

Systematic notes on Asian birds. 49

A preliminary review of the Aegithalidae, Remizidae and Paridae¹

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Proposed recent taxonomic changes in Paridae, Aegithalidae, and Remizidae are reviewed within the geographic scope of this series and their reliability is discussed in terms of the Biological Species Concept with respect to secondary contacts, hybridization, introgression, bioacoustics, and molecular genetics. Certain previously unpublished data are added to support the taxonomic decisions.

Introduction

This review benefits from the excellent treatment of these three passerine families in the monograph by Harrap (1996)², preceded by detailed work by Vaurie (1957a, b) on the Palearctic species set upon which Snow (1967) based his treatment for Peters's *Checklist of the Birds of the World*. Only after the publication of Harrap (op. cit.) has molecular genetics begun to furnish information on parid systematics and taxonomy. This has not only given insights into population structure and population genetics of various taxa, but also helped understanding of species evolution and species limits. Its influence on parid taxonomy is now quite pronounced. Papers like those of Gill et al. (1989, 2005), Kvist et al. (1996, 2001, 2003, 2006), Salzburger et al. (2002a, b), Päckert et al. (2005), Martens et al. (2006), to mention just a few, are milestones in this respect.

Research focused on contact zones in the Russian Far East and in the Himalayas (Kvist et al., 2003, Nazarenko et al., 1999, Päckert et al., 2005, Martens & Eck, 1995, Martens et al., 2006) has also provided detailed information suggestive of times of evolutionary divergence and possible refuge areas in the Himalayas and in China. These have turned out, in detail, to be considerably more complicated than was formerly believed. The main reason is that evolutionarily deeply split population units (haplotype clusters in terms of molecular genetics) often are not mirrored by external characters. Only molecular genetics makes them "visible".

¹ Results of the Himalayan Expeditions of J. Martens, No. 254. For No. 253 see: *Senckenbergiana biologica*, 86 (1): 11-36, 2006.

² Sometimes referred to as Harrap & Quinn, but the title page clarifies the authorship.

Acoustic work, so far as it is relevant to taxonomy, has also made strides forward and now allows consideration of nearly all the species of our area (sonagram collections of voices of Afghan, Himalayan, South Siberian and Chinese parids in Thielcke, 1968, Martens, 1975, Martens & Nazarenko, 1993, Martens et al., 1995, Martens & Eck, 1995, Thönen, 1996, Ivankina et al., 1997, Päckert et al., 2005). Over these years one of us (Eck, 1976, 1977, 1979, 1980a, b, 1982, 1988, 1992, 1996, 1998 and 2006) also contributed substantial fresh information on morphology that is relevant to the relationships and taxonomy of Asian species of the genus *Parus*.

These more modern approaches have not yet been applied to the study of the Aegithalidae and Remizidae. Although these groups are represented by only a few species in our area, taxonomic problems abound and in many cases these are still open to question.

When studying the detailed text of Harrap (1996), and the excellent plates by Quinn, it becomes evident that present taxonomic listings are relatively superficial and these will certainly change when more is known about contact zones, acoustics and molecular genetics.

Methodology

This contribution critically reviews systematic and taxonomic papers on Asian titmice and their allies. Consequently, it is purely descriptive in nature. Recommendations for taxonomic changes for nearly all cases proposed here have been published elsewhere, but they are critically discussed and partly revised. Personal experience with parid (*sensu lato*) taxonomy based on morphology, acoustics and molecular genetics has greatly influenced our views, and extended field experience mainly in the Himalayas, China and other parts of Palaearctic and Oriental Asia has informed our decisions. This paper was also much influenced by a detailed paper prepared by one of us, which reviews the present taxonomic situation in Palaearctic tits; published posthumously elsewhere (Eck, 2006).

The species accounts herein are often subdivided. Some or all of the following small sections are used:

- *Taxa included*: here we list the subspecies that we consider valid and which occur regularly within the area covered by this series (see Dickinson & Dekker, 2000: 5). We have added the type localities in square brackets, or occasionally a range statement. Sometimes we have found it appropriate to list a valid subspecies that is extralimital and in such cases the term 'EL' is added. Although our subspecific recognition is reflected in the 'sister' paper on the types of these families (Dickinson et al., 2006), and we use the spellings, dates and authorships used there, the additional geographic information given here should assist in understanding contact zones. This arrangement also allows us to minimise the number of citations we have to insert within each taxonomic account. Where Dickinson et al. (2006) list all relevant synonyms, we list only those we discuss.
- *Taxonomy*: generally, this section deals with the validity of subspecies and with species limits, but we also highlight the taxonomic questions which seem to us to require further research. Museum names are replaced by acronyms; these are listed at the end of this paper. In a few cases we provide a general introduction and go on to deal with one subspecies group at a time.

- *General characteristics*: this section contains notes on morphological generalities and peculiarities.
- *Distribution*: here we comment upon matters such as range gaps, and contact zones, and areas needing further research.
- *Colour images*: understanding this paper will, we think, be assisted by consulting published images, especially those we list here. Usually these are the work of Quinn in Harrap (1996) who depicted all the species and many of the subspecies in our area.

Aegithalidae

Aegithalos caudatus (Linnaeus, 1758)

Taxa included (7, extralimital subspecies listed for convenience: 1): *Ae. c. kamtschaticus* Domaniewski, 1933 [Kamchatka] EL; *Ae. c. sibiricus* (Seeböhm, 1890) [C Siberia]; *Ae. c. japonicus* Prázek, 1897 [N Japan]; *Ae. c. vinaceus* (Verreaux, 1870)³ [Ourato, 'Kansu' = Inner Mongolia]; *Ae. c. glaucogularis* (Moore, 1855)⁴ [China = Shanghai⁵]; *Ae. c. magnus* (Clark, 1907) [Kaiki District, Seoul, Korea]; *Ae. c. trivirgatus* (Temminck & Schlegel, 1848) [Japan; restricted to Honshu by Kuroda (1923c). Range: Honshu, Sado, Oki (Japan); Quelpart (Korea)]; *Ae. c. kiusiuensis* Kuroda, 1923c [N Kyushu].

Taxonomy: the Long-tailed Tit varies a great deal geographically, but the degree of variation is not constant. In some regions this variation is sharp and well differentiated subspecies have been described, but other names relate to slight differences and may be complicated by an exceptionally high degree of individual variation (Vaurie, 1959).

Based on external morphology there are several subspecies groups; three according to Vaurie (1959), or four in Harrap (1996). These appear to provide evidence of historic separation followed by recent, probably post-glacial, secondary contact with interbreeding. All three of the subspecies groups of Vaurie (1959) occur in our area (*caudatus*, *europeus* Hermann, 1804, and *alpinus* Hablizl, 1783); but Harrap (1996) separated a fourth group (*glaucogularis*, which Vaurie had included in his *alpinus* group). And according to him, this group in which he included just *glaucogularis* and *vinaceus* occurs in the area covered by this series, whereas his restricted *alpinus* does not.

Snow (1967) treated the *caudatus* 'group' as one wide-ranging form stretching across the northern Palaearctic taiga zone and extending eastwards to northern Japan. This approach was accepted by Harrap (1996) and Stepanyan (1990), but Stepanyan (2003) recognised *kamtschaticus*, a view supported by Red'kin (in litt.), and yet, like Snow, Stepanyan kept *sibiricus* Seeböhm, 1890, in the synonymy of *caudatus*⁶. Vaurie (1959) listed *japonicus*, although seeing it as weakly differentiated, and Morioka, in Orn. Soc. Japan (2000: 314), chose to follow Vaurie rather than Snow. Given our lack of fresh in-

³ Not 1871; see Dickinson et al. (2006).

⁴ Moore's name has priority over Gould's, which was used by Snow (1967: 55), see Dickinson et al. (2006).

⁵ Gould (1855) redescribed this and restricted the type locality.

⁶ Perhaps because the name was proposed in an unorthodox and almost conditional way.

formation we follow Stepanyan in recognising *kamtschaticus* and follow Morioka (op. cit. supra) in recognizing *japonicus*. This allows us to avoid the merger of populations that may well be found to differ markedly in their molecular genetics. We have not been able to examine specimens from NE China to see whether these best match *sibiricus* or *japonicus*.

Apart from *japonicus*, which is part of the *caudatus* group⁷, Korea and the Japanese islands are occupied by *magnus*, *trivirgatus* and *kiusiuensis* which are all considered by Vaurie, and by Harrap, to belong to the *europaeus* group, but from which they are widely separated. Intervening populations between the two halves make up the *caudatus* group. The wisdom of seeing these eastern forms as belonging to the *europaeus* group needs revisiting when molecular information becomes available as the characters that have suggested this relationship may instead result from morphological convergence between quite different haplotype groupings.

Because we think variation in Siberia requires further study and we find the split in the *europaeus* group questionable we consider that a detailed zoogeographic analysis drawing upon molecular information is urgently needed.

Colour images: Quinn in Harrap (1996), pl. 33, figs. 103k-l: *glaucogularis* (as well as figs. of various extralimital W Palaearctic subspecies).

Aegithalos leucogenys (Moore, 1854⁸)

Taxon included (1): *Ae. leucogenys* (Moore, 1854) [Woods above Balu Chughur' (= Chighu Serai), near Gusalek, Kunar valley, NE of Jalalabad]. – Monotypic.

Distribution: the White-cheeked Tit is a restricted-range endemic of dry central Asia, from Afghanistan and western Pakistan south to Baluchistan, and along the western Himalayas to about 74°E. Records east of 74°E, e.g., in Baltistan and Garhwal seem doubtful (Roberts, 1992: 351). No taxonomic problems are currently known.

Colour images: Quinn in Harrap (1996), pl. 35, figs. 104a-c.

Aegithalos concinnus (Gould, 1855)

Taxa included (6): *Ae. c. iredalei* (Baker, 1920a) [Himalayas = Simla⁹]; *Ae. c. manipurensis* (Hume, 1888) [eastern hills, Manipur]; *Ae. c. talifuensis* (Rippon, 1903) [E Tali, NW Yunnan]; *Ae. c. concinnus* (Gould, 1855) [? Chu Shan, Zhejiang]; *Ae. c. pulchellus* (Rippon, 1900) [southern Shan States, Myanmar]; *Ae. c. annamensis* (Robinson & Kloss, 1919) [Langbian Mts., Vietnam].

Taxonomy: the Black-throated Tit, as currently recognised, brings together highly distinct subspecies which were arranged in three subspecies groups (monotypic *iredalei* and *annamensis*, and polytypic *concinnus*) by Harrap (1996). The subspecies are remark-

⁷ But, as indicated, has often been treated as a synonym of nominate *caudatus*.

⁸ In full: Moore in Horsfield & Moore; Moore alone should be credited, *contra* Snow (1967).

⁹ Baker (1920a) was renaming *Parus erythrocephalus* Vigors, 1831, a name which was preoccupied. That had as type locality "Himalayas"; Baker restricted this to Simla (but there has been considerable dispute about the origin of the specimens that were described by Vigors and painted for Gould's 'Century').

able in that they differ not only in coloration of the crown (chestnut brown *vs.* greyish drab), but they also differ in pattern (i.e the presence or absence of supercilium and chestnut breast band).

Not surprisingly we have begun to find that these differences are paralleled by significant differences in the cytochrome-*b* gene. Three specimens have been sequenced. One from Rasuwa Distr. (Nepal, ssp. *iredalei*) differed from one from Omei Shan (Sichuan/China, spp. *talifuensis*) by 5.1% sequence divergence and from one from Natmataung (Mt. Victoria, Myanmar; ssp. *manipurensis*) by 5.3%. The Omei and Natmataung specimens differ by 6% (uncorrected, 663 bp). In the tree topology, the Nepal and the Omei specimens come out as 'sisters' and when these are compared with the Natmataung specimen the between-group distance is 5.6%. These are unexpected and remarkably strong differences at a level which, in songbirds, usually indicates a clear species difference (J.M., M. Päckert and D.T. Tietze, unpublished). All these three samples are from reddish-crowned subspecies, but *talifuensis* from West China also has a strong reddish breast band. There are two grey-headed subspecies (*pulchellus*, which has the reddish breast band, and *annamensis*, which does not), and by this character these differ sharply from the reddish-crowned ones.

Among these birds, crown colour seems particularly important as it may represent a plesiomorphic character state. Just-fledged juveniles of red-headed ssp. *talifuensis/concinnus* have the crown colour just like the grey-headed forms; but this is quite ephemeral as it is soon moulted, becoming chestnut apparently within a few weeks after fledging. Thus most field guides show juveniles with the forehead and crown reddish.

It seems possible that *Ae. concinnus* represents a hitherto unresolved species swarm. More data on contact zones of brownish- and greyish-crowned populations are needed, as well as molecular and vocal information.

Distribution: the Himalayas east to large parts of C and S China, Taiwan, Myanmar and parts of Thailand. Of the grey-headed subspecies, *annamensis*, in Vietnam and Laos is highly disjunct; *pulchellus* in northwest Myanmar seems to be in contact with the north-eastern Indian rufous-headed *manipurensis* (map in Harrap, 1996), but whether they intergrade is unknown.

Colour images: herein Pl. I, Figs. a-b: *talifuensis/concinnus*; Quinn in Harrap (1996), pl. 34, figs. 105a-b *iredalei* (reddish-headed), 105c *pulchellus* (grey-headed), 105d *talifuensis* (reddish-headed), 105e-f *annamensis* (grey-headed).

Aegithalos niveogularis (Gould, 1855)

Taxa included (4): A: the *niveogularis* 'group': *Ae. n. niveogularis* (Moore, 1855)¹⁰ [Northern India = N Punjab¹¹]; B: the *bonvaloti* 'group'¹²: *Ae. n. bonvaloti* (Oustalet, 1892¹³) [Tatsienlu = Kangding Xian, Sichuan, China]; *Ae. n. obscuratus* (Mayr, 1940) [Chengou Forks, 30 miles W of Wenchwan, Sunghan

¹⁰ Moore has priority over Gould, the author given by Snow (1967: 58), see Dickinson et al. (2006).

¹¹ Vaurie (1957b: 20) restricted the type locality of *niveogularis* Gould to N. Punjab. However, Moore published first and Gould's name is a primary homonym and permanently invalid. See Dickinson et al. (2006) for the parallel restriction of the type locality of *niveogularis* Moore.

¹² This grouping is for convenient discussion and based solely on geography.

¹³ For use of this date in place of 1891 see Dickinson et al. (2006).

district, northern Sichuan; given as Maowen by Cheng, 1987]; *Ae. n. sharpei* (Rippon, 1904) [Mt Victoria, S Chin Hills, Myanmar].

Taxonomy: although only a few taxa are concerned, species limits within the Sino-Himalayan long-tailed tits are not reliably worked out yet. The taxa *niveogularis* (W Himalayas), *iouschistos* (Blyth, 1845) (E Himalayas east to about the Tsangpo bend), and *obscuratus* (adjacent SW China) occupy a more or less coherent, but not quite continuous range, whereas *sharpei* (Chin Hills, Myanmar) is apparently entirely disjunct. Vaurie (1959) and Snow (1967) treated all these forms as conspecific, which reflects their overall similarity and largely continuous distribution along the Himalayan chain extending into south-west China.

However, western *niveogularis* is remarkably different from the adjacent *iouschistos* in coloration and slightly different in pattern. Furthermore, *niveogularis* is a form adapted to drier habitat, and its range ends in north-west Dhaulagiri in north-west Nepal. This is west of the start of the range of *iouschistos*. It is absent in the inner valley of the Kali Gandaki gorges (east of Dhaulagiri) and anywhere further east (Inskipp & Inskipp, 1991; Martens & Eck, 1995). By contrast, *iouschistos* inhabits mixed broad-leafed/coniferous forests within the influence of the monsoon. Syntopic occurrences of *niveogularis* and *iouschistos* are not yet known, nor are hybrids (Harrap, 1996). Thus it seems justified to treat *niveogularis* as a separate biological species; however overall relationships in this complex are unresolved. For instance, *bonvaloti* and *sharpei* are relatively long-tailed (as is *leucogenys*, which differs strongly in bill shape) while *iouschistos* and *niveogularis* are relatively short-tailed] (C.S. Roselaar pers. comm.).

Martens & Eck (1995: 314-315) united western *niveogularis* with *bonvaloti*, *obscuratus* and *sharpei* and treated them as conspecific. This arrangement is supported by external morphology, for *niveogularis*, *bonvaloti/obscuratus* and *sharpei* are very similar in pattern and coloration (cf. Vaurie 1957a). But this does not seem to fit with general zoogeography, and the limited ecological evidence is inconclusive. The habitat requirements of *niveogularis* seem to be dry forest and *obscuratus* lives well in dry forest too, e.g., in Yunnan (Jizu Shan; J.M.), however *bonvaloti* lives in wetter forest, while no clear habitat preference is recorded for *sharpei* of Mt. Victoria although one imagines this will not be dry forest. Wunderlich (1991) attached *obscuratus* to *iouschistos* but this is surely erroneous.

Harrap (1996) treated *niveogularis* as a monotypic species and united the eastern and south-eastern taxa with *iouschistos*. Dickinson (2003) felt unable to unite *iouschistos* and '*bonvaloti*' (made up of the three eastern and south-eastern representatives: *bonvaloti*, *obscuratus*, *sharpei*) and listed three species. We prefer to maintain the arrangement offered by Martens & Eck (1995), however we look forward to a molecular analysis, which will no doubt clarify the picture.

Colour images: Quinn in Harrap (1996), pl. 34, figs. 107a-b.

Aegithalos iouschistos (Blyth, 1845¹⁴)

Taxon included (1): *Ae. iouschistos* (Blyth, 1845) [Nepal].

¹⁴ The 1844 volume, and that date was used by Snow (1967: 58); however this paper appeared in 1845; see Dickinson & Pittie (2006).

Taxonomy: see above under *Ae. niveogularis*. – Monotypic.
Colour images: Quinn in Harrap (1996), pl. 34, figs. 107a-b.

***Aegithalos fuliginosus* (J. Verreaux, 1869)¹⁵**

Taxon included (1): *Ae. fuliginosus* (J. Verreaux, 1869) [E Tibet = W Sichuan]. – Monotypic.

Distribution: the Sooty Tit is a small-range Chinese species found in parts of Sichuan, Gansu, Shaanxi, and Hubei. It was quite common on the southern flanks of Taibai Shan, Shaanxi in June 1997 (J.M.). – No taxonomic problems known.

Colour images: Quinn in Harrap (1996), pl. 35, figs. 108a-c.

***Psaltria exilis* Temminck, 1836**

Taxon included (1): *Psaltria exilis* Temminck, 1836 [Java]. – Monotypic.

Colour images: Quinn in Harrap (1996), pl. 36, figs. 110a-b.

Remizidae

The Penduline Tit was most often treated as one wide-ranging species, *R. pendulinus* (as in Hartert 1905a, Vaurie 1959, Snow, 1967) until recently when Harrap (1996) accepted four species, *R. pendulinus sensu stricto*, *R. macronyx* (Severtsov, 1873), *R. coronatus* (Severtsov, 1873), and *R. consobrinus* (Swinhoe, 1870). Dickinson (2003: 530) retained the treatment of Snow (1967) but added some comments, in a footnote in which he mistakenly suggested that the last three subspecies listed would constitute the species *coronatus* if three species were recognised. In fact the name *consobrinus* Swinhoe, 1870, has priority over *coronatus* Severtsov, 1873. In addition to differences in coloration and pattern, the groups differ in size as well (Vaurie, 1950) and in relative bill length and structure of leg and foot (C.S. Roselaar pers. comm.) and that two quite different nest types occur.

That three species need to be recognised flows from the evidence of Kazakhstan (Gavrilov, 1972; see maps pp. 254, 259) where it is apparent that *R. r. macronyx* and *R. r. coronatus* are widely sympatric and that they differ not just structurally and morphologically but in habitat preference. If the appropriate recognised taxa are grouped with *pendulinus*, *macronyx* or *consobrinus* it is then apparent that *macronyx* meets with *pendulinus* and interbreeds in a narrow contact zone at the mouth of the river Ural and in “the southwest corner of the Caspian [basin]” (Harrap, 1996: 212). Whether and how any subspecies of *consobrinus* actually interacts is less clear. It was suggested by Hartert (1905) that *R. r. jaxarticus* may interbreed with *stoliczkae* (Hume, 1874), but this seems to have been based on museum specimens without field studies to determine the geography of any contact zone and how the birds interact. Thus *stoliczkae* is a desert form which may or may not meet and intergrade with *consobrinus*. It is said to intergrade

¹⁵ Snow (1967: 58) dated this 1870, implying a delay in publication. The volume title page is dated 1869 and no evidence of delay is apparent.

with *coronatus* in the Zaysan basin (Harrap, 1996: 215), and Harrap wondered whether *stoliczkae* as well as *consobrinus* might be involved in the increase of records in eastern China and Japan. We are unaware of any report that *stoliczkae* and *consobrinus* meet and interact on their breeding grounds.

