercus* species are highlighted in red. Values at nodes indicate posterior probabilities; \* indicates PP  $\geq 0.95$ . Labelling of nodes same as in Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

analyses; the three former were poorly supported by \*BEAST but strongly supported by concatenation, whereas clade P was only poorly supported by MrBayes. Within the second main clade,  $\beta$ , clade Y was only strongly supported by BEAST concatenation.

The strongly supported primary clades E, F, M, N, O, U, W and X are further corroborated by morphological features and/or geographical distributions. Within clade E, the species in clades A2 and B all have darker lateral and rather diffuse paler median crown-stripes, and usually uniformly pale orange lower mandibles, and all except one have distinct pale wing-bars; they are distributed through the Himalayas and mountainous regions of China and Southeast Asia. See below regarding clade A1. The species in clade D resemble the ones in clades A2 and B, and occur in partly the same area, but have even more contrasting crown patterns. Clade N comprises all the Afrotropical species, which are rather variable in plumage colouration, although they share a lack of pale wing-bars. The species in clade O have contrastingly yellowish undertail-coverts and all orange lower mandibles, and breed in Japan and neighbouring parts of Russia and China and the Philippines. Clade U contains the least conspicuously patterned species, which are all various shades of brown, grey or dull greenish above and whitish/brownish to yellowish below, without any contrasting crown, wing or tail markings. They breed across the Palearctic and temperate (mountainous) parts of the Oriental regions. The species in clade W are relatively small, with contrastingly patterned wings (including unique pale tertial markings) and in most species darker lateral and paler central crown-stripes and pale rump patches; in addition, the sister pair *P. maculipennis*–*P. pulcher* shows extensive white tail patterns. Their distributions are largely overlapping with those in clade U. The three species in clade X have contrastingly paler edges to the greater wing-coverts and tertials and have comparatively clean white underparts (except for yellow throat/upper breast in *P. sibilatrix*). They are mainly distributed in the Western Palearctic.

Clades F and M have traditionally been placed in *Seicercus*, and differ from the traditional *Phylloscopus* species by lacking contrasting pale supercilium and dark eye-stripe through the eye, while having distinct pale eye-rings. Clade F includes a group that has variously been classified as 2–4 small species (e.g. Eaton et al., 2016; del Hoyo and Collar, 2016) with very contrasting plumage patterns, including unique partly rufous head patterns and white eye-rings. The eight species in clade M all have very similar appearances, and six of them were previously treated as conspecific (cf. Table 1).

Clade K was not supported in the \*BEAST analysis, although it received PP 1.00 in the two concatenation analyses. The two major subclades I and J are well supported in all analyses, and both include groups of species that have previously been lumped into larger species units (cf. Table 1). Clade H, which received PP 0.92 in the \*BEAST tree, but PP 1.00 in the concatenation analyses, contains three species which until recently were considered conspecific (cf. Table 1). Because of the unresolved position of *P. emeiensis*, clade K is best considered a trichotomy. Except for *P. emeiensis*, the species in this clade are very similar morphologically: uniformly patterned above without any paler crown stripes, pale wing-bars and usually at least some dark on the tips of the lower mandibles. Their joint distribution covers much of the Palearctic.

Clade A1 is only well supported in the BEAST analysis. However, from a biogeographical point of view, this clade is reasonable, because all of the species in this clade occur in the Philippines, Sundaland and Melanesia. Moreover, most of them have contrastingly dark crown, some with a variably distinct paler median crown-stripe; the underparts usually show at least some yellow; and the lower mandible usually has at least a prominent dark tip (sometimes mostly dark).

#### 4.1.2. Relationships within closely related species groups

Clade A1 is poorly resolved, and more sequence data are needed to clarify the interrelationships within this clade. All of its species except *P. amoenus* are polytypic, and often strongly divergent in plumage and

vocalisations (del Hoyo et al., 2006; Eaton et al., 2016), so a more comprehensive sampling of these is warranted (Alström et al., in prep.). The relationships within clade A2 are uncertain, and also for these more sequence data are needed. Owing to its unusual colouration (cf. Fig. 1), *P. xanthoschistos* was previously placed in the traditional *Seicercus*, but was transferred to *Phylloscopus* based on molecular data (Olsson et al., 2005), later confirmed by analyses of songs and additional mtDNA (Päckert et al., 2009). The present study confirms that it is closely related to *P. davisoni*, *P. ogilviegranti* and *P. hainanus*, with all four being allopatric replacements of one another from the Himalayas to mainland Southeast Asia and southern China.

Although the phylogenetic relationships within clade B are not unanimously well supported, they make more sense from a biogeographical and morphological point of view than the sister relationship between *P. goodsoni* and *P. occipitalis* found by Alström et al. (2013a,b): *P. claudiae* and *P. goodsoni* are in close geographical proximity, whereas *P. goodsoni* and *P. occipitalis* are at the extreme ends of the joint distribution. Moreover, *P. reguloides*, *P. claudiae* and *P. goodsoni* are more similar in plumage, and were until recently considered conspecific (cf. Table 1). The relationships among the three species in clade D are unresolved.

The *P. trochiloides* complex (clade J) has been the subject of multiple detailed studies (see Table 1), and the most recent one, based on > 2300 SNPs, revealed a complex pattern which is not entirely consistent with the current taxonomy (Alcaide et al., 2014). Given that this species complex may be a rare example in nature of a ring species with complicated gene flow patterns, our data do not add anything to this discussion.

