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BUILD-UP OF THE HIMALAYAN AVIFAUNA THROUGH IMMIGRATION: A BIOGEOGRAPHICAL ANALYSIS OF THE *PHYLLOSCOPUS* AND *SEICERCUS* WARBLERS

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The Himalayan mountain range is one of the most species-rich areas in the world, harboring about 8% of the world's bird species. In this study, we compare the relative importance of immigration versus in situ speciation to the build-up of the Himalayan avifauna, by evaluating the biogeographic history of the *Phylloscopus*/*Seicercus* warblers, a speciose clade that is well represented in Himalayan forests. We use a comprehensive, multigene phylogeny in conjunction with dispersal-vicariance analysis to discern patterns of speciation and dispersal within this clade. The results indicate that virtually no speciation has occurred within the Himalayas. Instead, several speciation events are attributed to dispersal into the Himalayas followed by vicariance between the Himalayas and China/Southeast Asia. Most, perhaps all, of these events appear to be pre-Pleistocene. The apparent lack of speciation within the Himalayas stands in contrast to the mountain-driven Pleistocene speciation suggested for the Andes and the East African mountains.

KEY WORDS: Aves, biogeography, Himalayas, ***Phylloscopus***, ***Seicercus***, speciation.

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Mountains in tropical regions are the most species-rich areas on earth (Rahbek and Graves 2001; Orme et al. 2005). One possible explanation for this high species richness is that mountains promote a higher speciation rate, driven by the many opportunities for geographical isolation (Simpson 1964; Roy 1997; Graham et al. 2004; Weir 2006) and/or the possibility of adaptive diversification along altitudinal gradients (Endler 1982; Richman and Price 1992; Bates and Zink 1994; Graham et al. 2004; Smith et al. 2005) in these regions. In the Andes, allopatric speciation has been suggested to be the predominant mode of speciation (García-Moreno and Fjeldså 2000) and for example, Arctander and Fjeldså (1994) found that in the avian clade *Scytalopus* (Rhinocryptidae) the species found along an altitudinal transect in the Andes had their closest relatives at the same elevation on another mountain rather than among the neighboring species on the same slope. Alternatively, high diversity may result from an accumulation of species that have formed elsewhere and dispersed into these regions. Persistence of high species numbers in tropical montane regions has been related to a generally high primary productivity in the wet tropics (Hawkins et al. 2003a,b), a great diversity of climatic regimes and associated habitats along elevational gradients, ranging from tropical rainforest to alpine tundra (Terborgh 1977; Rahbek and Graves 2001), and the possibility that such regions are buffered from climatic extremes, for example, because habitats can shift elevationally in response to climate change (Fjeldså 1995; Fjeldså and Rahbek 2006).

The Himalayas are one of the world's two most prominent mountain ranges and contain about 8% of the world's bird species (Price et al. 2003). The high species diversity in the Himalayas is due to species turnover associated with elevational variation in habitat, as well as variation in species composition along the range (Martens and Eck 1995; Price et al. 2003). The formation of the Himalayan mountain range and the Tibetan plateau was initiated by the collision of the Indian plate with the Eurasian plate (reviewed by Le Fort 1996). The initial collision between the two continents occurred about 52–55 million years ago (mya) (Beck et al. 1995; Rowley 1996). By about 35 mya the Tibetan plateau had raised to an elevation of about 4000 m (Rowley and Currie 2006) and in the Himalayas elevations comparable to the present day were probably reached by at least 10 mya (Harrison et al. 1998; Rowley et al. 2001). At about 8–9 mya a major climate shift was associated with the onset of a modern-type monsoon (reviews in Molnar et al. 1993; Copeland 1997). It has been proposed that this climate change may have been driven by a rapid elevation of Tibet at that time (Molnar et al. 1993; Zhisheng et al. 2001), but given the high elevations prior to this time, this is probably unlikely (Rowley and Currie 2006).

The uplift of the Himalayas may have created opportunities for both vicariant speciation within the range (Randi et al. 2000) as well as speciation in response to ecological diversification as in adaptive radiation (Richman and Price 1992; Price and Gross 2005). Previous studies on the *Phylloscopus* warblers along an altitudinal gradient in Kashmir in the northwestern Himalayas indicated that the most closely related species along this gradient differed in habitat choice (altitude), whereas the older divergences relate to changes in body size and feeding method (Richman and Price 1992; Richman 1996). Price and Gross (2005) estimated that even the most closely related species in Kashmir are separated by 7–8 million years, and they suggested that speciation occurred in response to the formation of new habitats in association with climate changes and/or mountain uplift thought to have occurred around that time.

