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

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ARTICLE INFO

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 Subsaharan Africa, south to southern South Africa. The leaf warblers are very prominent members of many

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
Phylloscopus sibilatrix	*Rhadina sibilatrix*	*Rhadina sibilatrix*	*Phylloscopus sibilatrix*	*Phylloscopus sibilatrix*	
Phylloscopus bonelli	*Rhadina bonelli*	*Rhadina bonelli*	*Phylloscopus bonelli*	*Phylloscopus bonelli*	
Phylloscopus bonelli orientalis	***Rhadina orientalis***	***Rhadina orientalis***	***Phylloscopus orientalis***	***Phylloscopus orientalis***	Helbig et al. (1995)
Phylloscopus maculipennis	*Abrornis maculipennis*	*Abrornis maculipennis*	*Phylloscopus maculipennis*	*Phylloscopus maculipennis*	
Phylloscopus pulcher	*Abrornis pulchra*	*Abrornis pulcher*	*Phylloscopus pulcher*	*Phylloscopus pulcher*	
Phylloscopus inornatus	*Abrornis inornata*	*Abrornis inornata*	*Phylloscopus inornatus*	*Phylloscopus inornatus*	
Phylloscopus inornatus humei	***Abrornis humei***	***Abrornis humei***	***Phylloscopus humei***	***Phylloscopus humei***	Irwin et al. (2001a)
Phylloscopus subviridis	*Abrornis subviridis*	*Abrornis subviridis*	*Phylloscopus subviridis*	*Phylloscopus subviridis*	
—[a]	***Abrornis yunnanensis***	***Abrornis yunnanensis***	***Phylloscopus yunnanensis***	***Phylloscopus yunnanensis***	Alström et al. (1990), Alström et al. (1992), Martens et al. (2004)[b]
Phylloscopus proregulus[e]	*Abrornis proregulus*	*Abrornis proregulus*	*Phylloscopus proregulus*	*Phylloscopus proregulus*	
Phylloscopus proregulus proregulus[d]	***Abrornis kansuensis***	***Abrornis kansuensis***	***Phylloscopus kansuensis***	***Phylloscopus kansuensis***	Alström et al. (1997), Martens et al. (2004)
Phylloscopus proregulus chloronotus	***Abrornis chloronotus***	***Abrornis chloronotus***	***Phylloscopus chloronotus***	***Phylloscopus chloronotus***	Alström and Olsson (1990), Martens et al. (2004)
Phylloscopus proregulus chloronotus[c]	***Abrornis forresti***	***Abrornis forresti***	***Phylloscopus forresti***	***Phylloscopus forresti***	Martens et al. (2004)
Phylloscopus tytleri	*Phylloscopus tytleri*	*Phylloscopus tytleri*	*Phylloscopus tytleri*	*Phylloscopus tytleri*	
Phylloscopus armandii	*Phylloscopus armandii*	*Phylloscopus armandii*	*Phylloscopus armandii*	*Phylloscopus armandii*	
Phylloscopus schwarzi	*Phylloscopus schwarzi*	*Phylloscopus schwarzi*	*Phylloscopus schwarzi*	*Phylloscopus schwarzi*	
Phylloscopus griseolus	*Phylloscopus griseolus*	*Phylloscopus griseolus*	*Phylloscopus griseolus*	*Phylloscopus griseolus*	
Phylloscopus affinis	*Phylloscopus affinis*	*Phylloscopus affinis*	*Phylloscopus affinis*	*Phylloscopus affinis*	
(not yet described)	***Phylloscopus occisinensis***	***Phylloscopus occisinensis***	***Phylloscopus occisinensis***	*Phylloscopus affinis occisinensis*	Martens et al. (2008)
Phylloscopus fuligiventer[f]	*Phylloscopus fuligiventer*	*Phylloscopus fuligiventer*	*Phylloscopus fuligiventer*	*Phylloscopus fuligiventer*	
