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CHAPTER 4

PHYLOGENY, BIODIVERSITY, AND SPECIES LIMITS OF PASSERINE BIRDS IN THE SINO-HIMALAYAN REGION—A CRITICAL REVIEW*

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ABSTRACT.—We analyzed passerine biodiversity and phylogeography in the Sino-Himalayan region with respect to neighboring areas, especially the Siberian taiga zone to the north and tropical Asia southeast of the Himalayas and mountainous parts of southwest China. Fresh results, informative about evolutionary processes in that area, were obtained mainly by the application of new methods in passerine systematics, acoustic and molecular genetic markers. It became evident that species with areas in the Himalayas and southwest China and, in addition, often with disjunct areas in Siberia, actually belong to swarms of closely related, mostly allopatric species. In many cases these differ markedly in vocalizations and are deeply split according to molecular genetic markers. External morphology of the constituent taxa quite often remained surprisingly homogeneous and thus resulted in traditional subspecies status of single populations at best. Other such well-differentiated taxa were often overlooked and only discovered by molecular genetic techniques. Within the Himalayas, contrary to current thinking, intra-range differentiation is well developed in some taxa but still largely unresolved because of deficient sampling along the Himalayan chain. Both subspecies and allopatric species are also concerned here. Apparently, the Himalayas were mostly settled from the east following intra-range diversification. Immigration from the west into the Himalayas was a much rarer event and, impeded by the monsoons, immigrants reached just west Nepal and, with respect to evolutionary history, did not diverge further. Himalayan endemic passerines are few and mainly confined to the western part.

Key words: acoustics, China, Himalayas, molecular genetics, Siberia, Sino-Himalayan region, speciation.

Filogenia, Biodiversidad y Límites de las Especies de Aves Paserinas en la Región Sino-Himalaya—Una Revisión Crítica

RESUMEN.—Analizamos la biodiversidad y filogenia de paserinos en la región Sino-Himalaya con relación a las áreas vecinas, especialmente la zona de la taiga siberiana hacia el norte y Asia tropical al sudeste del Himalaya, y las partes montañosas del sudoeste de China. Nuevos resultados, que brindan información sobre los procesos evolutivos en aquellas áreas, fueron obtenidos principalmente por la aplicación de nuevos métodos en sistemática de paserinos, acústica y marcadores genéticos moleculares. Se hizo evidente que las especies distribuidas en el Himalaya y el sudoeste de China, que además usualmente se encuentran en áreas disjuntas en Siberia, pertenecen en realidad a enjambres de especies mayormente alopátricas y cercanamente emparentadas. En muchos casos éstas difieren marcadamente en vocalizaciones y están profundamente escindidas

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de acuerdo a los marcadores genéticos moleculares. La morfología externa de los taxones constitutivos con frecuencia fue sorprendentemente homogénea y, por ende, dio como resultado el estatus de subespecies tradicionales sólo para poblaciones individuales en el mejor de los casos. Otros taxones bien diferenciados fueron usualmente pasados por alto y sólo descubiertos por técnicas de genética molecular. Al contrario de lo que se piensa usualmente, dentro del Himalaya la diferenciación está bien desarrollada en algunos taxones, pero, en gran medida, permanece aún sin resolver debido a los muestreos deficientes a lo largo de la cadena del Himalaya. Tanto las subespecies como las especies alopátricas también son consideradas aquí. Aparentemente, el Himalaya fue mayormente colonizado desde el este, con una posterior diversificación dentro de esta zona montañosa. La inmigración desde el oeste hacia el Himalaya fue mucho más rara y, al estar impedida por los monzones, los inmigrantes llegaron sólo hasta el oeste de Nepal y no se diferenciaron más evolutivamente. Los passerinos endémicos del Himalaya son pocos y están principalmente confinados a la parte oeste.

THE HIMALAYAN REGION and, especially, its eastern parts and surrounding areas have long been considered a hotspot of avian diversity. Stattersfield et al. (1998) discriminated eight "important bird areas" (IBAs) in the area, with up to 22 endemic or restricted-range species in a single IBA. Because of its orographic diversity, ranging from the tropical lowlands and a variety of mountain forests up to the Himalayan snow peaks and Tibetan high-altitude steppes, the Sino-Himalayan area harbors a rich fauna. However, in the area under consideration, there is not simply a multitude of species attributable to orographic and ecological diversity. Many species and species complexes display a distinct and congruent distributional pattern that suggests they share a common history. In general, the historical complexity of various taxa seems to be enormous and enriches the fauna, which until recently was sampled and analyzed on the basis of traditional systematics and taxonomy. Fresh methods, like bioacoustics and molecular genetic analyses, enable us to draw a more complex picture that is appropriate to the orographic, geological, and climatic history of the area.

Our aim here is to provide an overview of the current state of knowledge from phylogenetic and bioacoustic research on some Himalayan passerine bird groups based on our own data from the past 10 years. In all study taxa the results of molecular research implied several taxonomic changes. In most species, relatively recent evolutionary steps seem to be concerned, because the areas of the taxa in question are allopatric and, occupying similar or even identical ecological niches, they apparently were unable to reach even partly sympatric distribution. Contact zones of closely related taxa are as yet unknown and have not been searched for. Consequently, population genetics in suture zones of closely related

representatives are unknown, too, but remain a constant challenge for field research.

In many of the species we treat here, a degree of geographic differentiation had long been known and was expressed by denomination of subspecies; thus, it was treated—in terms of current taxonomy—as subtle in most cases. Only the onset of comparative bioacoustics and molecular genetics provided the insight that population structure in Sino-Himalayan passerines is much more complicated and diverse, though quite often subject to a common pattern. Only the fruitful combination of acoustic and genetic characters gave evidence that differentiation formerly regarded as "subspecific" in reality represents populations that underwent long and independent evolution in geographic separation. Presently, in most cases these populations merit treatment as "species." Notwithstanding that issue, taxa that were formerly more or less indistinguishable morphologically—and, thus, unrecognized—came to light and needed to be named anew.

DEFINITIONS

Sino-Himalayan region.—Our focus is on the Himalayan chain between the upper Indus River in the west and Namcha Barwa Mountain or the Brahmaputra bent, respectively, in the east. The area further includes mountainous areas of southwestern China east and northeast of the Himalayas as an integral part of this biogeographic region. Relations to Southeast Asia and even Siberia are marked. At the western rim, faunal influences of adjacent parts of, for example, Afghanistan are sparse and did not much enrich Himalayan faunas either by immigration or by local speciation processes.

Species.—We adhere to Mayr's (1942, 1970) biological species concept throughout. The lack

of population interactions (lack or virtual lack of hybridization) is the precondition of the biological species concept. The flaw of this concept with regard to closely related allopatric populations is common sense. In these cases the yardstick approach is an important tool (Mayr and Ashlock 1991). Under this idea two taxa are affiliated to different species if important characters are at least as different from each other as they are between two proven species of the genus (or family) in question (compare Rheindt and Eaton 2010). With the onset of molecular systematics, "species" have often been reduced to strongly split clusters or lineages, leading to the definition of the phylogenetic species concept (Cracraft 1983), whereas the interactions of those clusters in nature have in most cases been neglected. Nevertheless, when discussing genetic distance values, the two species concepts meet. Low values may indicate independent lineages, not necessarily reproductive barriers, and are often regarded as defining a "species" according to the phylogenetic species concept. Higher values may indicate reproductive barriers and point to "biological species." For the time being, it is impossible to draw generalizations on molecular data alone.

Subspecies.—Subspecies indicate populations that inhabit parts of the area of a species. Mostly they are defined by external morphology, rarely by molecular genetic data.

Superspecies.—A superspecies is composed of two or more allospecies, and the term follows the ideas of Amadon (1966). Allospecies are actually allopatrically distributed and originate from the evolutionary split or splits of a former widespread ancestor species. Consequently, the former makes a superspecies monophyletic and its constituents closely related.

Species complex.—This is a more general term and denotes a set of species to which the term "superspecies" does not apply. In those complexes, common ancestry is less clear; it is camouflaged by further evolutionary processes and cannot be revealed unambiguously by molecular genetic analyses.

MATERIAL

The following review of passerine biodiversity and phylogeography in the Himalayas and surrounding areas is based mainly on the results of the working group of J.M. at Mainz University (and on the work of that group's later outliers).

It is entirely focused on passerines, with particular consideration of genera that include both Palearctic and Himalayan species, like *Certhia*, *Parus*, *Phylloscopus*, *Regulus*, *Seicercus*, and *Sitta*. In the Himalayas, the Palearctic avifaunal elements have a clear affiliation to the moist subalpine forests (*Rhododendron*-coniferous zone up to timberline; 2,800–4,200 m) whereas tropical Oriental species rarely occur above 2,000 m (Martens 1984, Belik 2006). Therefore, and because of our choice of study taxa, we can draw only limited conclusions on phylogeographic pattern and the degree of intra- as well as interspecific differentiation from our results, and it must be kept in mind that avian genera with an exclusively (sub-)tropical distribution might reveal different patterns. The material necessary for the various studies—skins, recordings of vocalizations, and tissue samples—was collected almost entirely during J.M.'s expeditions to parts of Asia, namely Nepal, India, China, the Philippines, Indonesia, Iran, and the former Soviet Union (western and eastern Siberia, Central Asia, and various parts of the Caucasus), and in Europe. Collecting trips were made nearly annually from 1969 to 2010.

METHODS

Molecular genetics.—Taxonomic and systematic conclusions drawn from our own molecular data were generally inferred from mitochondrial markers. Most of our own studies refer to the cytochrome-*b* gene, which for a long time was the most frequently used marker gene for phylogenetic inference. However, single-gene trees may significantly differ from species trees and may lead to conflicting results with respect to different mitochondrial and nuclear gene loci (Bensch et al. 2006, Liebers-Helbig et al. 2010, Wiens et al. 2010) but may also lead to concordant phylogenetic trees (Weibel and Moore 2002). In a comprehensive review of recent genetic studies on birds, Zink and Barrowclough (2008) found only a few examples of conflicts among phylogenies reconstructed from nuclear and mitochondrial DNA and concluded that mtDNA even provides the more sensitive markers for population structure. For a better resolution of older bifurcations in the molecular trees of highly diverse genera, additional mitochondrial and nuclear genes were used in some of our recent studies (Martens et al. 2008; Päckert et al. 2009a, b, 2010).

Depending on the study group, there were fresh blood and tissue samples available for molecular analysis; for the several taxa missing from the sample sets, we analyzed toe-pad or skin samples from museum specimens (up to ~90 years old). For extraction of DNA from blood and tissue samples, we used a High Pure PCR Template Preparation Kit (Roche, Mannheim, Germany). DNA extraction from toe pads was performed using an AGOWA sbeadex Forensic Kit (LGC, Berlin) in a separate clean room, and all steps of analysis (sampling, extraction, and polymerase chain reaction [PCR]) were performed on separate clean benches. Depending on the study group and the use of museum tissue samples, several internal primers were designed in order to amplify shorter gene fragments from degraded ancient DNA (aDNA). The PCR and sequencing protocols for cytochrome *b* followed Dietzen et al. (2003), and those for 16S rRNA followed Spicer and Dunipace (2004) with slight modifications. For aDNA analysis, internal primer design, and according PCR settings, see Martens et al. (2008) and Päckert et al. (2009a, 2010). Sequencing of the PCR products was performed with BigDye v. 3.0 and v. 3.1 Dye Terminator Cycle Sequencing Kits (Applied Biosystems, Foster City, California) according to the manufacturer's instructions, and reactions were electrophoresed with an ABI 377 automatic sequencer. Sequences were aligned by ClustalW using MEGA 3.1 (Tamura et al., 2007) and slightly adjusted by hand. Our own molecular data sets for the species discussed below comprise about 450 sequences of Asian passerines (cytochrome *b* only; west Palearctic taxa excluded, but far east Russian taxa included; for accession numbers of GenBank and standard phylogenetic reconstructions using maximum likelihood, neighbor joining, and Bayesian inference of phylogeny, see the original publications cited in the various sections below). To ensure comparability of genetic results from different studies, all intra- and interspecific genetic distances referred to below were recalculated from original data sets as uncorrected *p*-distances.

Bioacoustics.—Vocalizations of a number of Sino-Himalayan bird species are fairly well known and were often used as a flanking independent character set to verify the assumptions made on molecular systematics. A first, partly comprehensive Nepal avifauna by Martens and Eck (1995) provides a multitude of sonagrams, with a focus on passerine species; since then, knowledge of

acoustic differentiation among Himalayan, Central Asian, and Chinese populations of the same species group has significantly increased, mainly owing to the extensive collecting activities of J.M. (as shown in the examples below). Along with our molecular studies, sonographic analyses were conducted for all passerine groups discussed here. For sonographic measurements with Avisoft-SASLab Pro, version 4.36 (see Acknowledgments), we used digitized recordings of original recordings converted to a sampling rate of 22.1 kHz/16 bit. For details on sonographic measurements and analyses, see Martens et al. (2008) and Päckert et al. (2009a).

In order to test for a correlation of genetic and bioacoustic differentiation among taxa, mean pairwise genetic distances were compared with mean pairwise differences in discriminant functions 1 and 2 (as performed in Päckert et al. 2004, 2009a). In a more generalized approach, differences in song pattern (i.e., the order of notes, syllables, or distinct partitions of song [= syntax]) among taxa were categorized into three levels of differentiation: (1) same song pattern, in which subtle differences in frequency range may occur; (2) only parts of song show a different pattern (e.g., presence or absence of introduction notes in *Phylloscopus* and *Seicercus* [Päckert et al. 2004, Martens et al. 2008], trills or syllables in unit 1 of uniformly tripartite goldcrest song [Päckert et al. 2003]); or (3) song pattern completely different among taxa (e.g., trill and motif singers in treecreepers [*Certhia*; Tietze et al. 2008], song syntax in *Regulus* [U1U2U3 in *R. regulus*, U2U2 in *R. ignicapillus*, etc.; Päckert et al. 2003]).

RESULTS

Genetic and acoustic differentiation of Himalayan passerine species.—Pairwise genetic distances cover a broad range, even at the intraspecific level, according to the taxonomy in Dickinson (2003): most pairwise comparisons between currently recognized subspecies range below 3% *p*-distance values, but already a number of interspecific pairwise comparisons have been found at that comparatively low genetic divergence level (Fig. 1A). Examples for Himalayan–Chinese species pairs at a low level of genetic differentiation are *Aegithalos iouschistos* vs. *A. bonvaloti* vs. *A. fuliginosus*, *Phylloscopus xanthoschistos* vs. *P. davisoni*, and *Pyrrhula erythrocephala* vs. *P. erythaca*. On the other hand, several pairwise comparisons at the

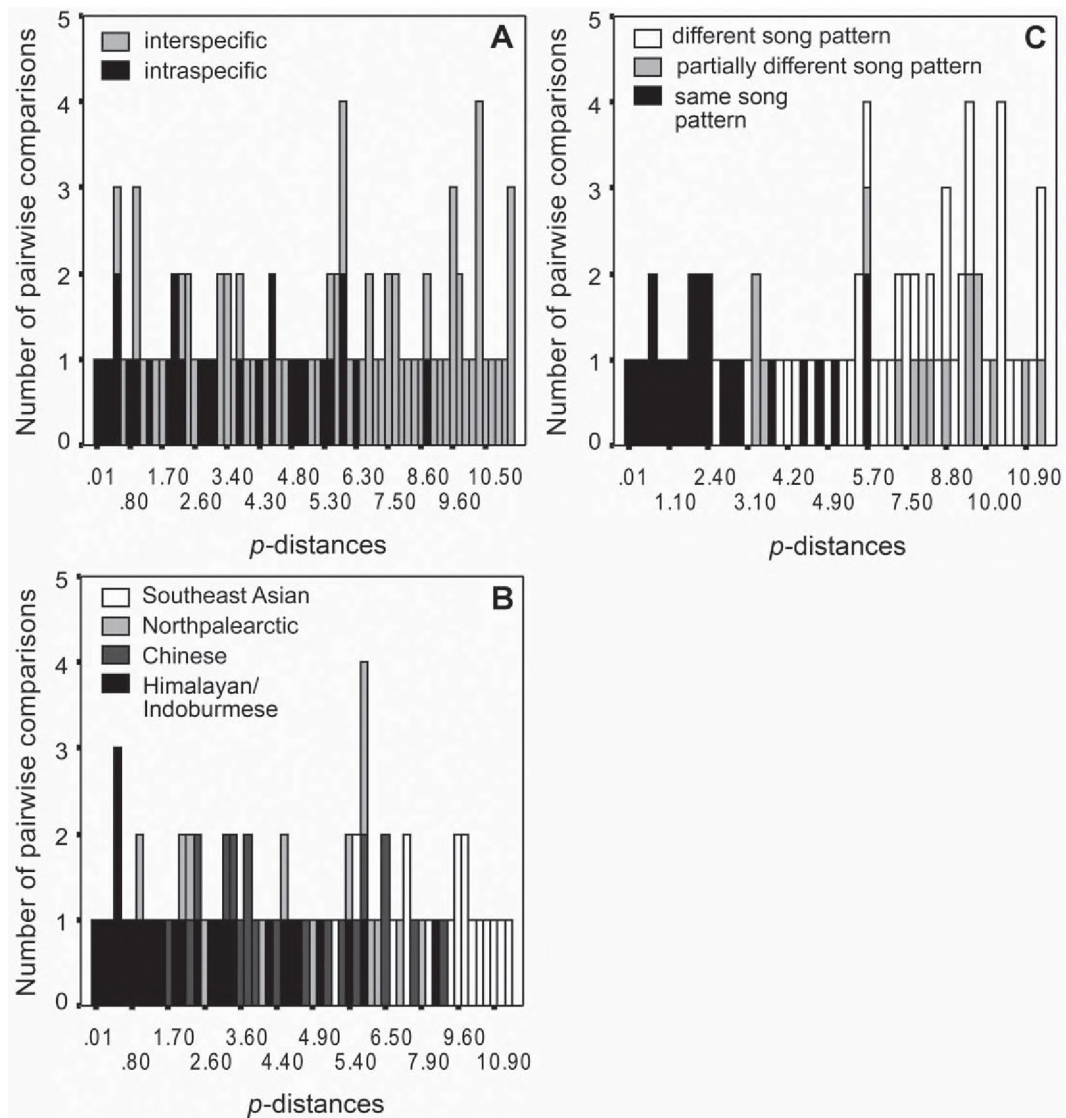


FIG. 1. Genetic versus acoustic differentiation of Himalayan taxa from their closest Chinese, Southeast Asian, and Palearctic relatives: p -distances (cytochrome b) plotted versus absolute number of pairwise comparisons (y -axis). (A) Intraspecific versus interspecific pairwise comparisons (taxonomy according to Dickinson 2003). (B) Comparison of Himalayan populations with those from other zoogeographic regions. (C) Comparison among three categories of pairwise acoustic differences: song pattern the same, partially different, or considerably different.

currently accepted intraspecific level have produced considerably high genetic distance values, up to a maximum of 8.8% among Himalayan and Chinese populations of *Phylloscopus affinis*. *Parus ater aemodius* and *P. a. melanolophus* also belong in this group (for details, see below). Other intraspecific comparisons at a high level of genetic differentiation comprise Himalayan and closely

related subspecies of the Goldcrest (*Regulus regulus himalayensis* vs. all other conspecifics), Black-throated Tit (*Aegithalos concinnus iredalei* vs. Southeast Asian ssp. *manipurensis*, *concinus*, and *talifuensis*), and Brown-throated Treecreeper (*Certhia discolor discolor* vs. *C. d. manipurensis*). But the latter taxon pair is now considered to represent two separate species.

Genetic differentiation within the Himalayas, and between Himalayan populations and those from the Indo-Burmese Mountains of Northeast India and Myanmar, ranges within the lowest distance values, generally lower than ~1.5%, but exceptions occur (Fig. 1B). Also, pairwise comparisons between Himalayan and Chinese sister clades (in most cases sister species) may range down to a comparatively low distance level of <2% but also yielded higher values of ≤5.4%. Regarding biogeographic affinities, the sister clade to several Sino-Himalayan species pairs (species groups) is represented by one north Palearctic species. Splits between these two clades correspond to a large range of pairwise genetic distances, even for intraspecific comparisons with lowest values for Coal Tits (~2%) and highest for Goldcrests (4.5–5.7%). Assuming a mean substitution rate of 0.0105 substitutions/site/lineage/Ma in cytochrome *b*, as recently reevaluated by Weir and Schluter (2008), most Sino-Himalayan and Palearctic sister clades separated during the (Late) Pliocene era.

Any differences in song pattern among taxa correspond to pairwise genetic distance values >2.5%. All pairwise comparisons below that value comprise taxa sharing the same song pattern (Fig. 1C). Most of the latter cases refer to subspecies pairs with identical song syntax, which, however, might well correspond to distinct clusters in discriminant analysis of sonographic parameters (see examples in warblers of the genus *Phylloscopus*, below). Some outliers with identical song patterns at relatively high distance values were found in (1) Himalayan *Regulus regulus himalayensis* and Taiwanese *R. goodfellowi*, and (2) Himalayan *Seicercus whistleri* and Chinese *S. soror* and *S. valentini* (black bars at highest distance values in Fig. 1C). Nevertheless, the highly similar songs of these species pairs are also distinguishable by differences in frequency range.

Pairwise differences of functions 1 and 2 from discriminant analyses with seven Himalayan warbler species (*Phylloscopus* and *Seicercus*) and their closest relatives from adjacent Southeast Asian regions (25 taxa included in total) showed a positive correlation with pairwise genetic distances (Fig. 2). Pairwise differences were compiled from four independent analyses of the following species complexes: *Phylloscopus reguloides* complex, *P. davisoni* complex, *Seicercus burkii* complex, and the superspecies *P. fuscatu*s, *P. affinis*, and *P. armandii*. Correlation between acoustic and genetic difference values were significant for function 1 (Pearson $P < 0.05$) but not for function 2 (Fig. 2).

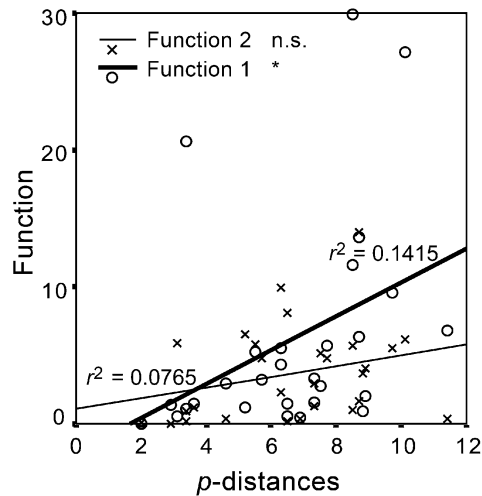


FIG. 2. Correlation of genetic versus acoustic differentiation in leaf-warblers (*Phylloscopus*, *Seicercus*). Plotted on the *x*-axis are uncorrected pairwise *p*-distances. Plotted on the *y*-axis are pairwise differences of functions 1 and 2 that resulted from four independent discriminant analyses with seven Himalayan warbler species (*Phylloscopus* and *Seicercus*) and their closest relatives from adjacent Southeast Asia (total 25 taxa).

In the following sections, we give an overview of intra- and interspecific differentiation of molecular and acoustic markers for superspecies and species complexes with different biogeographic affinities.

SUPERSPECIES AND SPECIES COMPLEXES WITHIN A TWOFOLD AREA: NORTHERN PALEARCTIC AND SINO-HIMALAYAS

COAL TIT (*PARUS ATER*)

Distribution.—Apart from a wide trans-Palaearctic distribution from north Africa to Japan, the Coal Tit has a second and isolated stronghold in the Himalayas and adjacent mountainous areas of western China and (heavily fragmented) in southeast China (Fujian and Jiangxi) and on Taiwan (Fig. 3).

Morphology.—Within Southeast Asian Coal Tit populations, color differences are remarkable and much more pronounced than throughout the extended north Eurasian area. Within Himalayan Coal Tits, color and pattern differences between eastern and western populations led to the conclusion that two small *Parus* (*Periparus*) species inhabit the Himalayan chain: *P. melanolophus* in

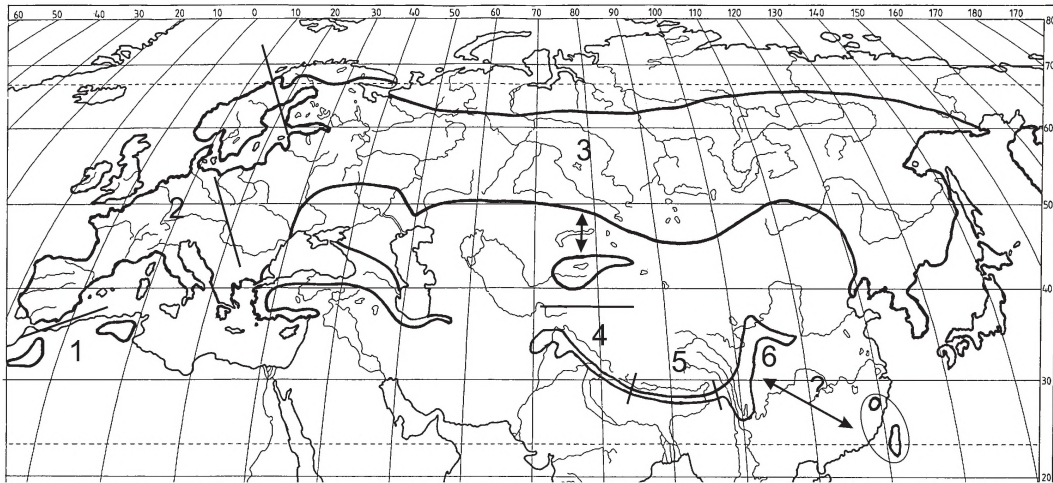


FIG. 3. Breeding range of the Coal Tit, *Parus ater*, including the Spot-winged Tit (*P. ater melanolophus*, lineage 4) with indication of alleged distribution limits of the six presently known cytochrome-*b* haplotype lineages (altered from Martens et al. 2006).

the west, extending into western Nepal; and *P. ater*, ranging from western Nepal all along the Himalayas into central China and to the highly isolated splinters in Fujian–Jiangxi and on Taiwan. Species status of *melanolophus* has been upheld by nearly all authorities writing on Asian birds (Cheng 1987, Dickinson 2003, Rasmussen and Anderton 2005, Gosler and Clement 2007) despite the long-known fact that in western Nepal both populations meet and hybridize in remote high-altitude valleys (Diesselhorst and Martens 1972, Martens and Eck 1995). In addition, it was largely overlooked that the isolated southeast Chinese population *fokiensis* is a rather dull and grayish form, bridging the colorations of the extreme western and eastern Himalayan forms *melanolophus* and *aemodius/martensi*.

Molecular genetics.—In the Palearctic, *P. ater* is divided into distinct cytochrome-*b* haplotype lineages, three of which occur in the Sino-Himalayan area (Martens et al. 2006): (1) “*P. melanolophus*” (western Himalayas), (2) *P. a. aemodius* (eastern Himalayas; including *P. a. martensi*), and (3) the recently described *P. a. eckodedicatus* (from southwest China; Martens et al. 2006). We know that there are variable hybrid populations between lineages 1 and 2, whereas the contact area between 2 and 3 is unknown but is suspected to be located in southwest China–northeast Himalayas. Lineage 3 was overlooked for so long because these birds are very similar to those of lineage 2.

Sequence distances between all trans-Palearctic cytochrome-*b* clusters are remarkably high (range: 2.4–4.1%; Martens et al. 2006) and suggest almost simultaneous Eurasian lineage splits during the Early Pleistocene. The distance values between the adjacent *melanolophus* and *martensi* in the Dhaulagiri in western Nepal amount to 2.2%, and those between *aemodius* and *eckodedicatus* to 2.4%.

Acoustics.—Vocal differentiation is said not to be marked within the Coal Tit complex (Martens 1993), though differentiation at least between north Eurasian and Sino-Himalayan populations is noticeable. In playback experiments in the field, certain verse types of Nepal and Afghan *P. a. melanolophus* are well “understood” by German *P. a. abietum* (Thielcke 1969), whereas other Himalayan or Chinese Coal Tit songs evoked significantly lowered or even no territorial reaction of German test birds (Tietze et al. 2011). Mensural differentiation of vocal characters is similar throughout the Palearctic (Tietze et al. 2011), and slight verse-pattern differences exist between north Palearctic and Sino-Himalayan populations, but not within Sino-Himalayan molecular lineages (Martens 1975).

Taxonomy.—Because it was only recently identified as the west Himalayan mitochondrial lineage of *P. ater*, the subspecies *melanolophus* was treated as a separate species, mainly for reasons of coloration and color pattern (e.g., Dickinson 2003, Rasmussen and Anderton 2005), despite good arguments not to do so. Taxon *melanolophus* simply

represents one of several distinct lineages within the wide-ranging trans-Palaearctic *P. ater*, and, accordingly, its taxonomic treatment as a separate species is not appropriate (Martens 1993, Eck and Martens 2006, Päckert and Martens 2008).

PALLAS'S WARBLER (*PHYLLOSCOPUS* [*PROREGULUS*])
SUPERSPECIES

Distribution.—This superspecies has a typical Sino-Himalayan distribution, with an eastward extension into the Qinling range; the distribution has a large, disjunct northern Siberian part (Fig. 4).

Morphology.—External morphology of representatives from all Sino-Himalayan populations is extremely homogeneous, and several available names partly referred to as subspecies or even species (*forresti* Hartert, *kansuensis* Meise, *yunnanensis* La Touche) for certain Chinese populations were generally placed in synonymy (Ticehurst 1938, Vaurie 1954, del Hoyo 2006). Only nominate *proregulus* from Siberia can easily be told apart from the Sino-Himalayan populations by a noticeably more yellowish tinge of the face. Consequently, all populations of the two main distributional areas have long been summarized under only one species name.

Molecular genetics.—Population structuring is considerably more pronounced than external morphology can indicate (Martens et al. 2004,

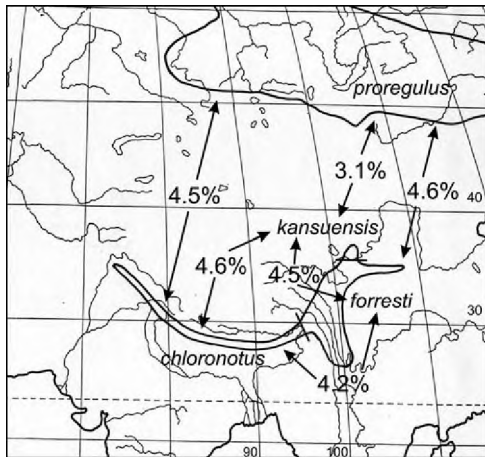


FIG. 4. Breeding range of the allospecies of the Pallas's Warbler complex, *Phylloscopus* [*proregulus*], with indication of (corrected) cytochrome-*b* distance values between, and alleged distribution limits of, the allospecies *P. proregulus* sensu stricto, *P. kansuensis*, *P. forresti*, and *P. chloronotus* (derived from Martens et al. 2004).

Johansson et al. 2007). Nominate *proregulus* from Siberia represents just one cluster of its own, but the disjunct Sino-Himalayan populations represent three further, deeply split haplotype clusters: one in northwest China (minute area in Gansu and northern Qinghai provinces; *kansuensis*), one in southwest China (Sichuan, Shaanxi, southeast Qinghai, and Yunnan provinces; *forresti*), and one along the Himalayan chain (*chloronotus*). Molecular distance values among most genetic lineages exceed population variation level. They are lowest between nominate *proregulus* and *kansuensis* across a huge distributional gap stretching across forestless northern China (divergence in cytochrome *b*: 2.0%) and are highest between *forresti* and nominate *proregulus* and between *kansuensis* and *chloronotus*, respectively (3.9–4.1% each; cf. Martens et al. 2004). Slight coloration differences within the Himalayan population (ssp. *chloronotus* Hartert, ssp. *simlaensis* Ticehurst) are not reflected by genetic differentiation.

Vocalizations.—Different song types and call notes (Fig. 5) strictly correspond to four cytochrome-*b* haplotype clusters. Territorial songs are distinguishable by various frequency and time parameters, resulting in an array of highly distinct song forms (Alström and Olsson 1990, Alström et al. 1997, Martens 1998, Martens et al. 2004). Song types vary between “endless songs” and distinctly partitioned “verse songs.” The former lack a distinct partitioning into verses; instead, they continue for minutes without marked pauses in between. “Endless songs” are composed of note blocks that comprise few or only one repeated element, and long trills may be interspersed (*proregulus* sensu stricto, *forresti* in part, *chloronotus*). Verse songs, on the other hand, are only up to 4.5 s long and consist of narrowly spaced trills with large frequency span (*kansuensis*, *forresti* in part). Highly similar partitioned verses of *kansuensis* and *chloronotus* differ by an important detail: in *kansuensis* the trill note steeply ascends, and in *forresti* it steeply descends—an important feature for species-specific recognition in warblers in the genus *Phylloscopus* (Becker et al. 1980, Martens and Hänel 1981). Innate calls (Fig. 5) of the superspecies' constituents are quite different but still show strong basic similarities (except for *P. kansuensis*) and impressively demonstrate the close relationships of the inherent taxa (Martens et al. 2004).

Taxonomy.—Molecular genetics and vocalizations of the *proregulus* complex indicate that four independent biological species are concerned

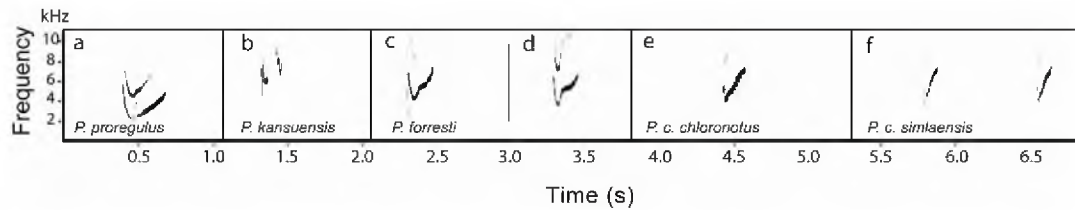


FIG. 5. Calls of several allospecies from the Pallas's Warbler complex, *Phylloscopus* [*proregulus*]. *Phylloscopus proregulus* sensu stricto: (a) Russia, Primorskiy Kray. *Phylloscopus kansuensis*: (b) China, Qinghai, Beishan. *Phylloscopus forresti*: (c) China, Sichuan, Omei Shan; (d) China, Sichuan, Wawu Shan. *Phylloscopus chloronotus*: (e) *P. c. chloronotus*, Nepal, Thodung, Those; (f) *P. c. simlaensis*, Nepal, Purano Marpha. (Recordings by J.M.)

(Martens et al. 2004, Johansson et al. 2007). However, alleged contact zones have not yet been discovered. It is, therefore, not a given fact that no hybridization occurs at the suture zones of the various areas, but, because of large vocal differences in song and calls between neighboring representatives, we expect none or only a little.

Surprisingly, one more taxon belongs in close relationship to the *proregulus* complex: *P. yunnanensis*. This escaped notice shortly after its formal description by La Touche (1922). A Chinese endemic, it occurs across the mountainous areas of Sichuan, Gansu, Shaanxi, Hubei, and Hebei provinces and lives sympatrically, and locally even syntopically, with two of the allospecies of the Pallas's Warbler (*P. kansuensis* and *P. forresti*). By external characters, *P. yunnanensis* is distinguishable from the Pallas's Warbler superspecies, but despite its monotonous, machine-like endless song type, it was overlooked for ~50 years. Alström et al. (1992) resurrected this taxon but described it under a different name. Genetic analyses confirmed a close relationship of the entire Pallas's Warbler complex with both *P. yunnanensis* and *P. subviridis*, but with poor support for any sister-group relationship among the three clades (Johansson et al. 2007).

EURASIAN TREECREEPER (*CERTHIA* [*FAMILIARIS*]) SUPERSPECIES

Distribution.—This superspecies is widely distributed in mountainous areas from western Europe across the Palearctic taiga belt to Japan. Apart from smaller and isolated areas on European islands and in Asian mountain systems, there is one additional extended area in southwest China and all along the Himalayan chain (Fig. 6). Until recently, this assemblage of 13 valid subspecies (Dickinson 2003) was believed to belong to a single species, *Certhia familiaris*.

Morphology.—Despite the considerable number of subspecies described, the coloration and pattern of all local subspecies are quite homogeneous, their camouflaging plumage matching tree-bark characters. Bill length varies, as does the color of the underside from grayish to whitish. The four Sino-Himalayan subspecies are the most diverse, especially the neighboring west (ssp. *hodgsoni*) and central-east Himalayan (ssp. *mandellii*) populations and the north Chinese (ssp. *bianchii*) and southwest Chinese (ssp. *khamensis*) populations, respectively, and concern bill length, underpart coloration, and hind-claw length (Martens and Eck 1995, Tietze and Martens 2009).

Molecular genetics.—A cytochrome-*b* phylogeny paints a quite complex picture (Tietze et al. 2006). One haplotype cluster spans all the north Palearctic from western Europe and Finland to Japan. At least nine of the current subspecies belong to this cluster; others have not been checked yet. Unexpectedly, the northernmost Chinese population (ssp. *bianchii*) also belongs to this northern Eurasian lineage and is separated from the nearest south Siberian populations by the deserts of Mongolia. The remainder of the Sino-Himalayan area harbors an additional three cytochrome-*b* lineages. One is represented by individuals from Sichuan and Shaanxi provinces (ssp. *khamensis*), one is in the central-east Himalayas (ssp. *mandellii*), and another is in the western Himalayas (ssp. *hodgsoni*). Sequence distances are pretty high, ranging from 4.9% to 5.1% between the north taiga area and the south Sino-Himalayan area and between 1.6% and 4.1% within the three Sino-Himalayan clusters. Sino-Himalayan (except for northern China, ssp. *bianchii*) and north Palearctic populations represent two deeply split clusters.

Vocalizations.—Territorial songs reflect the bipartite division between northern taiga populations (including the north Chinese *bianchii*) and all other Sino-Himalayan genetic lineages (Fig. 7). However,

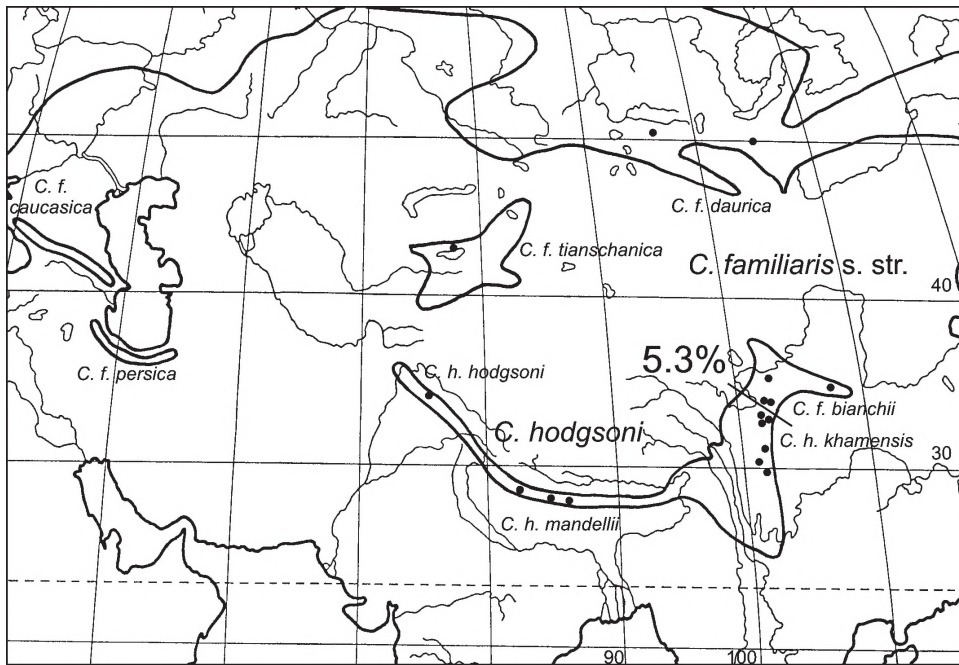


Fig. 6. East Palearctic breeding range of the Eurasian Treecreeper, *Certhia [familiaris]* superspecies with indication of cytochrome-*b* distance value between northern *C. familiaris* sensu stricto and *C. hodgsoni* and the alleged distribution limits between both allopecies in southwest China. Dots refer to origin of sequenced samples (slightly changed from Tietze et al. 2006).

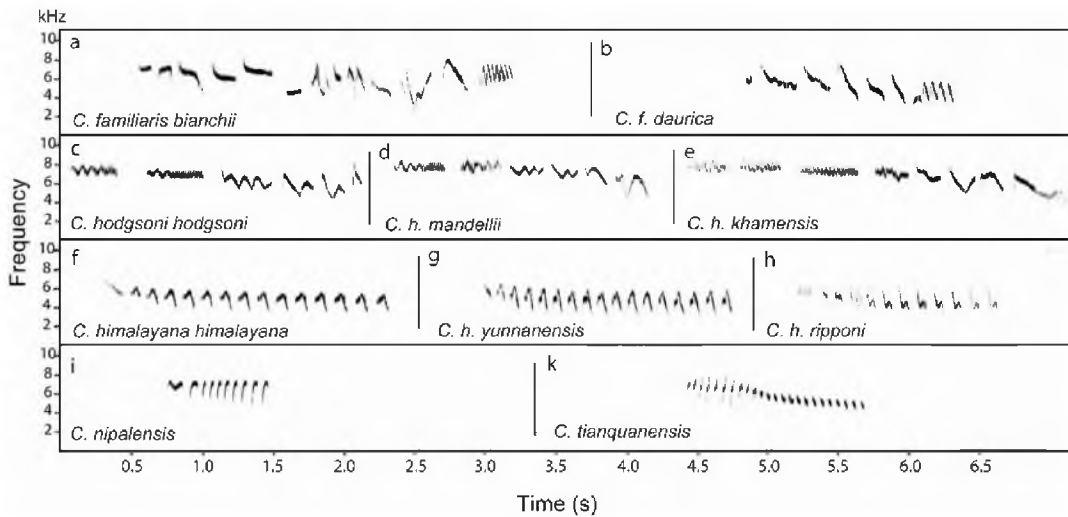


FIG. 7. Territorial songs of Sino-Himalayan treecreeper species. (a) *Certhia familiaris bianchii*, China, Qinghai. (b) *C. f. daurica*, Japan, Hokkaido. (c) *C. hodgsoni hodgsoni*, Pakistan, North-West Frontier Province. (d) *C. h. mandellii*, Nepal. (e) *C. h. khamensis*, China, Sichuan. (f) *C. himalayana himalayana*, India, Kashmir. (g) *C. h. yunnanensis*, China, Yunnan. (h) *C. h. ripponi*, Myanmar, Natnataung National Park. (i) *C. nipalensis*, Nepal. (k) *C. tianquanensis*, China, Shaanxi. (Recordings a, d–g, i–k by J.M.; b by T. Kabaya; c by P. Alström; h by D.T.T.)

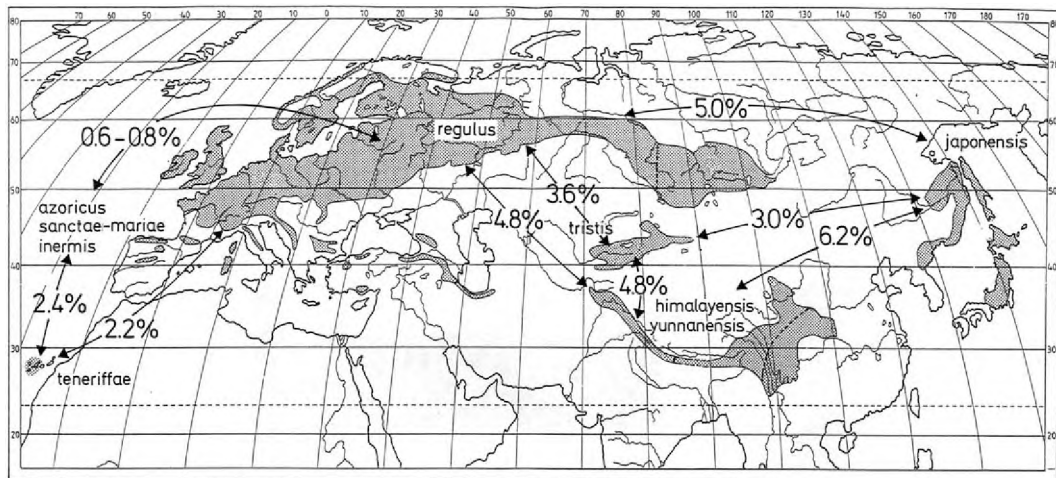


Fig. 8. Breeding range of the Goldcrest (*Regulus regulus*), with indication of cytochrome-*b* distance values between various lineages within the Palearctic region (reproduced from Martens and Päckert 2003).

although in terms of cytochrome-*b* differentiation the latter group is heavily substructured in itself, the trill-like territorial songs are relatively homogeneous and do not reflect the strong morphological and genetic differences between them. Substantial vocal differences between central European and Himalayan representatives have been reported (Martens 1981, Martens and Geduldig 1988, Tietze et al. 2008).

Taxonomy.—According to the genetic and acoustic differences, *C. familiaris* is now attributed to two allopatric species, *C. familiaris sensu stricto* and *C. hodgsoni* (Tietze et al. 2006). The latter comprises representatives of three well-differentiated lineages with morphological characters that are easily told apart. We may expect further species-level subdivisions upon better knowledge of contact zones of cluster representatives in the western Himalayas (ssp. *mandellii* vs. ssp. *hodgsoni*) because of their remarkably divergent external morphology (Martens and Eck 1995, Martens and Tietze 2006).

GOLDCREST (*REGULUS REGULUS*)

Distribution.—The trans-Palearctic area from the Canary Islands to Japan comprises a remarkable number of largely disjunct areas, including the Sino-Himalayan region (Fig. 8).

Morphology.—Although three valid subspecies occur in the area under consideration (*sikkimensis*,

yunnanensis, and *himalayensis*), external variation is minute (Vaurie 1959).

Molecular genetics.—Within the Sino-Himalayas, genetic differentiation in the Goldcrest is low. Cytochrome-*b* haplotypes from Nepal and Gansu are identical, and apparently all populations belong to only one lineage. The closest relatives live in Central Asia (Tian Shan, ssp. *tristis*), eastern Siberia–Japan, and the Siberian taiga belt (ssp. *japonensis*; cf. Päckert et al. 2003). Recent molecular analyses confirmed a close phylogenetic relationship of the endemic Taiwan *R. goodfellowi* to the *R. regulus* group (Päckert et al. 2008).

Vocalizations.—Molecular genetic lineages coincide with clearly distinct types of territorial song; one lineage may incorporate two rather different song types (eastern Siberian–Pacific coast vs. Japan). Throughout the entire Sino-Himalayan range, songs are identical and show a strong similarity to songs from Taiwanese *R. goodfellowi* (Päckert et al. 2008). Acoustic premating isolating mechanisms among largely allopatric subspecies groups were indicated by playback experiments (Martens et al. 1998).

Taxonomy.—Despite marked cytochrome-*b* distance values of the various lineages and distinct vocal differences, splits on the species level have never been proposed, and presently all trans-Palearctic Goldcrests range under one species name. Only Canary Island Goldcrests are

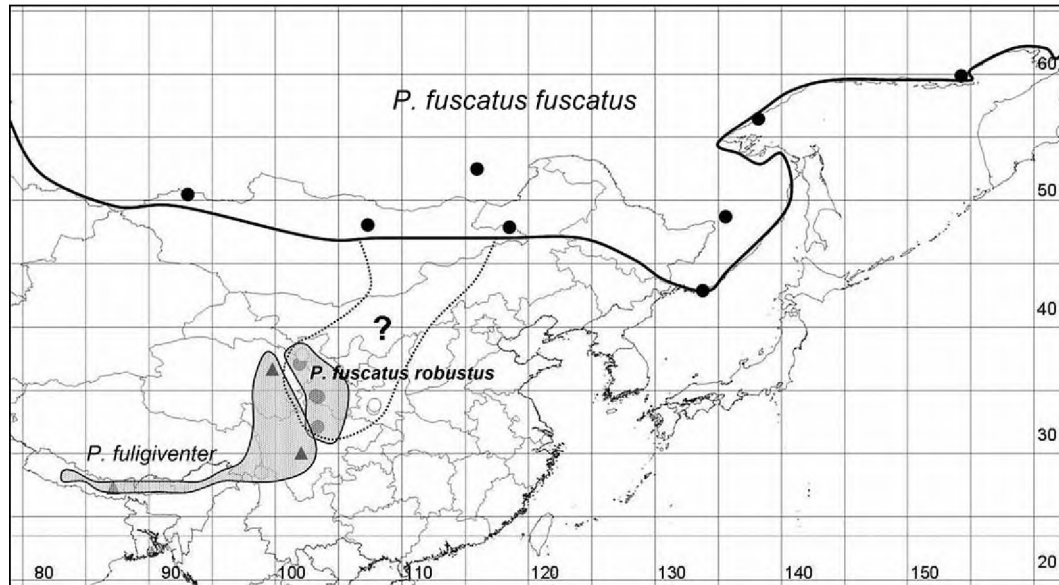


FIG. 9. Breeding range of the Smoky Warbler (*Phylloscopus fuligiventer*, including ssp. *weigoldi*; filled triangles) and the Dusky Warbler (*P. fuscatus*, including ssp. *robustus*; shaded circles). Distributional markers correspond to genetically identified specimens; dotted line indicates late spring records of northern *P. f. fuscatus* in western China and may refer to passage migrants rather than potential breeders (white circles). Distributional limits according to Chrabryj et al. (1989) and Martens et al. (2008).

sometimes treated as an independent species (Clements 2007).

SMOKY LEAF-WARBLER AND DUSKY LEAF-WARBLER (*PHYLLOSCOPUS FULIGIVENTER*–*P. FUSCATUS*) COMPLEX

Distribution.—The distribution of this complex is Sino-Himalayan, with a large, disjunct northern taiga part in Siberia in *P. fuscatus* but not in *P. fuligiventer*, which is exclusively Sino-Himalayan (Fig. 9).

Morphology.—At a first glance, all members of this group seem to represent a rather homogeneous morphological variation, with the exception of Himalayan and southeast Tibetan *P. fuligiventer*. These conspicuously dark birds differ from all other forms of the complex by having blackish-olive upperparts, breast, and flanks, and a rather small light-brownish to near blackish belly-patch. However, like the latter taxon, birds from Qinghai (ssp. *weigoldi*) lack the brown breast band and brownish tinge on the flanks, which are distinct characters of both Dusky Warbler populations from Siberia, Mongolia, and northeast China on

the one hand and populations from Gansu province (China) on the other.

Molecular genetics.—Martens et al. (2008) showed that a basal split divides this complex into two major clades, with the Himalayan *P. fuligiventer* clade including populations from Qinghai (traditional subspecies *P. fuscatus weigoldi*) at a surprisingly low level of genetic differentiation (1.4%). The *P. fuscatus* clade is bifurcated into a northern haplotype lineage of nominate *fuscatus* and a second one comprising haplotypes from Gansu in southwestern China (ssp. *robustus*). The northern cluster was found with several distinct haplotypes in southwest China (Shaanxi). It is likely that most of the Chinese birds carrying nominate *fuscatus* haplotypes are late migrants, because the three recent samples were taken in May. However, even a June bird from Gansu (Beick collection; see Martens et al. 2008) was genotyped as nominate *fuscatus*.

Vocalizations.—Territorial songs of all *P. f. fuscatus* and *P. f. robustus* are simple trills or double trills and are mostly preceded by an inconspicuous introductory note (Fig. 10). Songs from the Qinghai population (ssp. *weigoldi*) are given in a slower mode (i.e., the notes are more spaced) and are significantly

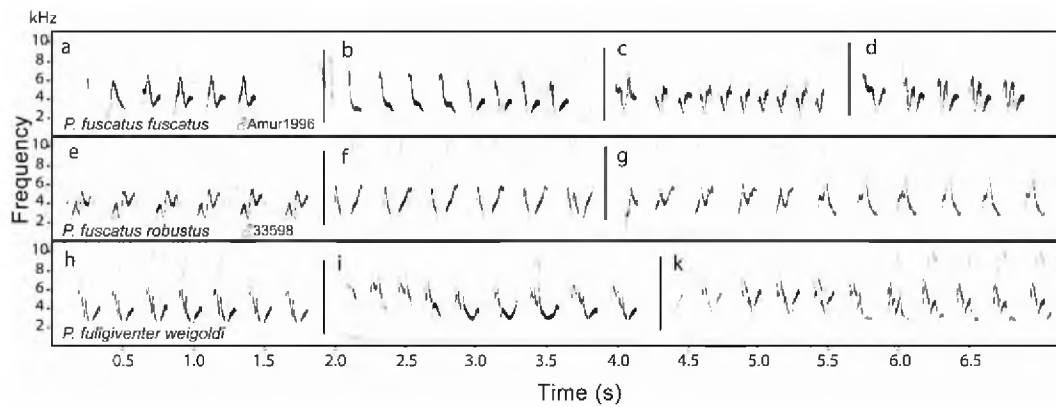


FIG. 10. Territorial songs of (a–g) the Dusky Warbler and (h–k) the Smoky Warbler. (a–d) *Phylloscopus fuscatus fuscatus*, far east Russia, Middle Amur, one male. (e–g) *P. f. robustus*, China, Gansu, Zhuoni, one male. (h–k) *P. fuligiventer weigoldi*, China, Qinghai, Koko Nor Lake, one male. (Recordings a–d by M.P., e–k by J.M.)

longer and much more complex. Even the individual note of the *weigoldi* verse is more structured and more strongly modulated than in nominate *fuscatus* and ssp. *robustus* and rather resembles a highly compressed syllable. In discriminant analysis, songs of *weigoldi* and *fuscatus* are well-separated clusters even when compared with other simple trill songs of *P. affinis* and *P. armandii* (Fig. 11).

Taxonomy.—On grounds of genetic and bioacoustic differentiation, Martens et al. (2008) suggested transferring the taxon *weigoldi* as a subspecies into *P. fuligiventer*. Consequently, Martens et al. (2008) declared a genotyped June bird from the *robustus* paratype series as a lectotype (the holotype was lost during World War II; Eck and Quaiser 2004), and other genotyped *P. f. robustus* specimens are

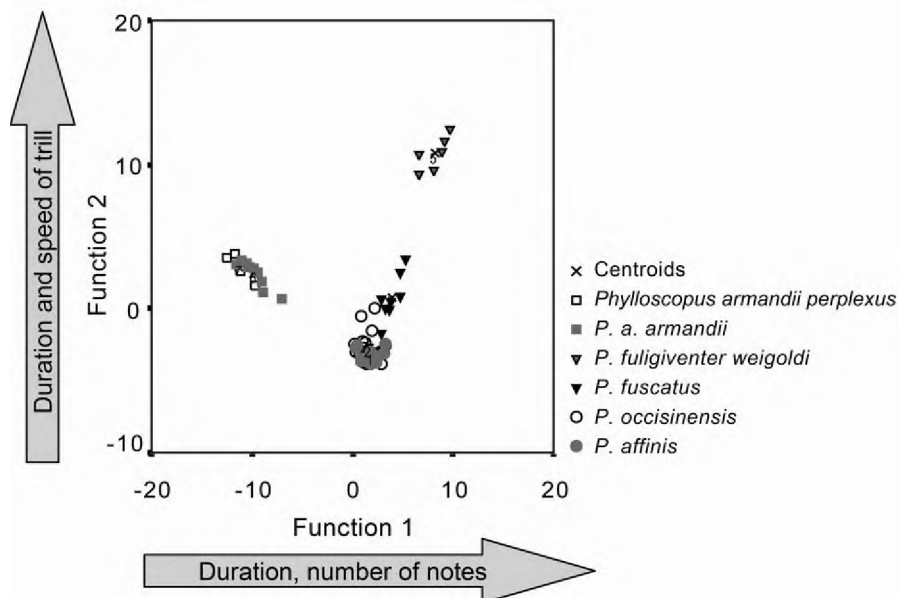


FIG. 11. Scatterplot of functions 1 and 2 from discriminant analysis based on eight song parameters of songs from *Phylloscopus fuscatus*, *P. fuligiventer* (ssp. *weigoldi* from Qinghai), *P. affinis*, *P. occisnensis*, and *P. armandii*. Song parameters with highest correlations with both functions are indicated at the *x*- and *y*-axes.

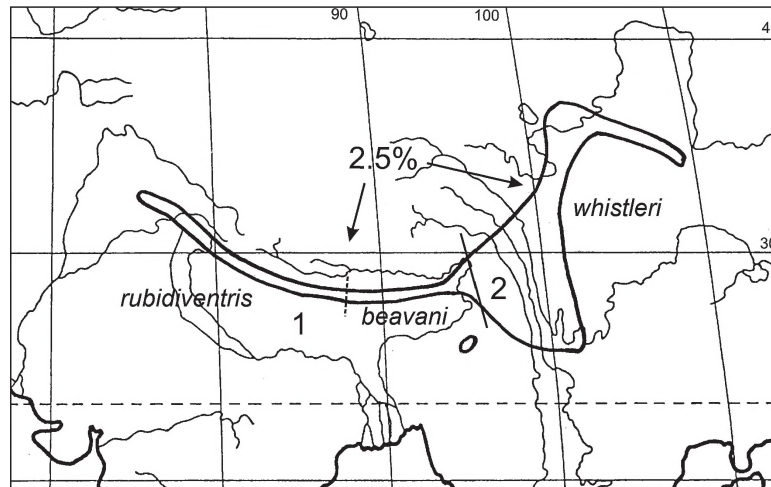


FIG. 12. Breeding range of the Rufous-vented Tit (*Parus rubidiventris*), with indication of cytochrome-*b* distance value of two molecular genetic lineages between gray-vented southwestern Chinese population (ssp. *whistleri*) and Himalayan populations (approximate alleged limit east and west of solid bar "2"); and range of red-vented western Himalayan (ssp. *rubidiventris*) and gray-vented eastern Himalayan (ssp. *beavani*) populations (approximate limit at stippled bar "1" in east Nepal). (Map slightly altered from Martens et al. 2006.)

so far known only from Sichuan and Gansu provinces, China.

SUPERSPECIES AND SPECIES COMPLEXES CONFINED TO THE SINO-HIMALAYAN AREA

RUFOUS-VENTED TIT (*PARUS RUBIDIVENTRIS*)

Distribution.—The Rufous-vented Tit is distributed from the western Himalayas to southwestern China, in the northeast to north Gansu and Shaanxi (Qinling range), thus conforming to the typical Sino-Himalayan pattern (Fig. 12).

Morphology.—Two distinct subspecies based on color differences are generally accepted, a cinnamon-bellied western Himalayan nominate *rubidiventris* and an eastern gray-bellied *beavani*. Another subspecies, *saramatii*, is known from south of the eastern Himalayas (Ripley 1961). Species rank of the former two groups had been proposed (Wolters 1980, Haffer 1993).

Molecular genetics.—There is a remarkable split, not as one might expect between cinnamon-bellied nominate *rubidiventris* and gray-bellied *beavani*, but within the gray-bellied populations in the eastern part of the area in the eastern Himalayas on the one hand and in southwest China on the other (Fig. 12). The between-lineage distance value amounts to ~2.8% (compared to ~6%

against sister species *P. rufonuchalis*). Apparently, the cinnamon versus gray underpart coloration distinguishing the two subspecies is quite young and is not reflected by any distinct molecular genetic differentiation.

Vocalizations.—No differences between the two mitochondrial lineages have yet been described.

Taxonomy.—The two molecular clusters are differentiated at the subspecies level. Martens et al. (2006) revalidated the Chinese subspecies *whistleri* Stresemann for the northeastern gray-bellied populations; both western subspecies, cinnamon-bellied nominate *rubidiventris* and the western of the two gray-bellied, *beavani*, are retained as different subspecies though traditionally based on coloration.

TICKELL'S WARBLER (*PHYLLOSCOPUS [AFFINIS]*) SUPERSPECIES

Distribution.—The area of *Phylloscopus affinis* sensu lato (Fig. 13) stretches all over the Himalayas and the mountainous areas of southwest China, including parts of east Qinghai, but the high-altitude Tibetan plateau is uninhabited (Vietinghoff-Scheel 1986). Throughout its area, the members of the *affinis* complex live in mountainous open bush and forest edges at high altitudes, and this holds true also for *P. griseolus* in Central Asia. All taxa of this group are mainly allopatric,

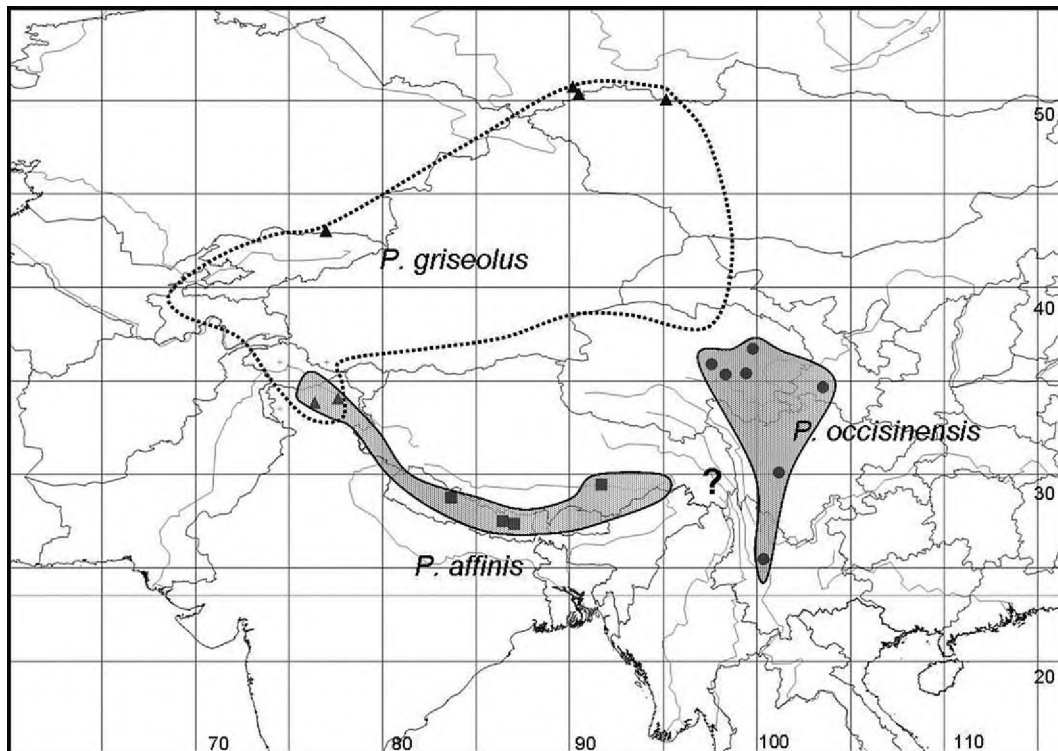


FIG. 13. Breeding range of three species taxa from the Tickell's Warbler (*Phylloscopus [affinis]*) superspecies. Data points correspond to genetically identified specimens; question mark indicates possible contact area, but so far no data are available (distributional limits according to Vietinghoff-Scheel 1986, Loskot and Vietinghoff-Scheel 1991, Martens et al. 2008).

but *P. griseolus* is believed to overlap with *P. affinis* in the westernmost parts of the Himalayas and in the Karakoram (Roberts 1992). Their areas embrace the Tibetan plateau, including *P. griseolus*, which also thrives as far as southwest Siberia (Loskot and Vietinghoff-Scheel 1991). The whole complex thus may have undergone the same north Palearctic-Sino-Himalayan diversification pattern as the truly arboreal species.

Morphology.—*Phylloscopus affinis* was believed to present a homogeneous external morphology throughout (Ticehurst 1938), and no subdivision into subspecies was ever proposed. However, variation all over the area is marked in the coloration and pattern of the underside. Three major population blocks are discernible. Birds of the western Himalayas are bright yellow below, in the central and eastern Himalayas the underpart is dull yellowish-greenish, and in southwestern China it is yellow with an orange touch and a marked breast-band (Martens et al. 2008).

Molecular genetics.—In two mitochondrial markers, Himalayan populations show strong differentiation from southwestern Chinese populations (Martens et al. 2008). These two lineages are separated by a surprisingly large cytochrome-*b* distance of 8.9%, and the markers used do not even represent a monophyletic group because of their unresolved phylogenetic relationships to the Central Asian *P. griseolus* (7.3% *p*-distance of the latter against *P. affinis* from Nepal). In addition, the eastern and western Himalayan populations also represent well-separated genetic lineages that are younger and more recently diverged during the Pleistocene.

Vocalizations.—In contrast to the extremely large genetic differences, only slight differentiation of territorial songs could be detected between eastern Himalayan (Nepal; *P. a. affinis*) and southwestern Chinese populations (*P. occisinensis*) of this group (Figs. 11, 14). Throughout the Sino-Himalayan range, territorial songs are made up of simple

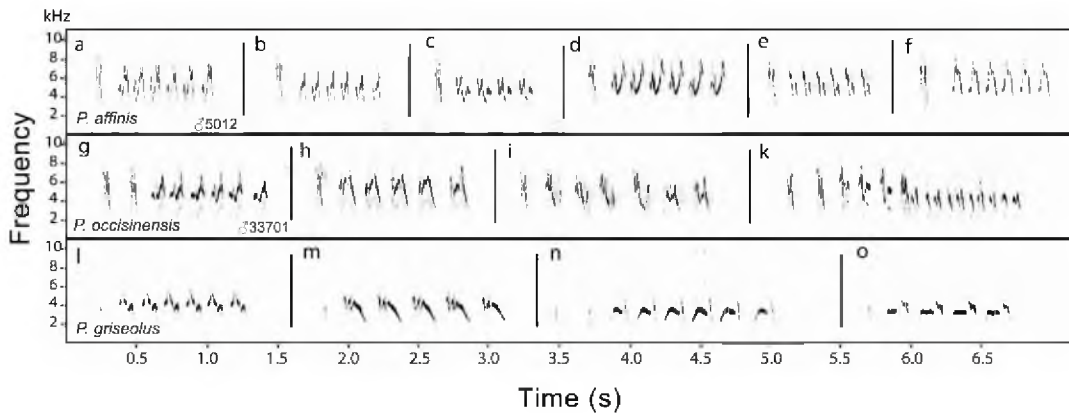


FIG. 14. Territorial songs of species from the Tickell's Warbler complex. (a–f) *Phylloscopus affinis*, Nepal, Mustang District, one male. (g–k) *P. occisinesis*, China, Qinghai, Donggi Cona Lake, one male. (l–o) *P. griseolus*, Russia, Rep. Tyva, one male. (Recordings a–k by J.M., l–o by B. Veprintsev.)

trills preceded by one or two sharp click-like call notes. Songs of western Himalayan populations have not been described by sonagrams. Central Asian *P. griseolus* songs have a similar trill pattern but cover a lower and narrower frequency range than those of *P. affinis* sensu lato.

Taxonomy.—*Phylloscopus affinis* is now attributed to two species, *P. affinis* sensu stricto (with a western ssp. *perflavus* and central–eastern Himalayan nominate *affinis*) and southwestern Chinese *P. occisinesis* from Qinghai, Gansu, Sichuan, and Yunnan (Martens et al. 2008). We may expect a further species-level subdivision upon better knowledge of a contact zone of cluster representatives in the western Himalayas (ssp. *perflavus* vs. ssp. *affinis*) and analysis of hitherto unknown territorial song of ssp. *perflavus*. Expected contact zones between all three taxa are yet undiscovered. Along with the two former species, the superspecies *Phylloscopus* [*affinis*] includes *P. griseolus*; however, phylogenetic relationships among the three allospecies are not yet fully resolved.

BLYTH'S LEAF-WARBLER (*PHYLLOSCOPUS REGULOIDES*) SPECIES COMPLEX

Distribution.—This complex of forms has a typical Sino-Himalayan distribution all along the Himalayan chain, with extended areas in north, southwest, and east China, to Indochina (Fig. 15).

Morphology.—This complex comprises medium-sized warblers with marked coronal stripes. *P. reguloides* sensu stricto (including *kashmirensis*, *assamensis* and *ticehursti*) has the least-developed

coronal stripes and is quite dull-greenish on the upper- and underparts, thus resembling ssp. *claudiae*. The latter shows marked coronal stripes tending to black at the rear. Subspecies *goodsoni* is brightest greenish (upperpart) and yellowish (underpart), also with distinct coronal stripes.

Molecular genetics.—Olsson et al. (2005), Johansson et al. (2007), and Päckert et al. (2009a) found considerable molecular genetic differentiation between three major genetic lineages within the complex. Neither of these studies supported the monophyly of all members of the Blyth's Leaf-Warbler group, because at least one further well-established species, *P. occipitalis*, was firmly nested in the respective clade. Monophyly is corroborated only for a clade comprising populations of the Himalayas (ssp. *reguloides*, ssp. *kashmirensis*), those from the adjacent mountains of Myanmar (ssp. *assamensis*), and those from southwest China (Yunnan), northwest Thailand, and south Vietnam (ssp. *ticehursti*). Genetic distance values within this clade range up to 2.9% of the cytochrome-*b* gene. Two further genetic lineages from north and northwest China (Hebei, Sichuan, Shaanxi, etc.; ssp. *claudiae*) and from south and southeast China (Fujian, Jiangxi, Guangxi, Guangdong; ssp. *goodsoni* and ssp. *fokiensis*) do not unambiguously form a monophyletic group with the latter Sino-Himalayan clade (Olsson et al. 2005, Johansson et al. 2007, Päckert et al. 2009a), but they are at least closely related to each other.

Vocalizations.—A discrete song pattern can be assigned to each of the three recently separated species *P. reguloides* sensu stricto, *P. claudiae*, and

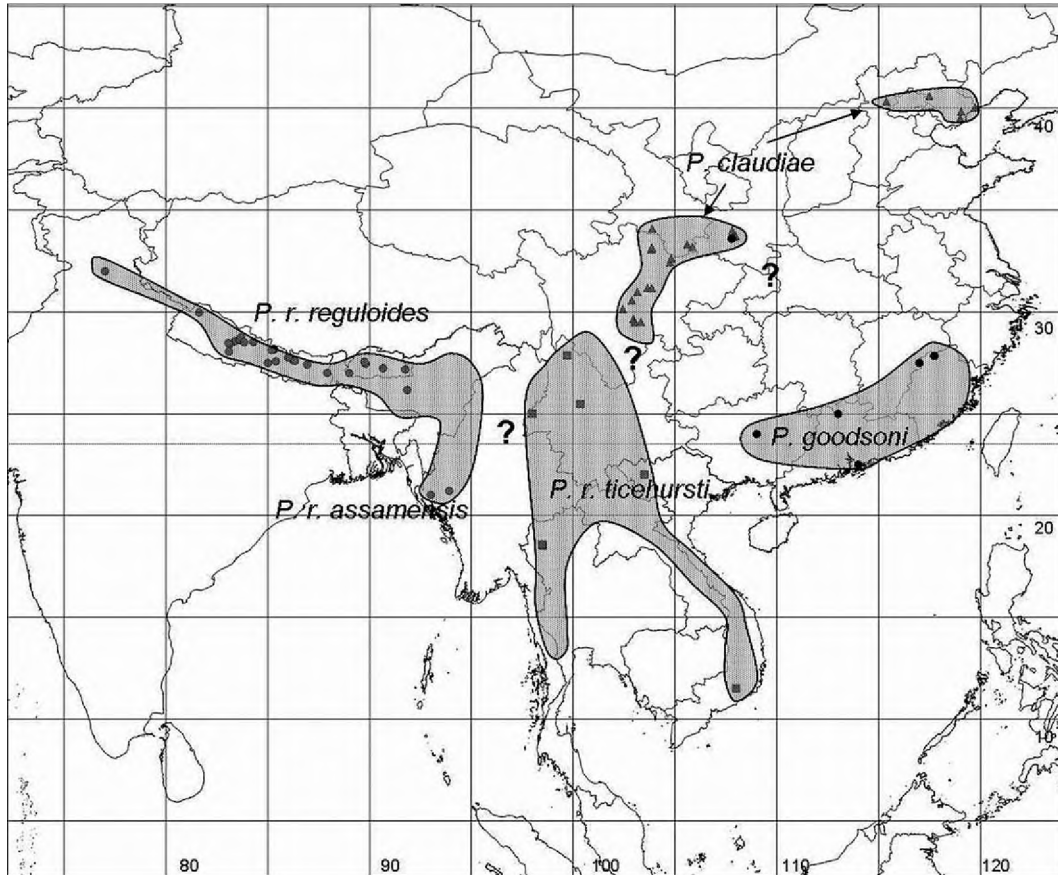


FIG. 15. Breeding range of species taxa from the Blyth's Warbler complex (*Phylloscopus reguloides* sensu lato). Data points correspond to specimens identified by molecular and/or acoustic markers (including data from Olsson et al. 2005, Päckert et al. 2009a); question mark indicates possible contact areas, but so far no data are available. Easternmost Himalayan records of ssp. "reguloides" belong to ssp. *assamensis*, too (distributional limits mainly according to Vietinghoff-Scheel 1989).

P. goodsoni (Figs. 16 and 17). In all Blyth's Leaf-Warbler populations, male repertoires comprise regularly structured songs with two- or three-note syllables (Martens 1980). Only repertoires of ssp. *claudiae* males include distinct trill song types with single notes repeated. Songs of *P. goodsoni* lack the typical introductory note of *P. claudiae* and *P. reguloides* sensu stricto and are introduced by two highly modulated notes of the same type. Discriminant analysis of song parameters revealed several distinct vocal clusters corresponding to genetic lineages (Päckert et al. 2009a). Song patterns in this group range from simply structured medium-speed songs ("speed" refers to the number of elements or syllables per second)

in *P. occipitalis* to low-speed and complex syntax structures in *P. goodsoni* (Fig. 17).

Taxonomy.—On the basis of molecular analyses, Olsson et al. (2005) distinguished three species in this group: *P. reguloides* sensu stricto breeds throughout the entire Himalayan chain (including the poorly differentiated western ssp. *kashmirensis*). Both form the little-differentiated sister clade to ssp. *assamensis* from Myanmar. The populations from southwest China (Yunnan), Thailand, and Vietnam were tentatively treated as ssp. *P. reguloides ticehursti* by Olsson et al. (2005). *Phylloscopus claudiae* and *P. goodsoni* were suggested to be ranked as separate species because of their strong genetic (Olsson et al. 2005, Päckert et al.

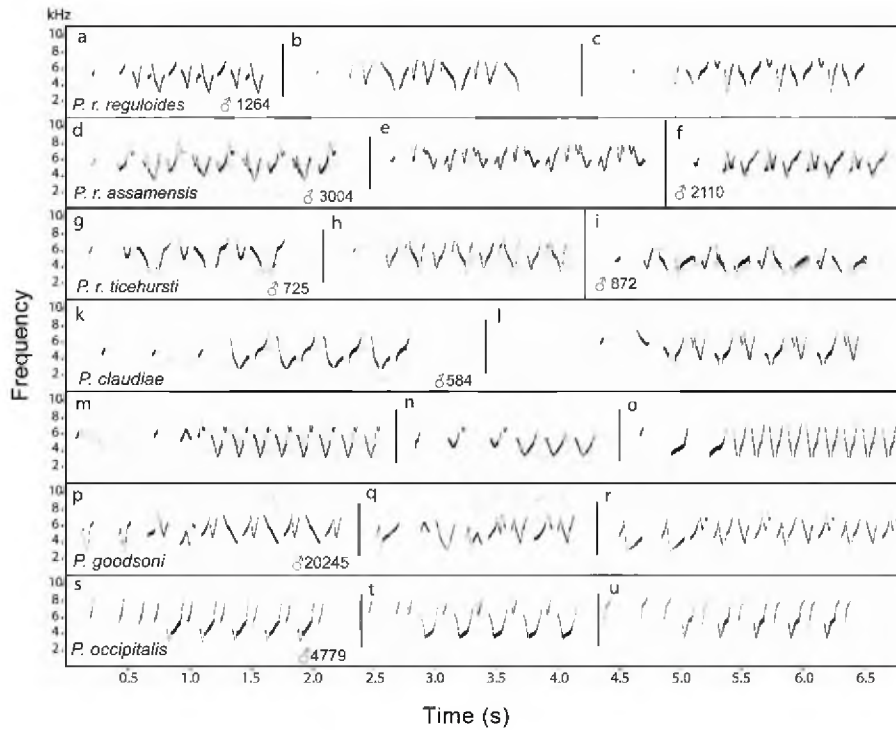


FIG. 16. Territorial songs in the *Phylloscopus reguloides* complex and allied species. (a–c) *P. reguloides reguloides*, one male from Nepal, Dolakha District. (d–e) *P. r. assamensis*, one male from India, Assam, Panbari Reserve Forest (rec. P. Holt). (f) *P. r. assamensis*, one male from Myanmar, Chin State, Natmataung National Park (rec. D.T.T.). (g–h) *P. r. ticehursti*, one male from China, Yunnan, north of Zhongdian. (i) *P. r. ticehursti*, one male from Thailand, Chiang Mai; Doi Inthanon. (k–o) *P. claudiae*, one male from China, Sichuan, Labahe. (p–r) *P. goodsoni*, one male from China, Jiangxi, Huanggang Shan. (s–u) *P. occipitalis*, one male from India, Kashmir. (Recordings by J.M. unless stated otherwise.)

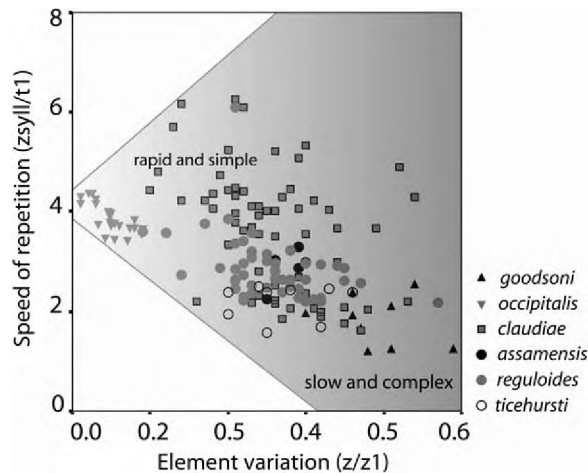


FIG. 17. Acoustic differentiation among species (and subspecies) of the *Phylloscopus reguloides* complex; scatter plot of the song-parameter element variation (number of different element types per song, x-axis) and speed of repetition (number of elements or syllables per time unit, y-axis).

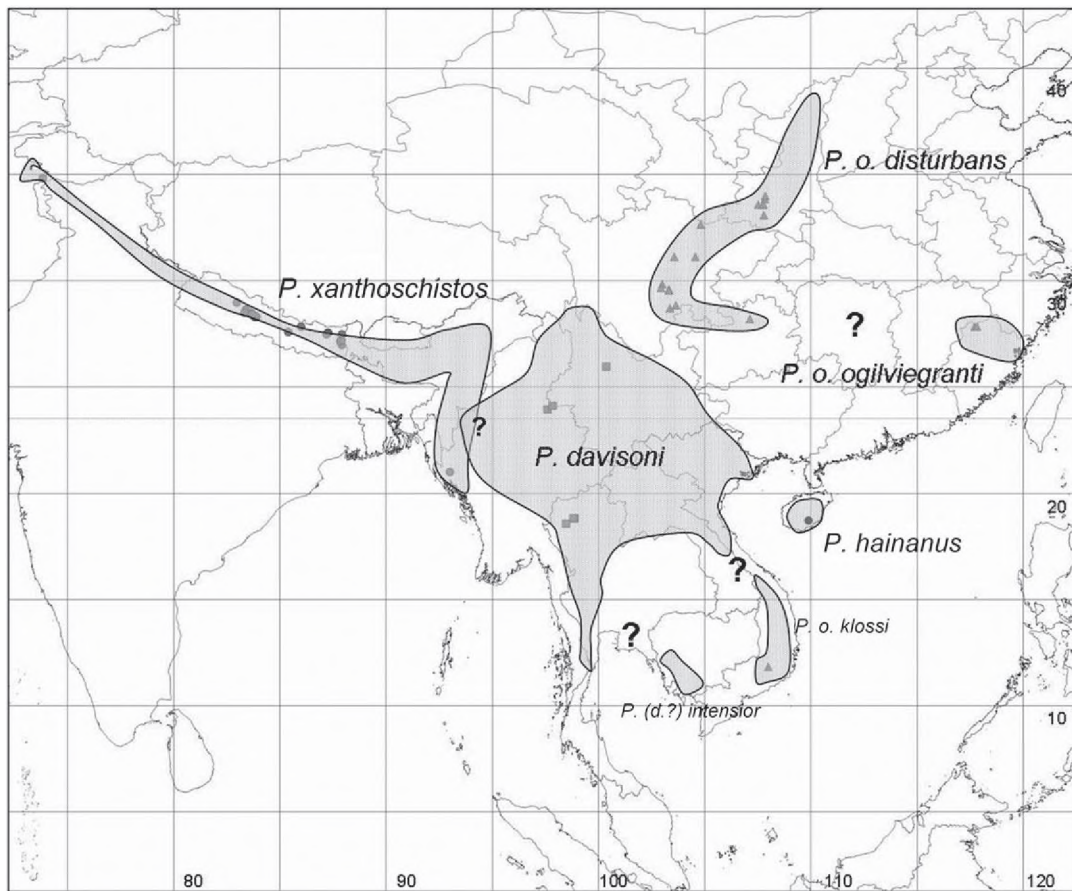


FIG. 18. Breeding range of species taxa from the White-tailed Warbler complex (*Phylloscopus davisoni* sensu lato). Data points correspond to specimens identified by molecular and/or acoustic markers (including data from Olsson et al. 2005, Päckert et al. 2009a); question mark indicates possible contact area, but so far no data are available (distributional limits drawn from Vietinghoff-Scheel [1987] and adjusted to the data points presented here).

2009a) and acoustic differentiation (Päckert et al. 2009a) from other species in this group.

WHITE-TAILED LEAF-WARBLER
(*PHYLLOSCOPUS DAVISONI*) SPECIES COMPLEX

Distribution.—This species complex has a typical Sino-Himalayan distribution, within China northward to the Qinling range in Shaanxi and also in southwest and south China, ranging into Indochina; there is a closely related taxon on Hainan (Fig. 18).

Morphology.—This complex group circumscribes small warblers with marked coronal stripes and whitish outer two rectrices (R5 and R6) differing in the extent of white. Depending on the taxon,

the underparts are whitish to yellowish-greenish; the upperparts are dull greenish to light yellowish-greenish in the southern populations, and on Hainan this tendency proceeds to yellowish-green (upperside) and bright yellow (underside). In general, the *davisoni* complex remarkably parallels the *P. reguloides* complex in distribution pattern, evolutionary history, and north-to-south coloration gradient.

Molecular genetics.—The Hainan Leaf-Warbler (*P. hainanus*) and the Gray-hooded Leaf-Warbler (*P. xanthoschistos*) are firmly nested in the molecular clade comprising all members of *P. davisoni* sensu lato (Olsson et al. 2005, Johansson et al. 2007, Päckert et al. 2009a). Accordingly, Olsson et al. (2005) suggested a species split between western

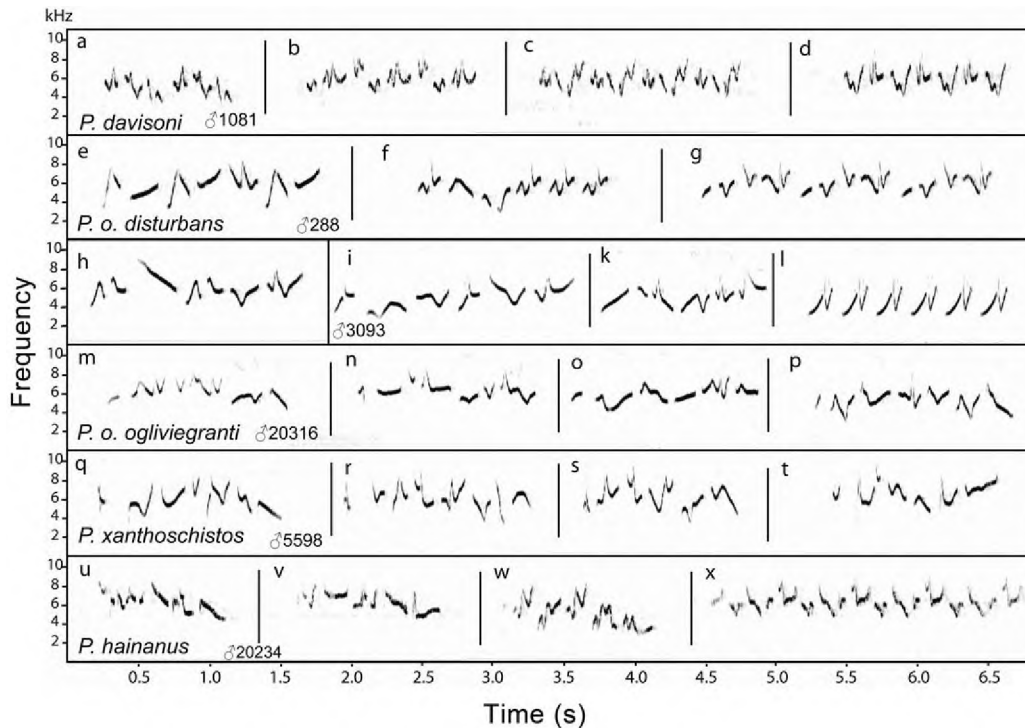


FIG. 19. Territorial songs of the *Phylloscopus davisoni* complex and allied species. (a–d) *P. davisoni*, one male from China, Yunnan, Jizu Shan. (e–h) *P. ogilviegranti disturbans*, one male from China, Shaanxi, Qinling Mountains. (i–l) *P. o. disturbans*, one male from China, Shaanxi (rec. P. Holt). (m–p) *P. o. ogilviegranti*, one male from China, Jiangxi, Huanggang Shan. (q–t) *P. xanthoschistos*, one male from Nepal. (u–x) *P. hainanus*, one male from China, Hainan, Diaoluo Shan. (Recordings by J.M. unless stated otherwise.)

and southern *P. davisoni* sensu stricto (southwest China [Yunnan] to north Thailand and northwest Vietnam) and more northern and southeastern Chinese *P. ogilviegranti*. Intraspecific genetic differentiation within the latter ranges at distance values <1.0% between nominate ssp. *ogilviegranti* from south China and northern ssp. *disturbans* from Shaanxi, Sichuan, and Gansu, despite an obviously large uninhabited area (Fig. 18). The sister clade of this species group comprises several species of Indo-Malayan origin, such as *P. trivirgatus*, *P. sarasinorum*, *P. presbytes*, and *P. amoenus* (Olsson et al. 2005), which are all little known with respect to vocal characters and internal molecular genetic structure. Strikingly, genetic distances within this group are highest among the two newly established species taxa of *P. davisoni* sensu lato (~3.2% cytochrome-*b* distance) but are considerably lower between terminal sister taxa of this group (e.g., between *P. ogilviegranti* and *P. hainanus*, only 1.0% cytochrome-*b* distance).

Vocalizations.—Territorial songs in this group are complex, with many different and often strongly modulated element types in the individual verse (Figs. 19 and 20). Repetitions of syllables or motifs in a single song are rare; often only the first two or three notes of a song are repeated. Regular song patterns with repeated syllables occur only in *P. davisoni* sensu stricto and *P. ogilviegranti disturbans* (but never in nominate *ogilviegranti*). In most species the maximum frequencies of the complex songs tend to decrease toward the end of a verse, most strikingly in *P. xanthoschistos* and *P. hainanus*. Songs of the latter species often end in a characteristic v-shaped element of relatively low frequencies.

Taxonomy.—With respect to paraphyly of the White-tailed Warbler and on grounds of their large genetic and bioacoustic differentiation, *P. davisoni* sensu stricto and *P. ogilviegranti* should be treated as separate species (Olsson et al. 2005, Päckert et al. 2009a). Apart from this split, species

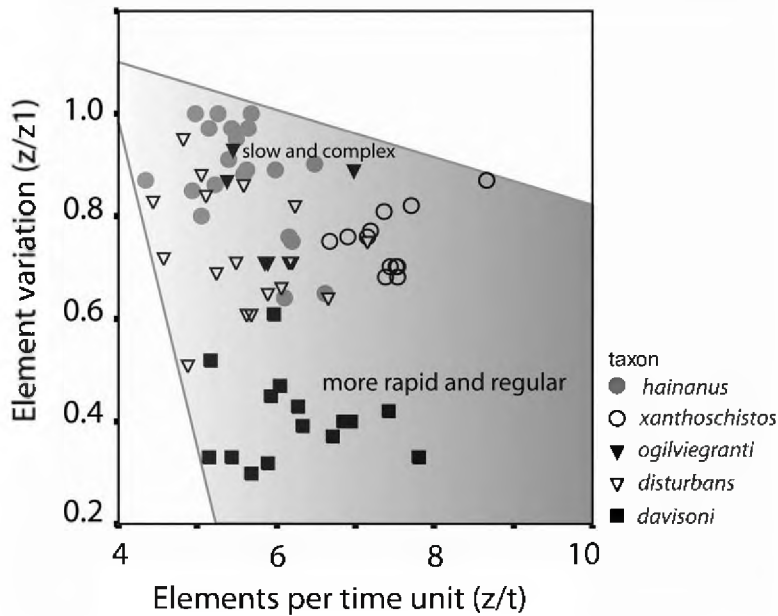


FIG. 20. Acoustic differentiation among species (and subspecies) of the *Phylloscopus davisoni* complex. Scatter plot of song-parameter element variation (number of different element types per song, y -axis) and speed of repetition (number of elements or syllables per time unit, x -axis).

delimitation among members of the White-tailed Warbler clade still causes difficulties. Whether species status of the island endemic *P. hainanus* is justified from a conservationist viewpoint remains questionable: genetic distances between this Hainan population and those from adjoining continental Chinese *P. ogilviegranti* are surprisingly low (1.0% cytochrome-*b* distance). Coloration and color patterns are remarkably different between insular (*hainanus*) and continental (*ogilviegranti*) populations, but morphological differences alone are a rather poor argument for species discrimination (see *Phylloscopus fulgiventis* and *Parus ater*, above).

GOLDEN-SPECTACLED WARBLER (*SEICERCUS BURKII*) SPECIES COMPLEX

According to the results of molecular, bioacoustic, and morphological analyses, the traditional polytypic *Seicercus burkii* sensu lato (Mayr et al. 1986, Cheng 1987) turned out to be a species swarm that underwent a complex evolutionary history resulting in both extant vicariance as well as vertical and presumably horizontal parapatry and local sympatry throughout the entire Sino-Himalayan region (Alström and Olsson 1999,

Martens et al. 1999, Martens and Eck 2000, Olsson et al. 2004, Päckert et al. 2004). Even the youngest splits among terminal sister species of this group were dated to the Pliocene–Pleistocene boundary and earlier (Johansson et al. 2007, Päckert et al. 2009b). The taxonomy, phylogeny, and breeding distribution of species within this highly differentiated group have already been revised several times (Martens et al. 2003, Alström 2006, Rheindt 2006), though considerable gaps in knowledge still exist.

The former *S. burkii* sensu lato proved to be a complex of at least six species that live partly sympatrically and partly allopatrically in the Himalayas, a large part of mountainous China, and parts of Southeast Asia, southward to south Vietnam (Alström and Olsson 1999, 2000; Martens et al. 1999, 2003; Olsson et al. 2004; Päckert et al. 2004). On a single mountain slope, up to four species may occur vertically separated, but up to three species have been found within a single forest edge and degraded secondary forest during the breeding season (Martens et al. 2003). The current state of knowledge is briefly summarized here. With respect to phylogenetic relationships and ecological diversification, two major subgroups of this complex are better described separately.

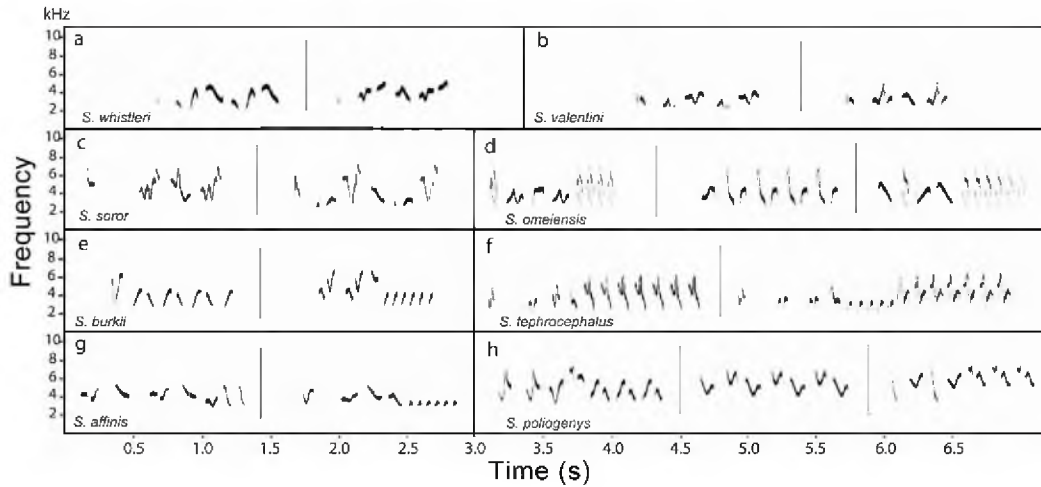


FIG. 21. Territorial songs of Sino-Himalayan spectacled warblers (*Scircercus*; two or three songs of one male per species). (a) *S. whistleri whistleri*, Nepal, Thodung. (b) *S. valentini latouchei*, China, Jiangxi, Huanggang Shan. (c) *S. soror*, China, Shaanxi, Taibai Shan. (d) *S. omeiensis*, China, Gansu, Kangxian. (e) *S. burkii sensu stricto*, Nepal, Thakkhola. (f) *S. tephrocephalus*, China, Gansu, Qing He. (g) *S. affinis*, China, Jiangxi, Huanggang Shan. (h) *S. poliogenys*, Bhutan (rec. P. Holt). (Recordings by J.M. unless stated otherwise.)

(I) SPECIES OF THE MEDIUM AND HIGH MOUNTAIN ELEVATIONS

Taxonomy.—All four species taxa of this group were formerly included in the Golden-spectacled Warbler at the subspecies level or were recently described as new to science. The closest relatives are two sister species from the upper mountain forest belt (ranked as two allospecies of the superspecies *Scircercus [valentini]*): *S. whistleri* occurs in the Himalayas up to 3,700 m (nominate *whistleri*) and in mountain forests of easternmost Himalayas–Myanmar up to 2,800 m (ssp. *nemoralis*) and is vicariant to the Chinese species *S. valentini* from the upper mountain regions of southwestern China (Shaanxi, Sichuan, Gansu, Yunnan provinces; spp. *valentini*) and of southern China (Guangdong, Jiangxi, Fujian) and adjacent Vietnam (ssp. *latouchei*).

Two other species from the middle elevations of Chinese mountain systems were described recently. Local breeding ranges of *S. omeiensis* (Martens et al. 1999) from southwest China (Shaanxi, Gansu, Sichuan, Hubei provinces) range from 1,300 m to ~2,300 m, but this differs locally. There, this species is vertically parapatric to *S. valentini* at its upper distributional range and in some places to *S. soror* (Alström and Olsson 1999), which inhabits lower elevations from 600 m to

1,300 m. Most species in this group have gray central crown stripes, and the inner vanes of R5 and R6 are fully or partly white. Only the central crown stripes of *S. whistleri* are green in the nominate subspecies, or mixed greenish-grayish in ssp. *nemoralis*; breast and underparts of the latter are tinged with a marked orange. Furthermore, *S. whistleri* differs from all other species in this group in having white on the three outer rectrices.

Vocalizations.—With the exception of *S. omeiensis*, all the species share the same song pattern: a repetition of two- or three-note syllables introduced by a short click note (Fig. 21a–d). Songs of the two upper mountain species (*S. whistleri* and *S. valentini*) are significantly lower and more narrow-banded. Strikingly, male *S. omeiensis* possess the most variable song repertoires of all Golden-spectacled Warbler species. Apart from the widely distributed syllabic songs, males of this species display simple and double trills, mixed song types comprising trills and syllables, and even complex nonrepetitive song types.

(II) SPECIES OF THE LOW MOUNTAIN ELEVATIONS

Taxonomy.—This group comprises two species formerly included in *S. burkii sensu lato* at the subspecies level: *S. burkii sensu stricto* from

the low elevations of the Himalayas is sister to *S. tephrocephalus* from Myanmar, parts of southwest China extending to the Qinling range, and Vietnam. These two species presumably separated during Pleistocene times and represent the youngest lineage split at the species level in the *S. burkii* sensu lato group. Both have white on the inner vane of the two outer rectrices (R5 and R6); central crown stripes are gray in *S. tephrocephalus* and green in *S. burkii*; lateral crown stripes are distinctly blackish and sharply outlined in both.

These two form a monophyletic group with the sister-species pair of *S. affinis* and *S. poliogenys*. The fact that the latter two were never subsumed under the large *S. burkii* sensu lato complex is certainly due to their distinctive head pattern of a broad bright eye-ring that is partly whitish or yellowish (in Sichuan) in *affinis* and broad whitish in *poliogenys*, and the general darkish head pattern of the latter. According to molecular data, Himalayan *S. poliogenys* populations are remarkably differentiated from those of southwest China and Vietnam, maybe even at the species level (Olsson et al. 2004).

Vocalizations.—Song structures of *S. affinis* and *S. tephrocephalus* are similar; repertoires are variable and contain repeated syllables, trills, and a combination of both (Fig. 21e–h). However, songs of *S. tephrocephalus* are distinct in having a regular introduction of one or two short call-like notes. Repertoires of *S. poliogenys* (Fig. 21h), at least in the eastern Himalayan population, comprise long and more complex song types and do not contain trills.

DISJUNCT SINO-HIMALAYAN DISTRIBUTIONS

WHITE-CHEEKED NUTHATCH (*SITTA* [*LEUCOPSIS*]) SUPERSPECIES

Distribution.—The two populations are largely disjunct in the western Himalayas (west to Afghanistan, in the east to western Nepal) on the one hand and in southwest China (Sichuan, Gansu, Qinghai) on the other hand. The gap between the two populations is ~1,500 km wide.

Morphology.—Quite pronounced differences exist between these population groups, the eastern *przewalskii* being larger and much more red-brownish on the flanks.

Molecular genetics.—The molecular genetics of this superspecies have not yet been investigated.

Vocalizations.—There are remarkable differences in territorial song (Fig. 22). That of *S. leucopsis* is multibanded and nasal throughout, and no other song forms were ever heard in the western Nepal breeding areas (Martens and Eck 1995). Also, Rasmussen and Anderton (2005) present sonagrams only of this type of vocalization. Song of *S. przewalskii* consists of long verses with slightly ascending whistles and short notes interspersed. In addition, Rasmussen and Anderton (2005) provide illustrations of further vocalizations, but these are not specified as to their behavioral context.

NEPAL TREECREEPER–SICHUAN TREECREEPER (*CERTHIA NIPALENSIS*–*C. TIANQUANENSIS*)

Distribution.—*Certhia nipalensis* is an east Himalayan species that extends slightly into Yunnan;

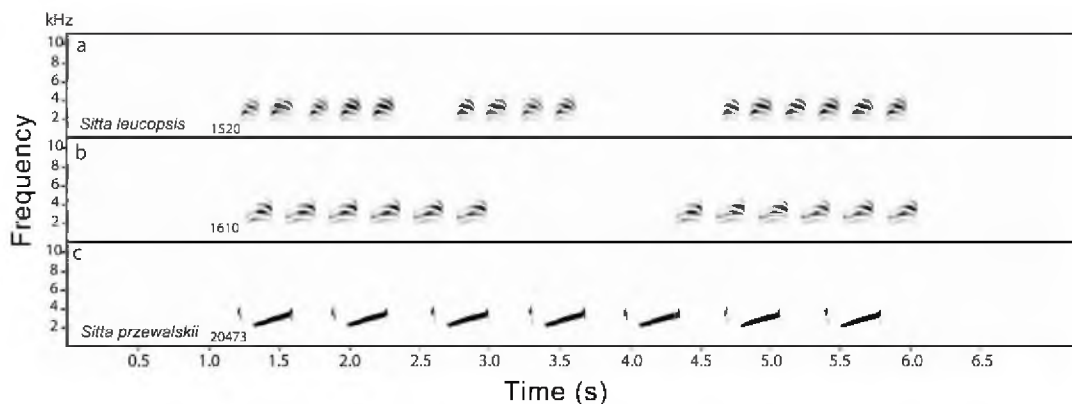


FIG. 22. Territorial songs of Sino-Himalayan White-cheeked Nuthatch (*Sitta leucopsis*) from (a) Nepal, Tarakot, and (b) Nepal, Phoksumdo Lake; and of (c) Przewalski's Nuthatch (*Sitta przewalskii*), from China, Gansu, Lianhua Shan. (Recordings by J.M.)

C. tianquanensis is confined to a minute area in Sichuan and Shaanxi. The latter taxon was originally described as a subspecies of *C. familiaris* (Li 1995), but molecular genetics brought to light the close relationship with *C. nipalensis* (Tietze et al. 2006).

Morphology.—As is consistent with the considerable molecular genetic distance, external morphology in this pair is quite different. With respect to coloration, the uniform dark underpart of Himalayan *C. nipalensis* contrasts with the light breast tapering to light gray in *C. tianquanensis*. Also, bill lengths are remarkably different (Martens et al. 2002), but in both species (which in general have similar body dimensions) the bills are much shorter than in other *Certhia* species (Tietze and Martens 2009).

Molecular genetics.—The cytochrome-*b* distance value between *nipalensis* and *tianquanensis* amounts to 5.7% and points to a long independent evolution of the two taxa that justifies species rank (Tietze et al. 2006).

Vocalizations.—Vocalizations are distinctly different in the two species; verses consist of short trills with ascending notes in *nipalensis*, whereas in *tianquanensis* the verse is bipartite, one part with ascending and the other with descending notes (Fig. 7i–k). Extremely narrowly spaced trills and remarkably short verses, the shortest within the genus *Certhia*, and short click-like calls that differ only in frequency are distinctive of this species pair (Tietze et al. 2008).

Taxonomy.—*Certhia tianquanensis* was described as a subspecies of *C. familiaris*, to which species it definitely does not belong (Tietze et al. 2006). Molecular phylogenetics and vocalizations demonstrated relationships at the species level with *C. nipalensis*, a Himalayan endemic with only slightly larger area than *C. tianquanensis*.

BAR-TAILED TREECREEPER (*CERTHIA HIMALAYANA*)

Distribution.—The Bar-tailed Treecreeper's distribution is remarkably disjunct from Afghanistan and the western Himalayas, not east of western Nepal (eastern records in Kali Gandaki Gorge), and restricted to dry, monsoon-protected areas (Martens and Eck 1995). The other parts of its area are confined to mountainous western China and quite isolated in the Natmataung National Park in Myanmar.

Morphology.—Subspecies have been described, and the disjunct populations in the western

Himalayas (and western outliers) are attributed to two subspecies, those in southwestern China and Myanmar to one each (Vaurie 1959).

Molecular genetics.—With 0.5–0.7% distance values in the cytochrome-*b* gene among the three main populations, differences are remarkably low and indicate the subspecies level at best (Tietze et al. 2006).

Vocalizations.—Although notes of the territorial song of individual males may differ considerably, song recognition between widely spaced populations of the Himalayas and China is obvious (Fig. 7f–h). In a population in north Yunnan, song types from western Nepal elicited strong territorial reactions, demonstrating a common species-specific pattern in both song types (Tietze et al. 2006, 2008).

Taxonomy.—On the basis of hardly recognizable differences in the territorial song of the various populations in the Himalayas and China and of low molecular genetic-distance values, all populations are best united within one species. Findings on vocal and molecular genetic investigations match current practice. The present disjunctions seem to be quite young.

DISCUSSION

Inner-Himalayan diversification pattern.—Distributional patterns of passerine birds in the Sino-Himalayan region are manifold, and the respective populations are differentiated at different levels of the time scale. The term "Sino-Himalayan" first points to a pattern of common occurrences of species in the Himalayan chain and in adjacent mountainous areas, mainly in southwest China. Martens (1984) pointed out that Himalayan passerine bird species have their origin in areas partly northeast and partly southwest of the Himalayan chain and, for a very small fraction, only from the northwest. He also stated that the Himalayan passerine fauna is to a large extent an "immigration" fauna that acquired its faunal wealth by immigration of taxa from outside the Himalayas. Additional recognition of diversification processes of Sino-Himalayan taxa within the Himalayan chain remained poor and, until recently, hardly surpassed the level of more or less well-marked subspecies. This was considered to be true of closely related representatives of the Himalayas and adjacent China as well. A nearly absent species-level diversification within the Himalayan chain was stressed by Johansson

et al. (2007) for *Phylloscopus* and *Seicercus* warblers. According to the latter study, speciation within the Himalayas is a rare case and can be referred to only two extant species pairs (*P. maculipennis*–*P. pulcher* and *S. affinis*–*S. poliogenys*). However, both species pairs harbor populations within the Himalayas as well as in China east of the Himalayas, and their individual distribution pattern is Sino-Himalayan. Consequently, in both cases an intra-Himalayan speciation process is not proven. Apparently, *Phylloscopus* and *Seicercus* species evolved in rather small areas either in the Himalayas or in China–Indochina east of the Himalayas, where they stayed until the recent past and finally spread into neighboring areas, including the Himalayan chain. Following this logic, only small-scale subspeciation occurred because of the small spans of time available for diversification in interglacials.

However, one should not generalize results drawn from a taxonomically narrowly circumscribed group, here phylloscopid warblers. Martens and Eck (1995:51, Fig. 41) pointed to distinct zones within the Himalayas where subspecies meet and possibly, but not necessarily, merge. They focused on four such areas in Nepal alone—the Karnali catchment transition zone, the Dhaulagiri transition zone, the Kathmandu transition zone, and the Arun catchment transition zone—and named up to 21 species that meet with different subspecies in a single transition zone. Almost none of these species were investigated vocally or genetically in sufficient detail to indicate whether evolutionarily distinct populations (in terms of genetic clusters or lineages) meet in these narrow zones or if only steps in clines are described. Such may be caused locally by different climatic conditions—for example, different temperature gradients or precipitation regimes along the Himalayan chain.

In fact, in some species, inner-Himalayan diversification of genetic markers was detected to some degree. The few cases occur in various passerine groups: titmice (*Parus ater* complex; Martens et al. 2006), bush warblers (*Bradypterus thoracicus* complex; Alström et al. 2008), leaf-warblers (*Phylloscopus affinis*; Martens et al. 2008), bush-tits (*Aegithalos concinnus iredalei*; Päckert et al. 2010), and treecreepers (*Certhia hodgsoni*; Tietze et al. 2006, 2008). In all these cases, a small-range western Himalayan population group is opposed to a more extensive eastern Himalayan area, followed by the southwest Chinese mountainous

area farther east. The latter normally harbors at least one further well-distinguishable taxon of given form-complexes. According to our molecular dating, all inner-Himalayan separation events were dated to the Pleistocene (with relatively narrow confidence intervals) and must thus be considered relatively recent (Päckert et al. 2009b). However, vocal differences among eastern and western Himalayan clades and their respective Chinese sister clade are subtle, if detectable at all, and would indeed indicate a rather low differentiation level. Undoubtedly, further detailed acoustic and genetic studies in species known to display striking morphological subspeciation along the Himalayan chain will reveal a wealth of further such inner-Himalayan diversifications, partly at the species level, partly at a well-advanced subspecies level.

Superspecies and species complexes with (continuous) Sino-Himalayan distribution.—In a number of cases, diversification within the Sino-Himalayan region is remarkably complex: a highly diverged array of populations are allopatrically distributed and represent deeply split haplotype clusters. In most of these cases vocalizations differ remarkably. We assume that the constituents of these form complexes (in most cases referred to here as “superspecies”) developed in allopatry, probably in single mountain stocks, perhaps in refuge areas prior to or within the Pleistocene glaciation periods. Secondarily, these supposed small-range populations enlarged their areas and came into secondary contact. How the individuals of the different haplotype clusters behave upon contact is virtually unknown. In no case have population interactions in contact zones been described, either by vocal behavior or by population genetics. Unlike the inner-Himalayan differentiation pattern, as in nearly all cases described above, vocal and genetic differences are marked and may well act as pre-mating isolating barriers, preventing pair formation between the differing vocal and genetic entities. Two general phylogeographic patterns are observed.

(1) The first pattern consists of superspecies with rather boreal representatives in parts of the northern Palearctic and a disjunct Sino-Himalayan portion of the range. This vast Eastern Palearctic part in Siberia, extending to Japan (sometimes reaching even the Western Palearctic), is homogeneous, at least in terms of molecular genetics, and belongs to a single haplotype cluster only (there are additional ones in the Western Palearctic, as

in *Parus ater* or *Regulus regulus*). The populations of the Sino-Himalayan part of the range, though much smaller than the former, are considerably more divergent and, in general, comprise three or four haplotype clusters. The respective areas are arranged in a more or less north–south order, as follows (depending on the superspecies or species complex): Ningxia, Gansu, Sichuan, Yunnan, and southeast Tibet, sometimes with an eastward extension along the Qinling range in south Shaanxi, in the south turning northward into the Himalayan chain. *Parus ater* comprises three such haplotype clusters (four valid subspecies), *P. [proregulus]* three (formerly four valid subspecies, now three allopecies), *Certhia [familiaris]* four (the northernmost populations in Sino-Himalayan China unexpectedly belong to the north Siberian taiga cluster), and *P. fuscatus* two. *Regulus regulus* comprises only one cluster; thus, Goldcrests are genetically uniform in the Sino-Himalayan region and so are their territorial songs. All species mentioned here are Palearctic, and their supposed origin was in the present southwest Chinese mountains. Range extension occurred northward into Siberia with extensions to the Western Palearctic. The present complicated cluster development may have occurred as a result of Late Pliocene and Early Pleistocene fragmentation and disjunction of areas and by additional range extension into the Himalayas combined with further diversification.

(2) The second phylogeographic pattern consists of species complexes and superspecies that are confined to the Himalayas and various mountainous parts of China east of the Himalayas only. This group is less homogeneous and mostly harbors true Chinese taxa with hardly any affiliation to the northern Palearctic. In addition to the Himalayas, these taxa are distributed in southwest China and often in south China, with extensions into tropical Indochina. Some species inhabit (as in the first pattern) high-altitude forest belts of the Himalayas and are found disjunctly in high-altitude southwestern Chinese forests, sometimes with relict area outliers in southeast China (Fujian, Jiangxi, and even Taiwan), the latter apparently being relicts from formerly more extended ranges, scattered during the Pleistocene. The *Seicercus burkii* complex in general has a tropical affiliation and origin and represents several evolutionary “layers” that allow even parapatric and locally sympatric occurrences of up to four species-level taxa on a single mountain slope

(Martens et al. 1999, 2003). It is noteworthy that, compared with the group described by pattern 1 above, in the tropical spectacled warblers separation times among Himalayan and Chinese sister clades (*S. valentini*–*S. tephrocephalus*; Himalayan and Southeast Asian *S. poliogenys*) were dated to older periods, prior to the Pliocene–Pleistocene boundary.

Other taxa that range to more southern parts of China and even Indochina represent a much more complex pattern. Besides a Himalayan cluster in the southwest, eastern and southern China, including Indochina, may harbor several populations that represent deeply split molecular genetic clusters, and this diversification pattern is best represented by the *Phylloscopus reguloides* and *P. davisoni* species complexes (Olsson et al. 2005, Päckert et al. 2009b). In addition to the Himalayan lineage, three additional ones exist in China and Indochina. Their areas are largely congruent but differ in details. This suggests a more or less synchronous diversification process of fragmentation that involved even parts of the Indonesian Archipelago (close relatives of *P. [davisoni]*). As in these leaf-warblers, other exclusively (sub-)tropical taxa apparently underwent a complex Southeast Asian radiation over long evolutionary time spans and formed highly diverse genera with many extant representatives in the Himalayas, particularly in the species-rich genera of the Timaliidae (former genus *Garrulax*: Luo et al. 2008; *Pteruthius*: Reddy 2008, Rheindt and Eaton 2009; *Yuhina*: Zhang et al. 2007, though this study neglected the Himalayan species; family level diversification: Gelang et al. 2009). *Cettia acanthizoides* also belongs to this distribution type, though its area parts are much smaller and isolated in southeast China and Taiwan (Alström et al. 2007).

Disjunct parts of areas within the Sino-Himalayan diversification pattern.—The reasons for these disjunctions are unclear, and at present they may be attributable to current differences in ecological conditions to which the western and eastern populations are adapted. Western Himalayan populations are adapted to dry, monsoon-reduced climate and presently can survive only in western Himalayan areas, mainly in inner valleys (Martens and Eck 1995:345). Differentiation levels are apparently very recent in terms of low cytochrome-*b* lineage differentiation and vocal similarity, as in *Certhia himalayana*. Slightly more marked differentiation exists in *Bradypterus thoracicus* between west Himalayan and southwest Chinese populations (Alström et al.

2008) and in *Sitta leucopsis*. Cytochrome-*b* divergence is unknown in the latter.

Pattern encircling the Tibetan Plateau.—Within Eurasia, the Tibetan Plateau facilitates ring-shaped distributional patterns of arboreal birds and was suggested to enhance the formation of so-called “ring species” (sensu Mayr 1942). Mayr’s isolation-by-distance theory is based on two main assumptions: (1) stepwise colonization around the geographic barrier in two chains of populations connected by gene flow and (2) significant differentiation and reproductive isolation of terminal populations of each of the two chains in secondary contact. The Greenish Warbler (*Phylloscopus trochiloides*) attracted some interest because it seemed to represent a well-established ring species with a nearly complete ring-shaped area only fragmented in the forestless deserts of northern China. In fact, the comprehensive analyses by Irwin (2000, 2002) and Irwin et al. (2001b, c, 2005) confirmed that the Greenish Warbler fulfills all basic assumptions made for a true ring species: (1) variation of song characters is clinal along both population chains, (2) populations along the eastern and western chain around the plateau are connected by gene flow, and (3) gene flow is interrupted and acoustic differences are highest between terminal populations of both chains in the Siberian secondary contact area of *P. trochiloides viridanus* and *P. plumbeitarsus*. In fact, the Greenish Warbler appears to be the only bird group for which mitochondrial, nuclear, and bioacoustic markers corroborate the isolation-by-distance theory around the Tibetan Plateau (for critical reviews of classical ring species, see Irwin and Irwin 2002, Martens and Päckert 2008).

A marginal debate raised the question of how and when the ring was actually formed, because certainly no such ring existed during the Pleistocene, at least in the northern arm, because of a lack of a continuous forest belt (Frenzel 1968) to which Greenish Warblers are confined (cf. Martens and Päckert 2008). Strikingly, the distributional patterns of some other monophyletic warbler groups at least partly encircle the Tibetan Plateau. However, more than two genetic units are involved: (1) the *Phylloscopus [inornatus]* superspecies, which includes three genetic units (*P. inornatus* and two further lineages of *P. humei*)—distribution gaps in the central Himalayas and northeast China—with initial separation similar to that in the Greenish Warbler at the beginning of the Pleistocene (cf. Irwin et al. 2001a); and (2) the *Phylloscopus [affinis]*

superspecies, which includes three genetic units (*P. affinis* sensu stricto, *P. occisinensis*, *P. griseolus*) with the ring nearly closed in the Qilian Shan of Gansu and Qinghai—separation of the three clades involved was dated considerably earlier than Pleistocene times, and very likely all three extant species evolved in allopatry (Martens et al. 2008). Apart from the warbler superspecies discussed, the breeding range of the White-browed Tit Warbler (*Leptopoeile sophiae*) encircles the Tibetan Plateau, too, absent only from parts of the western Himalayas. So far, it is not known whether the species comprises more than one genetic unit, but it may represent an older, pre-Pleistocene immigrant to the Tibetan Plateau, as suggested by Pliocene time estimates for the separation from its Chinese sister species, *L. elegans* (Päckert et al. 2010). All species discussed here, including the Greenish Warbler, inhabit high elevations of the Himalayas reaching from the subalpine forest belt considerably above 4,000 m to timberline and even into the alpine bush steppe and meadows. Apparently, the extant distributional patterns of these high-altitude species around the Tibetan Plateau date back to range and lineage separation during very different evolutionary time spans (some Early Pleistocene, others even before), and only the Greenish Warbler represents an exceptional case of isolation-by-distance around the geographic barrier.

Himalayan endemics.—Endemics without close relatives outside the Himalayas are a small group, and their relationships are diverse (Das 1966). Among passerines, one should note *Sitta cashmirensis* of the *S. europaea* complex; *Phylloscopus tytleri*, *P. subviridis*, and *Pyrrhula aurantiaca* in the west; and *Pnoepyga immaculata* and *Liocichla bugunorum* in the center and east of the mountain chain, respectively. However, in many cases their relations are not well worked out. In addition, it should be kept in mind that the Himalayas are richer in endemics than was formerly believed. Well-circumscribed subspecies (also in terms of molecular genetics) and allospecies of superspecies newly defined by vocal and genetic characters are confined to the Himalayas, and more are expected to be discovered.

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LITERATURE CITED

- ALSTRÖM, P. 2006. Species concepts and their application: Insights from the genera *Phylloscopus* and *Seicercus*. *Acta Zoologica Sinica* (Supplement) 52:429–434.
- ALSTRÖM, P., AND U. OLSSON. 1990. Taxonomy of the *Phylloscopus proregulus* complex. *Bulletin of the British Ornithologists' Club* 110:38–43.
- ALSTRÖM, P., AND U. OLSSON. 1999. The Golden-spectacled Warbler: A complex of sibling species, including a previously undescribed species. *Ibis* 141:545–568.
- ALSTRÖM, P., AND U. OLSSON. 2000. Golden-spectacled Warbler systematics. *Ibis* 142:495–500.
- ALSTRÖM, P., U. OLSSON, AND P. R. COLSTON. 1992. A new species of *Phylloscopus* warbler from central China. *Ibis* 134:329–334.
- ALSTRÖM, P., U. OLSSON, AND P. R. COLSTON. 1997. Re-evaluation of the taxonomic status of *Phylloscopus proregulus kansuensis* Meise. *Bulletin of the British Ornithologists' Club* 117:177–193.
- ALSTRÖM, P., U. OLSSON, P. C. RASMUSSEN, C.-T. YAO, P. G. P. ERICSON, AND P. SUNDBERG. 2007. Morphological, vocal and genetic divergence in the *Cettia acanthizoides* complex (Aves: Cettidae). *Zoological Journal of the Linnean Society* 149:437–452.
- ALSTRÖM, P., P. C. RASMUSSEN, U. OLSSON, AND P. SUNDBERG. 2008. Species delimitation based on multiple criteria: The Spotted Bush Warbler *Bradypterus thoracicus* complex (Aves: Megaluridae). *Zoological Journal of the Linnean Society* 154:291–307.
- AMADON, D. 1966. The superspecies concept. *Systematic Zoology* 15:245–249.
- BECKER, P., G. THIELCKE AND, K. WÜSTENBERG. 1980. Der Tonhöhenverlauf ist entscheidend für das Gesangserkennen beim mitteleuropäischen Zilpzalp (*Phylloscopus collybita*). *Journal für Ornithologie* 121:229–244.
- BELIK, V. P. 2006. Faunogenetic structure of the Palearctic avifauna. *Entomological Review* 86 Supplement 1:S15–S31.
- BENSCH, S., D. E. IRWIN, J. H. IRWIN, L. KVIST, AND S. ÅKESSON. 2006. Conflicting patterns of mitochondrial and nuclear DNA diversity in *Phylloscopus* warblers. *Molecular Ecology* 15:161–171.
- CHENG, T.-H. 1987. A Synopsis of the Avifauna of China. Parey, Berlin.
- CHRABRYJ, W. M., W. M. LOSKOT, AND E. V. VIETINGHOFF-SCHEEL. 1989. *Phylloscopus fuscatus* (Blyth). Dunkel-laub-sänger. Atlas der Verbreitung paläarktischer Vögel, Lieferung 16. Akademie-Verlag, Berlin.
- CLEMENTS, J. F. 2007. *Clements Checklist of Birds of the World*, 6th ed. Cornell University Press, Ithaca, New York.
- CRACRAFT, J. 1983. Species concepts and speciation analysis. Pages 159–187 in *Current Ornithology*, vol. 1 (R. F. Johnston, Ed.). Plenum Press, New York.
- DAS, S. M. 1966. Palearctic elements in the fauna of Kashmir. *Nature* 212:1327–1330.
- DEL HOYO, J., A. ELLIOTT, AND D. A. CHRISTIE, Eds. 2006. *Handbook of the Birds of the World*, vol. 11: Old World Flycatchers to Old World Warblers. Lynx Edicions, Barcelona, Spain.
- DICKINSON, E. C., Ed. 2003. *The Howard and Moore Complete Checklist of the Birds of the World*, 3rd ed. Christopher Helm, London.
- DIESSELHORST, G., AND J. MARTENS. 1972. Hybriden von *Parus melanolophus* und *P. ater* im Nepal-Himalaya. *Journal für Ornithologie* 113:374–390.
- DIETZEN, C., H.-H. WITT, AND M. WINK. 2003. The phylogeographic differentiation of the European Robin *Erithacus rubecula* on the Canary Islands revealed by mitochondrial sequence data and morphometrics: Evidence for a new robin taxon on Gran Canaria? *Avian Science* 3:115–131.
- ECK, S., AND J. MARTENS. 2006. Systematic notes on Asian birds. 49. A preliminary review of the Aegithalidae, Remizidae and Paridae. *Zoologische Mededelingen Leiden* 80-5:1–63.
- ECK, S., AND C. QUAISSER. 2004. Verzeichnis der Typen der Vogelsammlung des Museums für Tierkunde in den Staatlichen Naturhistorischen Sammlungen Dresden. *Zoologische Abhandlungen des Museums für Tierkunde Dresden* 54:233–316.

- FRENZEL, B. 1968. The Pleistocene vegetation of northern Eurasia. *Science* 161:637–649.
- GELANG, M., A. CIBOIS, E. PASQUET, U. OLSSON, P. ALSTRÖM, AND P. G. P. ERICSON. 2009. Phylogeny of babblers (Aves, Passeriformes): Major lineages, family limits and classification. *Zoologica Scripta* 38:225–236.
- GOSLER, A., AND P. CLEMENT. 2007. Family Paridae (Tits and Chickadees). Pages 662–750 in *Handbook of the Birds of the World*, vol. 12: Picathartes to Tits and Chickadees (J. del Hoyo, A. Elliott, and D. A. Christie, Eds.). Lynx Edicions, Barcelona, Spain.
- HAFER, J. 1993. Familie Paridae—Meisen. Pages 359–808 in *Handbuch der Vögel Mitteleuropas*, vol. 13 (U. N. Glutz von Blotzheim and K. M. Bauer, Eds.). Aula, Wiesbaden, Germany.
- IRWIN, D. E. 2000. Song variation in an avian ring species. *Evolution* 54:998–1010.
- IRWIN, D. E. 2002. Phylogeographic breaks without geographic barriers to gene flow. *Evolution* 56:2383–2394.
- IRWIN, D. E., P. ALSTRÖM, U. OLSSON, AND Z. M. BENOWITZ-FREDERICKS. 2001a. Cryptic species in the genus *Phylloscopus* (Old World leaf warblers). *Ibis* 143:233–247.
- IRWIN, D. E., S. BENSCH, J. H. IRWIN, AND T. D. PRICE. 2005. Speciation by distance in a ring species. *Science* 307:414–416.
- IRWIN, D. E., S. BENSCH, AND T. D. PRICE. 2001b. Speciation in a ring. *Nature* 409:333–337.
- IRWIN, D. E., AND J. H. IRWIN. 2002. Circular overlaps: Rare demonstrations of speciation. *Auk* 119:596–602.
- IRWIN, D. E., J. H. IRWIN, AND T. D. PRICE. 2001c. Ring species as bridges between microevolution and speciation. *Genetica* 112–113:223–243.
- JOHANSSON, U. S., P. ALSTRÖM, U. OLSSON, P. G. P. ERICSON, P. SUNDBERG, AND T. D. PRICE. 2007. Build-up of the Himalayan avifauna through immigration: A biogeographical analysis of the *Phylloscopus* and *Seicercus* warblers. *Evolution* 61:324–333.
- LA TOUCHE, J. D. 1922. [. . . descriptions of new forms of Chinese birds . . .]. *Bulletin of the British Ornithologists' Club* 43:20–23.
- LI, G.-Y. 1995. A new subspecies of *Certhia familiaris* (Passeriformes: Certhiidae). *Acta Zootaxonomica Sinica* 20:373–377.
- LIEBERS-HELBIG, D., V. STERNKOPF, A. J. HELBIG, AND P. DEKNIFF. 2010. The Herring Gull complex (*Larus argentatus—fuscus—cachinnans*) as a model group for recent Holarctic vertebrate radiations. Pages 351–371 in *Evolution in Action* (M. Glaubrecht, Ed.). Springer-Verlag, Heidelberg.
- LOSKOT, W. M., AND E. V. VIETINGHOFF-SCHEEL. 1991. *Phylloscopus griseolus* (Blyth) Felsenlaubsänger. In *Atlas der Verbreitung palaearktischer Vögel*, Lieferung 17. Akademie-Verlag, Berlin.
- LUO, X., Y. H. QU, L. X. HAN, S. H. LI, AND F. M. LEI. 2008. A phylogenetic analysis of laughingthrushes (Timaliidae: *Garrulax*) and allies based on mitochondrial and nuclear DNA sequences. *Zoologica Scripta* 38:9–22.
- MARTENS, J. 1975. Akustische Differenzierung verwandtschaftlicher Beziehungen in der *Parus* (*Periparus*)-Gruppe nach Untersuchungen im Nepal-Himalaya. *Journal für Ornithologie* 116:369–433.
- MARTENS, J. 1980. Lautäußerungen, verwandtschaftliche Beziehungen und Verbreitungsgeschichte asiatischer Laubsänger (*Phylloscopus*). *Advances in Ethology* 22: 1–71.
- MARTENS, J. 1981. Lautäußerungen der Baumläufer des Himalaya und zur akustischen Evolution in der Gattung *Certhia*. *Behaviour* 77:287–318.
- MARTENS, J. 1984. Vertical distribution of Palearctic and Oriental faunal components in the Nepal Himalayas. *Erdwissenschaftliche Forschung* 18: 323–336.
- MARTENS, J. 1993. Lautäußerungen von Singvögeln und die Entstehung neuer Arten. *Forschungsmagazin Universität Mainz* 9:34–44.
- MARTENS, J. 1998. Geographische Variabilität der Lautäußerungen von Sperlingsvögeln—Auswirkungen auf Artbildung und Artkonzept (Aves: Passeriformes: Oscines). *Zoologische Abhandlungen des Museums für Tierkunde Dresden* 50 Supplement:35–50.
- MARTENS, J., AND S. ECK. 1995. Towards an ornithology of the Himalayas: Systematics, ecology and vocalizations of Nepal birds. *Bonner Zoologische Monographien*, no. 38.
- MARTENS, J., AND S. ECK. 2000. Der *Seicercus burkii*-Komplex im Himalaya und China oder: Schätzen wir die Diversität der Singvögel falsch ein? *Ornithologischer Anzeiger* 39:1–14.
- MARTENS, J., S. ECK, M. PÄCKERT, AND Y.-H. SUN. 1999. The Golden-spectacled Warbler *Seicercus burkii*—A species swarm. *Zoologische Abhandlungen des Museums für Tierkunde Dresden* 50:282–327.
- MARTENS, J., S. ECK, M. PÄCKERT, AND Y.-H. SUN. 2003. Methods of systematic and taxonomic research on passerine birds: The timely example of the *Seicercus burkii* complex (Sylviidae). Part 2. *Bonner Zoologische Beiträge* 51:109–118.
- MARTENS, J., S. ECK, AND Y.-H. SUN. 2002. *Certhia tianquanensis* Li, a treecreeper with relict distribution in Sichuan, China. *Journal für Ornithologie* 143:440–456.
- MARTENS, J., AND G. GEDULDIG. 1988. Akustische Barrieren beim Waldbaumläufer (*Certhia familiaris*)? *Journal für Ornithologie* 29:417–432.
- MARTENS, J., AND S. HÄNEL. 1981. Gesangsformen und Verwandtschaft der asiatischen Zilpzalpe *Phylloscopus collybita abietinus* und *P. c. sindianus*. *Journal für Ornithologie* 122:403–427.
- MARTENS, J., AND M. PÄCKERT. 2003. Disclosure of song-bird diversity in the Palearctic/Oriental transition

- zone. Pages 551–558 in *Acta XVIII Congressus Internationalis Ornithologici* (A. Legakis, S. Sfentourakis, R. Polymeni, and M. Thessalou-Lagaki, Eds.). Pensoft, Sofia, Bulgaria.
- MARTENS, J., AND M. PÄCKERT. 2008. Ring species—Do they exist in birds? *Zoologischer Anzeiger* 246: 315–324.
- MARTENS, J., M. PÄCKERT, A. NAZARENKO, O. VALCHUK, AND N. KAWAJI. 1998. Comparative bioacoustics of territorial song in the Goldcrest (*Regulus regulus*) and its implications for the intrageneric phylogeny of the genus *Regulus*. *Zoologische Abhandlungen des Museums für Tierkunde Dresden* 50:99–128.
- MARTENS, J., Y.-H. SUN, L. WEL, AND M. PÄCKERT. 2008. Intraspecific differentiation of Sino-Himalayan bush-dwelling *Phylloscopus* leaf warblers, with description of two new taxa (*P. fuscatus*, *P. fuligiventer*, *P. affinis*, *P. armandii*, *P. subaffinis*). *Vertebrate Zoology* 58:233–266.
- MARTENS, J., AND D. T. TIETZE. 2006. Systematic notes on Asian birds. 65. A preliminary review of the Certhiidae. *Zoologische Mededelingen Leiden* 80-5:273–286.
- MARTENS, J., D. T. TIETZE, S. ECK, AND M. VEITH. 2004. Radiation and species limits in the Asian Pallas's Warbler complex (*Phylloscopus proregulus* s. l.). *Journal of Ornithology* 145:206–222.
- MARTENS, J., D. T. TIETZE, AND Y.-H. SUN. 2006. Molecular phylogeny of *Parus* (*Periparus*), a Eurasian radiation of tits (Aves: Passeriformes: Paridae). *Zoologische Abhandlungen des Museums für Tierkunde Dresden* 55:103–120.
- MAYR, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York.
- MAYR, E. 1970. *Populations, Species, and Evolution: An Abridgment of Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- MAYR, E., AND P. D. ASHLOCK. 1991. *Principles of Systematic Zoology*, 2nd ed. McGraw-Hill, New York.
- MAYR, E., M. A. TRAYLOR, AND G. E. WATSON. 1986. Genera *Phylloscopus* and *Seicercus*. Pages 221–262 in *Check-list of Birds of the World*, vol. 11 (E. Mayr and G. W. Cottrell, Eds.). Museum of Comparative Zoology, Cambridge, Massachusetts.
- OLSSON, U., P. ALSTRÖM, P. G. P. ERICSON, AND P. SUNDBERG. 2005. Non-monophyletic taxa and cryptic species—Evidence from a molecular phylogeny of leaf-warblers (*Phylloscopus*: Aves). *Molecular Phylogenetics and Evolution* 36:261–275.
- OLSSON, U., P. ALSTRÖM, AND P. SUNDBERG. 2004. Non-monophyly of the avian genus *Seicercus* (Aves: Sylviidae) revealed by mitochondrial DNA. *Zoologica Scripta* 33:501–510.
- PÄCKERT, M., C. BLUME, Y.-H. SUN, L. WEL, AND J. MARTENS. 2009a. Acoustic differentiation reflects mitochondrial lineages in Blyth's Leaf Warbler and White-tailed Leaf Warbler complexes (Aves: *Phylloscopus reguloides*, *P. davisoni*). *Biological Journal of the Linnean Society* 96:584–600.
- PÄCKERT, M., AND J. MARTENS. 2008. Taxonomic pitfalls in tits—Comments on the chapter Paridae of the *Handbook of the Birds of the World* (A. G. Gosler and P. Clement, HBW vol. 12, 2007). *Ibis* 150:829–831.
- PÄCKERT, M., J. MARTENS, J. KOSUCH, A. A. NAZARENKO, AND M. VEITH. 2003. Phylogenetic signal in the songs of Crests and Kinglets (Aves: *Regulus*). *Evolution* 57:616–629.
- PÄCKERT, M., J. MARTENS, AND L. LIU SEVERINGHAUS. 2008. The Taiwan Firecrest (*Regulus goodfellowi*) belongs to the Goldcrest assemblage (*Regulus regulus* s. l.): Evidence from mitochondrial DNA and the territorial song of the Regulidae. *Journal of Ornithology* 150:205–220.
- PÄCKERT, M., J. MARTENS, AND Y.-H. SUN. 2010. Phylogeny of long-tailed tits and allies inferred from mitochondrial and nuclear markers (Aves: Passeriformes, Aegithalidae). *Molecular Phylogenetics and Evolution* 55:952–967.
- PÄCKERT, M., J. MARTENS, Y.-H. SUN, AND D. T. TIETZE. 2009b. Phylogeography and the evolutionary time-scale of passerine radiations in the Sino-Himalayan region (Aves: Passeriformes). Pages 71–80 in *Biodiversity and Natural Heritage of the Himalaya III* (M. Hartmann and J. Weipert, Eds.). Naturkunde Museum Erfurt, Erfurt, Germany.
- PÄCKERT, M., J. MARTENS, Y.-H. SUN, AND M. VEITH. 2004. The radiation of the *Seicercus burkii* complex and its congeners (Aves: Sylviidae): Molecular genetics and bioacoustics. *Organisms, Diversity & Evolution* 4: 341–364.
- PALUMBI, S., A. MARTIN, S. ROMANO, W. O. McMILLAN, L. STICE, AND G. GRABOWSKI. 1991. *The Simple Fool's Guide to PCR*. Kewalko Marine Laboratory, University of Hawaii, Honolulu.
- RASMUSSEN, P. C., AND J. C. ANDERTON. 2005. *Birds of South Asia. The Ripley Guide*, vol. 2: Attributes and Status. Lynx Edicions, Barcelona, Spain.
- REDDY, S. 2008. Systematics and biogeography of the shrike-babblers (*Pteruthius*): Species limits, molecular phylogenetics, and diversification patterns across southern Asia. *Molecular Phylogenetics and Evolution* 47:54–72.
- RHEINDT, F. E. 2006. Splits galore: The revolution in Asian leaf warbler systematics. *BirdingASIA* 5:25–39.
- RHEINDT, F. E., AND J. A. EATON. 2009. Species limits in *Pteruthius* (Aves: Corvida) shrike-babblers: A comparison between the biological and phylogenetic species concepts. *Zootaxa* 2301:29–54.
- RHEINDT, F. E., AND J. A. EATON. 2010. Biological species limits in the Banded Pitta *Pitta guajana*. *Forktail* 26:86–91.
- RIPLEY, S. D. 1961. Some bird records from northern Burma with a description of a new subspecies. *Journal of the Bombay Natural History Society* 58:279–283.

- ROBERTS, T. J. 1992. The Birds of Pakistan, vol. 2. Passeriformes: Pittas to Buntings. Oxford University Press, Karachi, Pakistan.
- SPICER, G. S., AND L. DUNIPACE. 2004. Molecular phylogeny of songbirds (Passeriformes) inferred from mitochondrial 16S ribosomal RNA gene sequences. *Molecular Phylogenetics and Evolution* 30:325–335.
- STATTERSFIELD, A. J., M. J. CROSBY, A. J. LONG, AND D. C. WEGE. 1998. Endemic Bird Areas of the World: Priorities for Biodiversity and Conservation. BirdLife Conservation Series, no. 7. BirdLife International, Cambridge, United Kingdom.
- TAMURA, K., J. DUDLEY, M. NEI, AND S. KUMAR. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* 24:1596–1599.
- THIELCKE, G. 1969. Die Reaktion von Tannen- und Kohlmeise (*Parus ater*, *P. major*) auf den Gesang nahverwandter Formen. *Journal für Ornithologie* 110:148–157.
- TICEHURST, C. B. 1938. A Systematic Review of the Genus *Phylloscopus* (willow-warblers or leaf-warblers). Trustees of the British Museum (Natural History), London.
- TIETZE, D. T., AND J. MARTENS. 2009. Morphometric characterisation of treecreepers (genus *Certhia*). *Journal of Ornithology* 150:431–457.
- TIETZE, D. T., J. MARTENS, AND Y.-H. SUN. 2006. Molecular phylogeny of treecreepers (*Certhia*) detects hidden diversity. *Ibis* 148:477–488.
- TIETZE, D. T., J. MARTENS, Y.-H. SUN, AND M. PÄCKERT. 2008. Evolutionary history of treecreeper vocalizations (Aves: *Certhia*). *Organisms, Diversity & Evolution* 8:305–324.
- TIETZE, D. T., J. MARTENS, Y.-H. SUN, L. L. SEVERINGHAUS, AND M. PÄCKERT. 2011. Song evolution in the Coal Tit (*Parus ater*). *Journal of Avian Biology* 42:1–17.
- VAURIE, C. 1954. Systematic notes on Palearctic birds. No. 9. Sylviinae: The genus *Phylloscopus*. *American Museum Novitates* 1685:1–23.
- VAURIE, C. 1959. The Birds of the Palearctic Fauna: A Systematic Reference. Order Passeriformes. Witherby, London.
- VIETINGHOFF-SCHEEL, E. v. 1986. *Phylloscopus affinis* (Tickell). Himalaya-Laubsänger. In *Atlas der Verbreitung palaearktischer Vögel*, Lieferung 13. Akademie-Verlag, Berlin.
- VIETINGHOFF-SCHEEL, E. v. 1987. *Phylloscopus davisoni* (Oates). Weißschwanzlaubsänger. In *Atlas der Verbreitung palaearktischer Vögel*, Lieferung 14. Akademie-Verlag, Berlin.
- VIETINGHOFF-SCHEEL, E. v. 1989. *Phylloscopus reguloides* (Blyth). Streifenkopf-Laubsänger. In *Atlas der Verbreitung palaearktischer Vögel*, Lieferung 16. Akademie-Verlag, Berlin.
- WEIBEL, A. C., AND W. S. MOORE. 2002. A test of a mitochondrial gene-based phylogeny of woodpeckers (genus *Picooides*) using an independent nuclear gene, β -fibrinogen intron 7. *Molecular Phylogenetics and Evolution* 2:247–257.
- WEIR, J. T., AND D. SCHLUTER. 2008. Calibrating the avian molecular clock. *Molecular Ecology* 17:2321–2328.
- WIENS, J. J., C. A. KUCZYNSKI, AND P. R. STEPHENS. 2010. Discordant mitochondrial and nuclear gene phylogenies in emydid turtles: Implications for speciation and conservation. *Biological Journal of the Linnean Society* 99:445–461.
- WOLTERS, H. E. 1980. Die Vogelarten der Erde. Eine systematische Liste mit Verbreitungsangaben sowie deutschen und englischen Namen. Part 5:321–400. Parey, Berlin.
- ZHANG, S., L. YANG, X. YANG, AND J. YANG. 2007. Molecular phylogeny of the yuhinas (Sylviidae: *Yuhina*): A paraphyletic group of babblers including *Zosterops* and Philippine *Stachyris*. *Journal of Ornithology* 148:417–426.
- ZINK, R. M., AND G. F. BARROWCLOUGH. 2008. Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology* 17:2107–2121.