However, the Himalayas have relatively few endemic species (Martens and Eck 1995; Rasmussen and Anderton 2005, Fig. 4). Many Himalayan species are also found in the neighboring areas, for example, in the mountains of Central China and/or Southeast Asia, or Central Asia, and species found at lower elevations in the Himalayas extend into neighboring subtropical and tropical regions. One explanation for this pattern may be that many species formed in the Himalayas have expanded their range out of the region subsequent to speciation, that is, the mountains act as a speciation pump. This has been suggested as a general model for mountainous regions of South America and Africa (e.g., Roy et al. 1997; Jetz et al. 2004). But the pattern could, instead, indicate that the Himalayan fauna are predominantly composed of immigrants, from both the Palearctic and Indomalayan zoogeographical regions, with very little speciation in situ (Martens and Eck 1995).

To investigate the alternative explanations of in situ speciation and immigration, we examine recent and historical distribution patterns of *Phylloscopus* and *Seicercus* warblers in the Himalayas, using a comprehensive, multigene phylogeny of the group in conjunction with dispersal-vicariance analysis (DIVA) (Ronquist 1996, 1997). The *Phylloscopus*/*Seicercus* clade is well represented in the Himalayas with 19 species (almost one third of the species found across mainland Eurasia). The clade comprises in total more than 80 species, and is distributed in the Palearctic, Indomalayan, and Afrotropical regions.

Material and Methods

STUDY GROUP

Recent phylogenetic analyses have shown that neither the *Phylloscopus* nor *Seicercus*, as recognized in recent taxonomic treatments (e.g., Watson et al. 1986; Sibley and Monroe 1990; Dickinson 2003) are monophyletic (Olsson et al. 2004, 2005; Päckert et al. 2004). However, taken together, these two genera do form a monophyletic clade (Olsson et al. 2004, 2005; Päckert et al. 2004), and this is the reason why we consider them jointly in this article.

Our study encompasses 55 species of the *Phylloscopus* and *Seicercus* warblers, including all of the species in the Himalayas and all but six of the species in the Palearctic and Indomalayan regions (missing: western Palearctic *P. canariensis*, *P. ibericus*, *P. nitidus*, and central Asian *P. neglectus*, as well as two Indonesian species) (see Appendix/Supplementary Material available online). The taxonomy follows Dickinson (2003), except that we treat the following as distinct species based on recently published evidence: *P. claudiae* and *P. goodsoni* (previously subspecies of *P. reguloides*, Olsson et al. 2005); *P. ogilviegranti* (formerly subspecies of *P. davisoni*, Olsson et al. 2005); and *P. forresti* (previously united with *P. chloronotus*, Martens et al. 2004). Following Dickinson (2003), the species in the greenish warbler complex *P. trochiloides*, *P. viridanus*, and *P. plumbeitarsus* are treated as distinct species. However, it has been suggested that these form a single species (Irwin et al. 2001), and to account for this we performed an alternative analysis that treated this complex as a single species. This alternative treatment resulted in an almost identical reconstruction of ancestral areas and did not affect the conclusion regarding the Himalayas.

PHYLOGENETIC INFERENCE

Sequence data from the mitochondrial cytochrome b and 12S genes and the nuclear myoglobin intron 2 were used to infer the phylogenetic relationships within the clade (see Olsson et al. 2005 for details). The concatenated alignment consists of 2174 basepairs. The tree was rooted with *Sylvia atricapilla* and *Acrocephalus dumetorum*.