Phylloscopus fuscatus[i]	*Phylloscopus fuscatus*	*Phylloscopus fuscatus*	*Phylloscopus fuscatus*	*Phylloscopus fuscatus*	
Phylloscopus neglectus	*Phylloscopus neglectus*	*Phylloscopus neglectus*	*Phylloscopus neglectus*	*Phylloscopus neglectus*	
Phylloscopus affinis subaffinis	***Phylloscopus subaffinis***	***Phylloscopus subaffinis***	***Phylloscopus subaffinis***	***Phylloscopus subaffinis***	Alström and Olsson (1992), Alström et al. (1993)
Phylloscopus trochilus	*Phylloscopus trochilus*	*Phylloscopus trochilus*	*Phylloscopus trochilus*	*Phylloscopus trochilus*	
Phylloscopus sindianus	*Phylloscopus sindianus*	*Phylloscopus sindianus*	*Phylloscopus sindianus*	*Phylloscopus sindianus*	
Phylloscopus sindianus lorenzii	*Phylloscopus lorenzii*	*Phylloscopus sindianus lorenzii*[h]	*Phylloscopus sindianus lorenzii*	*Phylloscopus sindianus lorenzii*	
Phylloscopus collybita canariensis	***Phylloscopus canariensis***	***Phylloscopus canariensis***	***Phylloscopus canariensis***	***Phylloscopus canariensis***	Helbig et al. (1996)
Phylloscopus collybita	*Phylloscopus collybita*	*Phylloscopus collybita*	*Phylloscopus collybita*	*Phylloscopus collybita*	
Phylloscopus collybita tristis	*Phylloscopus collybita tristis*	*Phylloscopus collybita tristis*[h]	*Phylloscopus collybita tristis*	*Phylloscopus tristis*	Shipilina et al. (2017)
Phylloscopus collybita ibericus	***Phylloscopus ibericus***	***Phylloscopus ibericus***	***Phylloscopus ibericus***	***Phylloscopus ibericus***	Salomon 1989, Helbig et al. (1996), Helbig et al. (2001)
Phylloscopus collybita brehmii[g]					
Phylloscopus cebuensis	*Seicercus cebuensis*	*"Pycnosphrys" cebuensis*	*Phylloscopus cebuensis*	*Phylloscopus cebuensis*	
Phylloscopus olivaceus	*Seicercus olivaceus*	*"Pycnosphrys" olivaceus*	*Phylloscopus olivaceus*	*Phylloscopus olivaceus*	
Phylloscopus coronatus	*Seicercus coronatus*	*"Pycnosphrys" coronatus*	*Phylloscopus coronatus*	*Phylloscopus coronatus*	
Phylloscopus ijimae	*Seicercus ijimae*	*"Pycnosphrys" ijimae*	*Phylloscopus ijimae*	*Phylloscopus ijimae*	
Phylloscopus ruficapilla	*Seicercus ruficapilla*	*Pindalus ruficapilla*	*Phylloscopus ruficapilla*	*Phylloscopus ruficapilla*	
Phylloscopus umbrovirens	*Seicercus umbrovirens*	*Pindalus umbrovirens*	*Phylloscopus umbrovirens*	*Phylloscopus umbrovirens*	
Phylloscopus laetus	*Seicercus laetus*	*Pindalus laetus*	*Phylloscopus laetus*	*Phylloscopus laetus*	

Table 1 (*continued*)

Watson et al. (1986)	Dickinson and Christidis (2014)	Boyd (2017)	Gill and Donsker (2017)	del Hoyo and Collar (2016)	References
Phylloscopus laurae	Seicercus laurae	Tindalus laurae	Phylloscopus laurae	Phylloscopus laurae	
Phylloscopus budongoensis	Seicercus budongoensis	Tindalus budongoensis	Phylloscopus budongoensis	Phylloscopus budongoensis	
Phylloscopus herberti	Seicercus herberti	Tindalus herberti	Phylloscopus herberti	Phylloscopus herberti	
Seicercus affinis	Seicercus affinis	Seicercus affinis	Seicercus affinis	Phylloscopus intermedius[i]	
Seicercus poliogenys	Seicercus poliogenys	Seicercus poliogenys	Seicercus poliogenys	Phylloscopus poliogenys	
Seicercus burkii	Seicercus burkii	Seicercus burkii	Seicercus burkii	Phylloscopus burkii	Alström and Olsson (1999), Alström and Olsson (2000), Martens et al. (1999), Olsson et al. (2004), Päckert et al. (2004)
Seicercus burkii[j]	Seicercus tephrocephalus	Seicercus tephrocephalus	Seicercus tephrocephalus	Phylloscopus tephrocephalus	See S. burkii
Seicercus burkii[j]	Seicercus valentini	Seicercus valentini	Seicercus valentini	Phylloscopus valentini	See S. burkii
Seicercus burkii[j]	Seicercus whistleri	Seicercus whistleri	Seicercus whistleri	Phylloscopus whistleri	See S. burkii
(not yet described)	Seicercus omeiensis	Seicercus omeiensis	Seicercus omeiensis	Phylloscopus omeiensis	See S. burkii
(not yet described)	Seicercus soror	Seicercus soror	Seicercus soror	Phylloscopus soror	See S. burkii
Phylloscopus nitidus	Seicercus nitidus	Acanthopneuste nitidus	Phylloscopus nitidus	Phylloscopus nitidus	See P. trochiloides
Phylloscopus plumbeitarsus	Seicercus plumbeitarsus	Acanthopneuste plumbeitarsus	Phylloscopus plumbeitarsus	Phylloscopus plumbeitarsus	See P. trochiloides
Phylloscopus trochiloides	Seicercus trochiloides	Acanthopneuste trochiloides	Phylloscopus trochiloides	Phylloscopus trochiloides	Irwin (2000), Irwin et al. (2001b), Irwin et al. (2005), Irwin et al. (2008), Alcaide et al. (2014)
Phylloscopus trochiloides viridanus	Seicercus trochiloides viridanus	Acanthopneuste viridanus	Phylloscopus trochiloides viridanus	Phylloscopus trochiloides viridanus	See P. trochiloides
Phylloscopus trochiloides obscuratus	Seicercus trochiloides obscuratus	Acanthopneuste obscuratus	Phylloscopus trochiloides obscuratus	Phylloscopus trochiloides obscuratus	See P. trochiloides
(not yet described)	Seicercus emeiensis	Acanthopneuste emeiensis	Phylloscopus emeiensis	Phylloscopus emeiensis	Alström and Olsson (1995)
Phylloscopus magnirostris	Seicercus magnirostris	Acanthopneuste magnirostris	Phylloscopus magnirostris	Phylloscopus magnirostris	
Phylloscopus tenellipes	Seicercus tenellipes	Acanthopneuste tenellipes	Phylloscopus tenellipes	Phylloscopus tenellipes	
Phylloscopus tenellipes[l]	Seicercus borealoides	Acanthopneuste borealoides	Phylloscopus borealoides	Phylloscopus borealoides	Martens (1988)
Phylloscopus borealis xanthodryas	Seicercus xanthodryas	Acanthopneuste xanthodryas	Phylloscopus xanthodryas	Phylloscopus xanthodryas	See P. borealis
Phylloscopus borealis[k]	Seicercus borealis	Acanthopneuste borealis	Phylloscopus borealis	Phylloscopus borealis	Saitoh et al. (2006), Reeves et al. (2008), Saitoh et al. (2008), Saitoh et al. (2010), Martens, (2010), Alström et al. (2011c), Withrow et al. (2016)
Phylloscopus borealis xanthodryas	Seicercus examinandus	Acanthopneuste examinandus	Phylloscopus examinandus	Phylloscopus examinandus	See P. borealis
Seicercus castaniceps	Seicercus castaniceps	Pycnosphrys castaniceps	Seicercus castaniceps	Phylloscopus castaniceps	
Seicercus grammiceps	Seicercus grammiceps	Pycnosphrys grammiceps	Seicercus grammiceps	Phylloscopus grammiceps	
Seicercus grammiceps sumatrensis	Seicercus grammiceps sumatrensis	Pycnosphrys grammiceps sumatrensis[h]	Seicercus grammiceps sumatrensis	Phylloscopus sumatrensis	
Seicercus montis	Seicercus montis	Pycnosphrys montis	Seicercus montis	Phylloscopus montis	
(not yet described)	Seicercus calciatilis	Cryptigata calciatilis	Phylloscopus calciatilis	Phylloscopus calciatilis	Alström et al. (2010)
Phylloscopus cantator	Seicercus cantator	Cryptigata cantator	Phylloscopus cantator	Phylloscopus cantator	
Phylloscopus ricketti[m]	Seicercus ricketti	Cryptigata ricketti	Phylloscopus ricketti	Phylloscopus ricketti	
Phylloscopus occipitalis	Seicercus occipitalis	Cryptigata occipitalis	Phylloscopus occipitalis	Phylloscopus occipitalis	
Phylloscopus reguloides[n]	Seicercus reguloides	Cryptigata reguloides	Phylloscopus reguloides	Phylloscopus reguloides	
Phylloscopus reguloides claudiae	Seicercus claudiae	Cryptigata claudiae	Phylloscopus claudiae	Phylloscopus claudiae	Olsson et al. (2005), Päckert et al. (2009)

Table 1 (*continued*)

Watson et al. (1986)	Dickinson and Christidis (2014)	Boyd (2017)	Gill and Donsker (2017)	del Hoyo and Collar (2016)	References
Phylloscopus reguloides fokiensis + *P. ricketti goodsoni*	*Seicercus goodsoni*	*Cryptigata goodsoni*	*Phylloscopus goodsoni*	*Phylloscopus goodsoni*	Alström et al. (1995), Olsson et al. (2005), Päckert et al. (2009)
Phylloscopus davisoni	*Seicercus klossi*[r]	*Cryptigata davisoni*	*Phylloscopus davisoni*	*Phylloscopus intensior*[i]	Olsson et al. (2005), Päckert et al. (2009)
Seicercus xanthoschistos	*Seicercus xanthoschistos*	*Cryptigata xanthoschistos*	*Phylloscopus xanthoschistos*	*Phylloscopus xanthoschistos*	Olsson et al. (2005)
(not yet described)	*Seicercus hainanus*	*Cryptigata hainanus*	*Phylloscopus hainanus*	*Phylloscopus hainanus*	Olsson et al. (1993)
Phylloscopus davisoni ogilviegranti	*Seicercus ogilviegranti*[q]	*Cryptigata ogilviegranti*	*Phylloscopus ogilviegranti*	*Phylloscopus ogilviegranti*	Olsson et al. (2005), Päckert et al. (2009)
Phylloscopus trivirgata	*Seicercus trivirgata*	*Cryptigata trivirgata*	*Phylloscopus trivirgatus*[o]	*Phylloscopus trivirgatus*	
Phylloscopus trivirgatus nigrorum	*Seicercus trivirgatus nigrorum*	*Cryptigata nigrorum*	*Phylloscopus nigrorum*	*Phylloscopus trivirgatus nigrorum*	
Phylloscopus presbytes	*Seicercus presbytes*	*Cryptigata presbytes*	*Phylloscopus presbytes*	*Phylloscopus presbytes*	
Phylloscopus makirensis	*Seicercus makirensis*	*Cryptigata makirensis*	*Phylloscopus makirensis*	*Phylloscopus poliocephalus makirensis*	
Phylloscopus sarasinorum	*Seicercus sarasinorum*	*Cryptigata sarasinorum*	*Phylloscopus sarasinorum*	*Phylloscopus sarasinorum*	
Phylloscopus amoenus	*Seicercus amoenus*	*Cryptigata amoena*	*Phylloscopus amoenus*	*Phylloscopus amoenus*	
Phylloscopus poliocephalus[p]	*Seicercus poliocephalus*[p]	*Cryptigata maforensis*[p]	*Phylloscopus poliocephalus*[p]	*Phylloscopus poliocephalus*[p]	
Phylloscopus poliocephalus[p]	*Seicercus maforensis*[p]	*Cryptigata maforensis*[p]	*Phylloscopus maforensis*[p]	*Phylloscopus maforensis*[p]	
Phylloscopus poliocephalus misoriensis	*Seicercus maforensis misoriensis*	?	*Phylloscopus maforensis misoriensis*	*Phylloscopus misoriensis*	

[a] Not included, not even as a synonym, depite having been described in 1922.
