

**Differentiation processes in treecreepers (Aves: *Certhia*):  
phylogeny, vocalisations, morphometrics**

**Dissertation**

**zur Erlangung des Grades**

**„Doktor der Naturwissenschaften“**

am Fachbereich Biologie

der Johannes Gutenberg-Universität

in Mainz

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geboren am 2. November 1975 in Worms

Mainz, den 26. Juli 2007

Dekan: ...

Erstberichterstatter: ...

Zweitberichterstatter: ...

Tag der Prüfung: 5. September 2007

A slightly modified version of Chapter 2 of this thesis has been published at Blackwell Publishing:

Tietze DT, Martens J & Sun Y-H (2006): Molecular phylogeny of treecreepers (*Certhia*) detects hidden diversity. *Ibis* 148: 477–488.

Dedicated to  
Gerhard Thielcke  
(1931–2007)

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# **1 General introduction**

## **1.1 Modern avian systematics**

In the second half of the twentieth century traditional systematics of birds – almost exclusively based on morphological characters – had come to a (preliminary) end: further changes on higher and lower taxonomic levels were due to subjective judgement rather than to striking new findings. Recent revivals of research in the field of avian systematics were mainly triggered by two new methodological approaches: biochemical (mainly genetic) procedures on the one hand and bioacoustic comparisons on the other.

The latter were made possible by progressively smaller recording devices that could be taken into the field, including the more remote areas with avifauna practically unknown. Recordings could be played back in order to identify their originator and could be visualised as sonagrams for further investigation in the laboratory. Song syntax as well as single sonographic time or frequency parameters could be compared between taxa, and multivariate statistics were also introduced in order to facilitate discrimination of similar vocalisations (Sparling & Williams 1978). For a further review of the application of bioacoustics to bird classification see Alström & Ranft (2003).

Sibley & Ahlquist (1990) performed DNA-DNA hybridisations of a large selection of avian taxa and thus provided the scientific community with a “tapestry” for further, more detailed studies, thereby questioning many established higher-level relationships. Against this background, many taxa on lower taxonomic levels were evaluated by DNA data. But development continued in the field of morphology as well. For example, multivariate statistics were also applied to morphometric data (James & McCulloch 1990).

## **1.2 Cryptic species in passerines**

Besides the higher-level changes, at the other end of the taxonomic scale new insights are no less interesting. There are many examples of birds in which actual differentiation had been undetected and was now revealed by means of genetic or bioacoustic analysis. For example, subspecies had been overlooked in Coal Tits *Parus ater* (Martens et al. 2006), allopatric species had been erroneously treated as subspecies in the Chiffchaff *Phylloscopus collybita* (Helbig et al. 1996) and even sympatric species had been missed in other leaf-warbler complexes

such as *Ph. proregulus* (Alström et al. 1992, Martens et al. 2004) or *Seicercus burkii* (Martens et al. 1999).

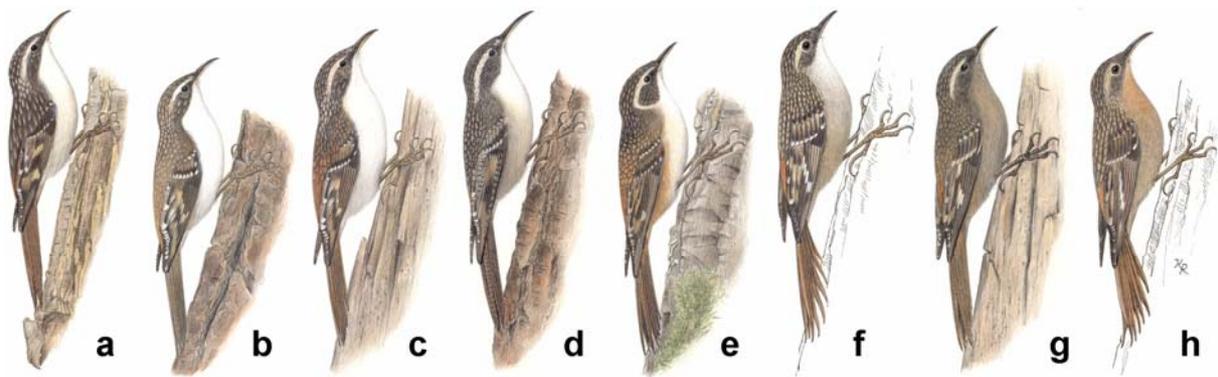
However, in the cases of allopatric populations that differ genetically and acoustically, the question arises which species concept is appropriate and thus has to be applied. Avian systematics in the second half of the twentieth century was mostly based on the biological species concept (Mayr 1942). But that fails in cases of allopatry, since no interactions between carriers of different distinct genetic or acoustic features can be observed with regard to whether they would mate under natural conditions or rather behave like reproductively isolated units. Taxonomic decisions must refer to inferences regarding various sets of characters of the populations in question, and consequently follow to a certain extent the phylogenetic species concept (Cracraft 1983), which is based on diagnosable “differences”, and are thus again more or less arbitrary. In order to become safer in taxonomic judgements, my approach combined genetic relationships and distances with – inborn and learnt – behavioural traits like vocalisations and with the phenotypic variation of body measurements; all results were discussed on the basis of our knowledge about biogeography, ecology and other aspects of tree-creeper biology.