Within clade M, Olsson et al. (2004) and Päckert et al. (2004) recovered the same topology (*S. poliogenys* not included by latter authors) based on mtDNA, except that they found *S. soror* to be sister to our clade M1b and *S. omeiensis* to be sister to the others in clade M1. The support for this was very low, but was raised in an analysis using non-molecular data (Olsson et al. 2004). In the present study, the sister relationship between *S. soror* and *S. omeiensis* (clade M1a) was high in the \*BEAST but low in the concatenation analyses. Examination of the single locus trees shows that this was only supported by myoglobin. We suggest that more sequence data are needed to evaluate this. Clade M1b is strongly supported by concatenation but not in the \*BEAST analysis. We consider this highly plausible because of the generally close similarities between *S. valentini* and *S. whistleri* in morphology, song and breeding habitat/altitude (Alström and Olsson 1999, 2000; Martens et al., 1999; Olsson et al., 2004; Päckert et al., 2004).

Clade M2b is poorly supported by our molecular data. However, as remarked by Olsson et al. (2004), this clade receives further support from a plumage synapomorphy: the eye-ring is broken above the eye (complete above the eye in the other species in clade M). Also clade M2a, which is strongly supported by our data, has a plumage synapomorphy (eye-ring thinly broken behind eye).

Watson et al. (1986) suggested based on morphological similarity that *P. ruficapilla*, *P. laurae* and *P. laetus* form a superspecies, but this is not supported by our data, although the sister relationship between *P. ruficapilla* and *P. umbrovirens* is not unanimously strongly supported. However, Watson et al.'s (1986) suggestion that *P. herberti* and *P. budongoensis* form a superspecies is supported by our analysis in as much as they are strongly supported as sisters.

The species in clade Q have all at some point been considered conspecific (e.g. Ticehurst, 1938; cf. Table 1). Our analyses fail to resolve the relationships among the different taxa. Likewise, Bensch et al. (2006a,b) found completely unresolved relationships between *P. collybita* and *P. ibericus* (= *P. collybita brehmii* in their paper) in four nuclear markers (different markers compared to ours). The sister relationship between clade Q and *P. trochilus* are, however, strongly supported. Bensch et al. (2006a,b) speculated that the lack of reciprocal monophyly between *P. collybita* (including *P. ibericus*) and *P. trochilus* found in three out of four analysed nuclear loci, but not in mtDNA, might be

due to ancient male-biased introgression. Zink and Barrowclough (2008) suggested that this could instead be explained by differences in effective population size between mtDNA and nuclear DNA, and that nuclear DNA is expected to be “lagging behind”. At any rate, our coalescent-based analyses (as well as concatenation) strongly support the sister relationship between clade Q and *P. trochilus*.

The sister relationship between *P. affinis* and *P. occisinsensis* (clade S) is strongly supported in the \*BEAST analysis, whereas the concatenation analyses found *P. occisinsensis* and *P. griseolus* as sisters with very low support. The relationship found by \*BEAST seems more reasonable in view of the extreme similarity in morphology and localisations between *P. occisinsensis* and *P. affinis* (Martens et al., 2008), and is also supported by the distributional pattern, with *P. affinis* and *P. griseolus* being sympatric in the western Himalayas whereas *P. affinis* and *P. occisinsensis* have parapatric distributions (Martens et al., 2008). More data are needed to resolve this. More sequence data are also needed to elucidate the relationships among the four species in clade V.

#### 4.2. Dating

Time estimates for up to almost 60 species of Phylloscopidae by Price (2010) and Päckert et al. (2012), using partly different calibrations and methods compared to our study and to each other's, agree fairly well with our calculations. However, the trees obtained in our study and those of Price (2010) and Päckert et al. (2012) differ slightly among each other in topology, which will affect some dates.

In a genomic study of the oscine radiation, Moyle et al. (2016) estimated the split between *Phylloscopus trochilus* and *Seicercus montis* to c. 9.4 mya (95% HPD 7.2–11.7 mya) (10.6 mya, 95% HPD 7.8–13.6 mya using different calibrations) (R. G. Moyle, in litt.), which would render their estimate of the split between our clades  $\alpha$  and  $\beta$  c. 1–2 my younger than our results, although the confidence intervals of the two studies are broadly overlapping.

In contrast, our divergence times are considerably younger than those in a recently published time tree of the Himalayan Phylloscopidae (Price et al., 2014). For example, the root of Phylloscopidae, excluding clade X which does not occur in the Himalayas, is at 16.4 mya (95% HPD 14.5–17.9 mya) in the Price et al. (2014) study, i.e. with non-overlapping confidence interval compared to our analysis. More recent splits have overlapping confidence intervals. For example, the split between *S. burkii* and *S. affinis* was estimated at  $4.4 \pm 3.0$ –5.7 mya by Price et al. (2014) vs.  $3.8 \pm 2.9$ –4.7 in our study, and the divergence between *P. pulcher* and *P. maculipennis* at  $8.3 \pm 6.6$ –10.3 mya vs.  $6.1 \pm 4.8$ –7.5 mya. These differences might be attributed to differences in taxon sampling and number of individuals per species (Price et al. (2014) analysed 21 species, vs. 76 in our study, and used only single individuals per species, vs. 3 individuals for most species in our study). However, they are more likely due to differences in calibration methods. Price et al. (2014) used multiple passerine fossils and biogeographic dates, many relating to Passeroidea and only one to Sylvioidea (a split between two closely related *Sylvia* species). Unfortunately, fossil dating is not possible for Phylloscopidae alone, because there are few fossils (oldest reliably identified one, *Phylloscopus* sp., is 1.6–1.8 mya; Mourer-Chauviré et al., 1977; Tommy Tyrberg, in litt.).

In the absence of a scientific consensus on the reliability of available calibration points, all node ages, here and in other publications, should be regarded as tentative.

#### 4.3. Revised classification

The non-monophyly of *Phylloscopus* and *Seicercus* necessitates a taxonomic revision. This was already suggested by Olsson et al. (2004, 2005) and Alström et al. (2013a,b), who, however, recommended awaiting a more comprehensive analysis before revising the taxonomy. Nevertheless, based on the earlier phylogenetic analyses, various

suggestions for a revised classification have been proposed (see Table 1). The first one by Dickinson and Christidis (2014) restricted *Phylloscopus* to our clade U, resurrected names for our clades W (*Abornis*) and X (*Rhadina*) and placed all *Phylloscopus* in our clade  $\alpha$  into a much expanded *Seicercus* (Table 1).

Boyd (2017) recognised no fewer than nine genera, which are largely in agreement with the clades recovered by us (and most of which were applied at the subgeneric level already by Watson et al., 1986 based on morphological similarities): clade E, *Cryptigata* Mathews, 1925 (type *Gerygone giulianetti* = *Phylloscopus maforensis giulianetti*); clade F, *Pycnosphrys* Strickland, 1849 (type *Pycnosphrys grammiceps*); clade K, *Acanthopneuste* H. Blasius, 1858 (type *Phyllopneuste borealis*); clade M, *Seicercus* Swainson, 1837 (type *Cryptolopha auricapilla* Swainson = *Sylvia burkii* E. Burton); clade N, *Pindalus* Gurney, 1862 (type *Pogonocichla ruficapilla*); clade O, “*Pycnosphrys*”; clade U, *Phylloscopus* Boie, 1826 (type *Motacilla trochilus*); clade W, *Abornis* J.E. and G.R. Gray, 1847 (type *Abornis erochroa* = *Phylloscopus pulcher*); and clade X, *Rhadina* Billberg, 1828 (type *Motacilla sibilatrix*).

We support the proposal by del Hoyo and Collar (2016) to synonymise *Seicercus* with *Phylloscopus*. This will lead to the fewest taxonomic changes compared to traditional classifications. The main changes are that *Seicercus affinis* needs to change name to *Phylloscopus intermedius* and *Phylloscopus davisoni* must change to *Phylloscopus intensor* (see explanations in del Hoyo and Collar, 2016). In order to apply Boyd's (2017) multigenus approach, one would have to propose a new generic name for clade O (as presumably indicated by Boyd (2017) by placing “*Pycnosphrys*” in quotation marks). Moreover, because clade K is not unanimously well supported, it might be better to restrict *Acanthopneuste* to clade I and propose new generic names for clade J and *Phylloscopus emeiensis*.

There is a current trend to break up large genera into smaller genera, especially when a small, often monotypic, genus is found to be nested within a larger clade. In our opinion, this practice does not facilitate communication, and the improved information about relationships obtained through recognition of multiple smaller genera is not necessarily more meaningful than showing that an odd taxon is actually part of a larger clade. We do not advocate taxonomic proliferation of names, and do not consider large genera a problem, as long as they represent monophyletic groups.

#### 4.4. Morphological evolution

Although not the focus of this paper, a few comments can be made on the morphological evolution (cf. Fig. 1 and Graphical Abstract). The leaf warblers are (1) overall rather homogeneous in size (9–14 cm; del Hoyo et al., 2006), structure and plumage. (2) Most of the main clades have evolved a novel “basic plumage type” (most striking for clades F and M), which has usually been highly conserved with only slight modifications over long time spans (e.g., the *P. borealis* complex [clade H] and *P. trochiloides* complex [clade J] are difficult to distinguish by appearance despite c. 7.5 my of independent evolution). (3) The rate of plumage divergence has been overall higher in some of the main clades (especially in the Philippine-Sundaland-Melanesian radiation [clade A1], where c. 35 taxa (most treated at subspecies rank) share a most recent common ancestor < 2.5 mya). (4) In clade A2, two of the species (*P. davisoni*, *P. ogilviegranti*) have presumably retained an ancestral plumage type shared with the species in clade B, whereas the two other species (*P. xanthoschistos*, *P. hainanus*) have diverged markedly in plumage (the former so much that it was previously placed in the traditional *Seicercus*). (5) There are several cases of convergent plumage evolution (e.g., striped crown, pale wingbars and bright yellow underparts appear to have evolved independently multiple times; *P. coronatus* and especially *P. emeiensis* are very similar to the species in clade B and to two of the species in clade A2).



## 5. Conclusions

The generally well resolved and well supported time calibrated phylogeny is a major step forward compared to earlier studies based on a smaller number of species and loci. This can provide a basis for future studies of other aspects of the evolution of this ecologically important group of birds.

## Acknowledgements

We are grateful to Sharon Birks (Burke Museum, University of Washington), Joel Cracraft, Paul Sweet and Thomas J. Trombone (American Museum of Natural History), Jon Fjeldså and Jan Bolding Kristensen (Zoological Museum, University of Copenhagen), Moe Flannery (California Academy of Sciences), Silke Fregin (Vogelwarte Hiddensee), Shannon Hackett (Field Museum, Chicago), Janet Hinshaw (University of Michigan Museum of Zoology), Paula Holahan (University of Wisconsin Zoological Museum), Ulf Johansson and Peter Nilsson (Swedish Museum of Natural History), Jan Lifjeld and Lars Erik Johannessen (Natural History Museum, University of Oslo), Richard Prum and Kristof Zyskowski (Yale Peabody Museum of Natural History), Robert Prys-Jones and Mark Adams (The Natural History Museum, Tring), Mark Robbins (University of Kansas Biodiversity Institute), Frederick H. Sheldon and Donna Dittman (LSU Museum of Natural Science Collection of genome Resources, Louisiana State University), Joanna Sumner (Museum Victoria), Hem Sagar Baral, Geoff Carey, Christian Cederroth, Ho-fai Cheung, Anders Dahl, Jonathan Eames, Joris Elst, Magnus Gelang, Magnus Hellström, Darren Irwin, Hannu Jännes, Peter Kennerley, Paul Leader, Pete Leonard, Jochen Martens, Lionel Maumary, Stephane Ostrowski, Trevor Price, Bo Petersson, Phil Round, Yoshimitsu Shigeta, Frank Steinheimer, Lars Svensson, Thor Veen, and William Velmala for providing samples. We are also grateful to the following persons for providing photos, some of which appear in Fig. 1 (F1) or Graphical Abstract (GA): Craig Brelsford (shanghaibirding.com) (F1: 7; GA: 14), James Eaton (F1: 2; GA: 2, 10, 18, 19), Göran Ekström (F1: 10; GA: 9, 15, 16, 22), Jocko Hammar (GA: 6), Jonathan Martinez (F1: 4, 5, 9; GA: 5, 7, 8, 11, 20), Yann Muzika (F1: 1, 3; GA: 1), Frédéric Pelsy (F1: 6; GA: 12), Megan & Chris Perkins (GA: 3), Nick Robinson (F1: 8; GA: 4, 13, 17, 21), and Hadoram Shir-ihai. Some of the analyses were run on the CIPRES Science Gateway. P.A. was supported by the Swedish Research Council (2015-04402), Jörnvalld Foundation, and Mark & Mo Constantine; P.E. and U.O. were supported by the Swedish Research Council (grant numbers 2013-5161 and 2015-04651, respectively).

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ympev.2018.03.031>.

## References

- Alcaide, M., Scordato, E.S., Price, T.D., Irwin, D.E., 2014. Genomic divergence in a ring species complex. *Nature* 511, 83–85.
- Alström, P., Olsson, U., 1990. Taxonomy of the *Phylloscopus proregulus* complex. *Bull. Br. Ornithol. Club* 110, 38–43.
- Alström, P., Olsson, U., Colston, P.R., 1990. Description of a possible new species of leaf warbler of the genus *Phylloscopus* from China. *Bull. Br. Ornithol. Club* 110, 43–47.
- Alström, P., Olsson, U., Colston, P.R., 1992. A new species of *Phylloscopus* warbler from central China. *Ibis* 134, 329–334.
- Alström, P., Olsson, U., 1992. Taxonomic status of *Phylloscopus affinis* and *P. subaffinis*. *Bull. Br. Ornithol. Club* 112, 111–126.
- Alström, P., Ripley, S.D., Rasmussen, P.C., 1993. Re-evaluation of the taxonomic status of *Phylloscopus subaffinis arcanus*. *Bull. Br. Ornithol. Club* 113, 207–209.
- Alström, P., Olsson, U., Colston, P.R., 1995. Reevaluation of the taxonomic status of *Phylloscopus ricketti goodsoni* Hartert. *Bull. Br. Ornithol. Club* 115, 53–57.
- Alström, P., Olsson, U., 1995. A new species of *Phylloscopus* warbler from Sichuan Province, China. *Ibis* 137, 459–468.
- Alström, P., Olsson, U., Colston, P., 1997. Re-evaluation of the taxonomic status of *Phylloscopus proregulus kansuensis* Meise. *Bull. Br. Ornithol. Club* 117, 177–193.
- Alström, P., Olsson, U., 1999. The Golden-spectacled Warbler: a complex of sibling species, including a previously undescribed species. *Ibis* 141, 545–568.
- Alström, P., Olsson, U., 2000. Golden-spectacled Warbler systematics. *Ibis* 142, 495–500.
- Alström, P., Ericson, P.G.P., Olsson, U., Sundberg, P., 2006. Phylogeny and classification of the avian superfamily Sylvioidea. *Mol. Phylogenet. Evol.* 38, 381–397. <http://dx.doi.org/10.1016/j.ympev.2005.05.015>.
- Alström, P., Davidson, P., Duckworth, J.W., Eames, J.C., Le, T.T., Nguyen, C., Olsson, U., Robson, C., Timmins, R.J., 2010. Description of a new species of *Phylloscopus* warbler from Vietnam and Laos. *Ibis* 152, 145–168.
- Alström, P., Fregin, S., Norman, J.A., Ericson, P.G.P., Christidis, L., Olsson, U., 2011a. Multilocus analysis of a taxonomically densely sampled dataset reveal extensive non-monophyly in the avian family Locustellidae. *Mol. Phylogenet. Evol.* 58, 513–526. <http://dx.doi.org/10.1016/j.ympev.2010.12.012>.
- Alström, P., Höhna, S., Gelang, M., Ericson, P.G.P., Olsson, U., 2011b. Non-monophyly and intricate morphological evolution within the avian family Cettiidae revealed by multilocus analysis of a taxonomically densely sampled dataset. *BMC Evol. Biol.* 11, 352. <http://dx.doi.org/10.1186/1471-2148-11-352>.
- Alström, P., Saitoh, T., Williams, D., Nishiumi, I., Shigeta, Y., Ueda, K., Irestedt, M., Björklund, M., Olsson, U., 2011c. The Arctic Warbler *Phylloscopus borealis* – three anciently separated cryptic species revealed. *Ibis* 153, 395–410.
- Alström, P., Barnes, K.N., Olsson, U., Barker, F.K., Bloomer, P., Khan, A.A., Qureshi, M.A., Guillaumet, A., Crochet, P.-A., Ryan, P.G., 2013a. Multilocus phylogeny of the avian family Alaudidae (larks) reveals complex morphological evolution, non-monophyletic genera and hidden species diversity. *Mol. Phylogenet. Evol.* 69, 1043–1056. <http://dx.doi.org/10.1016/j.ympev.2013.06.005>.
- Alström, P., Olsson, U., Lei, F., 2013b. A review of the recent advances in the systematics of the avian superfamily Sylvioidea. *Chinese Birds* 4, 99–131. <http://dx.doi.org/10.5122/cbirds.2013.0016>.
- Alström, P., Ranft, R., 2003. The use of sounds in avian systematics, and the importance of bird sound archives. *Bull. Br. Ornithol. Club Suppl.* 123A, 114–135.
- Bairlein, F., Alström, P., Aymí, R., Clement, P., Dyrce, A., Gargallo, G., Hawkins, F., Madge, S., Pearson, D., Svensson, L., 2006. Family Sylviidae (Warblers). In: In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), *Handbook of the Birds of the World Volume 12*. Lynx Edicions, Barcelona, pp. 492–709.
- Badyaev, A.V., Leaf, E.S., 1997. Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. *Auk* 114, 40–46.
- Bensch, S., Andersson, T., Åkesson, S., 1999. Morphological and molecular variation across a migratory divide in willow warblers, *Phylloscopus trochilus*. *Evolution* 53, 1925–1935.
- Bensch, S., Bengtsson, G., Åkesson, S., 2006a. Patterns of stable isotope signatures in willow warbler *Phylloscopus trochilus* feathers collected in Africa. *J. Avian Biol.* 37, 323–330.
- Bensch, S., Irwin, D.E., Irwin, J.H., Kvist, L., Åkesson, S., 2006b. Conflicting patterns of mitochondrial and nuclear DNA diversity in *Phylloscopus* warblers. *Mol. Ecol.* 15, 161–171.
- Boyd, J.H., 2017. Taxonomy in Flux Checklist 3.08. <http://jboyd.net/Taxo/List.html>.
- Brumfield, R.T., Liu, L., Lum, D.E., Edwards, S.V., 2008. Comparison of species tree methods for reconstructing the phylogeny of bearded manakins (Aves: Pipridae, *Manacus*) from multilocus sequence data. *Syst. Biol.* 57, 719–731.
- Chamberlain, C.P., Bensch, S., Feng, X., Åkesson, S., Andersson, T., 2000. Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. *Proc. Roy. Soc. London B: Biol. Sci.* 267, 43–48.
- Cibois, A., 2003. Mitochondrial DNA phylogeny of babblers (Timaliidae). *Auk* 120, 35–54.
- Cibois, A., Pasquet, E., Schulenberg, T.S., 1999. Molecular systematics of the Malagasy babblers (Passeriformes: Timaliidae) and warblers (Passeriformes: Sylviidae), based on cytochrome *b* and 16S rRNA sequences. *Mol. Phylogenet. Evol.* 13, 581–595.
- Cibois, A., Slikas, B., Schulenberg, T.S., Pasquet, E., 2001. An endemic radiation of Malagasy songbirds is revealed by mitochondrial DNA sequence data. *Evolution* 55, 1198–1206.
- Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* 9, 772–772.
- del Hoyo, J., Elliot, A., Christies, D.A. (Eds.), 2006. *Handbook of the Birds of the World Vol. 11*. Old World Flycatchers to Old World Warblers, Lynx Edicions, Barcelona.
- del Hoyo, J., Collar, N.J., 2016. *HBW and BirdLife International illustrated checklist of the birds of the world. Volume 2: Passerines*. Lynx Edicions, Barcelona.
- Dickinson, E. (Ed.), 2003. *The Howard and Moore Complete Checklist of the Birds of the World*, third ed. Helm, London.
- Dickinson, E.C., Christidis, L., 2014. *The Howard & Moore complete checklist of the birds of the world*, 4th ed., Vol. 2. Aves Press, Eastbourne, U.K.
- Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian Phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* 29, 1969–1973.
- Eaton, J.A., van Balen, B., Brickle, N.W., Rheindt, F.E., 2016. *Birds of the Indonesian Archipelago Greater Sundas and Wallacea*. Lynx Edicions, Barcelona.
- Edwards, S.V., 2009. Is a new and general theory of molecular systematics emerging? *Evolution* 63, 1–19.
- Edwards, S.V., Liu, L., Pearl, D.K., 2007. High-resolution species trees without concatenation. *Proc. Natl. Acad. Sci. U.S.A.* 104, 5936–5941.
- Forstmeier, W., Kessler, A., 2001. Morphology and foraging behaviour of Siberian *Phylloscopus* warblers. *J. Avian Biol.* 32, 127–138.
- Forstmeier, W., Bourski, O.V., Leisler, B., 2001. Habitat choice in *Phylloscopus* warblers: the role of morphology, phylogeny and competition. *Oecologia* 128, 566–576.
- Fregin, S., Haase, M., Olsson, U., Alström, P., 2009. Multi-locus phylogeny of the family Acrocephalidae (Aves: Passeriformes) – The traditional taxonomy overthrown. *Mol. Phylogenet. Evol.* 52, 866–878. <http://dx.doi.org/10.1016/j.ympev.2009.04.006>.
- Fregin, S., Haase, M., Olsson, U., Alström, P., 2012. New insights into family relationships within the avian superfamily Sylvioidea (Passeriformes) based on seven molecular markers. *BMC Evol. Biol.* 12, 157. <http://dx.doi.org/10.1186/1471-2148-12-157>.
- Gelang, M., Cibois, A., Pasquet, E., Olsson, U., Alström, P., Ericson, P.G.P., 2009. Phylogeny of babblers (Aves, Passeriformes): major lineages, family limits and



- classification. *Zoolog. Scr.* 35, 225–236. <http://dx.doi.org/10.1111/j.1463-6409.2008.00374.x>.
- Gill, F., Donsker, D., 2017. IOC World Bird List (v 7.2). doi : 10.14344/IOC.ML.7.2.
- Helbig, A.J., Seibold, I., Martens, J., Wink, M., 1995. Genetic differentiation and phylogenetic relationships of Bonelli's Warbler *Phylloscopus bonelli* and Green Warbler *Phylloscopus nitidus*. *J. Avian Biol.* 26, 139–153.
- Helbig, A.J., Martens, J., Seibold, I., Henning, F., Schottler, B., Wink, M., 1996. Phylogeny and species limits in the Palaearctic chiffchaff *Phylloscopus collybita* complex: mitochondrial genetic differentiation and bioacoustic evidence. *Ibis* 138, 650–666.
- Helbig, A.J., Salomon, M., Bensch, S., 2001. Male-biased gene flow across an avian hybrid zone: evidence from mitochondrial and microsatellite DNA. *J. Evol. Biol.* 14, 277–287. <http://dx.doi.org/10.1046/j.1420-9101.2001.00273.x>.
- Heled, J., Drummond, A.J., 2010. Bayesian inference of species trees from multilocus data. *Mol. Biol. Evol.* 27, 570–580.
- Huelsenbeck, J.P., Ronquist, F., 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17, 754–755.
- Irwin, D.E., 2000. Song variation in an avian ring species. *Evolution* 54, 998–1010.
- Irwin, D.E., Alström, P., Olsson, U., Benowitz-Fredericks, Z.M., 2001a. Cryptic species in the genus *Phylloscopus* (Old World leaf warblers). *Ibis* 143, 233–247. <http://dx.doi.org/10.1111/j.1474-919X.2001.tb04479.x>.
- Irwin, D.E., Bensch, S., Price, T.D., 2001b. Speciation in a ring. *Nature* 409, 333–337.
- Irwin, D.E., Bensch, S., Irwin, J.H., Price, T.D., 2005. Speciation by distance in a ring species. *Science* 307, 414–416.
- Irwin, D.E., Thimang, M.P., Irwin, J.H., 2008. Call divergence is correlated with geographic and genetic distance in greenish warblers (*Phylloscopus trochiloides*): a strong role for stochasticity in signal evolution? *J. Evol. Biol.* 21, 435–448.
- Johansson, U.S., Alström, P., Olsson, U., Ericson, P.G.P., Sundberg, P., Price, T.D., 2007. Build-up of the Himalayan avifauna through immigration: a biogeographical analysis of the *Phylloscopus* and *Seiurus* warblers. *Evolution* 61, 324–333.
- Johansson, U.S., Ericson, P.G., Fjelds, J., Irestedt, M., 2016. The phylogenetic position of the world's smallest passerine, the Pygmy Bushtit *Psaltira exilis*. *Ibis* 158, 519–529.
- Liu, L., Pearl, D.K., Brumfield, R., Edwards, S.V., 2008. Estimating species trees using multiple-allele DNA sequence data. *Evolution* 62, 2080–2091.
- Liu, L., Edwards, S.V., 2009. Phylogenetic analysis in the anomaly zone. *Syst. Biol.* 58, 452–460.
- Mahler, B., Gil, D., 2009. The evolution of song in the *Phylloscopus* leaf warblers (Aves: Sylviidae): a tale of sexual selection, habitat adaptation, and morphological constraints. *Adv. Stud. Behav.* 40, 35–66. [http://dx.doi.org/10.1016/S0065-3454\(09\)40002-0](http://dx.doi.org/10.1016/S0065-3454(09)40002-0).
- Marchetti, K., 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 362, 149–152. <http://dx.doi.org/10.1038/362149a0>.
- Marchetti, K., 1998. The evolution of multiple male traits in the yellow-browed leaf warbler. *Anim. Behav.* 55, 361–376. <http://dx.doi.org/10.1006/anbe.1997.0586>.
- Marchetti, K., Price, T., Richman, A., 1995. Correlates of wing morphology with foraging behaviour and migration distance in the genus *Phylloscopus*. *J. Avian Biol.* 26, 177–181.
- Martens, J., 1988. *Phylloscopus borealoides* Potenken—ein verkannter Laubsänger der Ost-Palaäktis. *J. Ornithol.* 129, 343–351.
- Martens, J., 2010. A preliminary review of the leaf warbler genera *Phylloscopus* and *Seiurus*. *Br. Ornithol. Club Occasional Publ.* 5, 41–116.
- Martens, J., Eck, S., Päckert, M., Sun, Y.-H., 1999. The Golden-spectacled Warbler *Seiurus burkii* – a species swarm (Aves: Passeriformes: Sylviidae), part 1. *Zool. Abhandl. Mus. Dresden* 50, 281–327.
- Martens, J., Tietze, D.T., Eck, S., Veith, M., 2004. Radiation and species limits in the Asian Pallas's warbler complex (*Phylloscopus proregulus* s.l.). *J. Ornithol.* 145, 206–222.
- Martens, J., Sun, Y.-H., Päckert, M., 2008. Intraspecific differentiation of Sino-Himalayan bush-dwelling *Phylloscopus* leaf warblers, with description of two new taxa. *Vert. Zool.* 58, 233–265.
- Mourer-Chauviré, C., Moya, S., Adrover, R., 1977. Les oiseaux des gisements quaternaires de Majorque. *Nouv. Arch. Mus. Hist. Nat. Lyon, Suppl.* 15, 61–64.
- Moyle, R.G., Marks, B.D., 2006. Phylogenetic relationships of the bulbuls (Aves: Pycnonotidae) based on mitochondrial and nuclear DNA sequence data. *Mol. Phylogenet. Evol.* 40, 687–695.
- Moyle, R.G., Andersen, M.J., Oliveros, C.H., Steinheimer, F., Reddy, S., 2012. Phylogeny and biogeography of the core babblers (Aves: Timaliidae). *Syst. Biol.* 61, 631–651.
- Moyle, R.G., Oliveros, C.H., Andersen, M.J., Hosner, P.A., Benz, B.W., Manthey, J.D., Travers, S.L., Brwn, R.M., Faircloth, B.C., 2016. Tectonic collision and uplift of Wallacea triggered the global songbird radiation. *Nat. Commun.* 7, 12709.
- Nguembock, B., Fjelds, J., Tillier, A., Pasquet, E., 2007. A phylogeny for the Cisticolidae (Aves: Passeriformes) based on nuclear and mitochondrial DNA sequence data, and a re-interpretation of a unique nest-building specialization. *Mol. Phylogenet. Evol.* 42, 272–286.
- Olsson, U., Alström, P., Colston, P.R., 1993. A new species of *Phylloscopus* warbler from Hainan Island, China. *Ibis* 135, 2–7.
- Olsson, U., Alström, P., Sundberg, P., 2004. Non-monophyly of the avian genus *Seiurus* (Aves: Sylviidae) revealed by mitochondrial DNA. *Zoolog. Scr.* 33, 501–510. <http://dx.doi.org/10.1111/j.0300-3256.2004.00166.x>.
- Olsson, U., Alström, P., Ericson, P.G.P., Sundberg, P., 2005. Non-monophyletic taxa and cryptic species – evidence from a molecular phylogeny of leaf-warblers (*Phylloscopus*, Aves). *Mol. Phylogenet. Evol.* 36, 261–276. <http://dx.doi.org/10.1016/j.ympev.2005.01.012>.