[b] Described as a new species, *Phylloscopus sichuanensis*, by Alström et al. (1992).
[c] Synonymised with *Phylloscopus proregulus chloronotus*.
[d] Synonymised with *Phylloscopus proregulus proregulus*.
[e] Includes *P. proregulus* (sensu stricto), *P. kansuensis*, *P. chloronotus* and *P. forresti*.
[f] 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.
[g] The name *ibericus* has priority over *brehmii*, as noted by later authors.
[h] No subspecies included, so this is inferential.
[i] See del Hoyo and Collar (2016) for explanation.
[j] Includes *S. burkii* (sensu stricto), *S. tephrocephalus*, *S. valentini* and *S. whistleri* (*S. soror* and *S. omeiensis* not yet described).
[k] Includes *P. examinandus* and *P. xanthodryas*.
[l] Synonymised with *P. tenellipes* (monotypic).
[m] Includes *P. goodsoni goodsoni*.
[n] Includes *P. claudiae* and *P. goodsoni*.
[o] Circumscription differs from other authors.
[p] Circumscription varies somewhat among authors.
[q] Treated as monotypic based on misinterpretation of results by Olsson et al. (2005) and Päckert et al. (2009).
[r] 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. occisinensis* (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* (cyt*b*) 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 + Γ + I model was selected for cyt*b*, and GTR + Γ 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 + Γ model was used also for cyt*b* (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 cyt*b*. 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 ≥ 0.95 for alternative reconstructions in both the *BEAST and concatenation trees (cf. Supplementary Figs. S2–S3). Two primary clades were recovered (α, β; Fig. 1), although clade β was only strongly supported in the concatenation trees (Supplementary Figs. S2–S3). Within clade α, there was strong support in all analyses (posterior probability, PP, ≥0.95) for seven main clades (E, F, I, J, M, N, O) and a single species (*Phylloscopus emeiensis*) with uncertain relationships. Within clade β, 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 ≥0.95 in one or both of the concatenation analyses (highlighted in orange in Fig. 1). In contrast, in three cases *BEAST reported PP ≥ 0.95, whereas concatenation produced considerably lower support (highlighted in blue in Fig. 1). Single-locus analyses varied in resolution and support, with cyt*b* 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 α and β, 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. fuligiventer*), 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. tytleri* 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 α, which includes both traditional *Phylloscopus* and *Seicercus* warblers, was strongly supported in all analyses. Clade β, which contains only traditional *Phylloscopus*, was only strongly supported by concatenation. Within clade α, none of the early splits into clades G, L, K and P received unanimously strong support across all
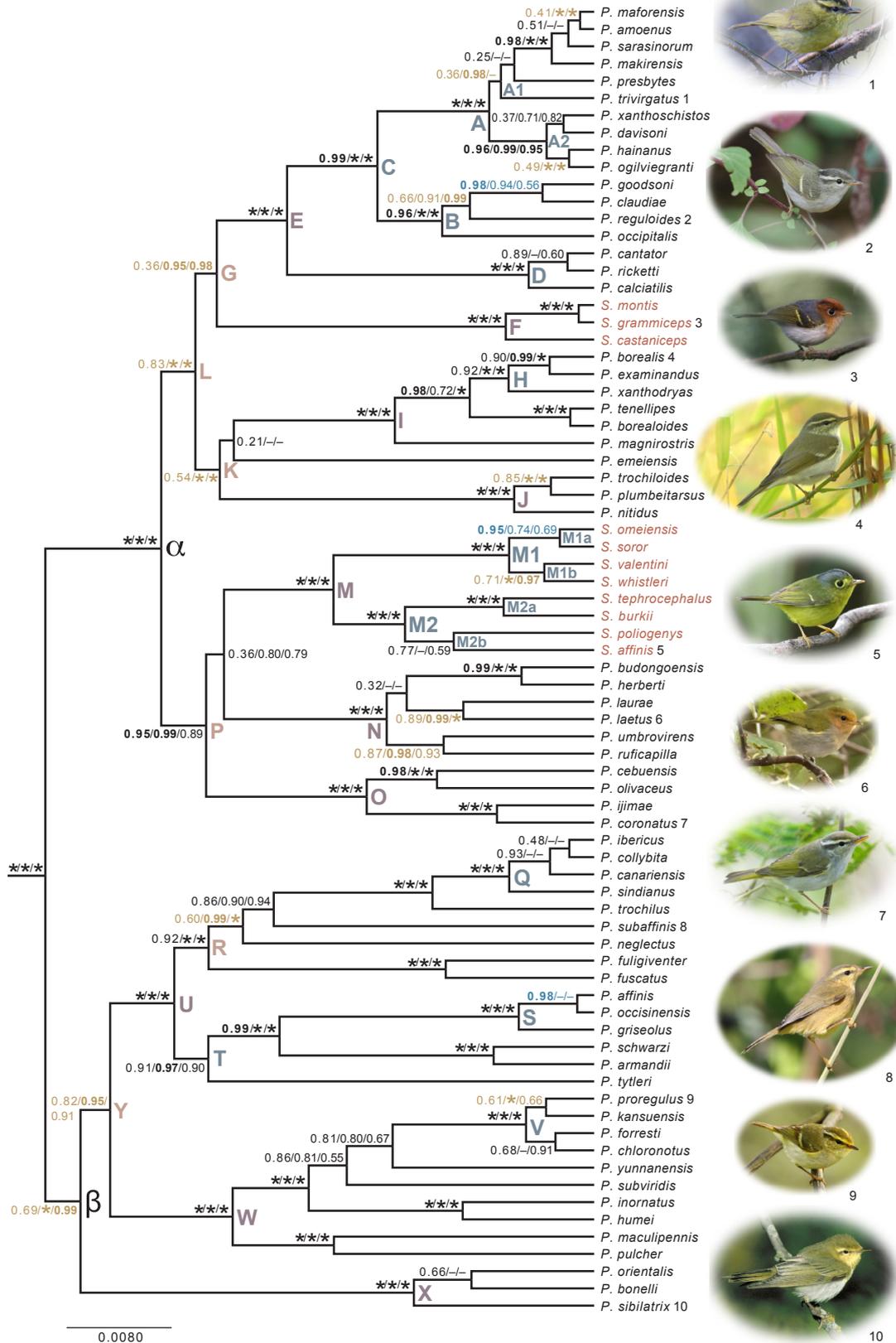
Fig. 1. Phylogeny of Phylloscopidae based on the mitochondrial cytochrome *b* and nuclear ODC, myoglobin and GAPDH introns inferred by *BEAST. Traditional *Seicercus* species are highlighted in red. Values at nodes indicate posterior probabilities (PP) in the order *BEAST/BEAST concatenated/MrBayes concatenated; * indictates PP ≥ 0.95. Nodes with PP < 0.90 in *BEAST but ≥0.95 in one or both concatenation trees are highlighted in orange, and nodes with PP ≥ 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.)