### 1.3 The genus *Certhia* as a model system

The genus *Certhia* (treecreepers) unites small passerine birds of uniform outer appearance. Because their backs are brownish-mottled in adaptation to their microhabitat, the bark of large trees, they draw little attention from diurnal predators. The combination of long curved pincer-like bills and stiff woodpecker-like tail feathers makes treecreepers unique and unmistakable among all Holarctic small passerines. But this shared pattern reduces the morphological variation between species (Fig. 1.1). Treecreepers are restricted to the Holarctic with local extensions to the tropics (Fig. 1.2). In the larger parts of the genus’ range, there is only one species present, but in Europe *C. brachydactyla* and *C. familiaris* occur together. In the Himalayas up to four species can be found sympatrically, but a tendency towards vertical segregation of species can be observed in all areas of sympatry (Fig. 1.3).

What makes treecreepers a good model for testing the applicability of the up-to-date approaches in avian systematics? Due to the lack of distinct morphological characters between species, the relationships within the genus have been difficult to ascertain, despite the small number of species concerned: debate about species limits in *Certhia* has a long history. I

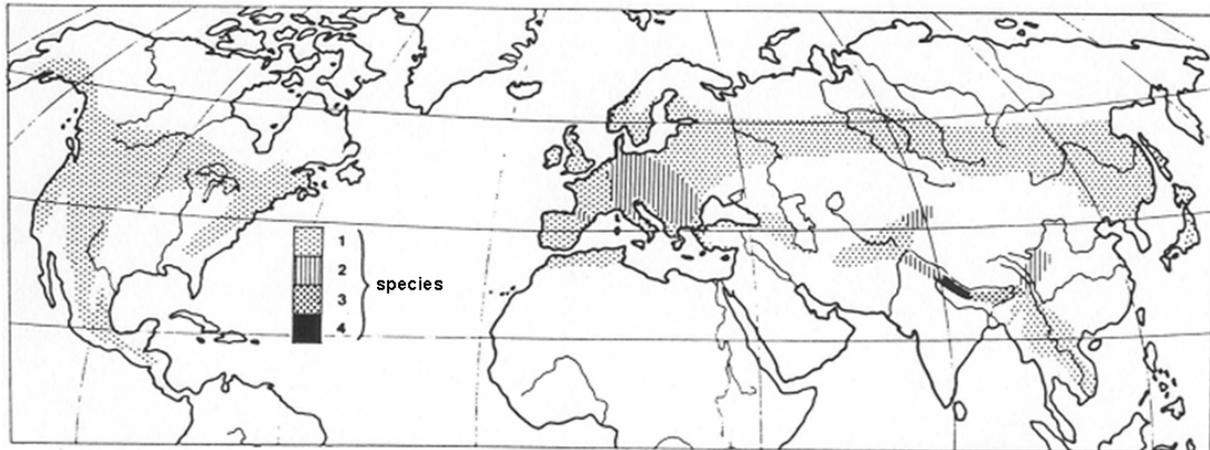
wanted (preliminarily) to put an end to this controversy by providing a molecular phylogeny of all *Certhia* species. I quite expected to uncover cryptic species because of experiences with other passerines having rather uniformly coloured plumage and because of hints from bioacoustics. There has been a long tradition of applying bioacoustics to treecreeper classification (e.g. Brehm 1820, Thielcke 1962, Martens et al. 2002). This is facilitated by the fact that a single treecreeper male almost invariably utilises the same verse of song and that even across larger distributional areas territorial songs remain extremely uniform. So I hoped to confirm the molecular-systematic results with a thorough analysis of the available sound recordings. Finally, I was eager to find morphometric characters for species delimitation. Therefore I had to provide comparable data for all described taxa within *Certhia*. Once this combined approach had yielded useful results, it could be recommended for other taxonomic studies on passerine birds with as yet unresolved taxonomic relationships.



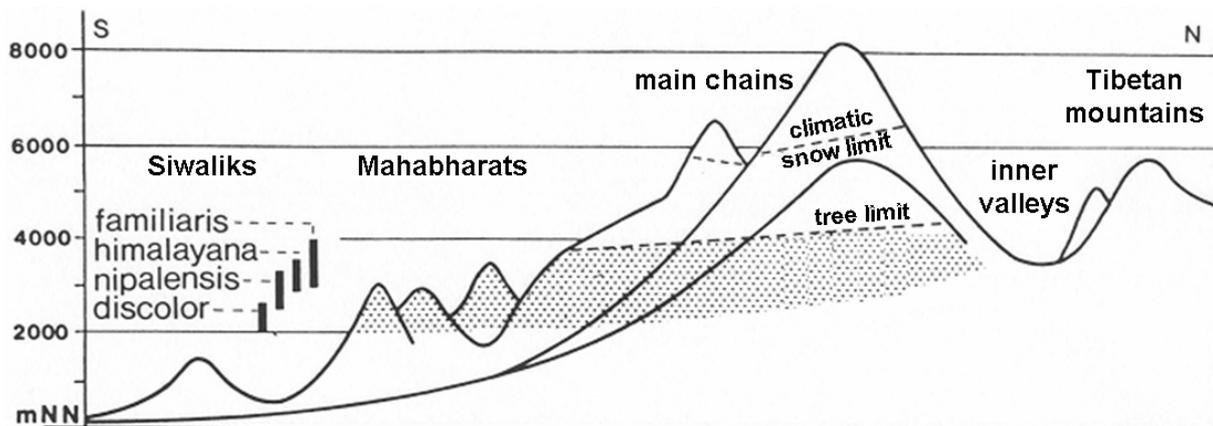
**Fig. 1.1:** Palaeartic treecreeper species of genus *Certhia*: a) *C. b. brachydactyla*, Spain, Salamanca, MTD C47333, b) *C. familiaris macrodactyla*, Czech Republic, Šumava, MTD C62629, c) *C. f. khamensis*, China, SE Tibet, NHM 1938.12.13.8, d) *C. h. himalayana*, Nepal, Mustang Distr., ZMFK 2000/203, e) *C. nipalensis*, Nepal, Myagdi Distr., ZMFK 71.807, f) *C. tianquanensis*, China, Sichuan, MTD C59560, g) *Certhia d. discolor*, Nepal, Sindhu Palchok, MTD C58570, h) *C. d. manipurensis*, Myanmar, Chin state, ZMB 39.345 (all drawings by K. Rehbinder).