Phylogenetic relationships were estimated with Bayesian inference in MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001). The model of sequence evolution was selected by the Akaike Information Criterion (Akaike 1973) and a hierarchical likelihood ratio test (Posada and Crandall 1998), both of which were calculated using MrModeltest 2.2 (Nylander 2004). The general time-reversible (GTR) model (Lanave et al. 1984; Tavaré 1986; Rodríguez et al. 1990), assuming rate variation across sites according to a discrete gamma distribution with four rate categories (Γ_4) (Yang 1994) and an estimated proportion of invariant sites (I) (Gu et al. 1995) was chosen for cytochrome b and 12s, whereas GTR + Γ_4 was chosen for myoglobin intron 2. Default priors were used. Four Metropolis-coupled MCMC chains were run for 3×10^6 generations and sampled every 100 generations. Samples collected during the burn-in period were discarded, and the posterior probabilities for the clades were estimated from the remaining generations. Two runs, starting from different, randomly chosen trees, were made to ensure that the individual runs had converged on the same target distribution (Huelsenbeck et al. 2002).

HISTORICAL BIOGEOGRAPHY

To evaluate the role of the Himalayas in the evolution of the warblers, we used DIVA to infer the ancestral distribution of the clades in the group (Ronquist 1996, 1997). This method is parsimony-based and takes into account the possibility of vicariance, dispersal, and extinction when inferring ancestral distributions. The method estimates the most likely ancestral area(s) at each node in a given phylogeny by using a three-dimensional cost matrix, which favors vicariance (zero cost) over dispersal and extinction (one cost per event). All species are assigned to one or several unit areas given their current distribution (cf. Fig. 1 and Appendix/Supplementary Material available online), and based on the reconstruction of ancestral areas the DIVA identifies four different events that can explain the distribution of the daughter species, that is, vicariance between areas, speciation within a single area (duplication), dispersal between areas, or extinction. Speciation is inferred to have been vicariant if the ancestral distribution involves two or more unit areas and the daughter lineages are distributed in mutually exclusive subsets of these areas. Speciation within a single unit area is assumed when the ancestral species is confined to that area, and both of the daughter species have at least parts of their distribution in that same area. DIVA

Figure 1. Map showing the approximate limits of the geographical regions used in the DIVA. (A) Central Asia, (B) Himalayas (including Hindu Kush and the mountains in Nagaland, Manipur, Mizoram, Cachar, and Meghalaya, India, and adjacent parts of Myanmar), (C) Central China, (D) tropical and subtropical Southeast Asia (including the southern provinces of China north to the Yangtze River [Chang Jiang]); (E) northeast China and adjacent parts of southeasternmost Russia, Korea, Japan, Sakhalin, and southern Kamchatka; (F) the Taiga; (G) Europe south of the Taiga.

has been widely used in the historical biogeography literature (see, e.g., Chesser 2000; Drovetski 2003; Burns and Naoki 2004 for additional examples). In particular, it has been used in several studies of Andean species, which forms the main point of comparison with the Himalayas. These studies have invariably identified much within-Andean speciation (Chesser 2000; Burns and Naoki 2004).

We set the Himalayas to be one of several unit areas in the Palearctic and Indomalayan zoogeographical regions (Fig. 1). Because our main focus is on Himalayan speciation, we chose two regions flanking the Himalayas as comparison, and then divided the rest of the group's range into four large regions based on standard biome classifications; these areas are coincident with many species ranges in this group. The seven areas are: (A) Central Asia; (B) the Himalayas (zoogeographically this region is considered to include, in addition to the Himalayan range, the Sulaiman range and Safed Koh of northern Pakistan, and the Mishmi Hills, Naga Hills, Khasi Hills, and Chin Hills in India, plus adjacent parts of Myanmar [cf. Stattersfield et al. 1998]); (C) the mountainous region of central China (corresponding to EBA 135–139 in Stattersfield et al. 1998); (D) tropical and subtropical Southeast Asia (including the southern provinces of China north toward the Yangtze River [Chang Jiang]); (E) the temperate northeast China and adjacent parts of southeasternmost Russia, Korea, Japan, Sakhalin, and southern Kamchatka; (F) the Taiga; (G) Europe south of the Taiga. Each species was allocated to one or several of these areas using published range maps (Baker 1997; Grimmet et al. 1998; MacKinnon and Phillipps 2000; Robson 2000; Rasmussen and Anderton 2005) and our own field observations.

We used DIVA 1.1 (Ronquist 1996) to conduct the analysis, with default settings, except that two different settings of the "maxarea" option were used to evaluate differences in reconstruction when the ancestral area was constrained to include a maximum of two or three unit areas, respectively; three being the maximum number of areas covered by any recent species. DIVA can only handle fully bifurcated trees, so we used the "all compatible" consensus tree from the Bayesian analysis for this analysis.