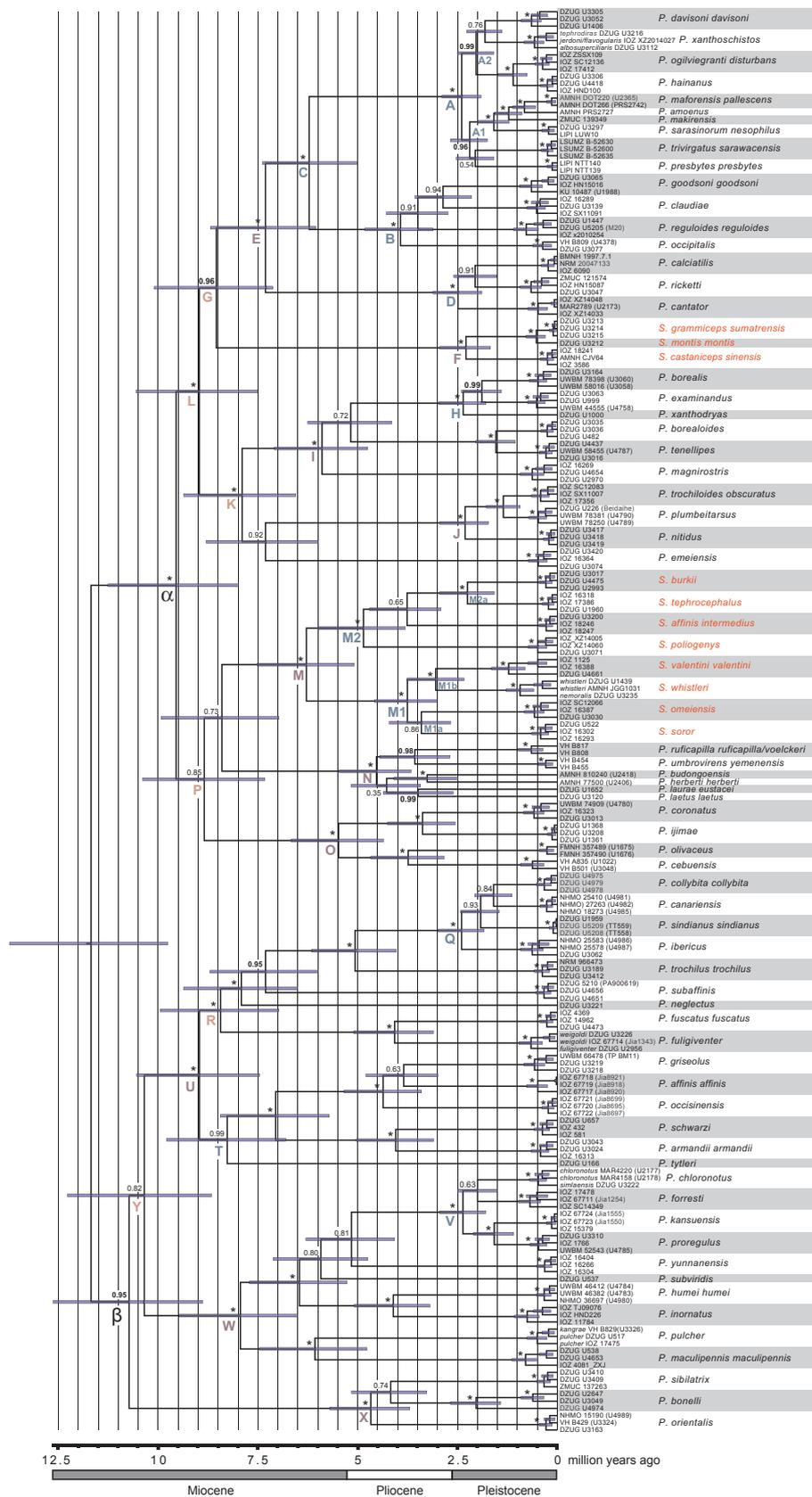
Fig. 2. Chronogram for Phylloscopidae based on same data as in Fig. 1, inferred by BEAST and a 2.1%/million year molecular clock for cytochrome *b*. *Seicercus* species are highlighted in red. Values at nodes indicate posterior probabilities; * indictates PP ≥ 0.95. Labelling of nodes same as in Fig. 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, β, 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 they 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. occisinensis* (clade S) is strongly supported in the *BEAST analysis, whereas the concatenation analyses found *P. occisinensis* 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 vocalisations between *P. occisinensis* 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. occisinensis* 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 α and β 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 ± 3.0–5.7 mya by Price et al. (2014) vs. 3.8 ± 2.9–4.7 in our study, and the divergence between *P. pulcher* and *P. maculipennis* at 8.3 ± 6.6–10.3 mya vs. 6.1 ± 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 (*Abrornis*) and X (*Rhadina*) and placed all *Phylloscopus* in our clade α 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, *Abrornis* J.E. and G.R. Gray, 1847 (type *Abrornis 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 intensior* (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 restict *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

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.

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