## 1.4 Aims of the thesis

In this thesis I studied differentiation processes within the avian genus *Certhia*. This relatively small group of passerine birds is well suited for this purpose because, despite the small number of species, taxonomic relationships within the genus had been difficult to ascertain on morphological grounds. In contrast to the similarity in outer morphology, vocalisations differ markedly and thus provide a good means for delimitation of evolutionary units.



**Fig. 1.2:** Total distributional area of the seven species of the genus *Certhia* recognised at the beginning of the investigation, marked by number of sympatric species. The highest number of species occurs in the central Himalayas (after Martens 1981).



**Fig. 1.3:** Vertical distribution of the four treecreeper species in Nepal during the breeding season. The dotted area represents the vertical area belt of all *Certhia* species of Nepal; only the upper half of the approximately 4000-m-wide forest belt is inhabited by treecreepers: *discolor* 2000–2700 m, *nipalensis* 2550–3400 m, *himalayana* 2900–3650 m, *familiaris* 3000–4000 m (after Martens 1981).

The first aim of my thesis was to resolve the intrageneric phylogenetic relationships in *Certhia* treecreepers. The second aim was to test the extent to which these relationships are reflected by similarities in bioacoustic features and whether parameters of inborn calls and learnt songs reliably delimit evolutionary units. The third aim was to search for acoustically isolating song parameters in the most widespread species, *C. familiaris*. The fourth aim was to characterise the accepted treecreeper taxa by several body measurements and to look for geographical trends therein and for those parameters most important in niche partitioning.

This thesis consists of four major chapters (Chapters 2 to 5) which can be read independently. Each chapter is organised like a journal publication, containing an introduction followed by methods, results and discussion sections and by a short summary. The thesis closes with general conclusions including the essentials of all four chapters.

In the first major chapter (Chapter 2) I reconstructed the phylogeny of the genus based on mitochondrial cytochrome-*b* sequences, using four different approaches. Next to the phylogram, I placed sonagrams of song verses in order to show that general song features support the phylogenetic structuring of the genus. Genetic distances between the main lineages were documented and taxonomic conclusions on species level were drawn.

The second major chapter (Chapter 3) deals with the detailed bioacoustic analysis. I measured time and frequency parameters of call and song recordings. These data were used to separate the species in a discriminant analysis and to perform a cluster analysis. Song features were mapped onto the molecular phylogeny in order to test for a phylogenetic signal. I tried to affiliate taxa not incorporated into the phylogenetic study with the correct species based on sonographic measurements.

The third major chapter (Chapter 4) treats the playback experiments in the field. I played territorial songs of closely related allopatric taxa to Central European *C. familiaris* in order to detect song components that are important for species recognition.

In the fourth major chapter (Chapter 5) I present standard body measurements of museum specimens and derived body indices for almost all accepted *Certhia* taxa. Sexes were treated separately due to a marked dimorphism. I worked out geographical trends and those parameters which differ most in sympatric forms.

## 2 Molecular phylogeny detects hidden diversity

### 2.1 Introduction

The genus *Certhia* (treecreepers) unites small passerine birds of highly uniform outer appearance. Because their backs are brownish-mottled, in adaptation to their microhabitat, the bark of large trees, they draw little attention from diurnal predators. The combination of long curved pincer-like bills and stiff woodpecker-like tail feathers make *Certhia* treecreepers unique and unmistakable among all Old World small passerines (Harrap & Quinn 1996).

Owing to the lack of distinct morphological characters between species, the relationships within the genus *Certhia* have been difficult to ascertain, despite the small number of species concerned: debate about species limits in *Certhia* has a long history. It dates back to C.L. Brehm (1820), whose lucidly described *C. brachydactyla* was rejected for decades. Misplacements of local populations came to a preliminary end when *C. tianquanensis* was wrongly positioned as a subspecies of *C. familiaris* (Li 1995).

Treecreepers are restricted to the Holarctic from Western Europe and North Africa to Japan with local extensions to the Indo-Malayan realm in Southeast Asia, and in the New World they penetrate southwards to mountainous Central America (Harrap & Quinn 1996). In the larger parts of the genus' range, northern Asia and North America, there is only one species present, but in Europe *C. brachydactyla* and *C. familiaris* occur together. In the Himalayas of Nepal as many as four species can be found sympatrically, three syntopically, but a tendency towards vertical segregation of species is obvious in all areas of sympatry (Martens 1981, Glutz von Blotzheim & Bauer 1993).

Martens (1981) and Martens et al. (2002) compared all known treecreeper territorial songs and redrew possible evolutionary pathways, which they saw reflected in song types. Treecreeper territorial songs seem to be useful for this purpose, because they are quite stereotyped, showing little variation in the single individual as well as in widely distributed populations (Thielcke 1961, 1970a). Consequently, they can be employed to delimit local populations, subspecies and even species. Thus, a bioacoustic approach is helpful when populations of uncertain taxonomic affiliation are to be correctly placed. Because of their uniformity in appearance and in their, frequently overlooked, vocalisations, it seems likely that cryptic differentiation and even overlooked species will be discovered in *Certhia*.

Here I present a phylogenetic reconstruction of the genus, based on parts of the cytochrome-*b* gene. In parallel, I demonstrate general patterns of territorial song. I included tissue samples of all presently accepted species of *Certhia* and of populations from several widespread parts of the large distributional areas in species to which this applies. Thus, I focus on possible still undetected cryptic differentiation up to the species level. Furthermore, I wish to draw special attention to the complicated evolutionary history in the Himalayas and in China, which includes vocal differentiation (Martens 1981).

## 2.2 Methods

### 2.2.1 Samples

I analysed parts of the cytochrome-*b* gene using 63 blood and tissue samples of the seven currently recognised treecreeper species (Dickinson 2003) and included one sequence from GenBank (Table 2.1). Eurasian Nuthatch *Sitta europaea* and Winter Wren *Troglodytes troglodytes* were used for hierarchical outgroup rooting. The choice of outgroups is based on the placement of the genera *Sitta* and *Troglodytes* as close relatives of the genus *Certhia* within the superfamily Certhioidea (Barker et al. 2004, Cracraft et al. 2004).

### 2.2.2 DNA extraction, PCR and sequencing

DNA was extracted using the High Pure PCR Template Preparation Kit (Roche Diagnostics). The following oligonucleotide primers, which were designed by me for this treecreeper project, were used for polymerase chain reaction (PCR) and sequencing: Certhia1 (5'-AATCGTCACCGGCCTACTG-3') and Certhia2 (5'-TTCTGGGTGCGCCTAGTTGG-3'). A 631-bp fragment was obtained with this primer combination. For PCR I used 0.2 mL PureTaq Ready-To-Go PCR Beads (Pharmacia Biotech), adding 4 µL DNA sample, 1 µL of each primer (20 pmol/mL) and 19 µL distilled water. PCR products were purified with the High Pure PCR Product Purification Kit (Roche Diagnostics). A total of 512 bp was consistently sequenced for all samples using Big-Dye Ready-Reaction Kit (Perkin Elmer). In the majority of cases, Primer Certhia1 was used to obtain this sequence. The sequences were analysed on an ABI Prism 3730 (Applied Biosystems) and aligned with MEGA version 3.1 (Kumar et al. 2004).

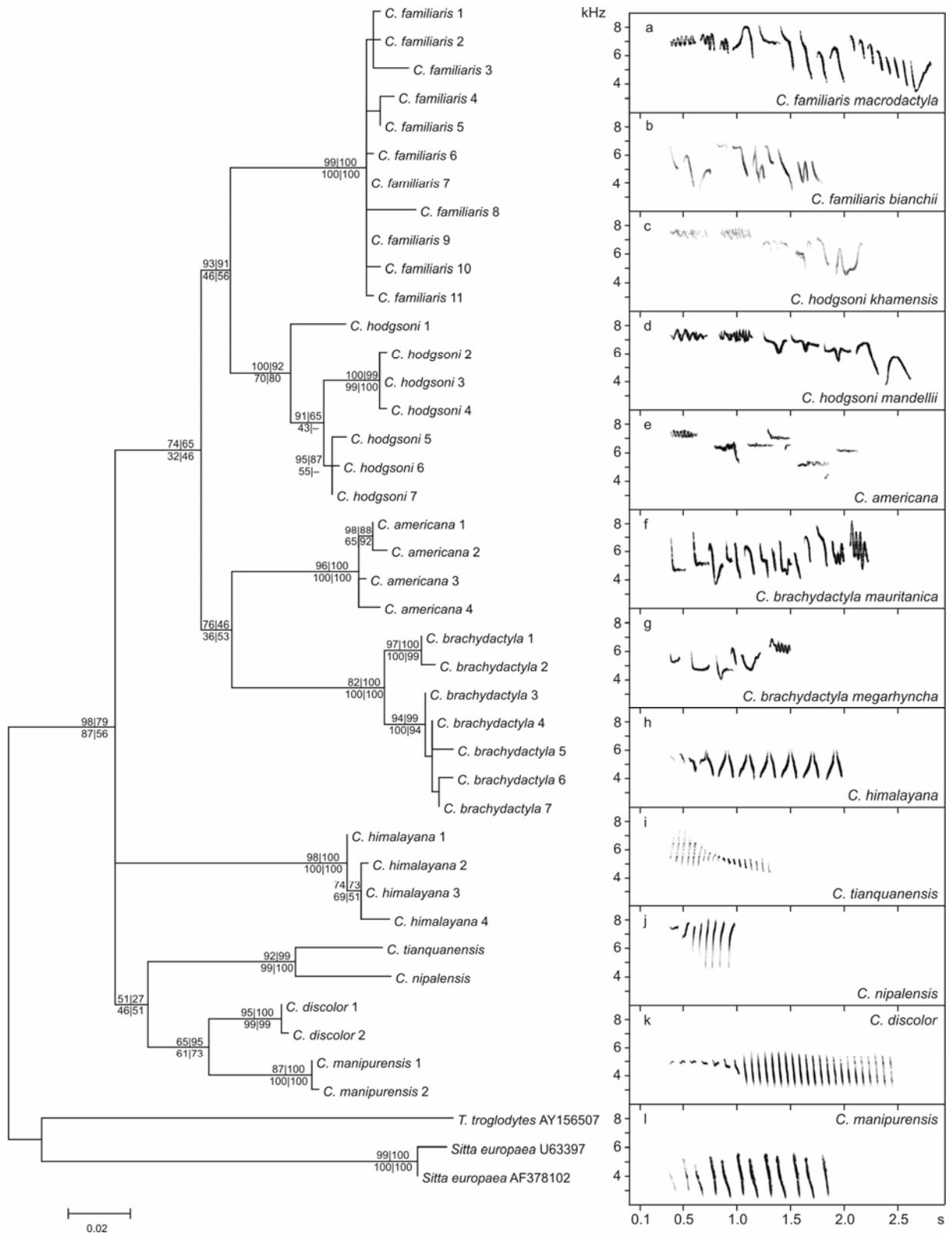
## 2 Molecular phylogeny

**Table 2.1:** Blood and tissue samples used for DNA extraction, sequencing and analysis, with corresponding haplotype numbers (as used for naming the leaves of the phylogenetic tree in Fig. 2.1), tissue types (1: blood, 2: muscle, 3: specimen toe pad), tissue collection numbers from MAR series, and GenBank accession numbers. N.N. indicates collector's name unknown; s.s., sensu stricto.

Haplotype	Subspecies	Locality	Date	Collector	Tissue	MAR	Accession no.
<b><i>Certhia americana</i></b>							
1	<i>americana</i>	Canada, Ontario, Long Point	1999-12-15	M. Peck	2	1048	DQ196363
2	<i>americana</i>	Canada, Ontario, Long Point	1999-12-15	M. Peck	2	1049	DQ196364
3	<i>americana</i>	USA, Illinois, Chicago City	2003-10-06	R. Price	2	3489	DQ196391
4	<i>ssp.</i>	USA, Illinois, Cook County	1987-09-24	N.N.			AY352523
<b><i>Certhia brachydactyla</i></b>							
1	<i>mauritanica</i>	Morocco, Dayet Aoua near Ifrane	2004-03-15	D.T. Tietze & K. Mally	2	4004	DQ196392
2	<i>mauritanica</i>	Morocco, Aguelmame Azigza	2004-03-17	D.T. Tietze & K. Mally	1	4009	DQ196393
3	<i>megarhyncha</i>	Germany, Sachsen-Anhalt, surroundings of Wittenberg	2002-09-25	M. Schönfeld	2	2840	DQ196402
4	<i>megarhyncha</i>	Germany, Rheinland-Pfalz, Mainz	2001-01-16	J. Martens	1	1025	DQ196359
4	<i>megarhyncha</i>	Germany, Sachsen, Weixdorf	2002-08-05	A. Kleefeld	2	2334	DQ196360
4	<i>megarhyncha</i>	Germany, Rheinland-Pfalz, Eich am Rhein	2005-06-11	D.T. Tietze	1	5166	DQ196361
4	<i>megarhyncha</i>	Germany, Rheinland-Pfalz, Eich am Rhein	2005-08-13	D.T. Tietze	1	5183	DQ196362
5	<i>megarhyncha</i>	France, Pyrénées-Orientales, Serralongue	1994-07-26	J. Martens	1	78	DQ196399
6	<i>megarhyncha</i>	France, Gironde, Montalivet S Soulac s. Mer	1996-08-27	J. Martens	1	500	DQ196355
7	<i>dorotheae</i>	Cyprus, Sayttas Forest	1955-02-02	G.A. Mavromoustakis	3	4342	DQ196411
<b><i>Certhia bicolor s.s.</i></b>							
1	–	Nepal, Bhojpur Distr., upper Myagdi Khola, NW Tumlingtar	2001-04-06	J. Martens	2	2657	DQ196379
2	–	Nepal, Myagdi Distr., upper Myagdi Khola, Dobang	1995-05-21	J. Martens	2	90149	DQ196380
<b><i>Certhia familiaris s.s.</i></b>							
1	<i>macrodactyla</i>	Czech Republic, Šumava, Nová Pec, SSE Volary	1994-10-19	J. Martens	2	104	DQ196401
2	<i>familiaris</i>	Finland, Muhos	1997-12-19	fide L. Kvist	2	2872	DQ196403
3	<i>macrodactyla</i>	Czech Republic, Šumava, Chlum	2003-05-15	D.T. Tietze	2	3095	DQ196398
4	<i>daurica</i>	Mongolia, Tes gol	2002-09-02	M. Stubbe	2	4024	DQ196394
5	<i>daurica</i>	Russia, Primorskiy kray, Ussuri valley, Oblachnaya	1996-05-27	M. Päckert	2	90351	DQ196397
6	<i>bianchii</i>	China, Shaanxi, Taibai Shan, above Houzhenzi	1997-06-16	J. Martens	1	743	DQ196356
6	<i>bianchii</i>	China, Shaanxi, Taibai Shan, above Houzhenzi	1997-06-16	J. Martens	2	746	DQ196357
6	<i>bianchii</i>	China, Shaanxi, Taibai Shan, Xianbansi	2005-05-07	J. Martens & Y.-H. Sun	2	4911	DQ196358
7	<i>daurica</i>	Japan, Hokkaido, Sapporo	1998-10-26	T. Kawaji	2	1722	DQ196367
8	<i>bianchii</i>	China, Gansu, Lianhua Shan, Bainuzui in the reserve	2000-10-15	Y. Fang	2	2097	DQ196369
9	<i>bianchii</i>	China, Shaanxi, Taibai Shan, Xianbansi	2005-05-08	J. Martens & Y.-H. Sun	2	4917	DQ196375
9	<i>bianchii</i>	China, Gansu, Zhuoni	2005-05-27	J. Martens & Y.-H. Sun	2	4958	DQ196376
9	<i>bianchii</i>	China, Gansu, Zhuoni	2005-05-28	J. Martens & Y.-H. Sun	2	4959	DQ196377
9	<i>bianchii</i>	China, Gansu, Lianhua Shan reservation	2004-07-23	Y.-H. Sun	2	4973	DQ196378
9	<i>daurica</i>	Russia, Tyva, zapovednik Aras, river Aras	2003-08-17	M. Stubbe	2	4025	DQ196374
9	<i>macrodactyla</i>	Germany, Sachsen-Anhalt, surroundings of Wittenberg	2001-03-01	M. Schönfeld	2	2478	DQ196370
9	<i>macrodactyla</i>	Germany, Baden-Württemberg, Lake Constance	2003-11-02	D.T. Tietze	1	3153	DQ196371
9	<i>tianschanica</i>	Kyrgyzstan, Ysyk Köl, Ananyevo	2001-03-30	A. Ostashenko	2	2883	DQ196372
9	<i>tianschanica</i>	Kyrgyzstan, Ysyk Köl, Ananyevo	2001-05-17	A. Ostashenko	2	2886	DQ196373

Table 2.1 continued

Haplotype	Subspecies	Locality	Date	Collector	Tissue	MAR	Accession no.
10	<i>daurica</i>	Russia, Chitinskaya Oblast, Is. Olchon, Lake Baikal	2004-09-16	A. Gamauf	2	4467	DQ196404
11	<i>bianchii</i>	China, Gansu, Zecha	2005-05-26	J. Martens & Y.-H. Sun	2	4956	DQ196412
<b><i>Certhia himalayana</i></b>							
1	<i>ripponi</i>	Myanmar, Chin State, Natmataung National Park, 8-mile camp	2005-04-02	D.T. Tietze	1	4558	DQ196406
1	<i>ripponi</i>	Myanmar, Chin State, Natmataung National Park, 8-mile camp	1999-08-11	N.N.	3	4717	DQ196407
1	<i>ripponi</i>	Myanmar, Chin State, Natmataung National Park, 8-mile camp	2005-04-02	D.T. Tietze	2	4734	DQ196408
2	<i>himalayana</i>	Nepal, Humla Distr., near Simikot	2002-06-24	M. Fischer & H. Grimm	2	3318	DQ196390
3	<i>himalayana</i>	Nepal, Humla Distr., near Simikot	2002-06-25	M. Fischer & H. Grimm	2	3319	DQ196366
3	<i>taeniura</i>	Kyrgyzstan, Tian Shan, Kirgis-Ata valley S Osh	1993-05-22	J. Martens	2	1561	DQ196365
4	<i>yunnanensis</i>	China, Yunnan, Geza, 60 km N Zhongdian	2002-05-01	J. Martens & D.T. Tietze	2	3241	DQ196385
<b><i>Certhia hodgsoni</i></b>							
1	<i>hodgsoni</i>	India, Kashmir, Naltar	1928-06-03	H. Whistler	3	977	DQ196368
2	<i>mandellii</i>	Nepal, Myagdi Distr., upper Myagdi Khola	1995-05-23	J. Martens	2	90170	DQ196396
3	<i>mandellii</i>	Nepal, Humla Distr., near Simikot, Chucho Khola	2002-06-28	M. Fischer & H. Grimm	2	3328	DQ196400
4	<i>mandellii</i>	Nepal, Rasuwa Distr., W Syabrubesi	2004-04-17	J. Martens	1	4213	DQ196395
5	<i>khamensis</i>	China, Sichuan, Longxi-Hongkou reserve	2002-05-24	J. Martens & D.T. Tietze	2	3297	DQ196389
6	<i>khamensis</i>	China, Sichuan, 16 km NW Kangding, eastern shore of lake Mugecuo	2004-04-11	A. Gebauer	2	3140	DQ196384
7	<i>khamensis</i>	China, Sichuan, Wawu Shan	2002-05-13	J. Martens & D.T. Tietze	2	3277	DQ196386
7	<i>khamensis</i>	China, Sichuan, Yaoji	2002-06-02	J. Martens & D.T. Tietze	2	3308	DQ196387
7	<i>khamensis</i>	China, Sichuan, road between Jiuzhaigou and Sungpan	2005-05-21	J. Martens	2	4949	DQ196388
<b><i>Certhia manipurensis</i></b>							
1	<i>manipurensis</i>	Myanmar, Chin State, Natmataung National Park, between field station and 8-mile camp	2005-03-29	D.T. Tietze	1	4554	DQ196405
2	<i>manipurensis</i>	Myanmar, Chin State, Natmataung National Park, 8-mile camp	2005-04-02	D.T. Tietze	1	4585	DQ196409
2	<i>manipurensis</i>	Myanmar, Chin State, Natmataung National Park, 8-mile camp	1999-08-10	N.N.	3	4737	DQ196410
<b><i>Certhia nipalensis</i></b>							
1	–	Nepal, Bhojpur Distr., Salpa La	2001-04-17	J. Martens	2	2741	DQ196381
1	–	Nepal, Rasuwa Distr., W Syabrubesi, Somdang	2004-04-09	J. Martens	1	4153	DQ196382
1	–	Nepal, Sindhu Palchok Distr., Dadar Danda, Kalinchok	1995-04-21	J. Martens	2	90050	DQ196383
<b><i>Certhia tianquanensis</i></b>							
1	–	China, Sichuan, Wawu Shan	2000-05-30	J. Martens & Y.-H. Sun	2	2073	DQ196350
1	–	China, Sichuan, Wawu Shan	2002-05-10	J. Martens & D.T. Tietze	2	3260	DQ196351
1	–	China, Sichuan, Wawu Shan	2002-05-13	J. Martens & D.T. Tietze	2	3273	DQ196352
1	–	China, Shaanxi, Taibai Shan, Xianbansi	2005-05-07	J. Martens & Y.-H. Sun	2	4913	DQ196353
1	–	China, Shaanxi, Huayang, Qangqing Panda Reservation	2005-05-14	J. Martens & Y.-H. Sun	2	4936	DQ196354



**Fig. 2.1:** See previous page. Maximum-likelihood tree based on 512 bp of the mitochondrial cytochrome-*b* gene from all nine treecreeper species recognised here (for taxonomic changes see Table 2.3). Bootstrap values indicated at nodes: maximum likelihood (1000 puzzling steps) and neighbour joining (2000 bootstrap replicates) above, maximum parsimony (1000 bootstrap replicates) and posterior probabilities of Bayesian inferences below branches. Numbers after species names refer to haplotypes of a given species and the corresponding subspecies in Table 2.1. Territorial song verses recorded in a) Germany, b) Gansu, China, c) Sichuan, China, d) Nepal, e) New York, USA, f) Morocco, g) Germany, h) Nepal, i) Sichuan, China, j–k) Nepal and l) Myanmar.

### 2.2.3 Sequence analysis

An adequate substitution model was estimated via hierarchical likelihood ratio tests (Modeltest version 3.7; Posado & Crandall 1998). Only the *Certhia* sequences were included in the input data set. The selected model according to the Akaike Information Criterion was HKY+I+G (Hasegawa et al. 1985) with the following parameters:  $\pi_A = 27.68\%$ ,  $\pi_C = 32.69\%$ ,  $\pi_G = 15.11\%$ ,  $\pi_T = 24.52\%$ ; transitions/transversions ratio = 5.66; proportion of invariable sites (I) = 0.5742; gamma distribution shape parameter  $\alpha = 1.3298$ .

Phylogenetic trees were constructed according to four approaches: neighbour joining (NJ) (Saitou & Nei 1987, MEGA 3.1 of Kumar et al. 2004); maximum likelihood (ML) (Tree Puzzle 5.2 of Schmidt et al. 2002), applying the above model, maximum parsimony (MP) (PAUP\* 4.0b10 of Swofford 2003); and Bayesian inferences (BI) (MrBayes version 3.1.1 of Huelsenbeck & Ronquist 2001), four runs with 500 000 generations, burnin 3000 and sample frequency 10 each). Robustness of clades was estimated by 2000/1000 bootstrap replicates (Felsenstein 1985) for NJ/MP and via quartet puzzling in ML (10 000 puzzling steps, Strimmer & von Haeseler 1996). The group-wise mean uncorrected p-distances and their standard errors (1000 bootstrap replications) were calculated by MEGA.

## 2.3 Results

### 2.3.1 Phylogenetic trees and relationships

In total, 512 bp of the cytochrome-*b* fragment could be analysed consistently for all haplotypes. There were 146 variable sites, 121 of which were parsimony-informative (ingroup only). I found 39 different *Certhia* haplotypes (out of 64 samples), which are listed in Table 2.1 and incorporated into all phylogenies (Fig. 2.1). In all of them, *Certhia* proved to be monophyletic with good support and monophyly is affirmed with respect to the chosen outgroups (except in BI).

All presently recognised species are represented as well-supported haplotype clusters, except for *C. familiaris* (ML and NJ only) and *C. discolor* (NJ only). Furthermore, the phylogenetic trees divide the traditional *C. familiaris* (Eurasia including China and the Himalayas) into two deeply split clusters, similar to the split between *C. brachydactyla* and *C. americana*, and the traditional *C. discolor* into two deeply split clusters, similar to the split between *C. tianquanensis* and *nipalensis*, which are sister taxa. In all phylogenies, the sister taxon of the latter two taxa is the split *C. discolor*. *Certhia himalayana* ranges between the cluster of the former three species and a large cluster mainly of the northern Palaearctic and the Nearctic realms. This is only supported by NJ and ML. It is deeply split into four subclusters: a western Palaearctic subcluster (Europe, North Africa; *C. brachydactyla*) is sister to a Nearctic one (*C. americana*), but support is weak. To both subclusters two additional subclusters are sister taxa, which represent the traditional *C. familiaris* of the Palaearctic (all northern Eurasia and, largely disjunct, the Himalayas/China).

Most haplotypes were rare and have been found only in one individual. Within each species I found different numbers of haplotypes, but in species with small distribution ranges, i.e. *C. nipalensis* and *C. tianquanensis*, all investigated individuals shared the same haplotype. In others, single haplotypes are shared by individuals of the same geographical origin. As an exception, within the northern Eurasian *C. familiaris* one haplotype exists in a huge area from Germany via central Asia (Kyrgyzstan), and central Siberia (Tyva) to China (Gansu and Shaanxi) (haplotype *familiaris* 9 in Table 2.1).

**Table 2.2:** Between-group distances from uncorrected pairwise distances of *Certhia* species and their standard errors estimated by bootstrapping (1000 replications). In the diagonal within-group distances are given – estimated in the same way: ame, *americana*; bra, *brachydactyla*; dis, *discolor*; *discolor* sensu lato (dis s.l.), *discolor* s.s. and *manipurensis*; fam, *familiaris*; *familiaris* sensu lato (fam s.l.), *familiaris* s.s. and *hodgsoni*; him, *himalayana*; hod, *hodgsoni*; man, *manipurensis*; nip, *nipalensis*; tia, *tianquanensis*.

	fam	hod	fam s.l.	ame	bra	him	dis	man	dis s.l.	nip	tia
fam	1.0 ± 0.2										
hod	5.3 ± 0.8	3.0 ± 0.4									
fam s.l.	–	–	3.6 ± 0.5								
ame	8.5 ± 1.1	7.4 ± 1.0	8.0 ± 1.0	0.8 ± 0.3							
bra	9.3 ± 1.2	8.5 ± 1.1	8.9 ± 1.0	8.6 ± 1.1	1.7 ± 0.4						
him	10.7 ± 1.2	9.7 ± 1.1	10.2 ± 1.1	9.7 ± 1.2	10.7 ± 1.3	0.7 ± 0.2					
dis	8.7 ± 1.2	8.4 ± 1.1	–	7.9 ± 1.1	9.4 ± 1.2	9.8 ± 1.2	0.2 ± 0.2				
man	10.1 ± 1.3	10.0 ± 1.2	–	8.9 ± 1.2	10.6 ± 1.3	10.1 ± 1.2	5.1 ± 1.0	0.2 ± 0.2			
dis s.l.	–	–	9.3 ± 1.0	8.4 ± 1.0	10.0 ± 1.2	9.9 ± 1.2	–	–	3.5 ± 0.7		
nip	11.4 ± 1.4	10.6 ± 1.3	11.0 ± 1.3	10.7 ± 1.3	11.6 ± 1.3	11.1 ± 1.4	9.5 ± 1.3	9.5 ± 1.2	9.5 ± 1.2	./.	
tia	11.3 ± 1.3	10.3 ± 1.2	10.9 ± 1.2	11.9 ± 1.4	11.9 ± 1.4	11.5 ± 1.3	9.7 ± 1.3	9.7 ± 1.3	9.7 ± 1.2	5.7 ± 1.0	./.

Almost all of the group-wise uncorrected p-distances between the recognised species fall into the range from 7.9 to 11.9%; only the distance between *C. nipalensis* and *C. tianquanensis*, 5.7%, appears as an outlier (Table 2.2).

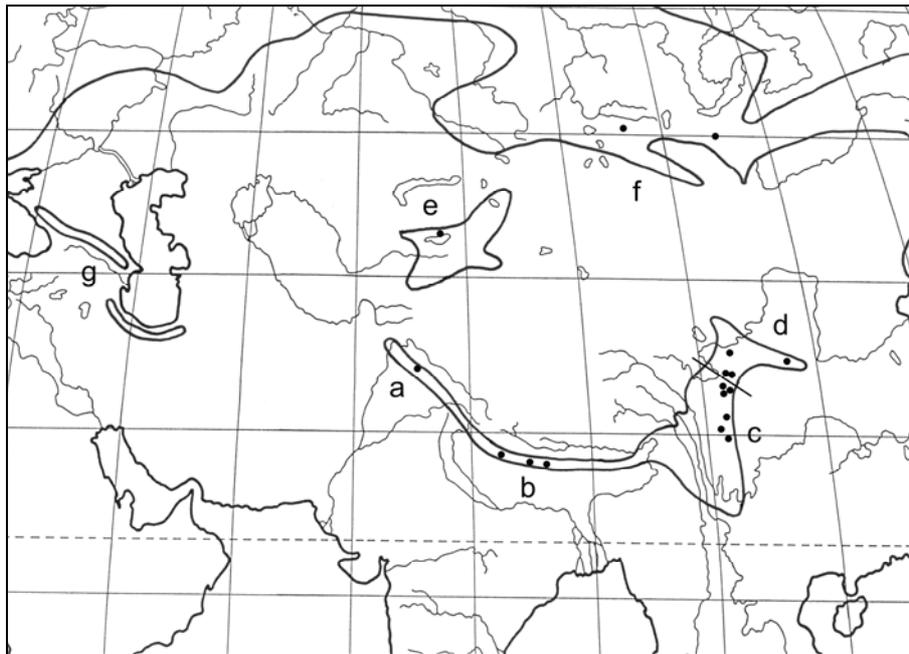
### 2.3.2 Within-group differentiation

The largest intraspecific differentiations exist in *C. familiaris* and *C. discolor*: within-group mean distances are 3.6 and 3.5%, respectively. In the case of *C. familiaris*, this is due to the fact that within an extended geographical area very diverse populations are incorporated: the northern haplotype cluster embraces birds from northern Eurasia (central Europe across Siberia to Japan) and the northern Chinese provinces Shaanxi and Gansu (no substructure given in the phylograms), while the southern haplotype cluster unites individuals from Kashmir/India, Nepal, and the western Chinese province of Sichuan (between-group distance of 5.3%, comparing northern and southern clusters). In addition, this southern cluster is divided into three clades, corresponding to the *C. familiaris* subspecies *hodgsoni* (western Himalayas; only one sample), *mandellii* (central and eastern Himalayas; well supported by all tree-reconstruction approaches) and *khamensis* (Sichuan; supported only by NJ and ML). Within this cluster, ssp. *hodgsoni* is the sister taxon to ssp. *mandellii* and ssp. *khamensis* (between-group distances of  $3.9 \pm 0.8$  and  $2.9 \pm 0.7\%$ , respectively; topology not given by BI, not supported by MP); even the mean distance between *mandellii* and *khamensis* is remarkably high at  $2.1 \pm 0.5\%$ . In the northern cluster, I have to include the (so far checked) subspecies *C. familiaris macrodactyla* (central Europe), nominate *familiaris* (North/East Europe), *tianschanica* (central Asia), *daurica* (central Siberia, