

Molecular phylogeny of *Parus* (*Periparus*), a Eurasian radiation of tits (Aves: Passeriformes: Paridae)*

Dedicated to Siegfried Eck † – the outstanding expert on palearctic birds

JOCHEN MARTENS¹, DIETER THOMAS TIETZE¹ & YUE-HUA SUN²

¹ Institut für Zoologie, Johannes-Gutenberg-Universität, 55099 Mainz, Germany,
E-mail: martens(at)uni-mainz.de, tietze(at)uni-mainz.de

² Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, P. R. China,
E-mail: sunyh(at)ioz.ac.cn

* Results of the Himalaya Expeditions of J. Martens, No. 251. – For No. 250 see:
Stuttgarter Beiträge zur Naturkunde, A 680, 2005.

Abstract. The subgenus *Parus* (*Periparus*) is most rich in species and subspecies in the Sino-Himalayan mountains and in subtropical/tropical Southeast Asia. We characterize the ingroup relationships of the subgenus by the cytochrome-b gene. Within the palearctic, we recognise: *P. ater* (incl. *melanolophus*), *P. rubidiventris* and *P. rufonuchalis*. Within the Indomalayan region, the taxonomic rank of *P. venustulus*, *P. amabilis* and *P. elegans* needs further study. Within its three large disjunct areas (Sino-Himalaya, northern Eurasia, northern Africa), *P. ater* is divided into six distinct cytochrome-b haplotype clusters. The Sino-Himalayan area comprises three cytochrome-b clusters; one of them is ssp. *melanolophus* (western Himalayas). In a variable hybrid population in western Nepal, mixing of *P. a. melanolophus* and *P. a. martensi* is proven, also by means of cytochrome-b haplotypes. *P. a. aemodius* is subdivided into two cytochrome-b clusters, which are restricted to the Himalayas and to western China. The Chinese cluster is named *P. a. eckodedicatus* n. ssp. In northern Eurasia, the ssp. *insularis*, *ater* and *rufipectus* extend from Japan via Siberia and central Asia to northern and east-central Europe. All belong to a single cytochrome-b cluster. Between the populations of northeastern and central/southern Europe there is a marked cytochrome-b difference. For these European mainland populations the name *abietum* BREHM, 1831, is revalidated. Within all *P. ater* clusters, ssp. *atlas* (North Africa) is genetically most distinct. The eastern cluster of *P. rubidiventris*, ssp. “*beavani*”, is bipartite as to cytochrome b and body size, and contains an eastern Himalayan and a western Chinese cluster. For the Chinese cluster the name *whistleri* STRESEMANN, 1931, is revalidated. Within Himalayan *P. rubidiventris*, red-bellied nominate *rubidiventris* and grey-bellied ssp. *beavani* belong to the same cytochrome-b-haplotype cluster. Concerning cytochrome b, there is no internal structure in *P. rufonuchalis*. The complicated evolutionary history of *P. ater* and *P. rubidiventris* have mainly been triggered by the early Pleistocene. At different times apparently three invasions of *P. ater* reached the western palearctic to form the present complicated distribution pattern.

Kurzfassung. In dieser Arbeit charakterisieren wir mit dem Cytochrom-b-Gen die verwandtschaftlichen Beziehungen der Untergattung *Parus* (*Periparus*) aus den sino-himalayanischen Gebirgen und aus dem subtropisch/tropischen SO-Asien. Folgende Arten werden anerkannt: In der Paläarktis *P. ater* (inkl. *melanolophus*), *P. rubidiventris* und *P. rufonuchalis*. Der taxonomische Rang der tropisch/subtropischen Arten *P. venustulus*, *P. amabilis* und *P. elegans* ist unklar. *P. ater* gliedert sich in den disjunkten Arealen Sino-Himalaya, N-Eurasien und N-Afrika in sechs eigenständige Cytochrom-b-Äste. Die sino-himalayanische Gruppe zerfällt in drei Äste, einer davon ist ssp. *melanolophus*. In Nepal wird Vermischung von ssp. *melanolophus* mit ssp. *martensi* morphologisch und über Cytochrom b nachgewiesen. Ssp. *aemodius* gliedert sich in zwei auch morphologisch differenzierbare Äste, von denen der chinesische Ast als *Parus ater eckodedicatus* n. ssp. neu benannt wird. In N-Eurasien reichen die Vertreter eines Cytochrom-b-Astes von Japan über Sibirien bis N-Skandinavien und O-Deutschland und umfassen die Subspezies *ater*, *rufipectus* und *insularis*. Dieser und der Cytochrom-b-Ast aus Mittel- und S-Europa sind durch einen Distanzwert von 3,4 % deutlich getrennt. Für diese Populationen wird der Name *abietum* C.L. BREHM, 1831, revalidiert. Innerhalb *P. ater* ist der am stärksten differenzierte Ast die N-afrikanische ssp. *atlas*. Der östliche Ast von *P. rubidiventris*, ssp. *beavani*, ist nach Cytochrom

b und Körpergröße zweigegliedert, in einen O-himalayanischen und einen chinesischen Ast. Für den chinesischen Ast wird der Name *whistleri* STRESEMANN, 1931, revalidiert. Innerhalb von *P. rubidiventris* gehören die rotbäuchige ssp. *rubidiventris* (W-Nepal) und die graubäuchige ssp. *beavani* (O-Himalaya) zum selben Cytochrom-b-Ast. *P. rufonuchalis* ist nach Cytochrom b nicht intern gegliedert. Die komplizierte Differenzierungsgeschichte von *P. ater* und *P. rubidiventris* wird überwiegend auf Separationsereignisse im frühen Pleistozän zurückgeführt. Wahrscheinlich hat *P. ater* in drei zeitlich gestaffelten Invasionswellen die W-Paläarktis erreicht.

Key words. *Parus (Periparus)*, cytochrome b, phylogeny, phylogeography, taxonomy, new subspecies, *Parus ater eckodedicatus* n. ssp.

Introduction

Within palearctic and Indomalayan *Parus* tits, the subgenus *Periparus* comprises only a few species, but the subgenus' delimitation is under dispute. Traditionally, only the palearctic species *P. ater* LINNÉ, 1758, *P. melanolophus* VIGORS, 1831, *P. rubidiventris* BLYTH, 1847, and *P. rufonuchalis* BLYTH, 1849 are placed under *Periparus* (HELLMAYR 1903, HARRAP & QUINN 1996). Recently, SLIKAS *et al.* (1996) added the SE-Asian species *P. venustus* SWINHOE, 1870 (China), *P. elegans* LESSON, 1831, and *P. amabilis* SHARPE, 1877 (both Philippines) to *Periparus* and, consequently, abandoned the subgenus name *Pardaliparus*. Even the number of taxa that qualify as species is controversial. *Periparus* in its enlarged composition is twofold. The palearctic species set covers a huge area in the taiga forests of northern Eurasia as well as a number of disjunct areas in East Asia, Europe and North Africa. The three Indomalayan species inhabit mainland China (with palearctic offshoots) and the Philippines, and all are allopatric. Members of *Periparus* in the palearctic are small to medium-sized tits with a large black bib, a whitish nuchal spot, greyish upper-side, grey-reddish to beige belly, and a marked crest in all Sino-Himalayan populations. Locally, like the coal tit in Europe, these are common birds, and the group is important with respect to Asian and European bird communities. The Indomalayan species are likewise small with *P. venustus* being most similar to *P. ater*. Of the Philippine species, *P. amabilis* differs most in that its head is entirely black in adults.

There are many highly diverse local representatives, especially in the Himalayas, China, and the Philippines. Their delimitation as to biological species has long been under discussion and tends to be even more controversial as additional genetic markers are brought forward. Rank of a species in its own right for *P. rufonuchalis* has been considered reasonable for several decades (MARTENS 1971), but the affiliation of *melanolophus* as a subspecies of *P. ater* (MARTENS & ECK 1995) is not generally accepted (DICKINSON 2003). The entire set of Himalayan forms is now not easy to survey, and their taxonomic history is presented here in some detail. This finally will facilitate a better understanding of the molecular-genetic results.