TIME

We obtained estimates of the timing of speciation events, for comparison with previous work in Africa and the Andes (Roy 1997; Roy et al. 1997; Burns and Naoki 2004; Weir 2006). Because the assumption of a molecular clock was rejected in a likelihood test, branch lengths proportional to time were estimated by rate-smoothing the tree obtained in MrBayes, using the program r8s and the method of penalized likelihood (Sanderson 2003). To convert sequence distances into time, the best approach is to use calibration points in the tree, either from biogeographical or fossil-based data, but the lack of reliable fossils of *Phylloscopus* and *Seicercus* warblers older than Late Pleistocene (Tyrberg 1998) precludes a more detailed clock calibration for the group. Instead, to calibrate the rate-smoothed tree, we equated the depth of the tree, to the depth of a tree obtained by enforcing a molecular clock in the maximum likelihood program TREE-PUZZLE (Schmidt et al. 2002) for the cytochrome b data only, using the HKY + Γ model with the parameters of the model estimated in TREE-PUZZLE ($\Gamma = 0.2$). We converted the depth of the tree into time using the estimated rate of 2% sequence divergence per million years for mitochondrial DNA (reviewed in García-Moreno 2004; Lovette 2004).

Results

PHYLOGENETIC RELATIONSHIPS

The two separate runs in the Bayesian analysis converged on similar, stable log-likelihood scores and resulted in identical topologies with only minor differences in posterior probabilities. The tree is generally well supported, with most nodes having posterior probabilities over 0.95 (Fig. 2). Most of the uncertainties pertain to the interrelationships within the small-bodied species (the clade containing, e.g., *P. maculipennis*, *P. pulcher*, *P. humei*, and *P. chloronotus*), and the relationship of this clade relative to the mainly European clade (*P. orientalis*/*P. sibilatrix*/*P. bonelli*) and a clade containing, for example, *P. trochilus*, *P. collybita*, *P. fuscatus*, and *P. tytleri*. Another uncertainty is the position of *P. emeiensis* relative to the clades containing *P. magnirostris* and *P. trochiloides*, respectively. The results of this study are similar to that of Olsson et al. (2005), who used the same three genes but a partly different taxon sampling to infer phylogenetic relationships of *Phylloscopus* and *Seicercus* warblers. The main discrepancies between these two studies pertain to the placement of *P. goodsoni* relative to *P. occipitalis* and *P. reguloides*/*P. claudiae* and to the placement of the clade containing, for example, *S. whistleri*, *S. burkii*, and *S. poliogenys* relative to *S. castaniceps*/*S. montis*, *P. coronatus*/*P. ijimae*, and the large clade containing, for example, *P. trochiloides*, *P. magnirostris*, and *P. reguloides*. In the former case both alternative hypotheses receive low nodal support, whereas in the latter case the placement of the *S. whistleri*, *S. burkii*, and *S. poliogenys* clade has a posterior probability over 0.95 in the present study, whereas the alternative placement of this clade in Olsson et al. (2005) has a posterior probability much lower than that.

HISTORICAL BIOGEOGRAPHY

The Himalayan species are scattered over the tree rather than forming a monophyletic group (Fig. 2). Except for two species pairs, *P. maculipennis*/*P. pulcher* and *S. poliogenys*/*S. affinis*, all of the Himalayan species have their closest relative outside the Himalayas. The optimal area reconstructions at each ancestral node from the constrained (maxarea = 3) DIVA indicate that the