- Olsson, U., Irestedt, M., Sangster, G., Ericson, P.G.P., Alström, P., 2013. Systematic revision of the avian family Cisticolidae based on a multi-locus phylogeny of all genera. *Mol. Phylogenet. Evol.* 66, 790–799. <http://dx.doi.org/10.1016/j.ympev.2012.11.004>.
- Ottosson, U., Ottvall, R. (Eds.), 2012. Fåglarna i Sverige: antal och förekomst. Swedish Ornithological Society.
- Päckert, M., Martens, J., Sun, Y.-H., Veith, M., 2004. The radiation of the *Seiurus burkii* complex and its congeners (Aves: Sylviidae): molecular genetics and bioacoustics. *Org. Div. Evol.* 4, 341–364.
- Päckert, M., Blume, C., Sun, Y.-H., Wei, L., Martens, J., 2009. Acoustic differentiation reflects mitochondrial lineages in Blyth's leaf warbler and white-tailed leaf warbler complexes (Aves: *Phylloscopus reguloides*, *Phylloscopus davisoni*). *Biol. J. Linn. Soc.* 96, 584–600.
- Päckert, M., Martens, J., Sun, Y.-H., 2010. Phylogeny of long-tailed tits and allies inferred from mitochondrial and nuclear markers (Aves: Passeriformes, Aegithalidae). *Mol. Phylogenet. Evol.* 55, 952–967. <http://dx.doi.org/10.1016/j.ympev.2010.01.024>.
- Päckert, M., Martens, J., Sun, Y.-H., Severinghaus, L.L., Nazarenko, A.A., Ting, J., Töpfer, T., Tietze, D.T., 2012. Horizontal and elevational phylogeographic patterns of Himalayan and Southeast Asian forest passerines (Aves: Passeriformes). *J. Biogeogr.* 39, 556–573.
- Pasquet, E., Han, L.-X., Khobket, O., Cibois, A., 2001. Towards a molecular systematics of the genus *Criniger*, and a preliminary phylogeny of the bulbuls (Aves, Passeriformes, Pycnonotidae). *Zoosystema* 23, 857–863.
- Price, T.D., 2010. The roles of time and ecology in the continental radiation of the Old World leaf warblers (*Phylloscopus* and *Seiurus*). *Philos. Trans. Roy. Soc. London B: Biol. Sci.* 365, 1749–1762.
- Price, T.D., Helbig, A.J., Richman, A.D., 1997. Evolution of breeding distributions in the Old World leaf warblers (genus *Phylloscopus*). *Evolution* 51, 552–561.
- Price, T., Zee, J., Jamdar, K., Jamdar, N., 2003. Bird species diversity along the Himalaya: a comparison of Himachal Pradesh with Kashmir. *J. Bombay Nat. Hist. Soc.* 100, 394–409.
- Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P., Olsson, U., Ghosh-Harihar, M., Ishitaq, F., Gupta, S.K., Martens, J.E., Harr, B., Singh, P., Mohan, D., 2014. Niche filling slows the diversification of Himalayan songbirds. *Nature* 509, 222–225. <http://dx.doi.org/10.1038/nature13272>.
- Rambaut, A., 2012. FigTree, Version 1.4.0 < <http://tree.bio.ed.ac.uk/software/figtree> > .
- Rambaut, A., Suchard, M.A., Xie, D., Drummond, A.J., 2014. Tracer v1.6, Available from <http://beast.bio.ed.ac.uk/Tracer>.
- Reeves, A.B., Drovetski, S.V., Fadeev, I.V., 2008. Mitochondrial DNA data imply a stepping-stone colonization of Beringia by arctic warbler *Phylloscopus borealis*. *J. Avian Biol.* 39, 567–575.
- Rheindt, F.E., 2006. Splits galore: the revolution in Asian leaf warbler systematics. *BirdingASIA* 5, 25–39.
- Richman, A.D., 1996. Ecological diversification and community structure in the Old World leaf warblers (genus *Phylloscopus*): a phylogenetic perspective. *Evolution* 50, 2461–2470.
- Richman, A.D., Price, T., 1992. Evolution of ecological differences in the Old World leaf warblers. *Nature* 355, 817–821.
- Ronquist, F., Huelsenbeck, J.P., 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572–1574.
- Saitoh, T., Nishiumi, I., Alström, P., Olsson, U., Ueda, K., 2006. Deep phylogeographical divergences among far eastern populations of the widespread Arctic Warbler. *J. Ornithol.* 147 (Suppl. 1), 242.
- Saitoh, T., Shigeta, Y., Ueda, K., 2008. Morphological differences among populations of the Arctic Warbler with some intraspecific taxonomic notes. *Ornithol. Sci.* 7, 135–142.
- Saitoh, T., Alström, P., Nishiumi, I., Shigeta, Y., Williams, D., Olsson, U., Ueda, K., 2010. Old divergences in a boreal bird supports long-term survival through the Ice Ages. *BMC Evol. Biol.* 10, 35.
- Salomon, M., 1989. Song as a possible reproductive isolating mechanism between 2 parapatric forms—the case of the chiffchaffs *Phylloscopus collybita collybita* and *Phylloscopus collybita brehmii* in the western Pyrenees. *Behaviour* 111, 270–290. <http://dx.doi.org/10.1163/156853989X00709>.
- Sheldon, F.H., Whittingham, L.A., Moyle, R.G., Slikas, B., Winkler, D.W., 2005. Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* 35, 254–270.
- Sibley, C.G., Monroe Jr., B.L., 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven.
- Singh, P., Price, T.D., 2015. Causes of the latitudinal gradient in birdsong complexity assessed from geographical variation within two Himalayan warbler species. *Ibis* 157, 511–527.
- Ticehurst, C.B., 1938. A Systematic review of the Genus *Phylloscopus* (Willow-Warblers or Leaf-Warblers). Trustees of the British Museum, London.
- Tietze, D.T., Martens, J., Fischer, B.S., Sun, Y.H., Klusmann-Kolb, A., Päckert, M., 2015. Evolution of leaf warbler songs (Aves: Phylloscopidae). *Ecol. Evol.* 5, 781–798.
- Winkler, D.W., Billerman, S.M., Lovette, I.J., 2015. Bird Families of the World: An Invitation to the Spectacular Diversity of Birds. Lynx Edicions, Barcelona.
- Mayr, E., Cottrell, G.W. (Eds.), 1986. Check-list of Birds of the World Vol. 11 Museum of Comparative Zoology, Cambridge, Massachusetts.
- Weir, J.T., Schluter, D., 2008. Calibrating the avian molecular clock. *Mol. Ecol.* 17, 2321–2328.
- Williamson, K., 1967. Identification for Ringers: The genus *Phylloscopus*, 2nd edn. British Trust for Ornithology, Tring, Herts.
- Withrow, J.J., Gibson, D.D., Gerasimov, Y., Gerasimov, N., Shestopalov, A., Winkler, K., 2016. Occurrence and taxonomy of Arctic Warblers (*Phylloscopus borealis*) sensu lato in North America. *Wilson J. Ornithol.* 128, 268–277.
- Zink, R.M., Barrowclough, G.F., 2008. Mitochondrial DNA under siege in avian phylogeography. *Mol. Ecol.* 17, 2107–2121.