In sum, the evidence would allow one to retain the *macronyx* group as a part of the species *pendulinus* and does not clearly resolve whether *coronatus* and *consobrinus* should be considered separate species. We prefer to treat these two as one species until more evidence is available. To add to the morphological and biological information already available, acoustic and molecular data are needed for sound decisions.

***Remiz consobrinus* (Swinhoe, 1870b)**

Taxa included (3): A: the *coronatus* group: *R. c. coronatus* (Severtsov, 1873) ['Nau, on Syrdar'ya below Khodzents' = Leninabad, Tajikistan]; *R. c. stoliczkae* (Hume, 1874) [no locality = Bora, Chinese Turkestan ¹⁶ = Bora, SE of Yecheng, Xinjiang, China]. B: the *consobrinus* 'group': *R. c. consobrinus* (Swinhoe, 1870b) [Sha-She, Hubei].

Distribution: the breeding range of eastern *consobrinus* is disjunct from the range of the western *coronatus* group.

Colour images: Quinn in Harrap (1996), pl. 11, figs. 35a-d: *coronatus*, 36a-d: *consobrinus*.

***Cephalopyrus flammiceps* (Burton, 1836)**

Taxa included (2): *C. f. flammiceps* (Burton, 1836) [Himalayas = Mussoorie ¹⁷]; *C. f. olivaceus* (Rothschild, 1923) [Tengyueh, N Yunnan].

Taxonomy: no problems need discussion.

Colour images: Quinn in Harrap (1996), pl. 12, figs. 43a-e: *flammiceps*, f: *olivaceus*.

Paridae

For many years ornithologists have followed traditional species limits in *Parus* but in recent years several of these limits have been questioned or changed, and further modifications are likely. Acoustics and present molecular genetics are influencing this progress, both in splitting and in lumping taxa. It now appears that marked morphological differences, mostly in coloration but some in overall pattern, do not reliably predict species limits in *Parus*. Taxa most affected by these investigations occur in five complexes: first, *Parus major* Linnaeus, 1758, *sensu lato*; second, *P. cyanus* Pallas, 1770, incl. *flavipectus* Severtsov, 1873; third, *P. ater* Linnaeus, 1758, incl. *melanolophus* Vigors, 1831; fourth, *P. montanus* Conrad, 1827; and fifth, *P. palustris* Linnaeus, 1758, incl. *hyper-melaenus* (Berezowski & Bianchi, 1891). Each is discussed in some detail in the species accounts that follow.

¹⁶ Designated by Hartert (1905a: 391).

¹⁷ The type locality was restricted by Whistler (1924).

This work on parids has offered additional insights into how well distance values of the cytochrome-*b* gene of the mitochondrial genome may indicate species limits even without additional biological data derived from morphology or full information on behaviour at contact zones and on hybridization events. Cytochrome-*b* differences of apparently “good” and long-established species, such as *P. caeruleus* Linnaeus, 1758, and *P. cyanus*, unexpectedly display very low cytochrome-*b* distances and by this seem to suggest only subspecies level distances. Rather higher distance values of above 3% are present between populations of *P. ater* that have traditionally been simply characterized as subspecies groups which apparently intergrade along suture zones, e.g., in China and in the western Palaearctic. These results should initiate fresh, general discussions of how reliably to apply mitochondrial distance values in avian taxonomy. Where relevant below, such discussions are begun herein.

The subspecies in *Parus* accepted here differ from those recognized in Peters’s Check-list (Snow, 1967) in two particulars. First, we include the post 1967 names of which we are aware: *Parus semilarvatus snowi* Parkes, 1971, *Parus ater martensi* Eck, 1998 and *Parus ater eckodedicatus* Martens, Tietze & Sun, 2006. Second, species limit concepts have changed since Snow (1967) and even since Harrap (1996), although this remains the most useful and comprehensive treatment of the family. There are significant differences between treatments in terms of the recognition or synonymization of some names and some views seem to have been based on limited access to specimens, or to be subjective. Such problems can be seen both in the grey tits (*Poecile*) and also in the great tit (*P. major sensu lato*) where conflicting views no doubt remain despite our attempts to elucidate Asian problems.

Taxonomy above the species level

In the 19th century attempts were already made to split the large genus *Parus* into genera or subgenera. The subgenus last erected was *Poeciloides* Bianchi, 1902, for *Parus superciliosus*. For *Parus sensu lato* 12 genus-level names are now in use. The species assigned to each were documented by Hellmayr (1903). Portenko (1954) and Wolters (1980) used these to label their genera. These subunits, until recently mostly used in the sense of subgenera¹⁸, are still in use without much variation as to the species incorporated, although some authors lost track of the type species of their genera (or subgenera).

In general, the circumscription of these units based on morphological characters was pretty good, although not based on a clear understanding of monophyly. Naturally the advent of molecular genetic phylogeny has inspired a re-examination of generic splits in songbirds and as *Parus* is a large genus it has received considerable attention. Gill et al. (2005: 139) stated: “The 51 species of titmice and chickadees constitute a well-defined, monophyletic assemblage of sylvioid passerine birds on the basis of both morphological and molecular characters ...”. They recommended (op. cit. p. 140) splitting *Parus* into six genera on grounds of cytochrome-*b* topology. “Each of the six recommended genera is a monophyletic group that displays distinctive behavioural and

¹⁸ Although for North America generic distinctions were accepted by the A.O.U. (1998).

morphological characteristics." However, this view is not unequivocal; different ones are possible especially when the entire genus *Parus sensu lato* is considered and all Asian and African species are accounted for.

The scope proposed by Gill et al. for the genus *Periparus* Selys-Longchamps, 1884, embraced the tropical and subtropical species (*amabilis*, *elegans*, *venustulus*) as well as true Palaearctic and often high-montane species (*ater*, *rubidiventris*, *rufonuchalis*). The species of these two groups by no means "...display [shared] distinctive behavioural and morphological characteristics...", furthermore their ecological requirements differ considerably, and it seems to us that it will be better to employ separate generic names for them.

In contrast, Gill et al. admit separate generic names of two Old and New World sister taxa, *Lophophanes* Kaup, 1829, and *Baeolophus* Cabanis, 1850. Are their species that distinct in morphology and behaviour as to sufficiently support this opinion? Their molecular split is not deeper than that between the two units of the broad genus *Periparus*. Thus decisions regarding a broad genus *Periparus* on one hand and narrow *Lophophanes* and *Baeolophus* on the other seem to be inconsistent.

There is one other apparent inconsistency in Gill's genus *Parus sensu stricto*, for this embraces two clades: the relatives of the great tit in Eurasia on the one hand and the species of sub-Saharan Africa on the other. The two are separated by a deep molecular split and under the conditions set by Gill et al. each of these may warrant separate generic treatment as well. Finally, the phylogeny of Gill et al. lacks one important species, *P. semilarvatus* (Salvadori, 1865) from the Philippines, the generic assignment of which is unresolved, although it may be close to *Poecile* Kaup, 1829.

Because of these open questions we refrain, for the time being, from adopting the generic recommendations of Gill et al. (2005) and use the generic name *Parus sensu lato* throughout. We have also avoided subgeneric names because of the Asian taxa that remain unsampled¹⁹ or insufficiently sampled at levels previously thought to be sub-specific²⁰. In the circumstances we have chosen to retain the species sequence used by Snow (1967).

The species accounts – taxonomy at the species level and below

Parus palustris Linnaeus, 1758

Taxa included (5; extralimital forms listed for convenience: 2): *P. p. altaicus* Johansen, 1952 [Buchtarma river, Katon-Karagai, S Altai, E Kazakhstan] EL; *P. p. brevirostris* (Taczanowski, 1872) [SW of Lake Baikal, Irkutsk Region, Russia]; *P. p. crassirostris* (Taczanowski, 1885) [Sidemi, S. Ussuriland, Russia]; *P. p. ernsti* Yamashina, 1933 [Naihoru, S. Sakhalin, Russia] EL; *P. p. hensoni* Stejneger, 1892 [Hakodate, Hokkaido, Japan]²¹; *P. p. jeholicus* Kleinschmidt & Weigold, 1922a [30 km north of Bali-

¹⁹ Table 2 in Gill et al. (2005) lacked the Asian taxa: *P. venustulus*, *P. nuchalis* and *P. semilarvatus*.

²⁰ Such as *P. hypermelaena* and *P. weigoldicus*.

²¹ Although we treat *seebohmi* Stejneger, 1892, as a synonym, as did Hartert (1905: 375) and later the Orn. Soc. Japan (1942) and Snow (1967: 74), we have not located the rationale by which Stejneger's distinctions between *hensoni* and *seebohmi* have been explained. The types may need re-examination despite acceptance of that synonymy by Deignan (1961: 342).

handián, NE Jehol ²² = Chengde Shi, Hebei, China]; *P. p. hellmayri* (Bianchi, 1902) [Peking = Beijing, China].

Taxonomy: historically the taxonomic treatment of the Marsh Tit has been characterised by strongly opposing views: extreme splitting and extreme lumping (for example see Kleinschmidt, 1897, for an account). Most systematists now follow Snow (1957, 1967) and Vaurie (1959). Of the numerous names given to eastern populations Vaurie (1957a) synonymised seven in *brevirostris* although, as he stated, he had only a single *brevirostris* at his disposal for comparison. Snow (1957: 37) was initially willing to recognize two of them (*altaicus* and *crassirostris*) thus dividing the Siberian population into three, but later (1967) decided to follow Vaurie (op. cit.).

One of us (Eck, 1980a) in an in-depth revision of the ‘*Poecile*’ group, which was based on a very substantial material, was able to offer a more detailed view. European and Asian Marsh Tits are not only widely disjunct, with a range gap of more than 1,000 km, they also differ significantly in morphology. These two widely disjunct subspecies groups are currently labelled as the *palustris* group (west Palaearctic and, for us, extralimital) and the *brevirostris* group (east Palaearctic or Asian). The Asian populations have a larger bib, smaller feet, and a clumsier bill. The differences between representatives of these groups seem to be insignificant in terms of mitochondrial genetic distance values (Gill et al., 2005: 127; J.M. unpublished), but more taxa need to be sequenced. The Asian populations between the Altai Mts. and Ussuriland are known by subtle colour differences and these, although placed in synonymy, should not be ignored. The population from Sakhalin (*ernsti*) closely resembles that of Japan (*hensoni*; Eck, 1980a: 144).

As concerns our area we accept *brevirostris*, *crassirostris*, *hensoni*, *jeholicus* and *hellmayri*, and in contrast to Cheng (1987) we recognise the distinctness of both *hellmayri* and *jeholicus* (see below). The first two of these, *crassirostris* and *hensoni*, form one morphological group, together with *ernsti* and extralimital *brevirostris*, occupying the central to eastern Palaearctic. A second morphological group encompasses *jeholicus* and *hellmayri* from more southerly north-east China. In north-east China the range of *jeholicus* is a continuation of that of *P. p. crassirostris* and presumably these intergrade, but this needs to be verified.

The Chinese taxon *hypermelaenus* is probably best excluded from *P. palustris* (see below).

General characteristics: compared with west Palaearctic populations the eastern ones have heavier bills and smaller feet. Within the group they vary in the coloration of the back and flanks, height of bill, and proportions of flight feathers. TWI (tail/wing index – see Abbreviations and Acronyms): ‘group 1’, from *altaicus* to *crassirostris* 96.6%, sd 2.26 (n = 28); group 2. *ernsti* 89.7%, sd 1.5 (n = 10); *hensoni* 89.5%, sd 2.1 (n = 24). In *hellmayri* and *jeholicus*, the dorsal coloration is equally brown, but the two subspecies differ in wing length. Relative tail length (TWI): *hellmayri* 86.2%, sd 1.15 (n = 13); *jeholicus* 92.5%, sd 1.52 (n = 11).

Distribution: when examining the detailed mosaic of varying populations within what was treated as *brevirostris sensu lato* by Snow (1967), the distribution is as follows:

²² Jehol Province was abolished in 1955 (Zhao & Adler, 1993: 434; for Chengdeh see p. 428).

brevirostris sensu stricto occurs in southern Siberia eastwards to the Shilka and Argun rivers including Mongolia and western parts of NE China, *crassirostris* inhabits Amurland and northern Korea, and probably easternmost north-eastern China, and *ernsti* is restricted to Sakhalin; *altaicus* is reported from the Altai and is sometimes considered a synonym of *brevirostris*, but is quite distinct in colour and is maintained by Eck (2006).

Colour images: Quinn in Harrap (1996): pl. 15, figs. 46d-e: *hellmayri*; Eck, 1980a: pl. 1: *brevirostris* and *hellmayri*.

Parus hypermelaenus (Berezowski & Bianchi, 1891)

Taxa included (1): *P. h. hypermelaenus* (Berezowski & Bianchi, 1891) [Landzya-kou, Shaanxi (locality of lectotype according to Stepanyan & Loskot 1998, at border between S Shaanxi and Gansu, China)]; Synonyms (provisional placement only): *dejeani* Oustalet 1897 [Tsékou, N Yunnan, China – Kangding according to Cheng, 1987²³]; *poecilopsis* (Sharpe, 1902) [Ch'ü-tung, W Yunnan, China]; *P. h.* ssp. (unnamed) [Mt. Victoria, Chin Hills, W Myanmar].

Taxonomy: the taxonomic rank of the Black-bibbed Tit, a local Chinese form, has often been discussed but, following Harrap (1996), Dickinson (2003) allowed it species rank, although essentially on hypothetical grounds. The case has still to be firmly established, but is not here refuted.

There are marked morphological differences from Marsh Tits, but a close relationship of *hypermelaenus* with the Marsh Tit is evident and has never been questioned. Though records of *P. palustris* exist close to *hypermelaenus* localities (maps in Cheng 1987, Harrap, 1996), no zone of contact is known and nor are intergrades or hybrids. Consequently, intermixing with *P. palustris* is open to question. The value of the cytochrome-*b* difference between the combined west and the east Palaearctic population groups of *P. palustris* on the one hand and *hypermelaenus* on the other amounts to 3.3% (J.M., unpublished). In view of the rather slight difference between the western and eastern population groups of *P. palustris*, of 0.65% (Gill et al., 2005), 3.3% is a remarkably high value and indicates prolonged independent evolution of about 1.6 m.y. when the 2% rule is applied. Without further information, however, species rank for *hypermelaenus* remains equivocal. In addition, we have to state that this value is of the same order of magnitude as those between various cytochrome-*b* clusters of *P. ater* (*q.v.*), in the east as well as in the west Palaearctic. The voice of *hypermelaenus* is unreported.

Geographical variation of *P. hypermelaenus* is only subtle (see Kleinschmidt, 1940: 29-30), and within China no subdivisions seem justified. The isolated population on Mt. Victoria (Chin Hills, Myanmar) was first considered a distinct subspecies by Stresemann (in Stresemann & Heinrich, 1940: 179), although he did not name it (see also Eck, 1980a: 144-145 and additional references; Harrap, 1996).

General characteristics: subtle geographic differences in coloration were discussed

²³ This is presumably Kangding Xian, Dardo, in Sichuan at 30°03'N 102°02'E rather than in Yunnan, but border changes that have taken place in the meantime might explain this. However, Zhao & Adler (1993: 446) thought the name equated with Tsu-kou at 28°00'N 98°52'E. This difference of opinion awaits resolution.

by earlier authors, but need further substantiation due to the lack of adequate series of specimens. The bib is even larger than in Chinese *P. p. jeholicus* and *P. p. hellmayri*, and *hypermelaeus* is also even shorter-tailed. Measurements in Harrap (1996: 244). TWI 79.5% (range 77-81), sd 1.6 (n = 5 from China alone, including a paratype; Eck 2006).

Distribution: recorded from the provinces of Yunnan, Sichuan, Gansu and Shaanxi in mountainous western China; details in Harrap (op. cit.). It has recently been rediscovered in the Qin Ling range (southern slopes of Taibai Shan; specimens in MTD), from where it was known historically (Cheng, 1987). This is now the northeastern-most confirmed locality.

Colour images: Quinn in Harrap (1996), pl. 15, fig. 47; Berezowski & Bianchi, (1891), pl. II: 2; Kleinschmidt (1938), Falco 34, pl. II; Eck, 1980a: pl. I.

Parus montanus Conrad, 1827

Introduction: in terms of species limits, systematics, taxonomy, and phylogeny, the Old World Willow Tit and its chickadee relatives in the New World are among the most intensively studied tits. There is a considerable body of knowledge of morphology, vocalizations and molecular phylogeny now available. This has influenced the recommendations made here.

In general, as in all '*Poecile*' tits the delimitation of subspecies is often difficult and somewhat subjective. It has been argued that too many subspecies have been described on minor local colour differences. This, to a point, is correct, especially in parts of the western Palaearctic. However, this was followed by overlumping of northern forms in the east Palaearctic by Vaurie (1957a, 1959) and Snow (1957, 1967) sometimes on the basis of quite limited material, followed by Stepanyan (1990, 2003). We follow here the arguments presented by one of us (Eck, 1980a) but also include new molecular results (Kvist et al., 2001, Salzburger et al. 2002b).

Hartert (1905a: 376) treated the Palaearctic Willow Tits and the Nearctic chickadees (the latter now being *P. atricapillus* Linnaeus, 1766, and *P. carolinensis* Audubon, 1834) as one single species. Mayr (1956), following several previous authors and relying quite strongly on vocalizations, separated Old and New World taxa as different species. This view was tentatively adopted by Mayr & Short (1970: 64). Eck (1980a), applying a broad species concept, stressed similarities more than the differences between Old and New World taxa and kept them in a single species, *P. atricapillus* (which although not followed here might have been his preference).

The distribution of Willow Tits spans almost the whole of the Palaearctic, from the British Isles continuously across northern Eurasia to Japan, with two disjunct range segments, one in central Asia (Tian Shan) and another in west to north-east China. The various populations display multiple variations in coloration and in flight feather proportions. However, mitochondrial molecular genetics (Kvist et al., 2001, Salzburger et al., 2002b) indicate that all northern populations are recent divergences. The southern populations (Tian Shan, China) are more varied, and drawing on these results a discussion of species limits is needed. Russian authors have generally treated *songarus* Severtsov, 1873 (Tian Shan), as a species (Stepanyan, 1990, 2003), and the Chinese endemics – *affinis* Przewalski, 1876, *stoetzneri* Kleinschmidt, 1921a, and *weigoldicus* Kleinschmidt, 1921b – were generally included in it despite having disjunct ranges. Harrap (1996) and

Dickinson (2003) adopted this view. Here we treat Palearctic Willow Tits as one species, separating only *weigoldicus*. This is upgraded to species rank on molecular evidence (see also Eck, 2006), while the rest of 'songarus' is replaced in *P. montanus*.

Using the evidence from morphology, acoustics and to some extent molecular genetics five subspecies groups can be distinguished (Eck 1980a), of which the *montanus* group and the *salicarius* Brehm, 1831, group are extralimital (Europe, east to the Urals). The other three groups – *borealis* Selys-Longchamps, 1843, *kamtschatkensis* Bonaparte, 1850, and *songarus* – occur in our area and we treat each separately below.

A molecular cytochrome-*b* study by Salzburger et al. (2002b) identified four distinct genetic clusters within trans-Palearctic Willow Tits, represented by three individual taxa, *Parus m. weigoldicus*, *P. m. songarus*, *P. m. affinis*, and a clade containing all six north Eurasian subspecies that were investigated: *borealis*, *montanus*, *rhenanus* Kleinschmidt, 1900, *baicalensis* Swinhoe, 1871, *sachalinensis* Lönnberg, 1908, and *restrictus* Hellmayr, 1900a. The three individual taxa *weigoldicus*, *affinis*, and *songarus* were reciprocally monophyletic and separated from each other by distances between 1.9 and 5.8%. Distances between the north Eurasian subspecies (central Europe to Japan) were low, only 0.65%. These latter subspecies are closely related and still share mitochondrial haplotypes, despite marked morphological and acoustic differences. The current classification which splits the species into the *songarus* and *montanus* subspecies groups and assigns them species rank is not in accord with the molecular results. However, the 'cluster' comprising *weigoldicus* appears to be a sister to all other subspecies and is deeply split from combined *montanus* and *songarus* by distance values of 4.6-5.8%. This unexpectedly great distance supports species rank for it and is paralleled by many well-defined Palearctic passerine species, including some sympatric ones (see, e.g., Päckert et al., 2004). So far, cytochrome-*b* results do not clarify any of the current subspecific delimitations in northern Eurasia.

The territorial song of Willow Tits now plays a major role in identifying evolutionary units that have a common history. Willow tit song is simple, and falls clearly into four main types, geographically defined 'regiolects' (Martens, 1996) which characterize Willow Tit populations all over the Palearctic. These are Lowland, Alpine, Siberian, and Sino-Japanese song types (Thönen, 1962, 1996, Martens & Nazarenko, 1993), all shown in Fig. 1²⁴. They do not fully mirror the molecular phylogeny and apparently differentiated on a different time scale, but they well indicate evolutionary units, too. Current data suggest that the mono-frequency song type (Alpine) may be ancestral being retained over a long evolutionary period in certain populations, but was altered or camouflaged by learning processes in others. Consequently, Willow Tit territorial song contributes important information in systematics and the interpretation of distributional histories (Thönen, 1962, 1996, Martens & Nazarenko, 1993, Martens et al., 1995).

We will now discuss geographic variation and subspecies belonging to the different groups introduced by Eck (1980a) who called them 'Sektoren' or sectors – and which were groups adopted by Harrap (1996).

²⁴ Fig. with a capital F refers to a figure included in this paper.

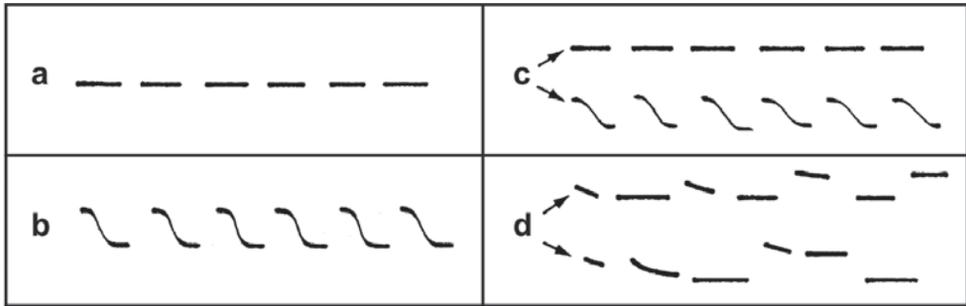


Fig. 1. *Parus montanus*: schematic sonagrams of territorial song. – a) Alpine song type; – b) Lowland song type; – c) Siberian song type; – d) Sino-Japanese song type. – The Siberian song type is a combination of the Lowland and Alpine song types; within its range every male disposes of both song types. Distribution: ‘Lowland’ occurs exclusively in Western Europe (extralimital to our area); ‘Alpine’ disjunctly all over the Palaearctic from the European Alps to Hokkaido, Japan; ‘Siberian’ from Scandinavia to Sakhalin; and ‘Sino-Japanese’ in central Asia, parts of China and Honshu/Japan. For more details of song type distribution see Quaiser & Eck (2003), Martens et al. (1995), Martens & Nazarenko (1993) and Thönen (1962, 1996). – Slightly modified from Quaiser & Eck (2003).

The *baicalensis* group:

Taxa included (2): *P. m. baicalensis* (Swinhoe, 1871) [Lake Baikal, Russia]; *P. m. shulpini* (Portenko, 1954) [Suchan, southern Ussuriland, Khabarovsk Region, Russia].

Unresolved (see below): ? *P. m. suschkini* (Hachlor [sic!], 1912; Hachlov in German spelling; Khakhlov in Russian spelling) [river Temir-Su in the Ssaour Mts.²⁵, the eastern extension of the Tarbagatai Mts.].

Taxonomy: the *baicalensis* group is most easily characterized by its Siberian song type, Fig. 1c (herein); see also Martens & Nazarenko (1993), and recordings depicted in Cramp & Perrins (1993: 179-180) and Thönen (1996: 8-9). Treatment of subspecies reaching our area differs: Vaurie (1957a) and Snow (1967) accepted *baicalensis* from western to north-eastern Siberia and north-eastern China, whereas Stepanyan (1990, 2003) favoured a much broader taxon, his subspecies *borealis* included all the populations of the western taiga sector from Scandinavia to east of Lake Baikal, but this is a minority opinion.

The measurements of *suschkini*, according to Hachlov (1912), suggest *baicalensis* but he distinguished *suschkini* on grounds of darker and browner upperparts than *baicalensis*, larger black bib, and virtual absence of white fringes along tail-feathers. These characters seem comparable to those of two skins from the Ssaour Mts in the Kazakh part of the Tarbagatay, the type locality of *suschkini*, thus close to our area. Hachlov emphasized the presence of very large bibs in his new form (specimens from June and July, with one from March) with the underparts or belly having a beige tinge (“isabellfarbiger Anflug”). The March skin had an ochre-brownish touch on the feathers of the shoulder of the wing. This name seems likely to have been applied to ‘hybrids’ between *songarus* and *borealis*, view supported by the position of the Ssaour Mts which lie between Dzhungarian Alatau

²⁵ An adult male and a juvenile female from Temir-su river were examined by SE and suggest that this form is intermediate between *songarus* and *baicalensis*.

and Tien Shan (*songarus*) and Altai (*baicalensis*). Clearly, such issues need better understanding but meanwhile it seems best not to recognise *suschkini*.

One of us (S.E.) checked about a dozen skins from the Altai. Their wing and tail measurements largely cover the two quite distinct size pools of *borealis* and *baicalensis*, respectively (on the whole, however, they are closer to *borealis*). The crown of these birds is not so deeply saturated with black as in *baicalensis* proper. From this area several song types have been noted (Ernst, 1991; Martens et al., 1995; Ernst & Hering, 2000), which may reflect an area of secondary contact between carriers of different song types and may indicate a complex historical situation which includes inter-breeding of populations of different Pleistocene origin.

The subspecies *shulpini* from Ussuriland (in the Russian Far East, close to the border with north-eastern China; type and additional skins checked by S.E. at ZISP) has the back slightly more yellow than *baicalensis* and is valid; it is smaller and relatively short-tailed, like extralimital *borealis*. One of us (J.M.) has song recordings from the Russian Far East (lower Amur and Ussuriland; *shulpini*); they match the Siberian song type.

General characteristics: the two subspecies accepted differ slightly in the coloration of the upper parts, *shulpini* being browner, in wing length and in relative tail length (Eck, 1982); changes are clinal. TWI: *baicalensis* 94.1%, sd 2.08 (n = 70); *shulpini* 92%, sd 1.97 (n = 10). Territorial song: Siberian type (Fig. 1c).

Distribution: *baicalensis* group members extend from N Europe to E Siberia and NE China, but exclude areas close to the sea of Okhotsk, the Anadyr basin, Koryakland and Kamchatka [Omolon and Penzhina basins are still *baicalensis*]. Type specimens of *P. m. suschkuni* were from the Kazakh parts of the Saur Mts, not from the Chinese part.

Colour images: Eck, 1980a: pl. IIIa: *baicalensis*; Quinn in Harrap (1996), pl. 16, fig. 50e: *baicalensis*.

The *kamtschatkensis* group:

Taxa included (2; extralimital forms listed for convenience: 3): *P. m. anadyrensis* Belopolski, 1932 [Markovo, Anadyr basin, Magadan Region, Russia] EL; *P. m. kamtschatkensis* (Bonaparte, 1850) [E Asia = Kamchatka, Russia ²⁶] EL; *P. m. sachalinensis* Lönnberg, 1908 [Sakhalin; Russia] EL (vagrant to Hokkaido); *P. m. ssp.* [Hokkaido, Japan]; *P. m. restrictus* Hellmayr, 1900a [Shimotsuke, Honshu, Japan].

Taxonomy: Stepanyan (1990: 566) thought *anadyrensis* and *baicalensis* might intergrade, but in general the subspecies of the far eastern Palaearctic ranging from the Koryak Highlands to Kamchatka, Sakhalin Is., and Japan are linked by stepwise character gradation (Eck, 1982: 139-140). Lobkov (1997) suggested the occurrence of a sharp boundary between *baicalensis* and *kamtschatkensis* just north of Tymlat and Shamanka Rivers, c. 60°N in Kamchatka; he also suggested splitting off *kamtschatkensis* as specifically distinct: he listed it as '*P. (m.) kamtschatkensis*' and considered its status 'close to specific independence' (p. 371). Shikoku Willow tits have been described as *abei* Mishima (1961) but this is not recognized as distinct (Orn. Soc. Japan, 2000).

²⁶ As restricted by Hartert (1905a).

The evidence of song types in relation to distribution is intriguing. Portenko (1939a: 95) described *anadyrensis* song as “tjou-tjou-tjou”, which is difficult to relate to the song forms currently known in eastern Asia. Instead his description seems closest to the Lowland song type (Fig. 1b, which would be unusual for the region). Adjoining *kamtschatkensis*, to the south, sings the Alpine song (Fig. 1a), and *sachalinensis* the Siberian song (Fig. 1c), while in Hokkaido the Alpine song type is known (Thönen, 1996, Thönen & Fujimaki, 1995). Finally, the Sino-Japanese song type (Fig. 1d) is reported for *restrictus* from Honshu (Thönen, 1996).

The taxonomic situation of Hokkaido Willow Tits is unresolved. Hartert (1905a) declared that these do not belong to *restrictus*, but later merged them into this subspecies without further comment (Hartert & Steinbacher, 1934: 196). According to the Orn. Soc. Japan (1922: 157) Hokkaido is inhabited by *sachalinensis*, but Vaurie (1959) and the Orn. Soc. Japan (1974: 283; 2000: 237) accepted *restrictus*. However the song of these birds is known to be Alpine in character (Thönen, 1996: 18). This distinct song type indicates a different history for this population, implying Hokkaido Willow Tits should neither be merged into *sachalinensis* nor into *restrictus*. Abe & Kurosawa (1984a, b) published measurements of Willow Tits from Hokkaido, but the population should be carefully circumscribed and named.

General characteristics: from north to south the populations tend to become greyer, smaller, and relatively more short-tailed.

Distribution: *kamtschatkensis* group members occupy easternmost Siberia from Anadyrland to Kamchatka, as well as Sakhalin and Japan. Apparently, there is a gap in distribution: they are absent in the Kuril Is., while birds on the mainland shore of the Sea of Okhotsk are *baicalensis*.

Colour images: Eck (1980a): pl. IIIb: *anadyrensis*, *restrictus*; Quinn in Harrap (1996), pl. 16, fig. 50f: *kamtschatkensis*.

The *songarus* group:

Taxa included: *P. m. songarus* Severtsov, 1873 [Tian Shan]; *P. m. affinis* (Przewalski, 1876) [Ala Shan and Gansu]; *P. m. stoetzneri* Kleinschmidt, 1921a [30 km N of Balihandien, NE Jehol²⁷ = Balihan, Nei Mongol].

Taxonomy: if *songarus* is compared in coloration with *baicalensis* (or *borealis*) the difference is remarkable and its treatment as a separate species by Russian authors (e.g., Stepanyan, 1978, 1990, 2003) might seem justified. Roselaar in Cramp & Perrins (1993: 185) and Harrap (1996) both accepted this. However, Thönen (1996: 17-18) disagreed based on vocalizations. The song type of *songarus* is just a slightly modified Siberian song (Martens et al. 1995: 375-377). The subspecies *affinis* uses two different forms of the Alpine song type, differing by locality (Martens et al., 1995: 377-378), while for *stoetzneri* only the Alpine song type is known (but see Martens et al., 1995: 378). For the exclusion of *weigoldicus* from this group see below.

²⁷ For Balihan see Zhao & Adler, 1993: 427.

General characteristics: all taxa of the *songarus* group are yellowish brown on the back, and in the eastern part of the range the populations are more greyish. Only in *songarus* is the bib brownish; it is blackish in *affinis* and *stoetzneri*. All members of the *songarus* group have a more or less dark brownish crown, very different from the black cap of northern willow tits of the *baicalensis* group. The colour of the crown of *affinis* was given by Hartert (1905: 368) as “Pelzrobbebraun” (“Seal Brown” according to Ridgway, 1886, III.1), and is shown by Ridgway (1912) in his plate XXXIX; that of *stoetzneri* which is blackish orange brown = “schwärzlichorangebraun” (Anon., 2000, Michel-Farbführer, pl. 17) is quite close. It is deeply brownish in *songarus* as well. In *affinis* and *songarus* the typical willow tit wing patch is hardly to be seen or virtually absent (see colour plate VI in Eck 1980a). The tail/wing relations of *songarus*, *affinis* and *stoetzneri* differ considerably, *stoetzneri* being the smallest form but relatively long-tailed. *Stoetzneri* also differs slightly in colour between western and eastern parts of its range (S.E., based on material in IZAS). All three forms differ in size, *songarus* is a large form with wing up to 73 mm, *affinis* up to 68 mm, *stoetzneri* is smallest (up to 66 mm). For detailed measurements and tail/wing proportions see Eck (1980a: 151-153, 2006).

Distribution: with *weigoldicus* (*q.v.*) excluded these forms are highly disjunct: *songarus* occurs in central Asia (Kazakhstan, and in our area in Xinjiang), *affinis* is found only in western China (NE Qinghai, Gansu, N Sichuan, SW Shaanxi and Ningxia); and *stoetzneri* in northeast China (Shanxi, Henan, Hebei, Beijing and SE Nei Mongol Zizhiqu).

Colour images: Eck, 1980a: pl. VI: *stoetzneri*, *affinis*, *songarus*; Quinn in Harrap (1996), pl. 16, figs. 51a: *songarus*, b: *stoetzneri*.

***Parus weigoldicus* Kleinschmidt, 1921b**

Taxon included (1): *P. weigoldicus* Kleinschmidt, 1921b [Atentze (= Atuntze, now Tehtsin)]²⁸. – Monotypic.

Taxonomy: the close relationships of the taxa perceived as the *songarus* group (*songarus*, *affinis*, *stoetzneri* and *weigoldicus*), were never called into question until Salzburger et al. (2002b) detected a marked cytochrome-*b* distance of 4.6-5.9% between *weigoldicus* and all other Willow Tits (incl. *songarus*, *affinis*).

In the phylogenetic topology generated *weigoldicus* is sister to all other Willow Tits including *affinis* and *songarus*. The unexpectedly high distance value indicates separate development by *weigoldicus* over the last two to three million years (based on the rule suggesting 2% distance per 1 million years of separate development (Lovette, 2004).

²⁸ Kleinschmidt (1921a) listed “z. B. Atentze”. This was thus an example of a collecting locality and he implies that there must have been two or more type specimens. It follows that although a specimen was labelled to suggest that it was a holotype, as indicated by Eck & Quaiser (2004: 290), we now note that it does not qualify (see Art. 73.1.3 of the Code, ICZN, 1999). Under the terms of Art. 74.7 this error did not accidentally result in a lectotype, and the specimen, C 23803, from Mauntschi (Barongschiba) remains a syntype. The other specimens listed by Kleinschmidt & Weigold (1922) are not all in Dresden, one is in the AMNH, and consultation seems desirable before any decision is made on whether lectotypification is appropriate, especially if the current name and coordinates of Mauntschi require clarification.

In size *weigoldicus* is similar to the Tian Shan Willow Tits (*P. montanus songarus*), but it differs conspicuously from parapatric *affinis* by larger wing length, shorter tail length, smaller TWI and less pronounced tail gradation, and in coloration (see Eck, 1980a: 151-153 and Eck, 2006 for details). The song type is Sino-Japanese (Thönen, 1996: 9, Martens et al., 1995) while that of *affinis* is the Alpine type. More work is needed on the Chinese Willow Tits but despite the present lack of additional biological data, especially regarding interactions with adjoining *affinis*, which would allow a better characterization of *P. weigoldicus*, the molecular evidence compels us to accept specific status for *weigoldicus*. We recommend the English vernacular name Sichuan Willow Tit.

General characteristics: conspicuously dark, earthy brown – “erdbraun”, (Kleinschmidt, 1921a) – on the back, the flanks very dark. For measurements and tail/wing length relationships see Eck (2006). No specimens are known which might indicate interbreeding with the parapatric *P. montanus affinis*.

Distribution: highly restricted; Sichuan and parts of northern Yunnan, China. The range is parapatric to that of *P. m. affinis* (see detailed map in Quaiser & Eck, 2003). The existence of a contact zone with the latter is so far unknown. *P. weigoldicus* is apparently a rare bird and not easily encountered.

Colour images: Eck, 1980a: pl. VI, bottom figure.

***Parus superciliosus* (Przewalski, 1876)**

Taxon included (1): *Parus superciliosus* (Przewalski, 1876) [alpine regions of ‘Gansu’²⁹]. – Monotypic.

General characteristics: the White-browed Tit is an unmistakable rather long-tailed tit with a white eye-brow. No taxonomic problems known.

The cytochrome-*b* molecular phylogeny places *P. superciliosus* at the base of the *Poecile* group or close to it (Gill et al., 2005). Detailed measurements are given in Eck (2006).

This tit inhabits tree-less high-altitude steppes, where only bushes persist. Nevertheless like all other *Parus* species, it is a hole-breeder, breeding in the burrows of pika and other rodents (Martens & Gebauer, 1993), or in fissures of rock faces. The first nest located (south of Koko Nor, Qinghai) held young and was situated in a rodent hole in a loess cliff and was entirely composed of moss (J.M., unpublished).

Distribution: high altitudes on the Tibetan plateau, China, but only locally: in NE and SE Tibet proper, E Qinghai and NW Sichuan.

Colour images: Pleske, pl. VIII: 3, 4; Kleinschmidt, 1911; Eck, 1980a, pl. 9, upper figure; Quinn in Harrap, 1996, pl. 18, fig. 56; Anderton in Rasmussen & Anderton, 2005, pl. 155, fig. 7.

²⁹ Vaurie (1972: 88, 88fn), who used the name Tibet in a geographic, not political sense, wrote of Przewalski’s specimens labelled ‘Gansu’ “I was not sure at the time that they had been collected in Tibet, but I believe now that these were probably taken in Tibet, chiefly in the South Tatung Range, not in Kansu proper”. Vaurie (1972: ix) mapped the Tatung River (now Datong He) north of Hsi-ning (now Xining), and the range, now the Daban Shan, is close to southern bank of the river. It is in fact in present day Qinghai.

***Parus davidi* (Berezowski & Bianchi, 1891)**

Taxon included (1): *Parus davidi* (Berezowski & Bianchi, 1891) [S Gansu]. – Monotypic.

Taxonomy: one of us (S.E.) has held varied views on the conspecificity of *P. davidi* Père David's Tit with west Palaearctic *P. lugubris* Temminck, 1820, the Sombre Tit; these forms seem related by morphology and geography and it has been hypothesised that connection was through *P. l. hyrcanus*. Eck (1976: 33) did not consider this, but later (Eck, 1980a), after a comparison with *hyrcanus*, came to accept it and used a broad species concept (see Eck, 1996).

However, one of the cytochrome-*b* topologies places *P. davidi* and *P. lugubris* as paraphyletic groups at the basis of the 'Poecile' tree (Gill et al., 2005) and the conspecificity of *P. davidi* and *P. lugubris* is not maintained here.

Distribution: central China.

General characteristics: a small, vivid and intensely-coloured tit with a thick bill. Wing length up to 71 mm, tail length up to 54 mm. TWI: 74.7%, sd 2.13 (n = 24).

Colour images: Berezowski & Bianchi, 1891, pl. II: 4; Eck, 1980a: pl. II; Quinn in Harrap, 1996, pl. 18, fig. 57.

***Parus cinctus* Boddaert, 1783**

Taxon included (1, extralimital form listed for convenience: 1): *P. c. cinctus* (Boddaert, 1783) [Siberia], *P. c. sayanus* (Sushkin, 1904) [W Sayan, Altai] EL.

General characteristics: *sayanus*, a southerly montane form, is similar to nominate *cinctus* in the relative length of wing and tail (TWI: 95.9%, sd 1.17, n = 10), but is markedly larger, wing up to 76 mm.

Taxonomy: the breeding localities in Mongolia are close to the type locality of *Parus (Póecila) obtectus* Cabanis, 1871 ('south of Lake Baikal'). That form is usually treated as a synonym of nominate *cinctus* (Snow, 1967, Stepanyan, 1990). Consequently, we list nominate *cinctus* for our area. However, according to Mauersberger (1983), Nazarenko (1978) identified new material from southern Transbaikalia with *sayanus* and treated this as extending into northern Mongolia.

Distribution: early suggestions that the Siberian Tit occurred in China have been discussed and finally rejected by Vaurie (1957a, 1959). Cheng (1976, 1987) also expressed doubts about old records and knew of no new records. Zheng (2005) did not even list the species for China. The species nonetheless reaches north-west Mongolia where it breeds in an area just west and east of Hövsgöl Nuur and in N Kentei (Hentyin Nuruu) (C.S. Roselaar pers. comm.). Whether *sayanus* reaches our area (as a breeding bird) remains unclear. Dickinson et al. (2006) consequently list it as 'probably extralimital'.

Colour images: Eck 1980a, pl. VIII: *lapponicus* (extralimital); Quinn in Harrap, 1996, pl. 19, fig. 58a-c: *lapponicus*, 58d: *cinctus* (both extralimital).

***Parus rubidiventris* Blyth, 1847**

Taxa included (4): *P. r. rubidiventris* Blyth, 1847 [Nepal]; *P. r. beavani* (Jerdon, 1863) [Mt. Tonglloo, Sikkim, India]; *P. r. whistleri* Stresemann, 1931 [near Lau-hu-kou, S Tetung (= Datong) Mts., NW Gansu,

China]; Syn.? *P. r. szetschwanensis* Meise, 1937; see below [Wa Shan, E Hsikang, now W Sichuan]; *P. r. saramatii* Ripley, 1961 [Mt. Saramati, Naga Hills ³⁰, Myanmar].

Taxonomy: until recently the Rufous-vented Tit posed no taxonomic problems except for the fact that the two Sino-Himalayan subspecies, *P. r. rubidiventris* (western Himalayas) and *P. r. beavani* (eastern Himalayas, China), were sometimes considered to represent different species (Wolters, 1980; Haffer, 1993), though on scant evidence except for marked differences in coloration of grey-bellied and rufous-bellied populations. No hybrid population of these strongly different subspecies had been detected, but, apparently, nobody paid special attention to this question. Allegedly, the range of *rubidiventris* overlapped with that of *beavani* (see Martens 1975); but there had been no recent confirmation. Even though such a zone of contact might have been expected in the upper course of Bhote Kosi valley (somewhat northeast of Kathmandu).

Cytochrome-*b* data depict a more complicated evolutionary situation (Martens et al., 2006). Within the continuous Sino-Himalayan region (Kashmir to Shaanxi, China) all *P. rubidiventris* populations fall into two deeply split clusters (with a distance value between them of about 2.5%) and these do not coincide with the current subspecific delimitation of rufous-bellied *rubidiventris* and grey-bellied *beavani* (Fig. 2).

³⁰ Mt. Saramati lies exactly on the border with India and is judged to be a part of the Naga Hills.

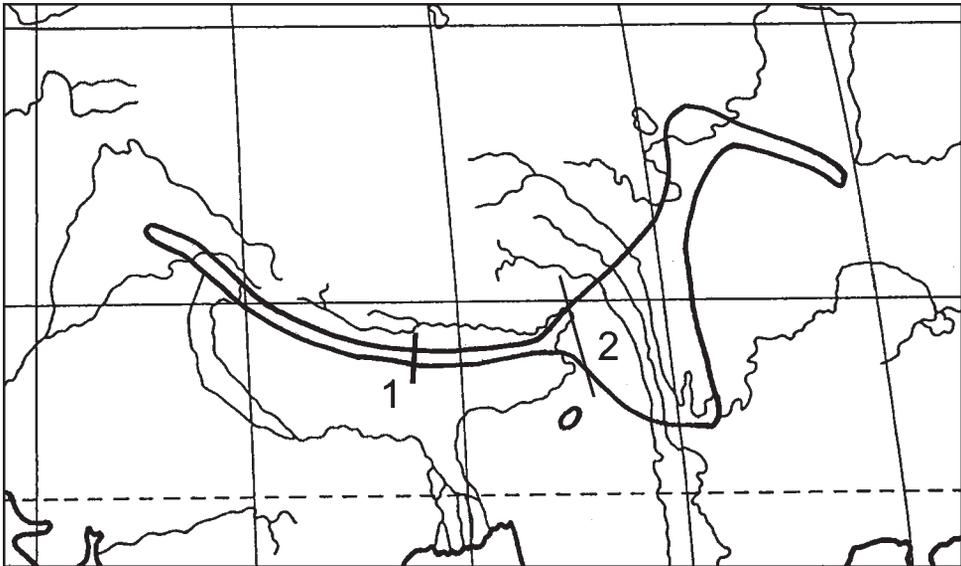


Fig. 2. Distributional map of subspecies and of cytochrome-*b* haplotype clusters of *Parus rubidiventris*. Solid bar (in Himalayas, 1) indicates the distribution limit of reddish-bellied western nominate *rubidiventris* and of grey-bellied eastern *beavani* and *whistleri*; isolated area: *saramatii* (grey-bellied). Thin bar (SW China, 2) separates cytochrome-*b* haplotype clusters, i.e. the Himalayan cluster (nominate *rubidiventris* and *beavani*) and the Chinese cluster (*whistleri*). Haplotype affiliation of *saramatii* unknown. – Slightly modified from Martens et al. (2006).

The populations in the Himalayas proper, i.e., western rufous-bellied nominate *rubidiventris* and grey-bellied *beavani*, belong to the same cytochrome-*b* haplotype cluster and can carry the same haplotype. Thus most of the western, Himalayan, part of the range of *beavani* belongs to a cytochrome-*b* cluster that is deeply different from the eastern cluster which relates to populations in the eastern parts of the range of *beavani*, i.e. in China. Representatives of the two clusters also differ in body size.

For the genetically different Chinese cluster (eastern grey-bellied "*beavani*") the oldest available synonym is *whistleri* and the use of this was revalidated by Martens et al. (2006). Originally, *whistleri* (from Gansu) was separated from *beavani* on the basis of its smaller size and lighter slaty-grey upperparts. Further south, birds from Sichuan were separated as *szetschwanensis*. Like *whistleri* they were considered to be smaller than *beavani* and they differed by being darker slaty-grey above (Meise in Stresemann et al., 1937). Both these small forms, which also differ from *beavani* in flight feather proportions, were unfortunately lumped with *beavani* by Vaurie (1957a). For the moment, we keep *szetschwanensis* in the synonymy of *whistleri*, which is clearly a valid form. A more thorough revision of the eastern grey-bellied tit 'cluster' is needed. *P. r. saramatii*, a disjunct population from the Naga Hills, is apparently smaller and differs in coloration from *beavani* and *whistleri*, its cytochrome-*b* cluster assignment is unknown.

The cytochrome-*b* sequence difference between the western cluster (rufous- and grey-bellied forms in the western central and eastern Himalayas) and the eastern cluster (in China and probably in parts of the easternmost Himalayas, but see below) is up to 2.5%. This is the same magnitude of difference as between the three southern cytochrome-*b* clusters of *P. ater* and to the values between the well-established species *P. venustus*, *P. amabilis* and *P. elegans* (see below).

General characteristics: centre of belly rufous or rusty red in *rubidiventris* from the western and west-central Himalayas. Measurements can be found in Martens & Eck (1995: 327). Belly grey in the eastern forms *beavani* and *whistleri*; and also in *saramatii*, but the nature of the grey tone differs (Ali & Ripley, 1973). Between the Himalayas and Gansu/China wing length decreases. Overall coloration differs locally. *P. r. beavani sensu stricto* has a TWI of 70.3%, sd 1.22 (n = 44) and a wing length of up to 74 mm (like *rubidiventris*); *whistleri/szetschwanensis* tend to have longer tails, their TWI is 71.9%, sd 1.30 (n = 31), maximum wing length 69 mm (see also Eck, 2006).

Distribution: nominate *rubidiventris* ranges from Kashmir (as a rare breeding bird, Jamdar & Price, 1990) east to at least Syng Gyang monastery in the Gosainkund Lekh at 85°21'E., just north of Kathmandu (Martens & Eck, 1995; specimen ZFMK). Even further east, in Helambu, Kandak-Kosi watershed, Malemchi Khola, rufous-vented birds were observed at about 85°31'E (Proud, 1951). Slightly further east, at appropriate altitude in the upper Bothe Kosi valley (at about 86°E, probably not in Nepal but in southern Tibet), nominate *rubidiventris* and *P. r. beavani* are thought likely to meet, but no such locality has yet been spotted. There is no information on the area where representatives of the two '*beavani*' clusters may meet; this may be somewhere in the eastern Himalayas or in SW China. C.S. Roselaar (*in litt.*) suggests that if size is a reliable basis for telling *beavani* from *whistleri*, the border between them is probably formed by the upper Mekong/Lancang rivers. According to Vaurie (1950), N Myanmar and NW Yunnan birds are still large, while Sichuan and Gansu birds are small. It is not yet clear whether birds from NE Burma should be associated with *whistleri* or with *szetschwanensis*.

Colour images: herein Pl. II, Fig. b: *rubidiventris*, c: *beavani*; *rubidiventris*; Martens & Eck (1995), pl. 2 is the same image; Quinn in Harrap (1996): pl. 20, figs. 62a-b: *rubidiventris*, c-d: *beavani*.

Parus rufonuchalis Blyth, 1849

Taxon included (1): *Parus rufonuchalis* Blyth, 1849 ["Range beyond Simla, near the snow-line", NW Himalayas. Synonyms? *blanchardi* Meinertzhagen, 1938 [Gardez Forest, E Afghanistan]; *parvirostris* Keve, 1943 [Naryn, Tian Shan]. – Monotypic.

Taxonomy: Martens (1971) discovered sympatric and even syntopic occurrences of *P. rubidiventris rubidiventris*, the Rufous-vented Tit, and the Rufous-naped Tit *P. rufonuchalis* during the breeding season in dry trans-Himalayan coniferous forests in west Nepal, proving the latter to be an independent species.

At different places either *P. a. melanolophus* or *P. a. martensi*, and *P. rubidiventris* occur in the same forest patches as *P. rufonuchalis*. Thus 'Periparus' is represented in the Himalayas by three different-sized species *rufonuchalis* (largest), *rubidiventris* (medium-sized) and *ater* Linnaeus, 1758 (smallest), and these size differences allow syntopic breeding. Sympatric occurrence of the two larger species in the western Himalayas has also been reported by Biswas (1963), Jamdar & Price (1990) and Gaston et al. (1993).

General characteristics: nuchal spot rusty; bib widely extended on lower breast. One of us (S.E.) found a maximum wing length of 79 mm and maximum tail length of 58 mm in *P. rufonuchalis* while *P. r. beavani* has a maximum wing length of 75 mm and a maximum tail length of 52 mm (Ali & Ripley, 1973: 183). When sexed correctly there seems to be considerable variation of measurements within sexes so that one may doubt whether *rufonuchalis* is uniform throughout its range (see measurement details in Eck, 2006). However, mitochondrial cytochrome-*b* haplotype evidence from Nepal and Kyrgyzstan (Martens et al., 2006) so far suggests there is no geographical variation. Should subspecific treatment be needed synonyms are available (see above).

Distribution: from the Tian Shan to the western Himalayas in west Nepal (eastern Dhaulagiri area), as far east as the dry Kali Gandaki river gorge in east Dhaulagiri/west Annapurna (Martens, 1971, Inskipp & Inskipp, 1991, Martens & Eck, 1995). In China it is restricted to SW Kokshaaltau and the E Pamir Mts in W Xinjiang (Vaurie, 1972). It also occurs in the uppermost Sulej valley just within SW Tibet, but this is not mapped in Cheng (1987). A record (dot) in Cheng (1987: 887, map 701; under *P. rubidiventris*) in eastern Tian Shan needs verification as this is far east of known distribution in this range (C.S. Roselaar pers. comm.).

Colour images: herein Pl. II, Fig. a; Martens & Eck, 1995, pl. 2 fig. a (same image); Quinn in Harrap, 1996, pl. 20, figs. 61a-b.

Parus ater Linnaeus, 1758

Introduction: the taxonomy of Coal Tits in the Himalayas is still in debate (Martens & Eck, 1995, Harrap, 1996, Dickinson, 2003), but a fresh evaluation can be offered based on surprising molecular genetic data obtained recently (Martens et al., 2006).

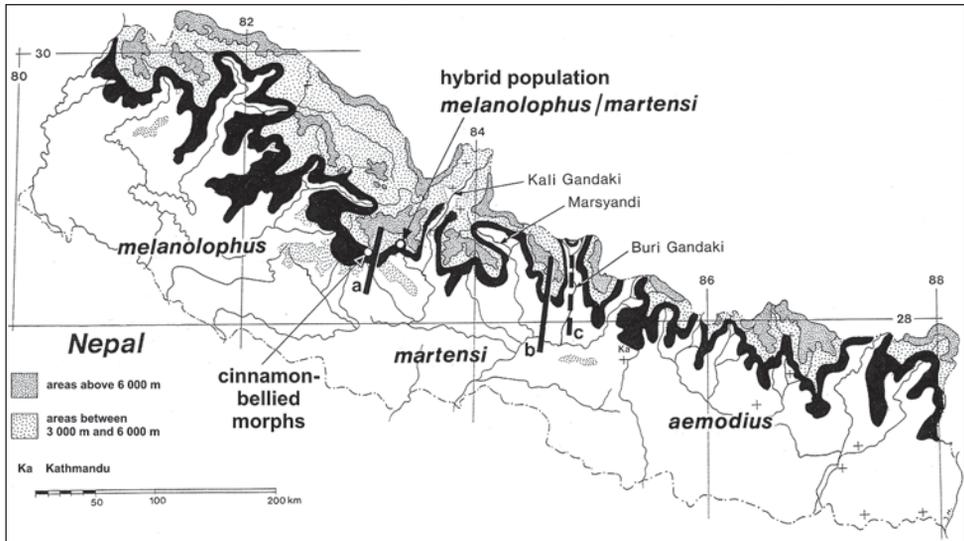


Fig. 3. Distribution of the Coal Tit complex (*Parus ater sensu lato*) in Nepal. In the upper Myagdi valley *melanolophus* and *martensi* meet and hybridise, *martensi* occupies a small area in the eastern Dhaulagiri and Annapurna ranges; east of the Annapurna massif *aemodius* occurs, extending to the easternmost Himalayas. Cinnamon-bellied morphs of *melanolophus* are known from the Dhorpatan valley only. Black shading: potential breeding zone of the *P. ater* group, roughly between 3000 and 4000 m. – Slightly modified from Eck (1998). Bars shown: a. eastern limit of *P. a. melanolophus*; b. eastern limit of *P. a. martensi*; c. the Buri Kandaki valley (Coal Tit population awaiting determination). Further east *P. a. aemodius* occurs.

Marked colour and pattern differences between western and eastern Himalayan Coal Tit populations (and Coal Tits in general) led to a conclusion with which nearly all recent authors agreed (Hartert 1905a, Harrap 1996, Inskipp et al., 1996, Dickinson, 2003), namely that two small ‘*Periparus*’ species inhabit the Himalayas: monotypic *P. melanolophus* Vigors, 1831, in the west, and representatives of *P. ater* (*martensi* Eck, 1998, and *aemodius* Blyth, 1845³¹) in the east, ranging into western China.

However the situation has steadily been revealed to be considerably more complex. In the south-western Dhaulagiri area of west Nepal “cinnamon-bellied hybrids” were discovered (Diesselhorst & Martens, 1972) (Fig. 3). These have a striking colour pattern, which differs from *melanolophus* in the dark chestnut-red centre of the belly, and differs strongly from typical Himalayan Coal Tits as well (Diesselhorst & Martens, 1972, Martens, 1994; Martens & Eck, 1995: 330-332, pl. 3 fig. d). An alternative hypothesis was that these birds were a local colour morph, not hybrids (Diesselhorst & Martens, 1972, Martens & Eck, 1995) – possibly a vanishing form (Eck, 2006). This *ater* population lives at low density within the range of *melanolophus*-coloured birds in a single high-altitude valley, the Dhorpatan valley at the south-western corner of the Dhaulagiri massif, and they interbreed freely with local *melanolophus* (Martens, 1975). Subsequently, small-sized ‘*Periparus*’ were found more continuously along the Himalayan chain and *P.*

³¹ Dated 1844 in Snow (1967: 93); for reasons to change see Dickinson & Pittie (2006).

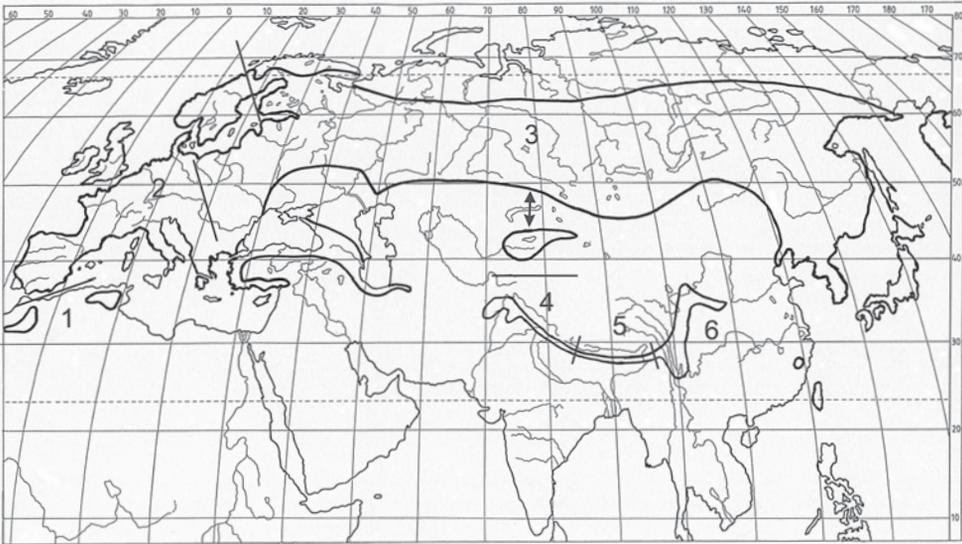


Fig. 4. Distribution of cytochrome-*b* haplotype clusters of *Parus ater sensu lato* in the Palearctic. Numbers indicate the cytochrome-*b* lineages and the bars signify the appropriate distribution limits between them (of which details are unknown). – 1: North African cluster; – 2: Central/South European cluster; – 3: Siberian cluster (several subspecies and includes disjunct Japanese *insularis* and Tian Shan *rufipectus*); – 4: West Himalayan cluster (*melanolophus*); – 5: East Himalayan cluster (*martensi*, *aemodius*); – 6: Chinese cluster (*eckodedicatus*). Cluster not yet determined and area without number: southeast China (*kuatunensis*) and Taiwan (*ptilosus*). Extralimital to the area under consideration are lineages 1 and 2. – Slightly modified from Martens et al. (2006).

melanolophus was reduced to a “semispecies” (Martens, 1975), and later to subspecies rank (Eck, 1996, Martens & Eck, 1995). More recently a population of the Coal Tit complex with a highly variable colour pattern was located in the upper course of the Myagdi valley in the south-eastern Dhaulagiri massif, some 50 km from Dhorpatan; these birds appeared to be ‘hybrids’ between *aemodius* and *melanolophus* (Martens & Eck, 1995: 337) and this was supported by their molecular genetics (Martens et al., 2006). About 30 km further northeast of the upper Myagdi Valley, along the upper course of the Kali Gandaki river another quite distinct and highly restricted Coal Tit population exists, which in colour is close to eastern Himalayan *aemodius*, not to *melanolophus* (colour plates in Martens, 1993, Martens & Eck, 1995, republished here). This was described as *P. ater martensi* by Eck (1998). From the neighbouring Marsyandi valley eastwards the Himalayan chain is inhabited by *P. ater aemodius*; its range extends to the mountains of western China.

More complete recent molecular genetic analyses paint a complicated, but different picture of the *Parus ater*/*P. melanolophus* complex (Martens et al., 2006). In the Palearctic it is divided into (at least) six distinct cytochrome-*b* haplotype clusters, of which four occur in our area (Fig. 4). The Sino-Himalayan area contains three of them: one is typical *melanolophus* (western Himalayas), the second is in the eastern Himalayas and the third in western China while the contact area between these two is not yet known. Fourthly, we have a variable ‘hybrid’ population (*melanolophus* × *martensi*) in a

restricted area in western Nepal, where the western cluster (*melanolophus*) mixes with the eastern Himalayan cluster as confirmed from cytochrome-*b* haplotype details and discussed above.

P. a. aemodius sensu lato is subdivided into two cytochrome-*b* clusters, which are restricted to the Himalayas and to western China respectively. The Chinese cluster, for which no name was previously available, has recently been described as *P. a. eckodedicatus* Martens, Tietze & Sun, 2006.

Another geographically extended cytochrome-*b* cluster ranges from northern and east-central Europe and central Asia via Siberia to Japan. It includes the proven subspecies, *ater* Linnaeus, 1758, *rufipectus* Severtsov, 1873, *amurensis* Buturlin, 1907, and *insularis* Hellmayr, 1902.

This clear-cut genetic structure is somewhat inconsistent with current subspecies limits (see below). The value distances between the eastern Palaearctic clusters are remarkably high, ranging from 2.6% to 3.2%. They indicate differentiation times of roughly 1.5 m.y. (based on the 2% rule) and the value distances are even higher (up to 3.4%) when the two remaining clusters from Europe and North Africa are compared with them.

This arrangement of geographical “forms” makes the Coal Tit one of the most variable passerine species of the eastern Palaearctic and in the Old World in general.

Below we arrange the Asian subspecies according to their cytochrome-*b* cluster affiliation. Within clusters some subspecies may be morphologically similar and others very different (as in the Siberian cluster for example); equally subspecies of different clusters may be very similar (East Himalayan and Chinese clusters).

The Siberian cluster:

Taxa included (4, extralimital forms listed for convenience: 1): *P. a. rossosibiricus* Johansen, 1952 [Popowo, 20 km SE of Kainsk, Baraba steppe, west Siberia] EL; *P. a. rufipectus* Severtsov, 1873 [C Tian Shan]; *P. a. amurensis* (Buturlin, 1907) [Amur Valley]³²; *P. a. insularis* Hellmayr, 1902 [Surugano-kumi, Honshu, Japan]; *P. a. pekinensis* David, in Swinhoe 1870a [Peking = Beijing].

Taxonomy: based on coloration and proportions this cluster can be recognised in a number of different forms. In our area, the populations in Siberia are rather uniform, and not all subspecies have been universally accepted. The individuals belonging to the Siberian populations are uncrested. In view of unexpectedly distinct mitochondrial genetic characteristics, even among extremely similar populations (e.g., the east Himalayan cluster, see below) it seems best to accept some less pronounced subspecies in order to signal evolutionary units within the genetic clusters. In regard to *amurensis* note that Buturlin (1907) had enough specimens to give a range of measurements but did not specify a type and the whereabouts of his type material is unknown (see Dickinson et al. 2006, this issue). He wrote “Diese Form bewohnt die Stromgebiete des Amur und Ussuri, ferner Sachalin und die südöstliche Küste des Ochotskischen Meeres” indi-

³² The type locality given by Snow (1967) appears to be a derivation of the scientific name that Buturlin selected and not a restriction of type locality. As quoted above the range Buturlin gave included both the Amur and Ussuri river basins and Sakhalin as well as the south-east coast of the Sea of Okhotsk.

cating a substantial range. It may prove desirable to restrict the type locality and the best means of doing so would be to designate a lectotype hence we appeal for information on any specimens that may be his types.

The disjunct central Asian *rufipectus* is very similar in coloration to Himalayan *aemodius* but has no distinct crest although the feathers on the hind crown are slightly elongated. This subspecies is proportionately extremely long-tailed (measurements and proportions in Eck, 2006).

Distribution: this subspecies group spans the northern Palaearctic from northern Scandinavia and eastern Germany to Japan and reaches our area via Mongolia and north-east China (*amurensis* and *pekinensis*). Isolated populations occur in central Asia (*rufipectus*) and Japan (*insularis*).

Colour images: herein Pl. III, Fig. b: *rufipectus* Tian Shan; Martens & Eck, 1995, pl. 3b: is the same image; Quinn in Harrap, 1996, pl. 21, fig. 64f: *pekinensis*.

Southern clusters:

General characteristics: members of these southern clusters are found in the Himalayas and the mountainous areas of western China with outliers in Fujian/Jiangxi and Taiwan, and they have a long crest in common. They are disjunct from the northern Euro-Siberian-Japanese area (which includes the Siberian cluster). They vary strongly in coloration, the western Himalayan form (*melanolophus*) being dark slaty grey, and the eastern Himalayan and Chinese forms beige or chamois coloured on the belly. There is a cline of increasing wing length from the western Himalayas to western China (*melanolophus* via *martensi* and *aemodius* to *eckodedicatus*).

a) The west Himalayan cluster:

Taxon included (1): *P. a. melanolophus* Vigors, 1831 [Himalayas = Simla-Almora ³³]

Taxonomy: where in the eastern range of *melanolophus* this taxon meets *P. a. martensi* (of the east Himalayan cluster) a variable local 'hybrid' population arises in the upper Myagdi valley of the south-western Dhaulagiri massif. This population incorporates haplotypes of the west and the east Himalayan cytochrome-*b* clusters. Measurements are given in Martens & Eck (1995) and in Eck (2006); and a detailed map of *melanolophus* distribution is found in Wunderlich (1989). Löhrl (1994) crossbred Afghan *P. ater melanolophus* and German *P. ater abietum* in captivity. Offspring were quite variable and included individuals similar to the cinnamon-bellied hybrids of west Nepal, though less intense in reddish coloration.

Colour images: herein Pl. III, Figs. c-d (d is the cinnamon-bellied morph); Martens & Eck, 1995, pl. 3 is the same plate). Quinn in Harrap, 1996, pl. 63, figs. a-c; cinnamon-bellied morph: fig. e.

³³ Restricted by Ticehurst & Whistler (1924: 471) but not without some dispute.

b) The east Himalayan cluster:

Taxa included (2): *P. a. martensi* Eck, 1998 [west-central Nepal, Chadziou Khola valley, Thakkhola, Mustang District, Nepal ³⁴]; *P. a. aemodius* Blyth, 1845 ³⁵, *sensu stricto* [Nepal ³⁶].

Taxonomy: *martensi* differs from both *aemodius* (*sensu stricto*, eastern Himalayas) and *eckodedicatus* (China) by its bright ochre-beige vent and belly, and this character makes it a clear-cut and easily distinguished subspecies (Eck, 1998). Measurements in Eck (2006).

Colour images: herein Pl. III, Fig. e: *martensi*, f: *aemodius*; Martens & Eck, 1995, pl. 3c is the same plate; Quinn in Harrap, 1996, pl. 21, figs. 63d: *martensi* (subspecies still undescribed when Harrap, 1996, was published), 64k-l: *aemodius*.

c) The Chinese 'cluster':

Taxon included (1): *P. a. eckodedicatus* Martens, Tietze & Sun, 2006 [Wawu Shan, Sichuan, China].

Taxonomy: in outward appearance this newly described subspecies is very similar to Himalayan *aemodius*, but it forms a distinct cytochrome-*b* haplotype cluster and differs morphologically by having slightly smaller wing measurements and a slightly different vent colour. Through haplotype analysis this subspecies can be confirmed from Gansu, Sichuan, Shaanxi and northern Yunnan (Martens et al., 2006). The contact area with *aemodius* is not yet known, but is presumably in southwest Yunnan or in the eastern-most Himalayas.

Colour images: Martens et al., 2006, fig. 6 (colour photograph p. 117).

d) Undefined cluster(s):

Taxa included (2): *P. a. kuatunensis* la Touche, 1923c [Kuatun = Guadun, Fujian, China], *P. a. ptilosus* Ogilvie-Grant, 1912 [Taiwan, China].

These are highly disjunct, restricted-range populations in Fujian, Jiangxi and Anhui, and in Taiwan, respectively, which may represent cytochrome-*b* clusters of their own. Their molecular genetic arrangement is not yet known. Both have pointed crests.

Colour images: Wang et al. (1991: 209).

Parus venustulus Swinhoe, 1870b

Taxon included (1): *Parus venustulus* Swinhoe, 1870b [gorges of Yangtze = Chang Jiang]. Monotypic.

³⁴ This lies west of the range of *aemodius sensu stricto* (see Fig. 3 herein).

³⁵ Dated 1844 in Snow (1967: 93); for reasons to change see Dickinson & Pittie (2006).

³⁶ Eck (1998: 130) noted that due to the wide distribution of *P. a. aemodius*, from EC Nepal to C China, and the corresponding establishment of this name in the literature it is justifiable to refer the name *aemodius* to the form which is widely distributed in the eastern Himalayas (combined with the erection of the subspecies *martensi* this is implicitly a restriction of the type locality to eastern Nepal. – Ed.).

Taxonomy: Parkes (1958: 96) for the first time, and no doubt correctly, combined *P. venustus*, the Yellow-bellied Tit, *P. amabilis* Sharpe, 1877, and *P. elegans* Lesson, 1831, in a superspecies. Based on cytochrome-*b* molecular genetics both Gill et al. (2005) and Martens et al. (2006) found these species form a monophyletic group.

However, the cytochrome-*b* distance values are quite low in so far as these values are derived from forms to which species rank is assigned: 3.3% between *amabilis* and *elegans*, 3.4% between *venustus* and *amabilis*, and 3.8% between *venustus* and *elegans*. These values are of much the same order of magnitude as those between the cytochrome-*b* clusters of *Parus ater* (*q.v.*)³⁷ which are all treated as belonging to one species. Apparently, and more puzzling, there is no clear lineage sorting as to species. Three samples of *P. venustus* belonged to a single haplotype (Sichuan, Shaanxi; Martens & al., 2006) and were sister to a sample of *P. e. elegans* (Luzon). One of *P. e. mindanensis* (Mearns, 1905) (Mindanao) appeared as sister to one *P. amabilis* (Palawan) and also to the *P. venustus* and *P. e. elegans* sisters. Material from several more Philippine islands is needed to shed more light on these unexpected findings.

Morphologically, *P. venustus*, *P. elegans*, and *P. amabilis* differ not only in size, coloration and colour pattern, but also in flight feather proportions. *P. venustus* is extremely short-tailed – TWI: 54.6%, sd 1.65 (n = 12); WTI 23.7%, sd 1.42 (n = 13). The large *P. amabilis*, the allospecies from Balabac, Palawan and Calauit, is relatively long-tailed – TWI: 62.2%, sd 2.1 (n = 4); WTI: 19.6%, sd 1.76. The last allospecies, the smaller polytypic *P. elegans* (for distribution in the Philippines see Dickinson et al., 1991, or Kennedy et al., 2000) is similar in tail/wing proportions to *P. amabilis*.

General characteristics: there is marked sexual dimorphism in colour, moult, and feather generations (Löhrl, 1988, Harrap, 1996: 311). The behaviour of captive *P. venustus* was investigated by Löhrl (1987, 1988) and compared to other species. Löhrl discovered interesting similarities to *Parus ater* and to *Sylviparus modestus* Burton, 1836.

Colour images: Berezowski & Bianchi, 1891, pl. II: 3; Quinn in Harrap, 1996, pl. 18, figs. 65a-f.

Parus elegans Lesson, 1831

Taxa included (9): Not detailed here; no taxonomic changes have occurred since Snow (1967) and Dickinson et al. (1991).

Taxonomy: the Elegant Tit, endemic to the Philippines, is currently divided into nine subspecies (Snow, 1967; Dickinson et al., 1991) which indicates the high evolutionary potential of this insular species. The unexplained intraspecific molecular-genetic situation of *elegans* has been discussed above under *P. venustus*. Parkes (1958) placed *panayensis* (Mearns, 1916) in the synonymy of ssp. *elegans*, but with some doubt. The resultant range of the lumped taxon although seemingly contiguous is zoogeographically surprising since Panay usually hosts the same form as is found on Negros (E.C. Dickinson, pers. comm.).

³⁷ Although that between *venustus* and *elegans* is somewhat higher.

Colour images: Quinn in Harrap, 1996, pl. 22, figs. 66a-d: *elegans*, 66e: *gilliardi*, 66f: *albescens*, 66g-h: *mindanensis*.

Parus amabilis Sharpe, 1877

Taxon included (1): *Parus amabilis* Sharpe, 1877 [Balabac, Philippines]. – Monotypic.

Taxonomy: no special comments on the Palawan Tit, a restricted-range species endemic to Balabac, Palawan and Calauit in the Philippines (Dickinson et al., 1991). Placement on the topology of *Parus* based on the cytochrome-*b* gene was discussed by Gill et al. (2005) and Martens et al. (2006).

Colour images: Quinn in Harrap, 1996, pl. 22, figs. a-d.

Parus dichrous Blyth, 1845³⁸

Taxa included (5): *P. d. kangrae* (Whistler, 1932) [Koti State = Kangra, N Punjab, India]; *P. d. dichrous* Blyth, 1845 [Nepal = northern C Nepal³⁹]; *P. d. izzardi* Biswas, 1955 [Thammu, Bhote Kosi valley, Khumbu, E Nepal; for recognition of this⁴⁰ see Martens & Eck (1995: 321-322)]; *P. d. wellsii* Baker, 1917 ['Big Bend of the Yangtze' = Chang Jiang, NW Yunnan, China]; *P. d. dichroides* (Przewalski, 1876) ['Gansu'⁴¹, China].

Taxonomy: Vaurie (1957a, 1959) accepted four subspecies of the Grey Crested Tit, and in his 1959 synoptic revision he described the colour differences between them as slight but well marked. Martens & Eck (1995: 321-322) pointed to a marked difference in wing length and relative tail length between *dichrous* (western Himalayas) and *izzardi* (eastern Himalayas). The easternmost known locality of *dichrous* (in Rasuwa Distr.; specimen in MTD) and the westernmost of *izzardi* (in Ramechhap Distr., specimen in ZFMK), both in Nepal, are about 125 km apart. It remains unknown whether there is a continuous cline connecting these two populations or whether they range closer and an abrupt character change occurs, but we repeat here that we feel it best to recognise *izzardi*. Though the material is still somewhat sparse (*dichrous* 4♂, 2♀, *izzardi* 9♂, 4♀; all from Nepal, the Martens and Diesselhorst collections, see Martens & Eck, 1995; Diesselhorst, 1968, and one additional specimen in MTD), the difference between the two is obvious: wing length of ♂: *dichrous* 65.5-69 mm (mean 67.1); *izzardi* 71-75 mm (mean 72.4). TWI of ♂: *dichrous* 63.8-66.4% (mean 65.4), *izzardi* 66.7-72.2% (mean 68.8, sd 1.68).

P. dichrous forms a superspecies with *P. cristatus* of the western Palaearctic (Martens & Eck, 1995: 331). These species share reddish eyes and have a similar voice (for sonagrams of *dichrous* see Martens & Eck, 1995, fig. 103a-i). Accordingly, in the cytochrome-*b* topology they fit as sisters (Gill et al., 2005).

Distribution: from the Himalayas to the Taibai Shan in the Qin Ling range, Shaanxi,

³⁸ Dated 1844 in Snow (1967: 93); for reasons to change see Dickinson & Pittie (2006).

³⁹ Restricted by Biswas (1955: 88).

⁴⁰ Vaurie (1959) and Snow (1967: 98) made this a synonym of nominate *dichrous*.

⁴¹ See footnote attached to *Parus superciliosus*. Most probably from Tibet.

in central China (Cheng, 1987) and north to NE Qinghai in the Qilian Shan (the former Richthofen Mts.) to about 38°N in N China (Stresemann et al., 1937).

Colour images: Quinn in Harrap, 1996, pl. 20, fig. 69a: *kangrae*, b: *wellsi*, c: *dichroides*.

Parus major Linnaeus, 1758, sensu lato

Introduction: the Great Tit is one of the most discussed species of Old World tits and this applies to its systematics and taxonomy. This is partly due to its vast range, which extends from North Africa across temperate Eurasia and into large parts of tropical South East Asia (Portenko & Wunderlich, 1984). This interest is also partly due to the considerable differences in colour, in mensural data and in morphology (e.g., tail/wing index, bill shape) of large population groups. This variety gave rise to numerous different named forms and to different ranking of the groups that seem to be composed of similar forms, rankings that even now differ markedly from author to author. Recently, substantial bioacoustic and molecular genetic work has been extended to the Great Tit. Fresh collecting, and field work in perceived contact zones, has helped to clarify some taxonomic problems.

Presently, four Sektoren ⁴² (singular Sektor), a term used by one of us (S. E.) in various papers, are accepted. Originally, these Sektoren were distinguished by colour alone (Stegmann, 1931), but later flight feather proportions were examined (Eck, 1977, 1980b, 1988), as well as vocalizations (Gompertz, 1968, Martens, 1994, 1996, Ivankina et al., 1997) and molecular genetics (Kvist et al., 2003, Päckert et al., 2005). Representative subspecies of all four Sektoren occur in the area we have under consideration, and two Sektoren are nearly confined to it (Fig. 5).

General characteristics: the *major* Sektor (group 1): yellow belly, greenish back; the *minor* Temminck & Schlegel, 1848, Sektor: greyish belly, greenish back; the *cinereus* Vieillot, 1818, Sektor: light grey belly, bluish-grey back; the *bokharensis* Lichtenstein, 1823, Sektor (= group 2 when placed within *major*): white belly, light grey back. Molecular phylogeny identifies the *major* and *bokharensis* groups and the *minor* and *cinereus* Sektoren, respectively, as close relatives (Kvist et al., 2003, Päckert et al., 2005) and in the case of the *major* and *bokharensis* groups we have merged the two into one Sektor (while retaining them as distinct groups of subspecies).

Formerly, the Great Tit was considered to be the classic example of a ring species (Rensch, 1933; Mayr, 1942: 182; a term still used by Kerimov & Formozov, 1986), but this was erroneous (Päckert et al., 2005). In a ring species the 'end' members of an uninterrupted and continuous ring of populations meet. In this case it was considered that they met in the middle Amur valley of eastern Siberia, and they were believed not to hybridize (Stegmann, 1928, 1929, 1931, Nazarenko, 1971). But for a long time the degree of reproductive isolation was not known.

Nevertheless, most western ornithologists grouped all these Sektoren into one extended, highly polymorphic species, *P. major sensu lato*, and the Sektoren were treated

⁴² Sektoren are groups of subspecies and may sometimes themselves comprise two or more identifiable groups of subspecies.

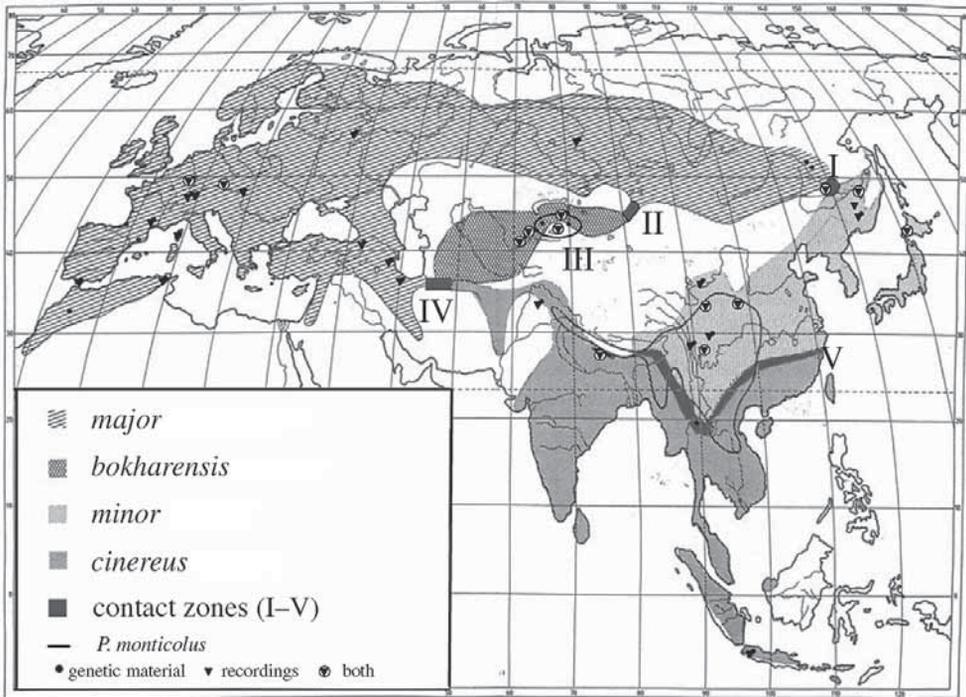


Fig. 5. Distribution of the component species of the great tit superspecies (*Parus [major]*) and their zones of secondary contact. Different shading indicates the areas of *P. major sensu stricto* (*major* and *bokharensis* Sektors, *P. minor* and *P. cinereus* and of *P. monticolus* (line only). Zones of contact and (restricted) hybridization are: – I. middle Amur valley, E Siberia (*P. major sensu stricto* and *P. minor*); – II. SW Mongolia, Bulugun valley (*major* Sektor and *bokharensis* Sektor of *P. major sensu stricto*); – III. Kyrgystan and Kazakhstan (man-made sympatry of *major* Sektor and *bokharensis* Sektor of *P. major sensu stricto*), – IV. trans-Caspian area of south Turkmenistan and north Iran (*major* Sektor and *bokharensis* Sektor of *P. major sensu stricto* and *P. cinereus*). – V. South China and parts of Indochina (*P. minor* and *P. cinereus*, hybridization resulting in *P. minor 'commixtus'*, full extent of hybridization unknown). – Slightly modified from Päckert et al. (2005).

as subspecies groups, with varying numbers of subspecies (Delacour & Vaurie, 1950). Vaurie (1957a) differed slightly, splitting off the *bokharensis* group as an independent species, *P. bokharensis*, from the rest of *P. major* on grounds of being “very distinct morphologically and apparently ‘overlapping’ in some regions [with *P. major*]... during the breeding season”. Most subsequent authors (Snow, 1967, Harrap, 1996, Dickinson, 2003) followed this view, but see Eck (1992; 1996: 47). By contrast Russian authors, adopting a typological view, treated all four Sektoren as independent species (e.g., Stepanyan, 1990, 2003), but rarely explained their rationale or logic, although Stepanyan (1983, 1988) was an exception.

Recent studies of vocalizations have clarified that at least two of the four Sektoren have different voice parameters for their territorial song (Martens, 1994, Ivankina et al., 1997, Päckert et al., 2005), and in part these are so different that an alien voice is not understood by members of another Sektor – for example *minor* group voices in the *ma-*

major group area (JM, unpublished). But vocalizations, in this case, may not be the most important pre-mating isolating mechanisms preventing hybridisation. Molecular genetic studies have demonstrated quite strong, but geographically differing, sequence distances between the Sektoren, and without doubt long-independent evolutionary histories of these Sektoren.

Here we treat the Great Tit as a superspecies, *Parus [major]*, which includes three allospecies, each of which requires species rank under the Biological Species Concept (Mayr, 1942): *Parus [major] major*, the Northern Great Tit, including the *bokharensis* group, *Parus [major] minor*, the Eastern Great Tit, and *Parus [major] cinereus*, the Southern Great Tit. Reasons are given below. We believe that treating these three taxa as allospecies within a superspecies best represents their close relationships and allows their geographic replacement to be kept in mind (see Helbig et al., 2002), as do the vernacular names suggested.

Parus [major] major Linnaeus, 1758 *sensu stricto*

Taxa included: A: *major* Sektor (2 relevant subspecies): *P. m. kapustini* Portenko, 1954 [Sretensk, eastern Siberia]; *P. m. bargaensis* Yamashina, 1939 [Lamagulusu, Lake Dalainor (now Hulun Nur), Manchuria, China ⁴³]. B: *bokharensis* Sektor (2 relevant subspecies, plus 2 extralimital ones added for clarity): *P. m. bokharensis* Lichtenstein, 1823 [Bukhara; ? Synonym *panderi* Zarudny & Härms, 1913 [Transcaspi] EL; *P. m. turkestanicus* Zarudny & Loudon, 1905 [Dsungaria, Semiratschja and Syr-Darja; implicitly restricted to the Syr-Darya area by Zarudny & Bilkewitsch, 1912 and further restricted to Tashkent by Eck, 1977: 197 ⁴⁴; Synonym *ferghanensis* Buturlin, 1912 [partem merid.-orient. Ferghanae (Mts. Alai) "hiemalis" ⁴⁵]; Synonym *meinertzhageni* Koelz, 1939 [Balkh, Afghanistan]; *P. m. iliensis* Zarudny & Bilkewitsch, 1912 [Djarkent (Semiratschja) = Zharkent, NE Kazakhstan] EL?; *P. m. dzungaricus* Zarudny & Bilkewitsch, 1912 [Orchu river, Dzungaria ⁴⁶] ⁴⁷.

Taxonomy and distribution: *P. major sensu stricto* covers most of temperate continental Eurasia and extends into eastern Siberia and northern China (Cheng, 1987). Nominate *major* is replaced by the lighter-coloured *kapustini* just east of Lake Baikal, and that meets *P. [major] minor* in the middle Amur valley, on both the Russian and Chinese sides of the Amur river.

Yellow-bellied and green-backed subspecies of the *major* Sektor that should be recognized within Chinese borders are not yet fully clarified. Cheng (1987) indicated

⁴³ Type in YIO, No. 00128; Yamashina No. 19037, adult male, 22.IV.1935; type locality given by Cheng (1987) as Lamuquer Miao, near Hulun Lake, Nei Mongol Aut. Reg.

⁴⁴ Because Zarudny & Loudon (1905) listed three areas and Zarudny & Bilkewitsch (1912) named new taxa from two of those the effect was to restrict the type locality of *turkestanicus* to Syr Darya. The restriction by Laubmann (1913) to the Orchu River was thus invalid and Vaurie (1950: 32) followed by Snow (1967: 110-111) were mistaken in following this, missing the fact that von Jordans (1923: 20-23) had already pointed out Laubmann's error.

⁴⁵ Snow (1967: 110) gave the type locality as "Kurshab, Alay valley, Kyrgyzstan; Ferghana (winter)" and Sudilovskaya (1959) reported that the type is from the 'Gul'cha area, Ferghana basin'.

⁴⁶ Dzungaria is in the northern part of Xinjiang and is indicated on modern maps by the Junggar Pendi (basin).

⁴⁷ For which recent authors, as explained in the earlier footnote, wrongly used the name *turkestanicus*.

kapustini for north-western Xinjiang Province and a disjunct presence in Nei Mongol. The first of these populations probably refers to birds representative of Siberian *major* which were released by hundreds between 1960 and 1965 in various localities in Kazakhstan, mostly close to Almaty (Dolgushin et al., 1972). These did well, enlarged their area considerably, e.g., into Kyrgyzstan (lake Issyk Kul basin) and also into SE Kazakhstan, in the Charyn valley close to the border of Xinjiang (Martens 1996), and they certainly have reached north-west China. The Nei Mongol population is indeed *kapustini* extending from the middle Amur into northern China, whose biological characters are now pretty well known (Päckert et al., 2005).

The type of *bargaensis*, held by the YIO and said to originate from Barga steppe near Hailar in Nei Mongol, has been kindly photographed by Hiraoka Takashi and, contrary to its placement by Cheng (1987: 879) in the synonymy of *artatus* Thayer & Bangs, 1909, which is part of the *minor* Sektor, belongs to the yellowish-greenish *major* Sektor.

The type localities of *kapustini* (Sretensk) and *bargaensis* (Dalai Nor, Barga steppe) are possibly only 350 km apart and Cheng (1987) may be correct that former Lamagusulu Monastery is now Lamuquer Miao, though Lamagusulu is some 100 km north of Lamuquer. Also, Barga steppe, from which the name *bargaensis* is derived, now Barag, is between Hailar and Hulun Nur (C.S. Roselaar pers. comm.). Consequently, *kapustini* and *bargaensis* may be synonyms, *bargaensis* being the older name. But see comments on *bargaensis* by Snow in Vaurie (1957: 42). The type of *bargaensis* seems unlikely to have been directly compared with topotypes of *kapustini* and until then we prefer to recognise both.

In the middle Amur valley, the yellow-bellied *major* Sektor meets the westernmost grey-bellied birds of the *minor* Sektor. The two differ in wing/tail proportions and size (Eck 1980b, 1988). The territorial songs of the two differ considerably in their elements, frequency range, and lower and upper frequency, and these differences are believed to act as premating isolating mechanisms, but they apparently do not hold in *P. major* (Päckert et al., 2005). Mitochondrial genome studies (control region [CR], Kvist et al., 2003; cytochrome-*b*, Päckert et al., 2005) showed that the *major* and *minor* aggregates are separated by a considerable genetic distance. In the faster evolving CR gene, this distance amounts to 5.9% (Tamura-Nei); using cytochrome-*b* the distance is 2.3% (uncorrected). This difference, at least in the case of cytochrome-*b*, is situated at a level which, in passerine birds, is sometimes used to define species limits, but at the lower end of the range for that indicator (Helbig et al., 1996). It seems important to us to add additional criteria to the complex of arguments.

Hybrids between the *major* and *minor* Sektors were reported by Portenko (1954), but not found by Nazarenko (1971). Later Eck (1980b) wrote of them again based on material in ZISP collected by I. A. Neufeldt, and Nazarenko et al. (1999) confirmed their occurrence. A detailed study by Päckert et al. (2005) discovered hybrids in a limited area of contact and overlap. But hybrids, determined in a collection of newly gathered skins by colour, flight feather proportions, and cytochrome-*b* cluster assignment, were quite rare: only seven of 52 specimens from the area of contact. Kvist et al. (2006) and Kvist & Rytönen (2006), largely based on the same material as Päckert et al. (2005), found a higher percentage of hybrids using nuclear microsatellite analyses rather than mitochondrial markers and morphological characters, indicating that hybridisation events are under-estimated by a cytochrome-*b*-analysis alone. A further population study in the

Amur contact zone by Fedorov et al. (2006) largely confirmed the results of Päckert et al. (2005), Kvist et al. (2006) and Kvist & Rytönen (2006). Thus there is, apparently, a zone of hybridization in existence but a large-scale swamping effect does not currently occur.

The two groups are also ecologically different; *major* Sektor tits are common in open habitat in villages, and *minor* birds on the outskirts of settlements and in nearby forests. *Major* seems to be a more aggressive species; its occurrence in the Amur valley is recent following human cultivation, as was first implied by Stegmann (1931), and it is still actively enlarging its range to the east (with single records in Khabarovsk close to the Pacific coast in 2000, see Päckert et al., 2005).

In the area of contact, *major* birds are also able to enlarge their vocal repertoire by learning and adding *minor* song elements. However, *minor* aggregate birds apparently do not learn *major* Sektor song elements. Consequently, their repertoire remains smaller and it seems difficult for them to find mates among the *major* birds and among hybrids within the zone of contact (Nazarenko et al., 1999). All these individual factors point to isolating mechanisms between *major* and *minor*, which prevent a swamping effect in the area of contact even though hybrids occur in considerable numbers.

Surprisingly, the *bokharensis* group is closest to the *major* group with cytochrome-*b* distances between them of only 0.8% (Päckert et al., 2005), a value typical of subspecies or even smaller population-level differentiation. In addition, territorial songs of the two Sektoren are remarkably similar with respect both to frequency range and form of elements (compare Fig. 6a-b with c-d). In a zone of contact in the Bulugun valley deserts of extreme south-west Mongolia, all specimens collected, about ten, turned out to be hybrids (Eck & Piechocki, 1977; Eck unpublished). In a new zone of secondary contact, caused by introduction, with resultant overlap of *major* and *bokharensis* birds in Kazakhstan, all specimens checked were considered to be hybrids (Formozov et al., 1993), yet in other areas (e.g., Charyn valley, SE Kazakhstan) they presently breed side by side apparently without large-scale mixing (Martens, 1996), and hybridization is not discernible from external morphology. Only one *bokharensis* from the Charyn valley carried a *major* haplotype (Kvist et al., 2003, Päckert et al., 2005). Thus, formation of mixed pairs between these morphologically very different forms is quite easily explicable and should not be seen as a remarkable occurrence as stated by Chalikova (2001). However the extent of mixing and further developments due to introductions of Siberian *major* birds deserve attention.

The *bokharensis* Sektor (of *P. major sensu stricto*) enters our area only marginally, in northern Afghanistan (*turkestanicus*), and in northern and central Xinjiang Province of north-west China *iliensis* and *dzungaricus* are involved (Delacour & Vaurie, 1950, Cheng, 1987)⁴⁸. The complicated taxonomy of the *bokharensis* group was reviewed by Delacour & Vaurie (1950, see their map), Vaurie (1957a), Eck & Piechocki (1977: 131) and Eck (1977, 1992). This group has a range that covers the central Asian desert areas and bridges the gap between the south-west Asian and Siberian parts of the *major* group within *P. major sensu stricto*. At the southern edge of this range, in 'Transcaspiä', the *bokharensis* group is in contact with the *cinereus* Sektor (Fig. 5) (Kerimov & Formozov, 1986). As Vaurie (1957a)

⁴⁸ Cheng (1987: 880) listed only *turkestanicus* but had *dzungaricus* in synonymy, mentioning the Junggar Basin; he did not mention *iliensis*, but the type locality, now called Zharkent, is just across the border from Yining and *iliensis* is very likely to occur in Xinjiang in the valley south of the Borohoro Shan.

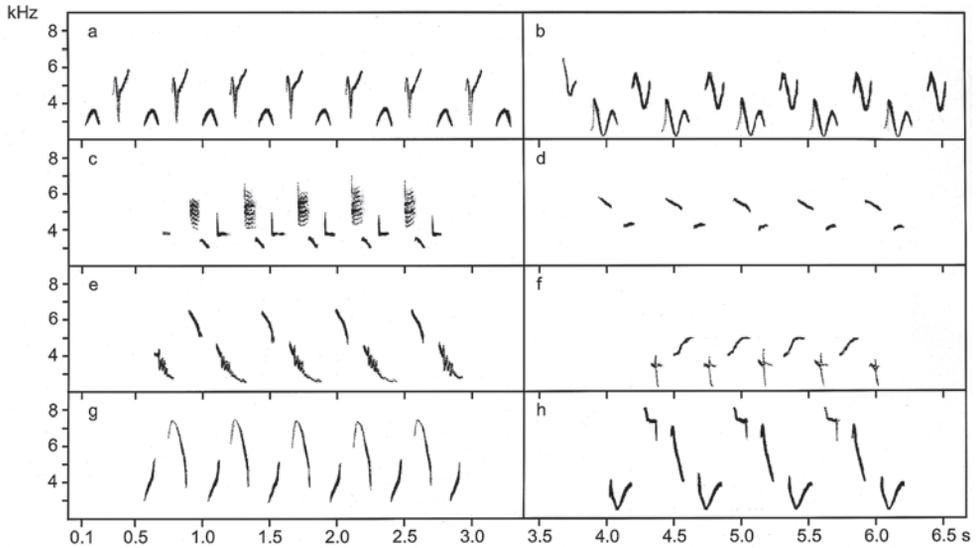


Fig. 6. Territorial song verses of *Parus major sensu lato*: a-b: *Parus minor*; c-f: *Parus major sensu stricto*, two each of the *major* Sektor (c-d) and of the *bokharensis* Sektor (e-f); g-h: *Parus cinereus*. - Recording localities: a) China, Yunnan, N of Zhongdian, 2002; b) Thailand, Chiang Mai, Doi Suthep, 1998; c) Kyrgyzstan, Issyk-Kol basin, SW of Kara-Kol, 1993; d) Iran, Mazandaran, Dasht-Nazir, 1978; e-f) Kyrgyzstan, Yarodar, 1993 (one verse each of two different males); g) India, vale of Kashmir, Tangmarg, 1976; h) Nepal, Bhojpur Distr., Arun valley W of Tumlingtar, 2001. - Recordings by J. Martens.

observed, the four subspecies of the *bokharensis* group are not only morphologically different, they also inhabit ecologically different areas. Though the differences between these subspecies are only slight, it presently makes sense to recognize them all.

As suggested by Päckert et al. (2005), *bokharensis* group is here merged with the *major* group of former *P. major sensu lato* to form *P. major sensu stricto* within a superspecies *P. [major]*.

Colour images: Martens, 1994, fig. 5a: *major*, fig. c: *bokharensis*; Quinn in Harrap, 1996, pl. 28, figs. 86a-e: *bokharensis*.

Parus [major] minor Temminck & Schlegel, 1848

Taxa included (10): *P. minor wladivostokensis* Kleinschmidt, 1913 [Vladivostok]; *P. minor dageletensis* Kuroda & Mori, 1920 [Dagelet I. (Ullungdo), Korea]; *P. minor minor* Temminck & Schlegel, 1848 [Japan = N Kyushu ⁴⁹ see Morioka et al., 2005: 87] Synonym *kagoshimae* Taka-Tsukasa, 1919 [S Kyushu] (see Morioka, 2000: 315); *P. minor artatus* Thayer & Bangs, 1909 [Yichang chi/Hubei, China]; *P. minor subtibetanus* Kleinschmidt & Weigold, 1922b [Tatsienlu (= Kangding), Sichuan, China]; *P. minor tibetanus* Hartert, 1905a [Chaksam, Tsangpo valley = Yarlung Zangbo, Tibet, China]; *P. minor*

⁴⁹ Restricted by Momiyama (1927: 29).

amamiensis Kleinschmidt, 1922 [Amami-Oshima I. ⁵⁰]; *P. minor okinawae* Hartert, 1905a [Okinawa, northern Riu Kiu Is.]; *P. minor nigriloris* Hellmayr, 1900b [Ishigaki, southern Riu Kiu Is. = S Nansei shoto]; *P. minor nubicolus* Meyer de Schauensee, 1946 [Doi Pa Hom Pok, border between Thailand and southern Shan States].

Taxonomy: there are several places across southern China and into Indochina where birds occur that show similar characteristics. These are thought to be of hybrid origin and Snow (1967) grouped them under the senior name: *Parus major commixtus* Swinhoe, 1868 [Tingchow = Dingzhou Mts., Fokien = Fujian]. The names *fohkiensis* la Touche, 1923a [Fujian], *indochinensis* Delacour, 1927 [NE Tonkin], and *makii* Momiyama, 1927 [Taiwan] are all treated as synonyms, but each needs further consideration.

On the border between north-east China and eastern Siberia *P. minor* is in contact with *P. major sensu stricto* but, as discussed above, hybridisation on the middle Amur is limited. In southern China *P. minor* is in contact with *P. cinereus*, and there are several locations where populations seem to be of hybrid origin (Fig. 5). According to Hartert (1923: 28, footnote), Delacour & Vaurie (1950) and Vaurie (1957a) *Parus major "commixtus"* can only be referred to hybrids from a contact zone between *P. minor* and *P. cinereus*. The mapped contact points occur within an elongated area from coastal south-east China west, probably, to parts of northern Thailand. But there are no recent investigations on population structure, extent of hybridization or vocalizations, let alone molecular genetics. Consequently, the population structure is virtually unknown and their interactions need to be studied.

General characteristics: the extent of the white markings on the tail feathers and of green on the back differs between subspecies.

Compared to nominate *minor*, *wladiwostokensis* is longer-winged and relatively long-tailed. In general, *P. minor* is longer-winged in the high-altitude areas in the south of its range (the wing in *tibetanus* is up to 82 mm). Birds from the islands of Japan are small and dark, but *nigriloris* from Ishigaki is a small, blue-backed and remarkably distinct form (T6 ⁵¹ is white-tipped; wing length ♂ 69 mm [type], 2 ♀♀ 62 and 65 mm), resembling *P. cinereus*, rather than being greenish-backed as is normal in *P. minor*. We recognize *P. minor wladiwostokensis* as it is longer-winged and has a greater relative tail length than nominate *minor* from Japan. Eck & Quaisser (2004) placed *tschiliensis* Kleinschmidt, 1922, in the synonymy of *wladiwostokensis*, which therefore reaches China.

One specimen from north-western Thailand (*nubicolus*, Mae Hong Sorn Prov., MTD) and two from northern Yunnan (*subtibetanus*, Zhongdian; MTD) represent the same cytochrome-*b* haplotype. This cluster is sister to all other specimens investigated from northern China, the Amur valley in eastern Siberia and Japan (M. Päckert, pers. comm., see topology in Päckert et al., 2005). These two groups are separated by distance values of between 0.9 and 1.7%. These differences amount to the cytochrome-*b* distances between the *major* group and *bokharensis* group of *P. major sensu stricto* and to those between *P. caeruleus* and *P. cyanus* in the western and eastern Palaearctic (Salzburger et al., 2002a). A complex pattern of what is probably Pleistocene diversification seems likely within the *P. minor* Sektor but this needs further study.

⁵⁰ Contrary to Snow (1967: 108) Amami-Oshima is not strictly a part of the Riu Kiu Islands (Morioka et al., 2005: 24).

⁵¹ T6 = the sixth pair of rectrices, thus the outer ones.

Territorial song of *P. minor* (Fig. 6e-f) largely differs from song of *P. major sensu stricto* by the much broader frequency range and sharp frequency changes within single notes of the song verse (Martens, 1996, Päckert et al., 2005), but there are similarities to the song of *P. cinereus* (*q.v.*).

When compared to the *bokharensis* group of *P. major sensu stricto*, *P. minor* is longer-tailed, with a relative tail-length (TWI) of up to 95% *vs.* 90% (Eck, 2006).

Distribution: from the middle Amur valley of Siberia across all China except for the barren and treeless parts of Qinghai, Tibet, Xinjiang and Nei Mongol and for southern China where it meets, and allegedly locally hybridizes with *P. cinereus* giving rise to "*commixtus*" (see above).

From Myanmar to Vietnam the distribution of the forms of *P. minor* and *P. cinereus* interdigitates and forms a rather complicated mosaic pattern, with various local subspecies involved. Snow (1967) listed *nipalensis* (of *P. cinereus* stock) in north-west Myanmar, with *tibetanus* in the north and *nubicolus* in the east (both of *P. minor* stock) and the largely disjunct form *ambiguus* Raffles, 1822, (of *P. cinereus* stock) in coastal Tenasserim. *P. cinereus* is also represented in north-east Thailand and neighbouring southern Vietnam by *templorum* Meyer de Schauensee, 1946. This part of the range of *P. cinereus* is isolated from that of *P. cinereus nipalensis* in north-east Myanmar by the interposition of *P. minor nubicolus* in north-west Thailand (Meyer de Schauensee, 1946, Vaurie & Delacour, 1950). In Thailand great tits occur only patchily (Lekagul & Round, 1991), and the exact distribution of the subspecies of *P. minor* and *P. cinereus* stock is yet not well documented. Lekagul & Round (1991) provided only one description although in addition to *nubicolus*, which is of *minor* stock, there is *templorum* on the eastern plateau and *ambiguus* in mangroves in the extreme south, both of *cinereus* stock.

Colour images: Martens, 1993, fig. 5b: *wladiwostokensis*, Quinn in Harrap, 1996, pl. 27, figs. 85f: *minor* (here given as similar to *wladiwostokensis*), i: *tibetanus*, j: *nigriloris* k: '*commixtus*'.

Parus [major] cinereus Vieillot, 1818

Taxa included (12): *P. c. ziaratensis* Whistler, 1929 [Ziarat, Baluchistan, Pakistan]; *P. c. decolorans* Koelz, 1939 [Jalalabad, eastern Afghanistan]; *P. c. caschmirensis* Hartert, 1905a [Gilgit, N Pakistan]; *P. c. nipalensis* Hodgson, 1837⁵² [Nepal]; *P. c. vauriei* Ripley, 1950 [Chabua, NE Assam, India]; *P. c. stupae* Koelz, 1939 [Sanchi, Bhopal, India]; *P. c. mahrattarum* Hartert, 1905b [Nuwara Eliya, Sri Lanka]; *P. c. templorum* Meyer de Schauensee, 1946 [Wat Pa, Lomsak, "central Siam" = eastern Thailand⁵³]; *P. c. ambiguus* Raffles, 1822 [Sumatra, Indonesia]; *P. c. cinereus* Vieillot, 1818 [Batavia, now Jakarta, Java, Indonesia]; *P. c. sarawacensis* Slater, 1885 [Bungal Hills, Sarawak, Malaysia]; *P. c. hainanus* Hartert, 1905b [Hainan I., China].

⁵² Not 1838 as in Snow (1967); this is in Vol. 2, part [1] comprising pages 1-74, within which on p. 52 there is the date Apr. 15, 1837.

⁵³ Meyer de Schauensee (1946) described Wat Pa as 'about 75 miles east of Pitsanulok', and Deignan (1963) placed this, the type locality, in Phetchabun province. Lomsak is a crossroad town where the road east from Pitsanulok meets a north-south road on the eastern side of the Dong Phaya Fai range. This places it on the eastern plateau and Deignan noted it from Ubon which is on the eastern side of the plateau. Snow (1967: 107) mentioned "western and central" Thailand, which does not agree, and included birds from southern Vietnam.

Taxonomy: the correct taxonomic rank for the *cinereus* Sektor of the *Parus major* complex is rather more difficult to establish. It is separated from the *minor* Sektor by a notable molecular genetic difference of 2.1 to 2.9% of the cytochrome-*b* gene (Päckert et al., 2005). These values, in themselves, are not a reason for a split at the species level. However, it is a level of the same magnitude as that between the *major* and *minor* Sektoren between which isolating mechanisms are established (see above).

Vocalizations of the *cinereus* Sektor (Fig. 6 g-h) are similar to those of the *minor* Sektor (Martens, 1996, Päckert et al., 2005) and considerably less different – both as evidenced by sonagrams and in song parameters – than those between the *major* and *minor* Sektoren, and while differences exist (Päckert et al., 2005) their meaning in a population context is unknown. External morphology, especially the flight feather proportions between these Sektoren is also similar. However, we must admit that morphological constraints, population structures (including hybridisation) and vocalizations in the south Chinese contact zone between the *minor* Sektor and the *cinereus* Sektor (where “*commixtus*” occurs) are little known. Outside our area at the north-western limit of the range of the *P. cinereus* Sektor, in north-eastern Iran and south-western and southern Turkmenistan, there is contact with the *major* group and the *bokharensis* group of *P. major sensu stricto*.

As suggested by Päckert et al. (2005), we give specific rank to the *cinereus* Sektor, as well the others, but substantial further research in zones of secondary contact is needed. See Helbig et al. (2002) for comments on the general taxonomic treatment of populations in areas of contact and (limited) hybridisation.

Distribution: the *P. cinereus* Sektor occurs across an enormous area from the central Afghan mountains and the subtropical foothills of the north-western Himalayas through India and deep into the Indo-Malayan archipelago. Conspecificity of *cinereus* from Java, and of the populations of Sumatra and Borneo, with those from the Asian mainland has not yet been investigated using modern techniques.

Although birds of the *major* Sektor carry lipochromes those of the *bokharensis* Sektor and of the *P. cinereus* Sektor do not, so that *cinereus* and *bokharensis* are somewhat similar in outward appearance, although differing in flight feather proportions. A detailed investigation of the great tits of Kopet Dag, the contact zone of these three taxa, will thus be particularly challenging and will be extremely interesting. To this area is ascribed “*Parus bocharensis* var. *intermedius*” Zarudny, 1890, [‘valleys of Karguy-Sou, Firouse, and Gujarmaou rivers, and hills and forests of Soumbar & Chandyr’ = along Kargy-su, Firyuza, Gyaur, Sumbar, and Chandyr rivers, Kopetdag Mts., SW Turkmenistan; extralimital]. It was suggested by Hartert & Steinbacher (1933: 176) that this name had been given to a hybrid population and this view was accepted by Delacour & Vaurie (1950), Vaurie (1957b), Mishchenko (1982) and Kerimov & Formozov (1985). However *intermedius* although said to have a greenish back and whitish underparts (similar to *minor* stock) may yet be shown to be best placed in the *cinereus* Sektor on non-morphological grounds. An understanding of this population will contribute importantly to our overall understanding of the allospecies treated here, as will a better knowledge of the *commixtus* zone (Fig. 5) and whether populations to the south of that (e.g., *hainanus*) truly belong with the *cinereus* Sektor.

For a fuller overview of western contact zones of Great Tits see Fig. 5 and Formozov et al. (1993).

Colour images: Martens, 1993, fig. 5c: *nipalensis*, Quinn in Harrap, 1996, pl. 28, figs. 85p-q: *caschmirensis*

Parus monticolus Vigors, 1831

Taxa included (4): *P. m. monticolus* Vigors, 1831 [Himalayas = Simla⁵⁴, N India]; *P. m. yunnanensis* la Touche, 1922 [Milati = now Zhicun, SE Yunnan, China]; *P. m. legendrei* Delacour, 1927 [Djiring, Langbiang Mts., S Annam, Vietnam]; *P. m. insperatus* Swinhoe, 1866 [mountains of S Taiwan, China].

Taxonomy: the Green-backed Tit is smaller than the Great Tit complex (*P. major sensu lato*), with coloration similar to parts of it, but with differences in the pattern of the inner vanes of outer tail feathers T4-6 (cf. Eck, 1980b: 388, fig. 3). Coloration increases in intensity from west to east (Vaurie, 1957a). It is a relative short-tailed species, TWI 79.9%, sd 2.38 (n = 9). In the cytochrome-*b* topology (Päckert et al., 2005) *P. monticolus* is sister to the whole *P. [major]* complex. The presence of lipochromes causing yellow and greenish coloration of belly and back in this complex thus seems to be a plesiomorphic trait, and its absence in *P. cinereus* and in the *bokharensis* group of *P. major sensu stricto* a secondary loss.

The highly disjunct *legendrei* has a conspicuously broad black ventral stripe. Vocal and molecular data for this form would be particularly interesting.

Distribution: the Himalayas, west and central China; disjunct populations in southern Vietnam and Taiwan.

Colour images: Martens 1993, fig. 5e: *monticolus*; Quinn in Harrap, 1996, pl. 29, figs. 87a-b: *monticolus*, c: *legendrei*

Parus nuchalis Jerdon, 1845

Taxon included (1): *Parus nuchalis* Jerdon, 1845 [Eastern Ghats, India]. Monotypic.

Taxonomy: the White-naped Tit is endemic to two apparently disjunct parts of India; locally present in the northwest though scarce, and rarer still in the south. This dry-country species, which is morphologically close to the *P. major sensu lato* complex and to *P. monticolus*, has not been sequenced for molecular genetic study and its voice has not been analysed.

It may form a superspecies with *P. monticolus* (for details see Eck, 1988: 115, footnote).

Recent distributional and ecological information of this little known species were presented by Hussain et al. (1992), Tiwari & Rahmani (1997), and Lott & Lott (1999).

Colour images: Quinn in Harrap, 1996, pl. 29, figs. 88a-c.

⁵⁴ Type locality restricted by Baker (1920b). Snow (1967: 111) dated this from the 1923 reprint; in fact this should be cited from J. Bombay Nat. Hist. Soc. 27 (2): 228-247 (for the date see Pittie, 2003). Note that Ticehurst & Whistler (1924) restricted the type localities of two other titmice (*P. melanolophus* and *P. xanthogenys*) from the same collection to Simla-Almora.

***Parus xanthogenys* Vigors, 1831**

Taxa included (3): *P. x. xanthogenys* Vigors, 1831 [Himalayas = Simla-Almora ⁵⁵, India]; *P. x. aponotus* Blyth, 1847 [Mts. of C India = Chaibasa, Singhbhun, Bengal ⁵⁶, India]; *P. x. travancoreensis* (Whistler & Kinnear, 1932) [Mynali ⁵⁷, S India].

Taxonomy: Rasmussen & Anderton (2005: 529) split the Black-lored Tit based on vocalizations and elevated *aponotus* of peninsular India to specific rank, with *travancoreensis* as a subspecies. The peninsular population is certainly disjunct from nominate *xanthogenys* of the western Himalayas, however there is no detailed information on territorial song, except for some sonagrams, and no acoustic playback experiments have been carried out yet. In addition no molecular genetic data seem to be available. The differences in colour in the wing bars of northern and southern populations may be no more than subspecific variation. For the time being we refrain from adopting this decision, believing more detailed studies are needed to support this split.

Distribution: endemic to India; two disjunct populations, widely separated by the Gangetic plain.

Colour images: Quinn in Harrap, 1996, pl. 31, figs. 89a: *xanthogenys*, b: *aponotus*, c-e: *travancoreensis*.

***Parus spilonotus* Bonaparte, 1850**

Taxa included (4): *P. s. spilonotus* Bonaparte, 1850 [Darjeeling, N Bengal, India]; *P. s. subviridis* Blyth, 1855 [Tenasserim, SE Myanmar]; *P. s. basileus* (Delacour, 1932) [Thateng, Bolovens Plateau, S Laos]; *P. s. rex* David 1874 [Kuatun, Fokien = Guadun, Fujian, E China].

Taxonomy: in the Yellow-cheeked Tit nominate *spilonotus* meets *P. xanthogenys*, the Black-lored Tit, in easternmost Nepal; but their interactions are so far unknown. A cytochrome-*b* difference of some 5.1% (Gill et al., 2005) strongly supports their validity as separate species; however the samples sequenced came respectively from “Nepal” and “Vietnam”. These are very distant populations, and if the sample from Vietnam came from the southern part of that country it may relate to a form totally disjunct from the Himalayan range. Further sampling is needed from closer to the contact area in eastern Nepal.

Distribution: mountainous subtropical areas from east Nepal through northern parts of Myanmar and Thailand to Laos, Vietnam and southern China, where perhaps the population of Fujian/Jiangxi is widely separated from more westerly Chinese birds now associated with it.

Colour images: Quinn in Harrap, 1996, pl. 31, figs. 90a-b: *spilonotus*, c-e: *rex*.

⁵⁵ Type locality restricted by Ticehurst & Whistler (1924).

⁵⁶ Type locality restricted by Whistler & Kinnear (1932).

⁵⁷ Not Mynall as in Snow (1967) and elsewhere. About 20 miles NNE of Trivandrum, in the shadow of two peaks greatly revered in South Travancore, Agastyamalai (6132 ft.) and Champunjimalai (5621 ft.).

Parus holsti Seebohm, 1894

Taxon included (1): *Parus holsti* Seebohm, 1894 [Taiwan]. Monotypic.

Taxonomy: the Yellow Tit is endemic to Taiwan. Monotypic with a peculiar and very distinctive morphology. The cytochrome-*b* topology places it as sister to *P. siltonotus* and *P. xanthogenys* (Gill et al., 2005).

Colour images: Quinn in Harrap, 1996, pl. 18, figs. 91a-c.

Parus cyanus Pallas, 1770

Taxa included: A. White-breasted Azure Tits (1, extralimital forms listed for convenience: 3): *P. c. koktalensis* (Portenko, 1954) [Koktal, Ili basin, Kazakhstan] EL; *P. c. hyperrhiphaeus* (Dementiev & Heptner, 1932) [Kustanai, Turgai region, Kirghiz steppe, Kazakhstan] EL; *P. c. yenisseeensis* Buturlin, 1911 [Konnyi near Krasnoyarsk, C Siberia, Russia] EL?; *P. c. tianschanicus* (Menzbier, 1884) [type locality restricted to Tian Shan; synonym *apeliotes* Meise, 1934, Tschen 21 km SE of Harbin, Heilongjiang, NE China]; B. Yellow-breasted Azure Tits (2, extralimital forms listed for convenience: 1): *P. c. carruthersi* Hartert, 1917 [Samarkand, Uzbekistan] EL; *P. c. flavipectus* Severtsov, 1873 ['Uylgum', not located, in Fergana basin *apud* Vaurie (1957a: 15)]; *P. c. berezowskii* (Pleske, 1893) [Guide, upper Chuan-che = Guide (36°04'N, 101°20'E) on upper Hoang-ho, NE Qinghai, China].

Taxonomy: once acoustic and molecular information was added to the taxonomic decision process species limits in the 'Cyanistes' complex changed substantially. Both in the west Palaearctic (blue tits) and in the east Palaearctic (azure tits) species limits are now drawn differently.

Traditionally, the split between Blue Tits (*P. caeruleus sensu lato*) and Azure Tits (*P. cyanus sensu lato*) had been thought to be older than that between the European Blue Tits (*caeruleus* group) and the North African/Canary Islands Ultramarine Tit group (based on *teneriffae* Lesson, 1831) (Martin, 1991). However, apparently the opposite is true and the "similar" African/Canary Islands and the European Blue Tits are the product of an older radiation and specific separation. These two "blue tit" groups, now *P. caeruleus sensu stricto* and *P. teneriffae*, were elevated to independent species by Salzburger et al. (2002a), based on remarkably high cytochrome-*b* difference values and distinct vocalisations. The average distance between the African and the European clade amounted to 4.9%. By contrast, distances were remarkably small (1.6-1.9%) between the European Blue Tits and the subspecies of the Azure Tit that have been analyzed. The value of 4.9% is quite enough to sustain specific rank, although the two Blue Tit groups are strictly allopatric (north and south of the Mediterranean) and no zone of contact is thought to exist. The 1.6-1.9% value is considerably closer to a subspecies level of distinction than to species rank. Equally the acoustic differences are more pronounced between the two "blue tit" species than those between the European Blue Tit and the Azure Tit (Becker et al., 1980; Martens & Schottler, 1991, Martens 1996, Schottler, 1993a, b, 1995).

P. caeruleus sensu stricto and *P. cyanus* are not strictly allopatric, and hybridisation occurs frequently; but that differs over time and may be dependent on population size (Johansen, 1952; Vaurie, 1957a; Meise, 1975; Portenko et al., 1982). Judging from territorial song and cytochrome-*b* distance values of below 2%, these two groups might be

seen as only subspecifically distinct, but no constant area of intergradation seems to exist and due to their different ecological preferences there may be no constant area of syntopy or even sympatry. We need to know their ecological requirements more precisely, as well as their behaviour in the area of potential sympatry.

The split between *P. caeruleus sensu stricto* and *P. cyanus* seems to be phylogenetically recent; and, in addition, no notable cytochrome-*b* distance is shown between white-breasted and yellow-breasted Azure Tits (see group members above), which even share the same haplotype cluster (Salzburger et al., 2002a). Premating isolating mechanisms may exist, but this seems very unlikely. Allegedly, mixed pairs and hybrids have 'often' been observed (Beaman, 1994), but the breeding area where they meet seems to be unknown. Because the species is supposed to be sedentary, one would expect such hybrids to occur in the Tian Shan at about 76°E, but Beaman gave no localities. Dolgushin et al. (1972) enumerates localities for *P. cyanus* west to Almaty and on the NW shore of Issyk Kul (Toraygur), for *P. flavipectus* east to SW Zailiskiy Alatau and upper Naryn River, with an occasional December find at Talgar, just east of Almaty. Dolgushin does not seem to list hybrids. In summary we cannot identify any sound reason to split white-breasted and yellow-breasted Azure Tits at the species level despite earlier suggestions and arrangements (Dolgushin et al., 1972, Stepanyan, 1990; Harrap, 1996, Inskipp et al., 1996, Sibley & Monroe, 1990, Dickinson, 2003) and we treat them as conspecific.

More information on the disjunct *berezowskii* from north-western China is especially needed. Within the last 100 years it has not been found within its presumed minute range.

General characteristics: white-breasted subspecies: crown and back vary, crown between white and lavender-grey, back between light grey and dark grey-blue, and the amount of white in the tail feathers varies (Meise, 1934: 31). So also does the thickness of the bill, which is remarkably thick in *koktalensis*. The underparts of young *yenisseensis* and *tianschanicus* are light yellow which may be further evidence of a link to *flavipectus* (Harrap, 1996), but juveniles of most white-breasted parids are pale yellowish below.

In the yellow-breasted subspecies the amount of white in the tail feathers varies, as does wing length; comparing *flavipectus* and *carruthersi* one finds the latter is shorter-winged. In disjunct *berezowskii* the crown is light grey, and there is no eye stripe behind eye, the neck collar is broken, and the belly lacks the median stripe. Wing length: up to 67 mm (very few skins available).

For measurements of all azure tit subspecies and comments on them see Eck (2006).

Distribution: white-breasted forms occur in the central Palaearctic from eastern Europe to eastern Asia, yellow-breasted forms from the Tian Shan to the Pamirs plus a widely disjunct tiny area in north-east Qinghai, China (see map in Portenko et al., 1982; Mauersberger, 1976).

Colour images: Quinn in Harrap (1996), pl. 30, figs. 93c: *hyperrhiphaeus*, d-e: *tianschanicus*, figs. 94a-c: *flavipectus*, d: *carruthersi*, e: *berezowskii*; Pleske (1890), pl. VII, fig. 3 and 4; *berezowskii*.

Parus varius Temminck & Schlegel, 1845

Taxa included (8): *P. v. varius* Temminck & Schlegel, 1845⁵⁸ [Japan = Honshu'⁵⁹]; *P. v. sunsunpi* Kuroda, 1919 [Tanegashima, Osumi Is., S Japan]; *P. v. namiyei* Kuroda, 1918 [Niishima, Seven Is. of Izu, Japan]⁶⁰; *P. v. owstoni* Ijima, 1893 [Miyakeshima, Seven Is. of Izu, Japan]; *P. v. orii* (Kuroda, 1923b) [Minami-Daitojima, Borodino Is. = Daito shoto, Japan]; *P. v. amamii* (Kuroda, 1922) [Amami Oshima]; *P. v. olivaceus* (Kuroda, 1923a) [Iriomote I., S Riu Kiu Is. = Nansei shoto, Japan]; *P. v. castaneiventris* Gould, 1863⁶¹ [Taiwan, China].

Taxonomy: because the Varied Tit occurs both on the Asian mainland and on the Japanese islands and Taiwan its relatively small and isolated populations show considerable geographic variation. Consequently, numerous, indeed too many, subspecies were erected (Kuroda, 1927), so that for decades infraspecific nomenclature was rather unstable. Vaurie (1957a) revised the group and accepted nine subspecies. Snow (1967) largely agreed, but synonymised *yakushimensis* with *sunsunpi*⁶². We have retained Snow's arrangement.

Gill et al. (2005) found a cytochrome-*b* distance between nominate *varius* (based on one specimen from Korea) and *castaneiventris* of Taiwan of 6%. This difference needs validation through molecular sequencing of the Japanese populations from the main islands south to Iriomote before species limits for *P. varius* can be seriously reconsidered. However, C. Roselaar informs us that *castaneiventris* stands well apart in its smaller measurements and remarkably short tail compared to the other geographical representatives of *P. varius*. See also the comments by Chikara (2002).

General characteristics: the main variable features are the overall colour pattern, the extent of the rufous on the nape and on the upper back, the wing length (longest in *owstoni*, 84 mm) and bill length. The light parts of the face may be whitish (in nominate *varius*) or dark chestnut (as in *owstoni*).

Between 1830 and 1966 six hybrids between *P. varius* and *P. montanus* are known to have been found in Japan. The most recent one was intermediate in colour, but in voice was close to *varius* (Mishima, 1969). Does this perhaps hint at an affiliation of *P. varius* to the *Poecile* group? Gill's et al. (2005) cytochrome-*b* phylogeny placed *P. varius* close to the basis of *Poecile*. The possible relationship to the rather similar *P. semilarvatus* of the Philippines is unresolved because its cytochrome-*b* has not yet been determined. In morphology it is somewhat similar to *P. varius* as it has a white frontal patch. But the Philippine species has a strongly down-curved, and thus very differently shaped, bill.

⁵⁸ Not 1848 as used by Snow (1967: 117). See Morioka et al. (2005).

⁵⁹ Type locality restricted by Hartert (1905a: 354).

⁶⁰ Morioka (2000: 315) observed that this might not justify recognition.

⁶¹ Not 1862; see Duncan (1937).

⁶² A position not taken by Orn. Soc. Japan (2000: 239), but Morioka (op. cit. p. 315), although he had not seen specimens from Tanegashima (*sunsunpi*), implied that probably both *yakushimensis* and *sunsunpi* should be subsumed in nominate *varius*. That he did not act on this view in the Checklist itself suggests that his material was too scanty to be relied upon.

Distribution: somewhat scattered. Found in north-eastern China in Liaoning and Jilin Provinces (Cheng, 1987, Meyer de Schauensee, 1984), Korea, S Kuril Islands, throughout Japan, Taiwan, and also Sakhalin where it seems likely to have been a vagrant (but is perhaps a sporadic breeder)⁶³.

Colour images: Quinn in Harrap (1996), pl. 18, figs. 95a-b: *varius*, c: *owstoni*, d: *castaneiventris*.

Parus semilarvatus (Salvadori, 1865)

Taxa included (3): *P. s. snowi* Parkes, 1971 [N Luzon]; *P. s. semilarvatus* (Salvadori, 1865) [Mt. Arayat, Luzon]; *P. s. nehrkorni* (Blasius, 1890) [Mindanao].

Taxonomy: if the genus *Parus* is to be satisfactorily divided into genera this species needs molecular sampling so that we can determine its generic assignment. It was not included by Gill et al. (2005).

Colour images: Quinn in Harrap (1996), pl. 22, figs. 96a-c: *semilarvatus*, d-e: *snowi*, f: *nehrkorni*.

Melanochloa sultanea Hodgson, 1837

Taxa included (4): *M. s. sultanea* (Hodgson, 1837)⁶⁴ [Nepal]; *M. s. flavocristata* (Lafresnaye, 1837) [Sumatra]; *M. s. seorsa* Bangs, 1924 [Yenping, Fujian, China]; *M. s. gayeti* Delacour & Jabouille, 1925 [Bana, C Annam = Vietnam].

Taxonomy: these three isolated populations show significant colour differences. For example, *gayeti* from Vietnam has a black crest rather than a yellow one.

In the Paridae cytochrome-*b* topology *Melanochloa* is placed close to the base of the tree, the only other clade that is sister to all other parids being '*Cyanistes*' (Gill et al., 2005). Löhrl (1997) examined *Melanochloa* behaviour in a general parid context and found many behavioural traits were conspicuously unlike parids. This seemed especially true in its marked 'panic' in reaction to unusual noise or unexpected encounters with other species inhabiting the same pen.

Distribution: from east Nepal to south-east Asia including peninsular Malaysia, with disjunct and local forms in Sumatra, S China, and Vietnam.

Colour images: Quinn in Harrap (1996), pl. 31, figs. 102a-c: *sultanea*, d: *gayeti*.

⁶³ Based on 2 birds observed 21 Sep 1976 at Pugachevka river basin, Sakhalin (Bardin, 1987 *apud* Harrap, 1996).

⁶⁴ Dickinson et al. (2006) re-examined the old question of whether the specific name should be *sultanea* or *flavocristata* and showed that as far as can be determined *sultanea* has a couple of months priority over *flavocristata*.

Sylviparus modestus Burton, 1836

Taxa included (3): *S. m. simlaensis* Baker, 1917 [Simla]; *S. m. modestus* Burton, 1836 [Himalayas = Nepal⁶⁵]; *S. m. klossi* Delacour & Jabouille, 1930 [Langbian Mts., S Annam = Vietnam].

Taxonomy: local differences are small. The greenish feathering which camouflages the bird in the canopy of broad-leaved forests, as in the case of *Phylloscopus* warblers, apparently does not allow much variation. Vaurie (1957a) and Snow (1957, 1967) concluded that although numerous names are available, only three subspecies should be accepted. Martens & Eck (1995: 318) agreed adding that “it seems more appropriate merely to call attention to the differences [of local populations] that can exist, rather than finding a new subspecies for each of them”. However, in view of apparent gaps in the range it will be interesting to learn about possible molecular differences between populations.

Distribution: Himalayas and many isolated populations in southern China and in northern parts of tropical SE Asia.

Colour images: Quinn in Harrap (1996), pl. 12, figs. 101a-b: *modestus*, c: *simlaensis*.

Pseudopodoces humilis (Hume, 1871)

Taxon included (1): *Pseudopodoces humilis* (Hume, 1871) [above Kichik-Yailagh at 36°47'N, 78°16'E, near Sanju Pass, SW Xinjiang, China]. – Monotypic.

Taxonomy: Dickinson et al. (2004a, b) discussed this species within the preliminary review of the Corvidae and signalled in a footnote the proposal that this species be re-assigned. It is now fully apparent that this species of the Tibetan highlands belongs to the parids. This new position is based on morphological and anatomical studies (James et al., 2003), on molecular genetics (James et al., 2003, Gill et al., 2005) and even on biochemical traits of the uropygial glands (Gebauer et al., 2004).

In the cytochrome-*b* topology *Pseudopodoces* is not, as one would expect, a sister to the bulk of ‘true’ *Parus*, but it is placed as sister to the species around *P. major* though with low support (Gill et al., 2005), thus in a broad genus *Parus* it would need to be included there.

Geologically the high plateau of Asia is due to relatively recent uplift, but it would appear to have been invaded twice by parids. This species, due to its distinctiveness, is assumed to be the first of the invaders, or did it evolve on the spot despite the orogenic disturbances? *P. supercilialis* which also occurs at high-altitude and occupies the same novel niche is thought to be a younger immigrant to the high plateau. See also Gill et al. (2005).

Colour images: Anderton in Rasmussen & Anderton, 2005: pl. 155 fig. 6 (head only), James et al. (2003, fig. 1b).

⁶⁵ Type locality restricted to Nepal by Baker (1920b). Snow (1967: 111) dated this from the 1923 reprint; in fact this dates from the J. Bombay Nat. Hist. Soc. 27 (2): 228-247.

Abbreviations and acronyms

HI	Handflügel Index (or wing-tip index)
IZAS	Institute of Zoology, Academy of Sciences, Beijing.
MTD	Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Dresden.
m.y.	million years
sd	standard deviation (omitted when sample too small)
TWI	Tail wing index
WTI	Wing tip index
YIO	Yamashina Institute for Ornithology, Abiko City
ZFMK	Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn
ZISP	Zoological Institute, Russian Academy of Science, St. Petersburg.

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⁶⁶ The 1923 reprint (240 pp.) was entitled: A Handlist of genera and species of birds of the Indian Empire.

⁶⁷ We accept 1850 for pp. 1-106 (see Dickinson et al., 2004: 138); the subsequent pages are best dated 1851.

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⁶⁸ The author is given as "Hauptmann Thom. Conr. von Balenstein in Graubünden" but see Conti (1947) for reason not to accept the title 'von Balenstein'.

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⁶⁹ Mitt. zool. Mus. Berlin (Suppl. for Vol. 53).

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⁷¹ Spelled Hachlor in the original and doubtless a typographical error for Hachlov or Hachlow which is the normal German spelling; Khakhlov in Russian.

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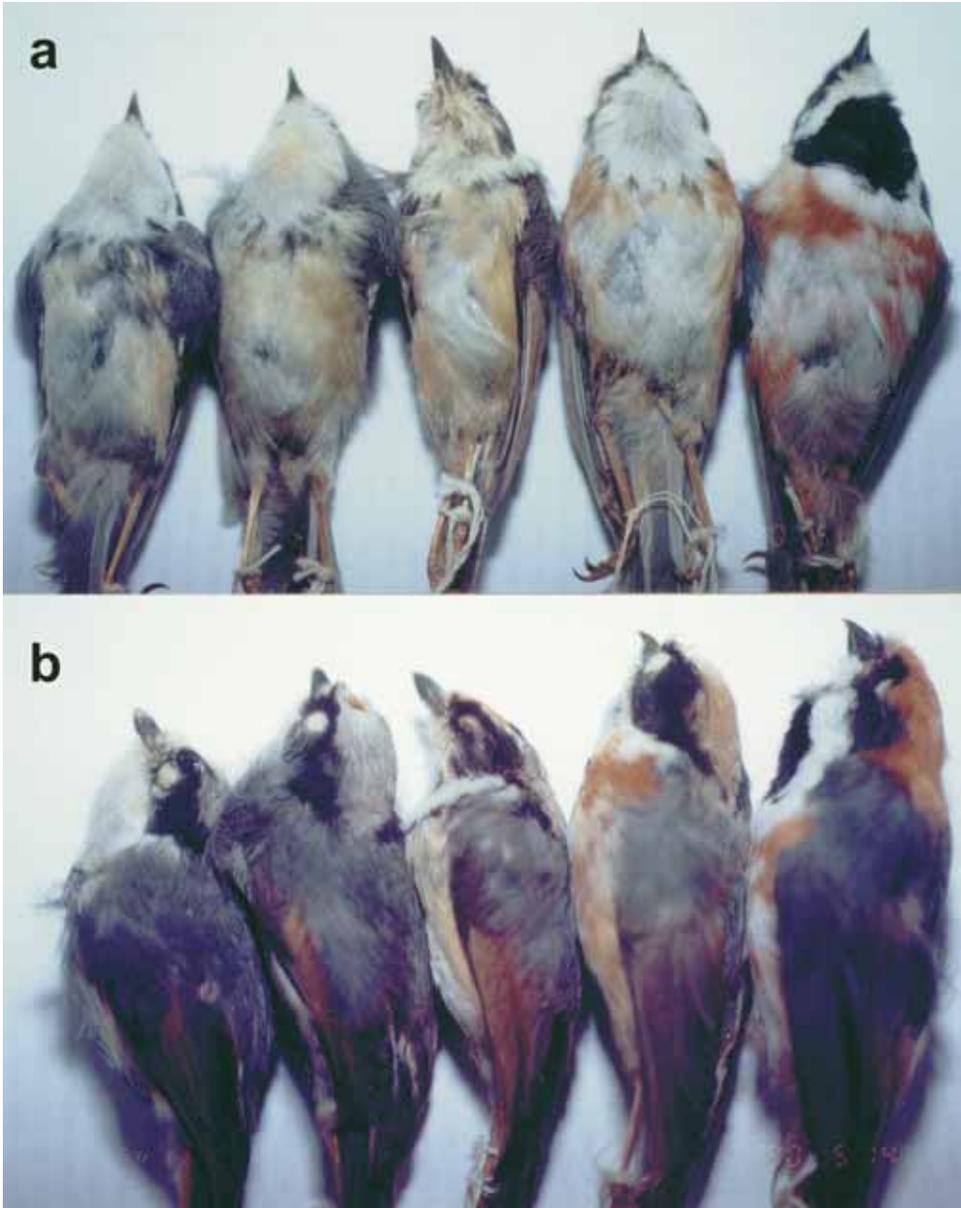


Plate I: A series of *Aegithalos concinnus* from China (*talifuensis* and/or *concinnus*) in different plumage states, from newly fledged juveniles to the adult state. Note the grey crown in the youngest birds (left), changing to chestnut in the older/adult ones (right). – In a. and b. the same series is shown from below and from the left side. Based on material in the collection of the Chinese Academy of Sciences, Beijing (IZAS). – Photo: J. Martens.

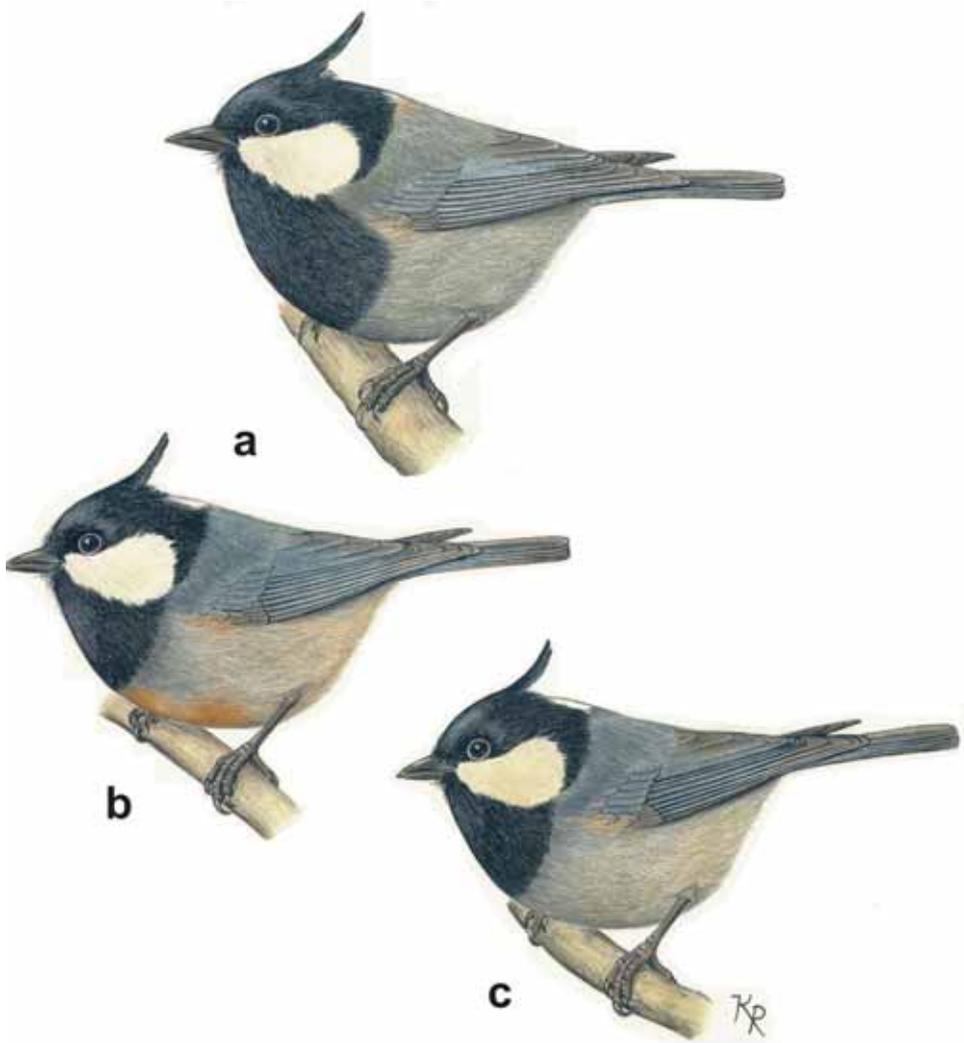
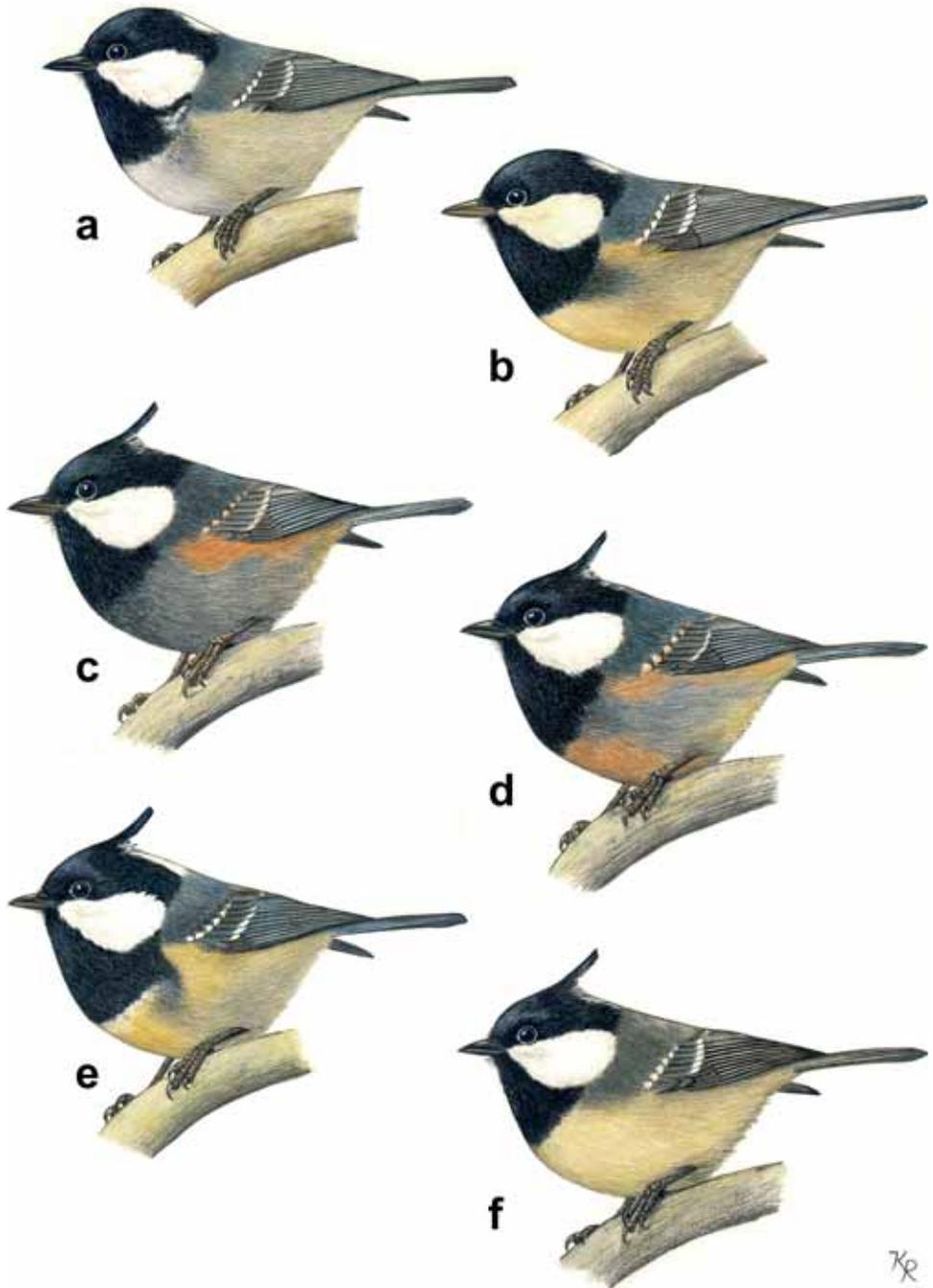


Plate II: Himalayan representatives of *Parus rufonuchalis* and *Parus rubidiventris*. – a) *P. rufonuchalis*, Nepal, Dolpo Distr., Phoksumdo Lake (ZMFK 71.1055); – b) *P. r. rubidiventris*, Nepal, Myagdi Distr., Dhorpatan valley (ZMFK 71.1064); – c) *P. r. beavani*, Nepal, Solukhumbu Distr., Pare (ZMFK 71.61). – *P. r. rubidiventris* and *P. r. beavani* from Nepal belong to the same haplotype cluster. All drawings to scale. – Originals by K. Rehbinder (first published in Martens & Eck, 1995).



◀ Plate III: European, central Asian and Himalayan subspecies of the Coal Tit, *Parus ater*. – a) ssp. *abietum*, Austria (MTD C 52967); – b) ssp. *rufipectus*, Kazakhstan or Xinjiang/China; east ‘Turkestan’ (ZFMK GX1f.b.gamma); – c) ssp. *melanolophus*, ‘normal’ morph, Nepal, Dolpo Distr., Phoksumdo Lake (ZFMK 95.026); – d) ssp. *melanolophus*, cinnamon-bellied morph, Nepal, Myagdi Distr., Dhorpatan valley; – e) ssp. *martensi*, holotype, Nepal, Mustang Distr., Chadziou Khola valley (ZFMK 95.024); – f) ssp. *aemodius*, Nepal, Solukhumbu Distr., Imja/Phunki Drangka valley (ZFMK 95.023). All drawings to scale. – Original by K. Rehbinder (first published in Martens, 1993 and Martens & Eck, 1995).