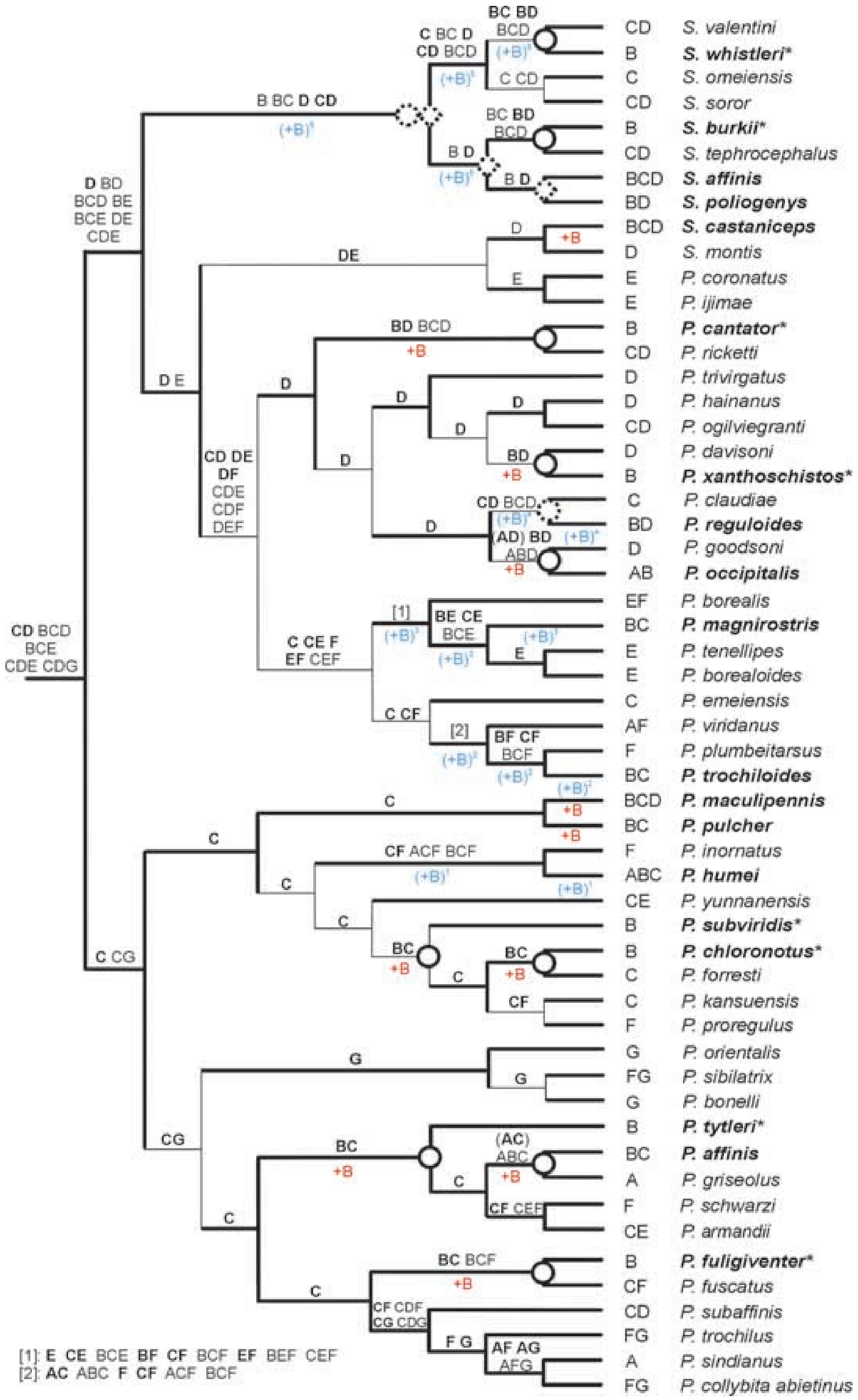

Figure 2. Reconstruction of the biogeographic history of the *Phylloscopus/Seicercus* clade using a constrained (maxarea = 3) DIVA (Ronquist 1997). The topology is from Bayesian analysis of a combined data set of mitochondrial cytochrome *b* and 12S and nuclear myoglobin intron 2 sequences. Thick branches indicate nodes with posterior probabilities $\geq$0.95. Letters at nodes refer to the geographical regions shown in Figure 1 and indicate the ancestral areas inferred for that node. Areas indicated in bold also arise in the "maxarea = 2" optimization. Symbols: "+B" indicates a dispersal event into the Himalayas; "(+B$^{1\text{-}5}$)" indicates dispersal into the Himalayas, but that the point in the phylogeny is uncertain given uncertainties in the reconstruction of the ancestral areas. Symbols denoted with an identical superscript (numbers 1–5), refer to the same bifurcation event and denote alternative inferences for that event; *circle*: vicariance; *diamond*: speciation within the Himalayas; *stippled symbol*: inferred mode of speciation only under certain optimizations of the ancestral area(s). Names in bold indicate species found in the Himalayas; those marked with * are endemic to the Himalayas.

majority of the Himalayan species independently originated from ancestral species that dispersed into the Himalayas from Central China or Southeast Asia (Fig. 2). In at least half of these cases, subsequent vicariance between the Himalayan and the ancestral population has resulted in an endemic species in the Himalayas. In one case, speciation is inferred to have taken place between Central Asia and the Himalayas (between *P. affinis* and *P. griseolus*), but this clade is inferred to have originated from an ancestor that dispersed into the Himalayas from the east (Central China).