The taxonomic situation of the coal tit assemblage of the Himalayas is still under debate (MARTENS & ECK 1995, HARRAP & QUINN 1996, DICKINSON 2003). The present results are apt to favour *one* opinion in the ongoing discussions. Marked colour and pattern differences between western and eastern Himalayan coal tit populations (and coal tits in general) lead to the conclusion, with which nearly all present scholars agree, that two small *Periparus* species inhabit the Himalayas: *P. melanolophus* (western) and *P. ater* (ssp. *aemodius*; eastern, extending to West China). In the southwestern Dhaulagiri area of western Nepal "cinnamon-bellied hybrids" have been discovered (DIESELHORST & MARTENS 1972). These are striking by their colour pattern, which differs from *melanolophus* in the dark chestnut-red centre of the belly and strongly differ from Himalayan coal tits as well (DIESELHORST & MARTENS 1972, MARTENS 1993; MARTENS & ECK 1995: 330–332). Such birds live in low density within *melanolophus*-coloured birds in a single high-altitude valley, the Dhorpatan valley at the southwestern corner of the Dhaulagiri massif (MARTENS 1975). Alternatively, these birds have been regarded as a local colour morph, not hybrids (DIESELHORST & MARTENS 1972, MARTENS & ECK 1995). Nevertheless, a continuous distribution of small-sized *Periparus* along the Himalayan chain

was ascertained and *P. melanolophus* was degraded to “semispecies” rank (MARTENS 1975). Later, in the upper course of the Myagdi valley in the southeastern Dhaulagiri massif, some 50 km apart from Dhorpatan, a highly variable-coloured population of the coal tit complex was located, and these birds were regarded as hybrids between *aemodius* and *melanolophus* (MARTENS & ECK 1995: 337). About 30 km further northeast of the upper Myagdi Valley, along the upper course of the Kali Gandaki river, which cuts deeply through the Dhaulagiri and Annapurna massifs, another quite distinct and highly restricted coal tit population exists, which, with respect to coloration, is close to the eastern Himalayan ssp. *aemodius*, not to *melanolophus* (colour plates in MARTENS 1993, MARTENS & ECK 1995). It was described as *P. ater martensi* by ECK (1998). From the neighbouring Marsyandi valley eastward the Himalayan chain is inhabited by *P. ater aemodius*, and it extends to the mountains of western China. A detailed map indicating the distribution of the subspecies of *P. ater* in Nepal was presented by ECK (1998). This Himalayan arrangement of “forms” makes the coal tit one of the most variable passerine species of the eastern palearctic.

In this paper, we present a molecular phylogeny of *Parus (Periparus)* in order to approach the following questions:

Can the cytochrome-b gene be used to elucidate the phylogeography of *Periparus* species with large palearctic areas and obviously distinct subspeciation (*P. ater*, *P. rubidiventris*)?

Is the cytochrome-b gene apt to support decisions on disputed species limits, especially in the controversial case of *P. ater* and *P. melanolophus*?

Materials and methods

Definitions

Hybrid/Hybridisation: Both terms play a role in the analysis of population relations between *Parus ater* and *P. melanolophus* in western Nepal. We demonstrate hybridisation between these taxa by two observations:

(i) In a limited area in western Nepal there is a variably coloured population, displaying parts of the distinct colour characters of both *P. ater martensi* and *P. (a.) melanolophus* (MARTENS & ECK 1995).

(ii) In this population individuals exist which carry a cytochrome-b haplotype of *P. ater martensi* (incl. *aemodius*) or a cytochrome-b haplotype of *P. (a.) melanolophus* (see below).

Cytochrome-b haplotype: A cytochrome-b differentiation of an individual bird within a given population.

Cytochrome-b haplotype cluster: Several cytochrome-b haplotypes which form a monophyletic group. A single haplotype cluster may embrace a single traditionally defined subspecies (mostly by morphology) or may comprise several of them.

Subspecies: Traditionally, they are characterised by external morphological characters. Subspecies of a given species are allopatric (geographic representative principle). Here we admit the possibility that within biospecies (according to E. MAYR) populations representing allopatric haplotype clusters may serve to characterise subspecies. Empirical studies have shown that cytochrome-b cluster-distance differences of up to 3 % (sometimes beyond) are sufficient to define subspecies within biospecies. A proof of hybridisation or even introgression in critical cases is needed.

Genetic samples

We analysed parts of the cytochrome-b gene using 58 blood and tissue samples from the seven current *Parus (Periparus)* species (SLIKAS *et al.* 1996, DICKINSON 2003, GILL *et al.* 2005) and included eight ingroup and three outgroup sequences from GenBank (Appendix 2). European Nuthatch (*Sitta europaea*), Chiffchaff (*Phylloscopus collybita*), and Willow Warbler (*P. trochilus*) were used for hierarchical outgroup rooting.

DNA extraction, PCR, and sequencing

DNA was extracted using the “High Pure PCR Template Preparation Kit” (Roche Diagnostics). The following oligonucleotide primers were used for PCR and sequencing: L14841-Cyt b (5'-AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA-3' (KOCHER *et al.* 1989) and H15547-Cyt b (5'-AAT AGG AAG TAT CAT TCG GGT TTG ATG-3'; EDWARDS *et al.* 1991) were applied. A 706-bp fragment was obtained with these primer combinations, respectively. For PCR we used 0.2 ml “PureTaq Ready-To-Go PCR Beads” (Pharmacia Biotech), adding 4 μ l DNA sample, 1 μ l of each primer (20 pmol/ml), and 19 μ l distilled water. PCR products were purified with the “High Pure PCR Product Purification Kit” (Roche Diagnostics). A total of 633 bp was consistently sequenced for all samples using “Big-Dye Ready-Reaction Kit” (Perkin Elmer). The corresponding L primer was used to obtain the sequence. The sequences were analysed on an ABI Prism 3730 (Applied Biosystems) and aligned with MEGA version 3.1 (KUMAR *et al.* 2004).

Sequence analysis

An adequate substitution model was estimated via hierarchical Likelihood Ratio Tests (Modeltest 3.7; POSADA & CRANDALL 1998). Only the *Parus (Periparus)* sequences were included in the input data set. The selected model according to the Akaike Information Criterion was TrN+I+G with the following parameters: $\pi_A = 27.57\%$, $\pi_C = 36.11\%$, $\pi_G = 14.10\%$, $\pi_T = 22.22\%$; rate matrix = (1, 17.5296, 1, 1, 12.2294, 1); proportion of invariable sites = 0.4791; gamma distribution shape parameter $\square = 0.5502$.

Phylogenetic trees were constructed according to three approaches: Neighbor Joining (SAITOU & NEI 1987, MEGA 3.1 of KUMAR *et al.* 2004), Maximum Likelihood (Tree Puzzle 5.2 of SCHMIDT *et al.* 2002), applying the above model, and Maximum Parsimony (PAUP 4.0b10 of SWOFFORD 2003). Robustness of clades was estimated by 2000/1000 bootstrap replicates (FELSENSTEIN 1985) for Neighbor Joining/Maximum Parsimony and via quartet puzzling in Maximum Likelihood (10000 puzzling steps, STRIMMER & VON HAESLER 1996). Group-wise uncorrected p-distances were calculated by MEGA.

Measurements

All measurements were taken by SIEGFRIED ECK except for three specimens of *Parus ater* from China (J.M.). Wing length: maximum-chord method. Tail length: from the point of emergence of the central tail feather pair to the tail tip in the normally formed tail.

Results

Phylogenetic trees and relationships

633 bp of the cytochrome-b fragment could be consistently analysed for all haplotypes. There were 187 variable sites, 126 of which were parsimony informative. We found 39 different *Periparus* haplotypes (out of 66 samples), which are listed in Appendix 2 and which are incorporated into all phylogenies (Fig. 1).

Periparus proved to be monophyletic with good support. All species presently united under *Periparus* are represented as well-supported haplotype clusters, but there is one exception in the Indomalayan species set (see below). *Periparus* consists of three main clades with unresolved relationships: the *Parus ater* complex (including *P. melanolophus*), the tropical/subtropical species set which comprises *P. venustus*, *P. amabilis*, and *P. elegans*, and a monophyletic group of the species *P. rufonuchalis* and *P. rubidiventris* which are sisters to each other.

Within each species we found different numbers of haplotypes, but in species with small distribution ranges, *P. rufonuchalis* and *P. venustus*, the investigated individuals share the same or very similar haplotypes. In others, more often single haplotypes are shared by individuals of the same geographic origin. As an exception, within the northern Eurasian

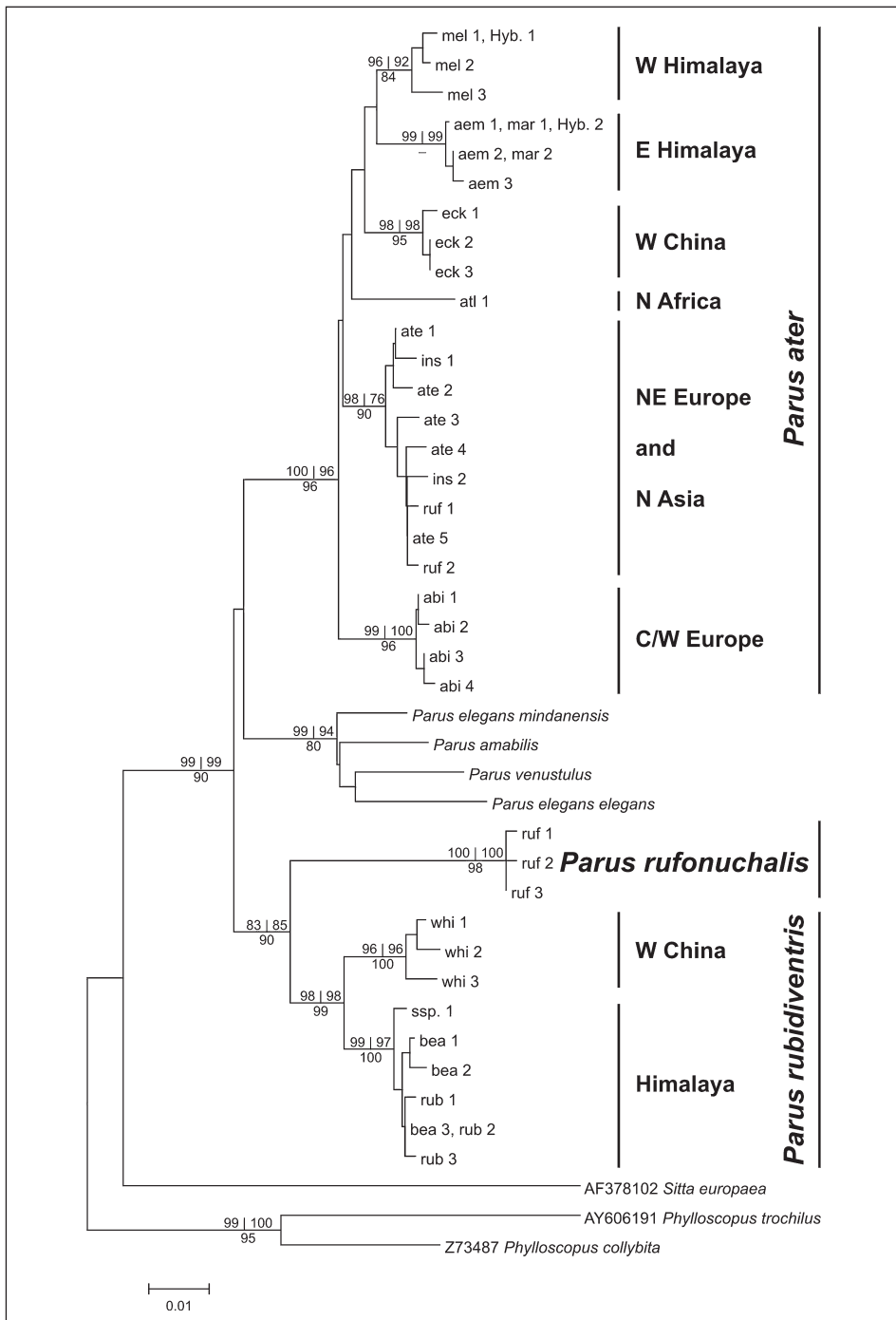


Fig. 1. Neighbor-joining tree based on 633 bp of the mitochondrial cytochrome-b gene. Values indicated at nodes: bootstrap from neighbor joining (2000 bootstrap replicates) and maximum parsimony (1000 bootstrap replicates) above, maximum likelihood (10000 puzzling steps) below branch.

Table 1. Between-group distances (in %) from uncorrected pairwise distances of *Parus (Periparus)* species (in lower left) with their standard errors estimated by bootstrapping (1000 replications). In the diagonal within-group distances are given – estimated in the same way.

	<i>ater</i>	<i>rufonuchalis</i>	<i>rubidiventris</i>	<i>amabilis</i>	<i>elegans</i>	<i>venustus</i>
<i>ater</i>	2.4±0.3					
<i>rufonuchalis</i>	7.9±1.0	0.2±0.2				
<i>rubidiventris</i>	6.2±0.8	5.8±0.9	1.6±0.3			
<i>amabilis</i>	6.1±0.9	7.2±1.1	6.4±0.9	./.		
<i>elegans</i>	6.4±0.9	7.7±1.1	7.0±0.9	3.3±0.6	3.4±0.7	
<i>venustus</i>	6.7±1.0	7.8±1.1	7.6±1.1	3.4±0.8	3.8±0.7	./.

Table 2. Between-group distances (in %) from uncorrected pairwise distances of *Parus ater* haplotype lineages (in lower left) with their standard errors estimated by bootstrapping (1000 replications). In the diagonal within-group distances are given – estimated in the same way.

	N Africa	C/S Europe	NE Europe/N Asia	W China	E Himalaya	W Himalaya
N Africa	./.					
C/S Europe	3.4±0.7	0.3±0.1				
NE Europe/N Asia	3.0±0.7	2.6±0.5	0.7±0.2			
W China	3.3±0.7	3.0±0.6	2.6±0.6	0.3±0.2		
E Himalaya	3.1±0.7	2.9±0.7	3.2±0.7	2.5±0.6	0.2±0.2	
W Himalaya	3.2±0.7	2.8±0.6	2.6±0.5	2.3±0.6	2.3±0.6	0.7±0.3

populations of *P. ater*, the same haplotype exists in the Russian Far East (island of Sakhalin) and in East Germany (Appendix 2).

Almost all of the group-wise uncorrected p-distances between the recognised species fall into the range from 3.3% to 7.9%. Among these, the distances between the Indomalayan species *P. amabilis* and *P. elegans* are lowest (3.3%), and the distance between *P. venustus* and these two is only slightly higher (3.4–3.8%) (Table 1).

The palearctic species set *Parus ater*, *P. rubridiventris*, and *P. rufonuchalis*

Parus ater

Six highly distinct lineages can be identified within *P. ater* (Fig. 2): a North African lineage (i), two North Eurasian clusters (ii, iii), three Sino-Himalayan clusters (iv–vi), namely a West Himalayan cluster (iv), an East Himalayan cluster (v), and a West Chinese cluster (vi). The relations of all lineages within *P. ater* remain uncertain due to low bootstrap support. The between-lineage mean distances range between 2.3% and 3.4% (Table 2).

(i) The North African cluster. *P. a. atlas* from Morocco presents the highest cytochrome-b distance found within *P. ater*: 3.0–3.4% to neighbouring European and all Asian populations. The other subspecies from North Africa, *P. a. ledouci*, was not available for this study. – 1 sample analysed.

(ii) The Central/South European cluster: It is represented by populations from southern and northern Germany (federal states Baden-Württemberg and Niedersachsen), from southern

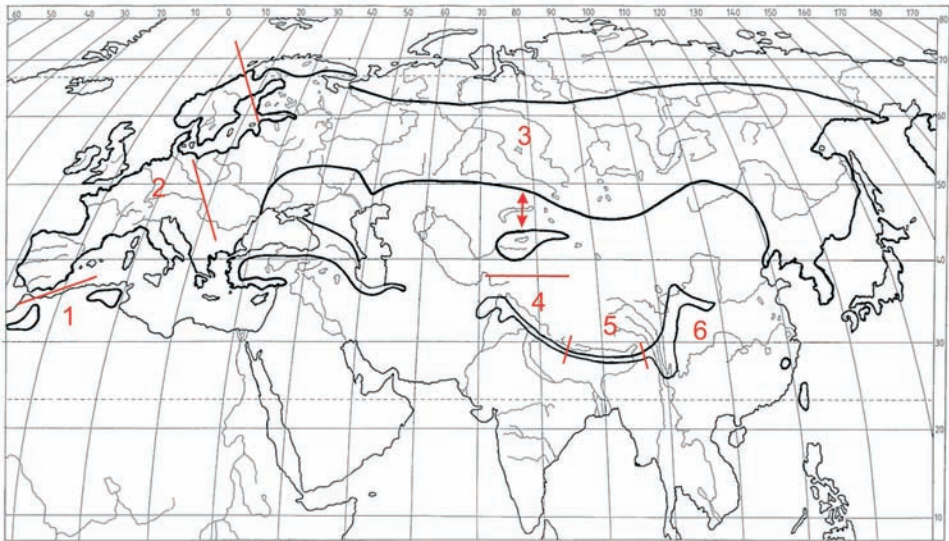


Fig. 2. Distributional map of *Parus ater*. Numbers indicate the cytochrome-b lineages and the bars signify the approximate distribution limits between them. Map drawn from various sources. – 1: North African lineage (ssp. *atlas* [western] and ssp. *ledouci* [eastern]); – 2: Central/South European cluster (ssp. *abietum*; only mainland); – 3: Siberian cluster (nominate *ater* [taiga zone], ssp. *insularis* [Japan], and ssp. *rufipectus* [disjunct, central Asia]); – 4: West Himalayan cluster (ssp. *melanolophus*); – 5: East Himalayan cluster (ssp. *aemodius*); – 6: Chinese cluster (ssp. *eckodedicatus*).

France (Dép. Pyrénées-Orientales), and Greece. The area covered by these samples normally falls under nominate *ater*; see below. – 8 samples analysed, incl. 1 from GenBank.

(iii) The North Eurasian cluster: It comprises coal tit populations from the entire North Eurasian coniferous forest belt; our samples cover Japan, the Russian Far East, and central Asia and extend to northern (Finland) and central Europe (East Germany). The samples represent the current subspecies *insularis* (Japan), *rufipectus* (central Asia), and nominate *ater* (taiga zone). – 14 samples analysed.

(iv) The West Himalayan cluster: It mainly includes the former *P. melanolophus* and embraces one specimen with external hybrid characters between ssp. *martensi* and ssp. *melanolophus*. This cluster covers the western Himalayas to mid/western Nepal. – 4 samples analysed, including 1 from GenBank.

(v) The East Himalayan cluster: It is represented by individuals from west/central Nepal (southern flanks of eastern Dhaulagiri massif) to eastern Nepal (Bhojpur Distr.). This cluster comprises individuals of ssp. *martensi* and, to the east, ssp. *aemodius*, and, in addition, represents three individuals which appear intermediate in coloration between ssp. *martensi* (E Dhaulagiri/W Annapurna area) and ssp. *melanolophus* (W Dhaulagiri). The latter birds are regarded as hybrids between the clusters (iv) and (v). One additional hybrid-coloured bird from the same locality carried a haplotype that normally occurs in the West Himalayan cluster. The area covered by this cluster extends from mid/western Nepal to the eastern Himalayas with unknown eastern limitation. – 9 samples analysed.

(vi) The West Chinese cluster: It comprises coal tits from the Chinese provinces of Gansu, Sichuan, and Yunnan, and belongs to *P. ater* “*aemodius*”. But this cluster strongly differs from the East Himalayan *aemodius* cluster, by 2.5%. – 6 samples analysed incl. 1 from GenBank.

Parus rubidiventris

The rufous-vented tit is a well supported monophyletic group and falls into two significant cytochrome-b clusters. The between-cluster distance values are about 2.5%.

(i) The Himalayan cluster: Representatives comprise the quite differently coloured *P. rubidiventris beavani* (grey-bellied) and *P. r. rubidiventris* (cinnamon-bellied). Our samples originate from far western to central Nepal (ssp. *rubidiventris*) and from eastern Nepal (Sindhu Palchok Distr.; ssp. *beavani*). Five out of ten sequences of these morphologically conspicuously distinct geographical representatives are even shared by both subspecies. – 10 samples analysed: 5 nominate *rubidiventris*, 5 ssp. *beavani* s. str.

(ii) The West Chinese cluster: It harbours the grey-bellied ssp. “*beavani*” from western China and covers the area at least of all Chinese populations of *P. rubidiventris*; it may extend to the easternmost Himalayas. Samples from Shaanxi und Gansu were available. – 4 samples analysed incl. 1 from GenBank.

Parus rufonuchalis

Specimens from Kyrgyzstan, the western Himalayas, and from one unknown Asian locality carry only slightly different haplotypes.

The Indomalayan species set *Parus venustus*, *P. amabilis*, and *P. elegans*

These three species make up a monophyletic group with high bootstrap support for the entire group. The relationships between the species remain unresolved, and two *elegans* samples from different islands do not appear as sisters. Distance values are quite low and range between 3.3 % (*amabilis* vs. *elegans*) and 3.4–3.8 % (*venustus* vs. *amabilis/elegans*).

Within-group distances

Within species

Amounting to 3.4%, the intraspecific differentiation is largest in *P. elegans*. In *P. ater* the within-group mean distance is 2.4% and is reduced to 1.6% in *P. rubidiventris*. The lowest intraspecific differentiation is found in *P. rufonuchalis*, 0.2%. In *P. venustus* we could only find a single haplotype (Appendix 2).

Within subspecies

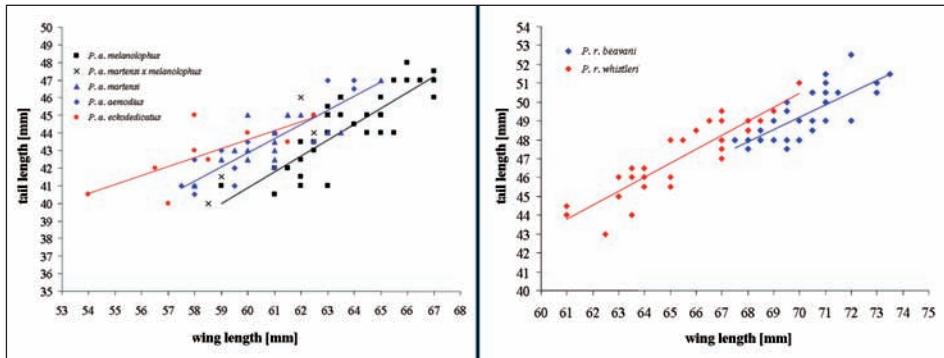
The traditional subspecies only partly coincide with the haplotype lineages, and up to three may belong to the same lineage in *P. ater*. Within the regional clusters (Fig. 1, Table 2), the within-group variation is again low and ranges from 0.2% to 0.7%. The highest value stems from the nearly trans-continentially distributed Eurasian cluster. Distance values between the cytochrome-b clusters are quite high, and range from 2.3% to 3.4%.

In *P. rubidiventris* the two cytochrome-b clusters likewise differ markedly, by 2.5%. The Himalayan cluster includes the ssp. *rubidiventris* and ssp. *beavani*, which are distinguished by vent coloration.

A morphological addition: wing-tail proportions

In both *P. ater* and *P. rubidiventris*, a single subspecies is accepted for each of the regions eastern Himalayas and western China. These geographic representatives differ in contour-feather measurements.

In *P. ater*, there is an obvious tendency for wing and tail lengths to become reduced from west to east (from ssp. *melanophus* via *martensi* to Nepalese *aemodius*) which extends even into



Figs. 3–4. 3. Scatter plot of wing and tail lengths from Sino-Himalayan *Parus ater* subspecies. Note: *P. a. eckodedicatus* was previously included in *P. a. aemodius*, which we now restrict to the eastern Himalayas. 4. Scatter plot of wing and tail lengths from the two eastern *Parus rubidiventris* subspecies. Note: *P. r. whistleri* was previously included in *P. r. beavani*, which we now restrict to the eastern Himalayas.

western China (Chinese *aemodius*, named “*eckodedicatus*” in Fig. 3; see below). Additionally, in western Chinese *aemodius* the wing-tail ratio (73.3%) is larger than in *melanolophus* (69.5%) and Himalayan *martensi* and *aemodius* (71.5%).

In *P. rubidiventris*, the same phenomena appear, but are even more conspicuous: there is almost no overlap in the scatters of ssp. *beavani* from Nepal and China (the latter named “*whistleri*” in Fig. 4). Tail-wing index differs similarly between Nepal (70.3%) and Chinese *beavani* (71.9%).

Discussion

Taxonomy and biogeography

Our phylogenetic reconstructions reflect the current taxonomy of the *Periparus* group quite well, but with a few restrictions. The traditional *P. melanolophus* falls within a set of six *P. ater* cytochrome-b lineages and is not, as one would expect, a sister to the remainder of the coal tit assemblage. The tropical species *P. venustus*, *P. amabilis*, and *P. elegans* do not turn up as clearly and deeply separated lineages, but represent a yet unresolved assemblage of unclear species delimitation (cf. GILL *et al.* 2005). Their study placed the two species sets, palearctic and tropical ones, as sister groups; our data neither support nor reject their result. Their sample set was smaller than ours, but they analysed a longer gene fragment. We were unable to further clarify the within-subgenus relationships with all analyses applied. The tree presented here agrees with GILL *et al.* (2005) insofar as *P. rubidiventris* and *P. rufonuchalis* are sister taxa.

The highest species number of the northern *Periparus* taxa exists in the Himalayas. Two of them, *P. ater* and *P. rubidiventris*, are highly differentiated into colour- and size-defined subspecies. The genetically defined clusters may have undergone similar evolutionary histories. Coloration differences are not always as old as the cytochrome-b clusters, and consequently, population-bound colour patterns and cytochrome-b haplotype clusters do not necessarily coincide. One cytochrome-b cluster may comprise several subspecies, as in *P. ater* and *P. rubidiventris* (Fig. 1). In *P. ater*, this holds true also for the two northern clusters.

Divergence distance values within the clusters of *P. ater* and *P. rubidiventris* range between 2.3% and 3.4%. These are distinct differences and they suggest separate, but quite recent evolutionary histories of these clusters (see below). In terms of species limits, all these values

indicate within-species limits to the extent that the MAYRIAN biospecies concept is applied (HELBIG *et al.* 1996, DIETZEN *et al.* 2003).

The differentiation processes fall into the Pleistocene period and are not older than about 2.1 million years according to a calculation of FLEISCHER *et al.* (1997). Accordingly, within *P. ater* we have to consider disjunct Pleistocene refuge and evolutionary areas for *melanolophus*, one each for the western *aemodius* (in the eastern Himalayas), and the northeastern “*aemodius*” (in China). Most important is the position of the four highly variable birds from the upper Myagdi valley, out of the morphologically defined “hybrid population” (MARTENS & ECK 1995: 331 f.): One bird carries a *melanolophus* haplotype, identical to one of the *melanolophus* specimens from far western Nepal, some 250 km away. Three other specimens from the same forest patch fall into the East Himalayan cluster, which comprises ssp. *martensi* and ssp. *aemodius*. Because ssp. *martensi* and neighbouring ssp. *aemodius* on the one hand and ssp. *melanolophus* on the other hand are highly different in terms of coloration, the hybrid population is easy to recognise. Only this affiliation of haplotypes of the different clusters to these hybrid specimens enables us also to use a mitochondrial marker to recognise and to further prove this hybridisation event.

For *P. rubidiventris* the situation is similar (Fig. 5): We have to postulate a refuge area for nominate *rubidiventris* (western Himalayas) and one each for *beavani* (eastern Himalayas and western China, respectively). Though coloration differs most in ssp. *rubidiventris* and ssp. *beavani* from Nepal, their separation time must have been even shorter, at least in terms of cytochrome-b differentiation. Their haplotypes form one narrow cluster with little sequence variation. In post-Pleistocene times, formerly isolated refuge areas fused secondarily and *P. rubidiventris* nowadays forms a continuous area band in coniferous forests at high altitude – as *P. ater* does.

In *P. ater* the situation is even more complicated and characterised by large-range area rearrangements. Postulating an eastern palearctic origin of what is now *P. ater* (GILL *et al.* 2005), three settlement waves must have reached the western palearctic: The North African populations (ssp. *atlas*, probably also ssp. *ledouci*) represent the oldest layer, with no other population traces left. The second wave is represented by the central to southern European ssp. *abietum*, which probably spent the Pleistocene “winter” on the Balkan Peninsula (see below, Taxonomy). The last post-Pleistocene immigrant from the east is the eastern, central and northern European ssp. *ater*, which probably reached Europe from a Siberian refuge area after the last glaciation.

Taxonomic recommendations

Parus ater

Though quite different in coloration, the western (*melanolophus*) and eastern representatives (*martensi*, *aemodius*) of the Himalayan coal tit complex are most closely related, their areas are in contact (Fig. 2) and in the contact zone they apparently hybridise freely. The hybrid belt is only small, but this may be due to the rugged mountainous habitat and the highly sedentary behaviour of these tits. LÖHRL (1994) successfully crossbred German ssp. *abietum* with Afghan ssp. *melanolophus* in captivity and reared variably coloured offspring, similar to the Nepal hybrid population.

Parus ater aemodius is a composite and paraphyletic taxon embracing two haplotype clusters (Himalayas and West China) with ssp. *melanolophus* as a close relative. The name *aemodius* BLYTH, 1844, applies to the Himalayan population (type locality “Nepal”, restricted by ECK [1998] to “East Nepal”). The Chinese “*aemodius*” population requires a new name (see Appendix 1). Contact zone with Himalayan *P. ater aemodius* is not yet known, but is to be expected in the easternmost Himalayas or Yunnan.

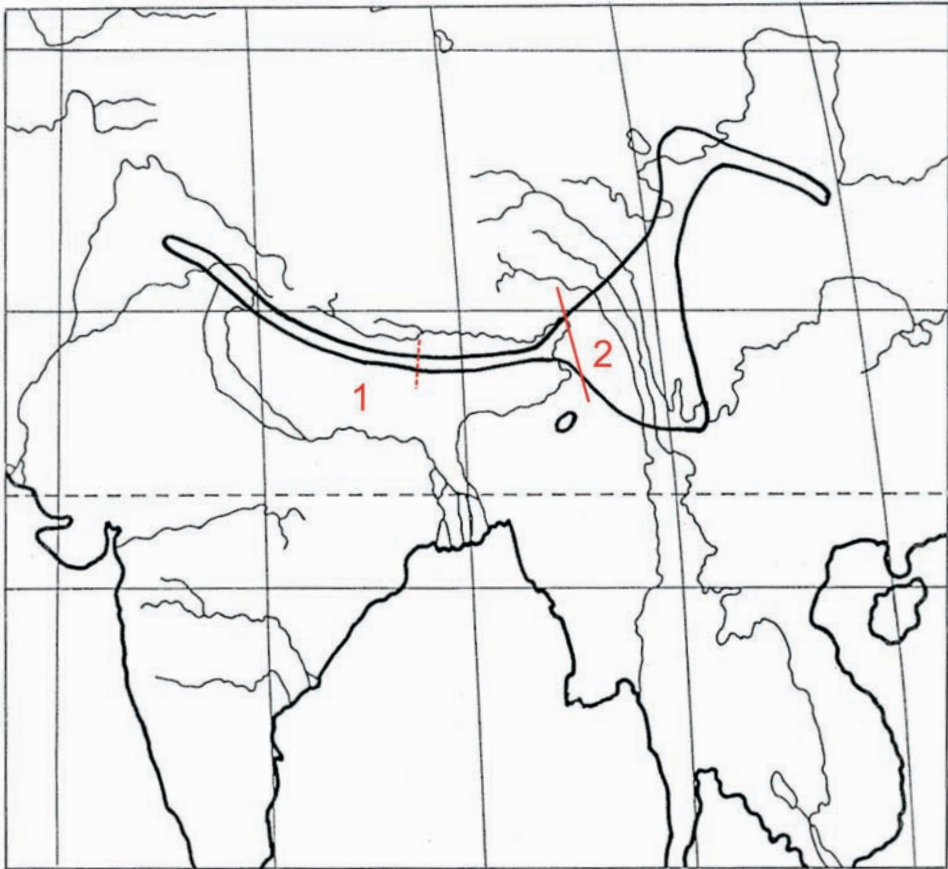


Fig. 5. Distributional map of *Parus rubidiventris*. Numbers indicate the cytochrome-b clusters. The solid bar signifies the approximate distribution limit of cytochrome-b clusters. Map drawn from various sources. – 1: Himalayan cluster (nominate *rubidiventris* and ssp. *beavani*; range limits indicated by broken bar); – 2: Chinese cluster (ssp. *whistleri*).

The taxonomic situation of European coal tits is complicated, too, and a couple of subspecies are generally accepted: ssp. *vieirae* in the Iberian Peninsula, ssp. *sardus* in Corsica and Sardinia, and nominate *ater* in all other parts of Europe as a westward extension of the northern Asian area. We could not include peripheral populations in our study, but we recommend that the central and southern European mainland population be treated, on the basis of morphology (for details see ECK 1984: 84) and molecular genetics, as a separate taxon, *Parus ater abietum* C.L. BREHM, 1831 (type locality: Schwarzwald [Black Forest], Germany).

Parus rubidiventris

Concerning cytochrome-b sequences and size, the grey-bellied population (“*beavani*”) falls into two groups: the larger birds originate from the eastern Himalayas (Nepal, Sikkim) and the smaller birds from western and southwestern China. In addition, the proportions of contour feathers differ. Subspecies “*beavani*” s. str. from the Himalayas (Loc. typ. Mt. Tongloo, Sikkim) is the largest form, with wing lengths up to 74 mm (tail/wing ratio: 70.3 ± 1.25 , $n = 31$; MARTENS & ECK 1995: 329). From China two further grey-bellied subspecies have been

described: *P. r. szetschwanensis* MEISE, 1937 (Loc. typ. Waschangipfel [summit of Wa Shan, Sichuan]) and *P. r. whistleri* STRESEMANN, 1931 (Loc. typ. S. Tetung-Geb. [southern Tetung mountains, Gansu]). The former is coloured like *beavani* from Nepal/Sikkim, but is smaller, although as large as the slightly greyer *whistleri* (wing length up to 70 mm, tail/wing ratio of *whistleri* and *szetschwanensis* combined: $71.9 \pm 1.30\%$, $n = 31$; S. ECK, pers. comm.). Thus, the more short-winged populations tend to be relatively long-tailed.

VAURIE (1959) lumped *whistleri* and *szetschwanensis* with *beavani*, but as concerns size and cytochrome-b genetics this does not seem to be appropriate. Here we revalidate the older name *whistleri* and treat *szetschwanensis* as a junior synonym. We refer this name to the short-winged and relatively long-tailed populations of western China (Yunnan to Gansu and Shaanxi). The contact zone between nominate *beavani* and ssp. *whistleri* is not yet known, but may be situated in the easternmost Himalayas or in southwestern Yunnan (Fig. 5).

Subspecies *rubidiventris* and *beavani* (western and eastern Himalayas, respectively), which form a common cytochrome-b cluster, possess the same contour feather proportions, but the bill/wing ratio is higher in nominate *rubidiventris* than in *beavani* (MARTENS & ECK 1995: 327). Being based on pronounced colour differences, both subspecies are retained here.

Taxonomic changes

According to present cytochrome-b findings, we recommend the following taxonomic changes:

Parus ater melanolphus VIGORS, 1831 (downgrading to subspecies level as already proposed by MARTENS & ECK 1995). – Type locality: Simla-Almora distr., India. – Distribution: from the western Himalayas (southwestern Dhaulagiri area) to eastern Afghanistan.

Parus ater abietum BREHM, 1831 (revalidation) – Type locality: Schwarzwald, Germany. – Distribution: probably all western to central and southern Europe except the insular-based subspecies (British and Mediterranean island populations not analysed). The relevant cytochrome-b cluster is known from northwestern and southern Germany (in East Germany the nominate *ater* haplotype was found), southern France (eastern Pyrenees), and Greece (locality unknown; fide GILL *et al.* 2005). Morphological differentiation as stated by ECK (1984).

Parus ater eckodedicatus n. ssp. (new taxon comprising the Chinese “*aemodius*” populations, based on size, coloration, and marked differences in cytochrome-b arrangement; see Appendix 1) – Type locality: China, Sichuan, Wawu Shan. – Distribution: Proven occurrences originate from Yunnan, Sichuan, and Gansu. Morphological differentiation: slightly smaller in wing and tail measurements (but larger tail-wing index) than Himalayan ssp. *aemodius*; vent coloration brighter than in the latter.

Parus rubidiventris whistleri STRESEMANN, 1931 (revalidation) – Type locality: China, Sichuan, Wa Shan. – Distribution: Proven occurrences (partly by morphology, partly by cytochrome-b sequence) originate from Yunnan, Sichuan, Qinghai, Gansu, and Shaanxi. Morphological differentiation: smaller and greyer than ssp. *beavani* from the eastern Himalayas.

Acknowledgements

This paper results from a multitude of expeditions to Nepal, China, and the former Soviet Union within the last 37 years (1969–2005), on which J.M. collected blood/tissue samples and voucher specimens of tits. Additional tissue samples were provided by M. FISCHER, M. GRIMM, L. KVIST, T. LUBJUH, A.A. NAZARENKO, ISAO NISHIUMI, A. OSTASTSHENKO, and O. P. VALCHUK. D. PLATH accompanied J.M. to Nepal in 1973, A. AUSOBSKY and B. FRÜHBEIS in 1980, W. SCHAWALLER in 1988 and 1995, G. GEDULDIG in 1988, P. KESSLER in 2001, C. and F. MARTENS in 2004, A. GEBAUER and M. KAISER to China in 1996 and 1998, C. FISCHER, P. JÄGER and J.M.’s wife Beate to China in 1997, Y.-H. S. and Y. FANG in China in 1999, 2000, and 2002, D.T.T. and partly Z. BI in 2002, and Y.-H. S. and J. LI in 2005. K. MALLY accompanied D.T.T. to Morocco in 2004. An early state of this paper including only the coal tit phylogeny was part of S. CORBET’S diploma thesis from 2004. – Deutscher Akademischer Austauschdienst, Deutsche Forschungsgemeinschaft, Feldbausch-

Stiftung und Wagner-Stiftung, both at Fachbereich Biologie of Mainz University, Vereinigung "Freunde der Universität Mainz", Deutsche Ornithologen-Gesellschaft (East Asia grants to J.M., A. GEBAUER, and M. KAISER), and Gesellschaft für Tropenornithologie provided travel funds. Authorities of the Chinese Academy of Sciences helped to organise the travels within China. L. KVIST and M. PÄCKERT commented on an earlier draft of the manuscript. Many cordial thanks are due to all friends, colleagues, and organisations mentioned.

References

- CHENG, T.-H. (1987): A synopsis of the avifauna of China. – Beijing, Hamburg: Parey.
- DICKINSON, E. (ed.) (2003): The Howard & Moore Complete Checklist of the Birds of the World. – 3rd edn. London: Christopher Helm.
- DIESSELHORST, G. & J. MARTENS (1972): Hybriden von *Parus melanolophus* und *P. ater* im Nepal-Himalaya. – J. Ornithol. **113**: 374–390.
- DIETZEN, C., H.-H. WITT & M. WINK (2003): The phylogeographic differentiation of the European robin *Erithacus rubecula* on the Canary Islands revealed by mitochondrial DNA sequence data and morphometrics: evidence for a new robin taxon on Gran Canaria? – Avian Science **3**: 115–131.
- ECK, S. (1984): Katalog der ornithologischen Sammlung Dr. U. Bährmanns (3. Fortsetzung). – Zool. Abh. (Dresden) **39**: 72–98 (for 1983).
- ECK, S. (1998): *Parus ater martensi* subsp. nov., die Tannenmeise der Thakkhola, Nepal (Aves: Passeriformes: Paridae). – Zool. Abh. (Dresden) **50**: 129–132.
- EDWARDS S.V., P. ARCTANDER & A.C. WILSON (1991): Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. – Proc. R. Soc. Lond. B **243**: 99–107.
- FELSENSTEIN, J. (1985): Confidence limits on phylogenies: an approach using the bootstrap. – Evolution **39**: 783–791.
- FLEISCHER, R.C., C.E. MCINTOSH & C. TARR (1997): Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. – Molecular Ecology **7**: 533–545.
- GILL, F.B., B. SLIKAS & F.H. SHELDON (2005): Phylogeny of titmice (Paridae): II. Species relationships based on sequences of the mitochondrial cytochrome-b gene. – Auk **122**: 121–143.
- HARRAP, S. & QUINN, D. (1996): Tits, nuthatches & treecreepers. – London: A & C Black.
- HELBIG, A.J., J. MARTENS, I. SEIBOLD, F. HENNING, B. SCHÖTTLER & M. WINK (1996): Phylogeny and species limits in the palearctic chiffchaff *Phylloscopus collybita* complex: mitochondrial genetic differentiation and bioacoustic evidence. – Ibis **138**: 650–666.
- HELLMAYR, C.E. (1903): Paridae, in: SCHULZE, F.E. (ed.): Das Tierreich **18**. Berlin.
- KOCHER, T.D., W.K. THOMAS, A. MEYER, S.V. EDWARDS, S. PÄÄBO, F.X. VILLABLANCA & A.C. WILSON (1989): Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. – Proc. Natl. Acad. Sci. USA **86**: 6196–6200.
- KUMAR, S., K. TAMURA & M. NEI (2004): MEGA3: Integrated Software for Molecular Evolutionary Genetics Analysis and Sequence Alignment. – Brief. Bioinformatics **5**: 150–163.
- LÖHRL, H. (1994): Beitrag zum noch offenen Fragenkomplex der Hybridisation von Tannen- und Schopfmeise (*Parus ater*, *P. melanolophus*) (Aves: Passeriformes: Paridae). – Zool. Abh. (Dresden) **48**: 149–157.
- MARTENS, J. (1971): Artstatus von *Parus rufonuchalis* Blyth. – J. Ornith. **112**: 451–458.
- MARTENS, J. (1975): Akustische Differenzierung verwandtschaftlicher Beziehungen in der *Parus* (*Periparus*)-Gruppe nach Untersuchungen im Nepal-Himalaya. – J. Ornith. **116**: 369–433.
- MARTENS, J. (1993): Lautäußerungen von Singvögeln und die Entstehung neuer Arten. – Forschungsmagazin Johannes Gutenberg-Univ. Mainz **9**: 34–44.
- MARTENS, J., & S. ECK (1995): Towards an ornithology of the Himalayas: systematics, ecology and vocalizations of Nepal birds. – Bonn. Zool. Monogr. **38**: Zoologisches Forschungsinstitut und Museum Alexander Koenig.
- POSADO, D. & K.A. CRANDALL (1998): MODELTEST: testing the model of DNA substitution. – Bioinformatics **14**: 817–818.
- SAITOU, N. & M. NEI (1987): The neighbor-joining method: a new method for reconstructing phylogenetic trees. – Mol. Biol. Evol. **4**: 406–425.
- SCHMIDT, H.A., STRIMMER, K., VINGRON, M. & VON HAESLER, A. 2002. Tree-Puzzle: maximum likelihood phylogenetic analysis using quartets and parallel computing. – *Bioinformatics* **18**: 502–504.
- SLIKAS, B., F.H. SHELDON & F.B. GILL (1996): Phylogeny of titmice (Paridae): Estimate of relationships among subgenera based on DNA-DNA hybridization. – J. Avian Biol. **27**: 70–82.

- STRIMMER, K. & A. VON HAESELER, A. (1996): Quartet puzzling: a quartet maximum likelihood method for reconstructing tree topologies. – *Mol. Biol. Evol.* **13**: 964–969.
- SWOFFORD, D.L. (2003) *Phylogenetic Analysis Using Parsimony (and Other Methods)*, Version 4. Sunderland, MA: Sinauer, Associates.
- VAURIE, C. (1959): *The Birds of the Palearctic Fauna. A systematic reference. Order Passeriformes.* London.
- ZHENG, G. (ed.) (2005): *A checklist on the classification and distribution of the birds of China.* Beijing.

Received 24.10.2005, accepted 1.11.2005.

Appendix 1

Parus ater eckodedicatus n. ssp.

Holotype: ♂, China, Sichuan, Wawu Shan, 2650 m, J. Martens & D. T. Tietze *leg.* 13 May 2002; 29°38'N, 102°57'E (tissue sample MAR 3280; [MTD C 62481](#)).

Paratypes: ♂, China, Yunnan, Geza, 60 km N Zhongdian, 3300 m, J. Martens & D. T. Tietze *leg.* 2 May 2002; 28°12'N, 99°44'E (tissue sample MAR 3242; song specimen; tape China 2002 **6**: 2.5–5; [MTD C 62482](#)); – ?, China, Gansu, Lianhua Shan, 2900 m, J. Martens & Y. Fang *leg.* 15 April 1999; 34°55'N 103°43'E (tissue sample MAR 1876; [MTD C 59782](#)); – ?, China, Gansu, Lianhua Shan, 2900 m, J. Martens & Y. Fang *leg.* 15 April 1999; 34°55'N 103°43'E (tissue sample MAR 1880; [MTD C 59783](#)); – ♂, China, Shaanxi, Huayang, Changqing, 2400 m, Y.-H. Sun & J. Martens *leg.* 13 May 2005; 33°42'N, 107°36'E (tissue sample MAR 4934; song specimen; tape China 2005 **5 b**: 114–170; Zool. Inst. Beijing, IZAS; Fig. 6).

Of the following additional material, neither cytochrome-b haplotypes nor song recordings are available. Therefore, these specimens are not included into the type series.

♂, China, Sichuan, Kwanshien [presently: Dujiangyan, NW of Chengdu], H. Weigold *leg.* 1 December 1914 ([MTD C 23814](#)); – ?, China, Sichuan, Kwanshien, H. Weigold *leg.* 22 January 1915 ([MTD C 23815](#)); – ♂, China, Sichuan, Waschangipfel [summit of Wa Shan], H. Weigold *leg.* 14 April 1915 ([MTD C 23816](#)); – ♂, China, Sichuan, Kwanshien, Berge [mountains], H. Weigold *leg.* 5 December 1914 ([MTD C 23813](#)).

Diagnosis. A subspecies of the Sino-Himalayan subspecies complex of the coal tit (*Parus ater*), wing is 57.0–61.5 (58.8±1.6) mm, tail is 40.0–45.0 (43.0±1.7) mm in ♂ (n = 6). In recently collected specimens (from April, May) belly and vent more bright beige with a slight reddish touch in centre of belly and vent, tending to more grey laterally (compared to Himalayan *aemodius*). Back steel grey without any admixture of yellowish tinge. Compared to all other *Parus ater* populations, cytochrome-b cluster of the mitochondrial genome unique (see GenBank accession numbers in Appendix 2).

Comparison. *P. ater eckodedicatus* n. ssp. is smaller than *P. a. aemodius*, but otherwise similar to it. Belly and vent are less yellowish beige, more grey in *aemodius* in a series of 15 Ex. from the same season (March, April). Measurements of *P. a. aemodius* from Nepal: wing: 57.5–64.0 (60.9±2.1) mm, tail: 41.0–47.0 (43.6±2.2) mm. Cytochrome-b sequences of *eckodedicatus* n. ssp. form a unique cluster differing by 2.5% from *P. a. aemodius* (East Himalayan cluster), by 2.3 % from *P. a. melanolophus* (West Himalayan cluster) and by 2.6% from *P. a. ater* (North Eurasian cluster; see also Table 2).



Fig. 6. *Parus ater eckodedicatus* n. ssp., paratype, MAR 4934, China, Shaanxi, Huayang, Changqing Panda Reservation, 13 May 2005. Photo: Y.-H. SUN.

P. ater martensi ECK, 1998 (type locality: Nepal, Mustang Distr.; west of the area of *P. a. aemodius*) differs by bright ochre-beige vent and belly from both ssp. *aemodius* (s. str.) and ssp. *eckodedicatus* and by this character is a clear-cut and easy-to-distinguish subspecies (ECK 1998).

Note. The four Sichuan specimens in the WEIGOLD collection (see above), which were collected roughly 90 years ago and partly in the same season, differ markedly. Belly and vent lack any bright reddish-beige but tend to markedly more “dirty” grey. The same holds true for primaries and secondaries, which are not black or dark grey but are markedly lighter with brownish tinge. But direct comparison is needed to see the differences. This seems to be an effect of ageing and needs to be considered for further taxonomic work in that group.

Distribution. This new subspecies inhabits coniferous forests at high altitude (from about 2600 m upwards) in the mountains of western China; cytochrome-b proven occurrences are in Yunnan, Sichuan, Gansu, and Shaanxi. Probably also the populations of Qinghai, South-East Xizang, and the easternmost parts of the Indian Himalayas belong to *eckodedicatus* n. ssp. (see CHENG [1987] and ZHENG [2005] for coal tit distribution in China).

Derivatio nominis. This subspecies is dedicated to Dr. h. c. SIEGFRIED ECK (1942–2005), who for decades contributed so much to our understanding of palearctic birds and whose scrutiny also initiated and helped to correctly evaluate the systematics and taxonomy of Chinese passerine birds.

Appendix 2

Blood and tissue samples which were used for DNA extraction, sequencing, and analysis with corresponding haplotype number (no. from MAR series). Outgroup sequences were taken from GenBank.

Species	Subspecies	Ht.	No.	Locality	Date	Collector	Accession no.
<i>Parus amabilis</i>				Philippines, Palawan	< 2003-05-28	fide Gill et al. (2005)	AY308730
<i>Parus ater</i>	<i>abietum</i>	1	267	Germany, Baden-Württemberg, Grafenhausen	1996-03-31	J. Martens	DQ217844
<i>Parus ater</i>	<i>abietum</i>	1	1134	France, Pyrénées-Orientales, Serralongue	1993-08-19	J. Martens	DQ217850
<i>Parus ater</i>	<i>abietum</i>	1	3094	Czech Republic, Šumava, Slunečna	2003-05-08	J. Martens	DQ217868
<i>Parus ater</i>	<i>abietum</i>	1	90231	Germany, Niedersachsen, Lingen	2002-06-30	T. Lubjuhn	DQ217900
<i>Parus ater</i>	<i>abietum</i>	1	90232	Germany, Niedersachsen, Lingen	2002-06-30	T. Lubjuhn	DQ217901
<i>Parus ater</i>	<i>abietum</i>	2	1120	France, Pyrénées-Orientales, Serralongue	1993-08-14	J. Martens	DQ217849
<i>Parus ater</i>	<i>abietum</i>	3	526	France, Pyrénées-Orientales, Serralongue	1997-08-17	J. Martens	DQ217845
<i>Parus ater</i>	<i>abietum</i>	4		Greece	< 2003-05-28	fide Gill et al. (2005)	AF347959
<i>Parus ater</i>	<i>aemodius</i>	1	4156	Nepal, Rasuwa District, Somdang	2004-04-09	J. Martens	DQ217873
<i>Parus ater</i>	<i>aemodius</i>	2	4196	Nepal, Rasuwa District, Somdang	2004-04-13	J. Martens	DQ217874
<i>Parus ater</i>	<i>aemodius</i>	2	90019	Nepal, Sindhu Palchok Distr., Dadar Danda, Kalinchok	1995-04-20	J. Martens	DQ217879
<i>Parus ater</i>	<i>aemodius</i>	3	90053	Nepal, Sindhu Palchok Distr., Dadar Danda, Kalinchok	1995-04-22	J. Martens	DQ217881
<i>Parus ater</i>	<i>ater</i>	1	1416	Russia, Sakhalinskaya oblast, island of Sakhalin, Chaplanovo	1995-06-12	A. A. Nazarenko	DQ217851
<i>Parus ater</i>	<i>ater</i>	1	1446	Russia, Primorskiy kray, Vladivostok	1994-10-15	A. A. Nazarenko	DQ217853
<i>Parus ater</i>	<i>ater</i>	1	1450	Russia, Primorskiy kray, Vladivostok	1994-10-15	A. A. Nazarenko	DQ217855
<i>Parus ater</i>	<i>ater</i>	1	5125	Germany, Mecklenburg-Vorpommern, Serrahn	2005-05-20	D. T. Tietze	DQ217878
<i>Parus ater</i>	<i>ater</i>	2	90223	Finland, Liminka	1996-06-30	L. Kvist	DQ217895
<i>Parus ater</i>	<i>ater</i>	3	90224	Finland, Lammi	1996-06-30	L. Kvist	DQ217896
<i>Parus ater</i>	<i>ater</i>	4	90225	Finland, Lammi	1996-06-30	L. Kvist	DQ217897
<i>Parus ater</i>	<i>ater</i>	5	1444	Russia, Primorskiy kray, Vladivostok	1994-10-15	A. A. Nazarenko	DQ217852
<i>Parus ater</i>	<i>ater</i>	5	1448	Russia, Primorskiy kray, Vladivostok	1994-10-15	A. A. Nazarenko	DQ217854
<i>Parus ater</i>	<i>ater</i>	5	1471	Russia, Evreyskaya avtonomnaya oblast, settlement Londoko	1996-09-04	O. P. Valchuk	DQ217856
<i>Parus ater</i>	<i>atlas</i>	1	4008	Morocco, near Cèdre Goureaud	2004-03-16	D. T. Tietze & K. Mally	DQ217872
<i>Parus ater</i>	<i>eckodedicatus</i>	1	1876	China, Gansu, Lianhua Shan	1999-04-15	J. Martens	DQ217859
<i>Parus ater</i>	<i>eckodedicatus</i>	1	1880	China, Gansu, Lianhua Shan	1999-04-15	J. Martens	DQ217860
<i>Parus ater</i>	<i>eckodedicatus</i>	1	3280	China, Sichuan, Wawu Shan	2002-05-13	J. Martens & D. T. Tietze	DQ217870

Species	Subspecies	Ht.	No.	Locality	Date	Collector	Accession no.
<i>Parus ater</i>	<i>eckodedicatus</i>	1	4934	China, Shaanxi, Huayang, Changqing Panda Reservation	2005-05-13	J. Martens & Y.-H. Sun	DQ217876
<i>Parus ater</i>	<i>eckodedicatus</i>	2	3242	China, Yunnan, Geza N Zhongdian	2002-05-02	J. Martens & D. T. Tietze	DQ217869
<i>Parus ater</i>	<i>eckodedicatus</i>	3		China, Sichuan	< 2003-05-28	fide Gill et al. (2005)	AF347958
<i>Parus ater</i>	<i>insularis</i>	1	90229	Japan, Hokkaido, Nagano	2002-03-14	Isao Nishiumi	DQ217899
<i>Parus ater</i>	<i>insularis</i>	2	90228	Japan, Hokkaido, Nagano	2003-01-14	Isao Nishiumi	DQ217898
<i>Parus ater</i>	<i>martensi</i>	1	90101	Nepal, Parbat Distr., between Chitre and Deorali	1995-05-02	J. Martens	DQ217885
<i>Parus ater</i>	<i>martensi</i>	2	90132	Nepal, Mustang Distr., Purano Marpha	1995-05-10	J. Martens	DQ217888
<i>Parus ater</i>	<i>martensi x melanolophus</i>	1	90165	Nepal, Myagdi Distr., upper Myagdi Khola	1995-05-24	J. Martens	DQ217891
<i>Parus ater</i>	<i>martensi x melanolophus</i>	2	90156	Nepal, Myagdi Distr., upper Myagdi Khola	1995-05-23	J. Martens	DQ217889
<i>Parus ater</i>	<i>martensi x melanolophus</i>	2	90163	Nepal, Myagdi Distr., upper Myagdi Khola	1995-05-24	J. Martens	DQ217890
<i>Parus ater</i>	<i>martensi x melanolophus</i>	2	90166	Nepal, Myagdi Distr., upper Myagdi Khola	1995-05-24	J. Martens	DQ217892
<i>Parus ater</i>	<i>melanolophus</i>	1	2918	Nepal, Humla Distr., Saipal	2001-07-06	M. Fischer	DQ217867
<i>Parus ater</i>	<i>melanolophus</i>	2	3324	Nepal, Humla Distr., Chucho Khola	2002-06-29	M. Fischer & H. Grimm	DQ217871
<i>Parus ater</i>	<i>melanolophus</i>	3		Nepal	< 2003-05-28	fide Gill et al. (2005)	AF347960
<i>Parus ater</i>	<i>rufipectus</i>	1	2879	Kyrgyzstan, Issyk-Kul	2001-03-29	A. Ostastshenko	DQ217864
<i>Parus ater</i>	<i>rufipectus</i>	2	2878	Kyrgyzstan, Issyk-Kul	2001-03-29	A. Ostastshenko	DQ217863
<i>Parus elegans</i>	<i>elegans</i>			Philippines, Luzon	< 2003-05-28	fide Gill et al. (2005)	AF347964
<i>Parus elegans</i>	<i>mindanensis</i>			Philippines, Mindanao, Bukidnon	1992-05-13	fide Gill et al. (2005)	AY308719
<i>Parus rubidiventris</i>	<i>beavani</i>	1	90041	Nepal, Sindhu Palchok Distr., Dadar Danda, Kalinchok	1995-04-21	J. Martens	DQ217880
<i>Parus rubidiventris</i>	<i>beavani</i>	1	90065	Nepal, Sindhu Palchok Distr., Dadar Danda, Kalinchok	1995-04-23	J. Martens	DQ217884
<i>Parus rubidiventris</i>	<i>beavani</i>	2	90055	Nepal, Sindhu Palchok Distr., Dadar Danda, Kalinchok	1995-04-22	J. Martens	DQ217882
<i>Parus rubidiventris</i>	<i>beavani</i>	3	2745	Nepal, Bhojpur Distr., Salpa La	2001-04-18	J. Martens	DQ217862
<i>Parus rubidiventris</i>	<i>beavani</i>	3	90057	Nepal, Sindhu Palchok Distr., Dadar Danda, Kalinchok	1995-04-22	J. Martens	DQ217883
<i>Parus rubidiventris</i>	<i>rubidiventris</i>	1	90168	Nepal, Myagdi Distr., Myagdi Khola	1995-05-24	J. Martens	DQ217894
<i>Parus rubidiventris</i>	<i>rubidiventris</i>	2	2906	Nepal, Humla Distr., Saipal	2001-07-05	M. Fischer	DQ217865
<i>Parus rubidiventris</i>	<i>rubidiventris</i>	2	2920	Nepal, Humla Distr., Saipal	2001-07-05	M. Fischer	DQ217866
<i>Parus rubidiventris</i>	<i>rubidiventris</i>	2	90167	Nepal, Myagdi Distr., Myagdi Khola	1995-05-24	J. Martens	DQ217893
<i>Parus rubidiventris</i>	<i>rubidiventris</i>	3	4248	Nepal, Rasuwa District, W Syabrubesi	2004-04-15	J. Martens	DQ217875
<i>Parus rubidiventris</i>	<i>ssp.</i>	1		Nepal	< 2003-05-28	fide Gill et al. (2005)	AY308725

Species	Subspecies	Ht.	No.	Locality	Date	Collector	Accession no.
<i>Parus rubidiventris</i>	<i>whistleri</i>	1	731	China, Shaanxi, Taibai Shan, above Houzhenzi	1997-06-14	J. Martens	DQ217846
<i>Parus rubidiventris</i>	<i>whistleri</i>	2	1875	China, Gansu, Lianhua Shan	1999-04-15	J. Martens	DQ217858
<i>Parus rubidiventris</i>	<i>whistleri</i>	3	754	China, Shaanxi, Taibai Shan, above Houzhenzi	1997-06-16	J. Martens	DQ217847
<i>Parus rufonuchalis</i>		1	1568	Kyrgyzstan, Kirgis Ata valley	1993-05-23	J. Martens	DQ217857
<i>Parus rufonuchalis</i>		2	90130	Nepal, Mustang Distr., Purano Marpha	1995-05-10	J. Martens	DQ217886
<i>Parus rufonuchalis</i>		2	90131	Nepal, Mustang Distr., Purano Marpha	1995-05-10	J. Martens	DQ217887
<i>Parus rufonuchalis</i>		3		?	< 2003-05-28	fide Gill et al. (2005)	AY308729
<i>Parus venustus</i>		1	773	China, Shaanxi, Taibai Shan, above Houzhenzi	1997-06-24	J. Martens & P. Jäger	DQ217848
<i>Parus venustus</i>		1	2033	China, Sichuan, Qincheng Shan	2000-05-14	J. Martens & P. Jäger	DQ217861
<i>Parus venustus</i>		1	4938	China, Shaanxi, Huayang, Changqing Panda Reservation	2005-05-14	J. Martens & Y.-H. Sun	DQ217877