No speciation event is unequivocally inferred to have occurred within the Himalayas, but in three cases, all in a clade of *Seicercus* warblers and including internal nodes, a Himalayan origin is indicated as one of two or more equally optimal alternatives (Fig. 2). In these three cases, Southeast Asia is inferred as an equally likely ancestral area, and when the DIVA analysis is constrained to allow the ancestor to occur only in a maximum of two areas (maxarea = 2), only Southeast Asia (and in one case Southeast Asia and Central China) is optimized as being the ancestral region. Under this optimization, no internal node is inferred as Himalayan, but apart from this, there is generally good agreement between the optimization where maxarea = 3 and the one where maxarea = 2 (Fig. 2).

TIMING

The rate-smoothed tree (Fig. 3) indicates that among the Himalayan species, only six of the 19 species are separated from their closest relative by less than 4% sequence divergence. In all these cases, the nearest relative's range is outside the Himalayas. If the analysis is confined to only the species that occur within the Himalayas, none are separated by less then 4%, and only two splits (separating the species *S. affinis*/*S. poliogenys* and *P. reguloides*/*P. occipitalis*, respectively) are separated by less than 8%. If the conventional clock of 2% divergence/million years is assumed, only six speciation events that involve at least one Himalayan species occurred in the Pleistocene, that is, are younger than 2 million years old, and no splits separating two Himalayan species are younger than Pleistocene. Even if the rate of molecular evolution is twice as fast, only two splits that include two Himalayan species could have occurred in the Pleistocene. Standard GTR + Γ distances (in the absence of rate smoothing) between pairs of species indicate even older splits for many species pairs. Only two pairs, *S. castaniceps*/*S. montis* and *P. trochiloides*/*P. plumbeitarsus* are separated by less than 4%. No two Himalayan species are separated by less than 10% in the GTR + Γ distance matrix.

Discussion

As in all historical analyses, inference of ancestral areas may be sensitive to uncertainties in the phylogeny, especially for a trait likely to be as generally labile as geographical range. The phylogenetic tree used for the DIVA is in general well supported, but also contains some weakly supported nodes (Fig. 2). These uncertainties may possibly affect specific reconstructions, but even with these uncertainties in mind, our data clearly indicate that speciation is not centered in the Himalayas. Even in the two cases where both presumed sister species are found in the Himalayas (Fig. 2), it is doubtful if the speciation took place there. In the case of the sister species *P. maculipennis* and *P. pulcher*, both species are also distributed in central China, and the DIVA reconstruction implies that speciation occurred in this region, with immigration into the Himalayas of both sister species at a later stage. The other Himalayan sister pair, *S. affinis* and *S. poliogenys*, is inferred as potentially having originated in the Himalayas, but only in one of the two different DIVA optimizations, and then too as one of two equally optimal alternatives (the other implying immigration of both species from Southeast Asia). Furthermore, none of the internal, more ancient, nodes unambiguously support speciation in the Himalayas, and in only two cases, in one of the two optimizations, is the Himalayas inferred as a possible ancestral area, but in both cases other regions are inferred as equally likely (Fig. 2).

Speciation within the Himalayas, as suggested by Richman and Price (1992) and Price and Gross (2005), is not supported by the present study. Instead, most species appear to have originated from ancestors that lived east of the Himalayas, either in Central China or Southeast Asia. This includes even the species *P. tytleri* and *P. subviridis*, which both have very restricted distributions in the western Himalayas (Fig. 2). DIVA does indicate several examples of vicariance between the Himalayas and the apparent ancestral area, and many of the Himalayan endemics appear to be a result of dispersal or range expansion of an ancestral species into the Himalayas from the east, with subsequent vicariance between the Himalayas and the area of origin; for example, *P. chloronotus*, *P. xanthoschistos*, and *P. cantator* (Fig. 2). Six of the eight Himalayan endemics have a parapatric sister species east of the range, and five of these sister pairs meet in a fairly restricted area in the Salween–Mekong–Yangtze region in southeastern Tibet and western Yunnan, China (Baker 1997; Rasmussen and Anderton 2005). This region is characterized by a series of parallel north–south trending high mountain ridges intercepted by deep gorges formed by the Salween, Mekong, and Yangtze rivers. The concordance of the distribution of these species pairs suggests that these mountain ranges constitute an effective barrier to dispersal. Although DIVA infers vicariance as the mode of speciation in these groups, it cannot be established whether the ancestral distribution was divided by the uplift of the Salween, Mekong, and Yangtze divides (vicariance in a strict sense) or whether the ancestral species crossed this barrier after it had been established. The results of DIVA are consistent with both these scenarios. However, the r8s analysis indicates different divergence times for these species pairs (Fig. 3), suggesting that these splits may not have

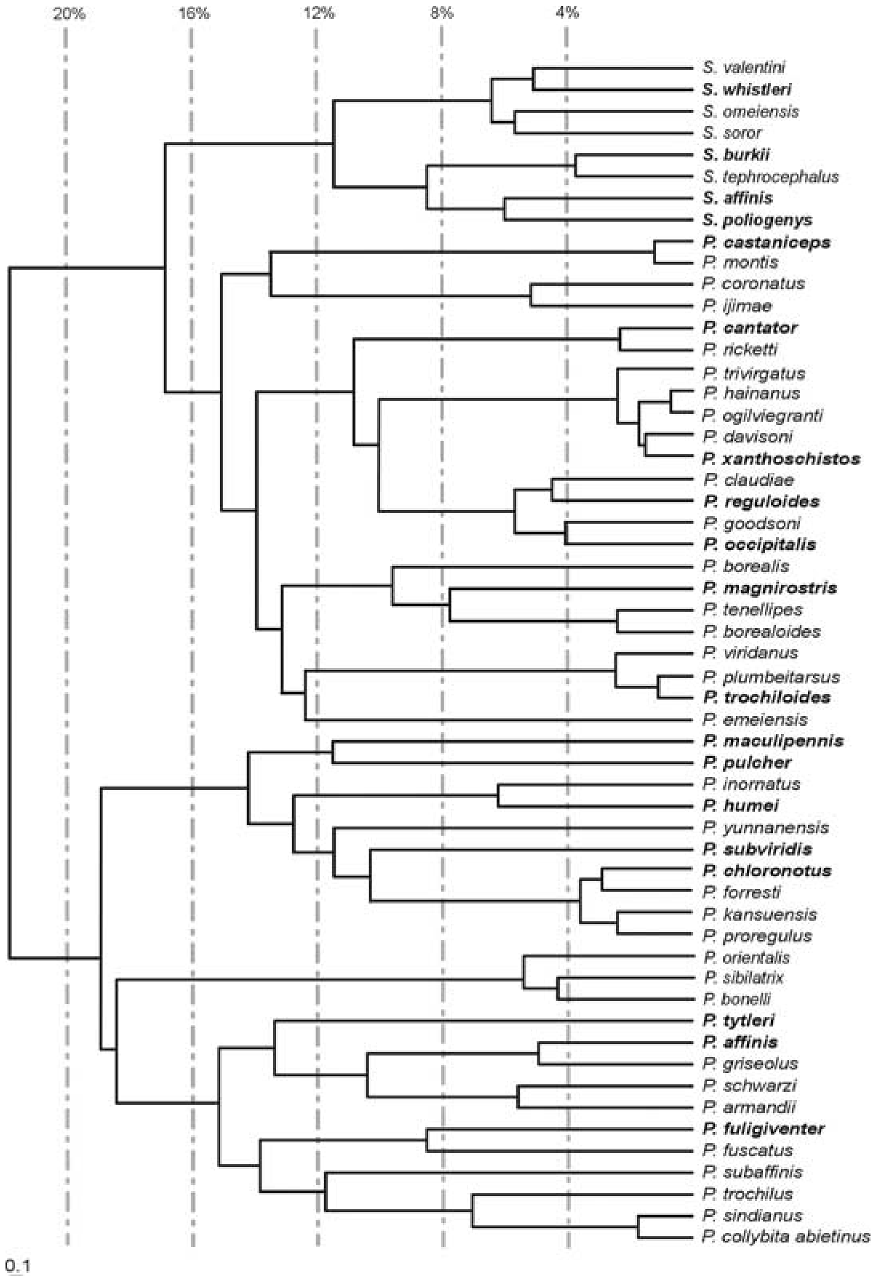

Figure 3. A rate-smoothed tree with the topology and branch lengths (GTR $+ \Gamma +$ I) from a Bayesian analysis of a combined data set of mitochondrial cytochrome *b* and 12S and nuclear myoglobin intron 2 sequences. The depth of the tree was estimated at 10.97% (i.e., 21.94% sequence divergence across the root) in a separate analysis that used the cytochrome *b* data only in a maximum likelihood enforced clock with no outgroups, and mid-point rooting. Species in bold have Himalayan distributions as in Figure 2. Scale bar indicates inferred amount of evolution along a branch; dashed lines indicate inferred sequence divergence at 4% intervals.

been concurrent. Alternatively, this region represents a secondary contact zone and other barriers in this region have fostered the vicariant patterns in the group.

Genetic distances between warbler species currently present in the Himalayas indicate that they diverged before the Pleistocene. In contrast, both in the Andes (García-Moreno et al. 1999; Weir 2006) and in some African mountains (Roy 1997; Roy et al. 1997), many speciation events are inferred as Pleistocene. In particular, much recent speciation has happened in the Andes. Weir (2006) found in an analysis of 146 species from diverse groups that 43% were <5% divergent from their closest Andean relative. In contrast, among the 19 Himalayan warblers studied here using the same methods as Weir, none of the species that live in the Himalayas are separated by divergence times of <5% (Fig. 3). However, splits separating some of the Himalayan endemics from their parapatric sister species may have occurred in the

Pleistocene, for example, *P. chloronotus*/*P. forresti*, *S. castaniceps*/*S. montis*, and *S. burkii*/*S. tephrocephalus*.

Although only a few other groups of Himalayan birds have been studied, there seems to be little evidence for vicariant speciation within the Himalayas in general. Ripley and Beehler (1990) documented the role of barriers in causing vicariance in the Indian subcontinent. They concluded that the river gorge Karnali in western Nepal formed a barrier between the hybridizing tits *Parus melanolophus* and *P. ater*. All other barriers separating allospecies were in regions outside the Himalayas, for example, the Palk strait between India and Sri Lanka, and the Ganges River basin (Ripley and Beehler (1990). A possible example of vicariant speciation within the Himalayas was presented by Randi et al. (2000), who suggested that events in the Pliocene and early Pleistocene fostered vicariant speciation in tragopans (*Tragopan* spp.).

We suggest three possible reasons for the apparent lack of Pleistocene divergences among the Himalayan species, as well as the absence of speciation in the Himalayas in general. First, glacial barriers such as those invoked for North American species (Weir and Schluter 2004) and suggested as being important for Andean speciation (Weir 2006) may have been absent. The glacial advance in the Himalayas during Pleistocene glaciations is thought to have been relatively small, as a result of low precipitation (Mark et al. 2005; Owen and Benn 2005). Second, habitats along the range may have been largely unsuitable for warblers for long periods. Although a detailed picture of the forest distribution in the Himalayas during the last glacial maximum (c.18,000 years before present) is lacking, the generally dry and cold conditions that prevailed may have led to an absence of temperate forest in the region (Adams and Faure 1997; Ray and Adams 2001). Third, the lack of speciation in the Himalayas may be more apparent than real, if inclement conditions in the Pleistocene have led to a high rate of extinction.

In conclusion, we find that the present species composition in *Phylloscopus* and *Seicercus* warbler communities in the Himalayas has resulted mainly or exclusively from the immigration of taxa from areas east of the range. The build-up of the Himalayan avifauna may have been driven by the appearance of new habitats in association with mountain building or climate change (Price and Gross 2005), but the formation of species that were able to invade the region to exploit these habitats appears to have been driven by speciation events outside the range. Thus, it appears that while ecological opportunity per se may have been important in enabling species build-up in the Himalayas, it may not have been critical in driving speciation. If this is a correct interpretation, adaptive diversification and speciation are largely independent of each other, and not coupled as in the classic conception of adaptive radiation where ecological opportunity drives speciation (Schluter 2000).

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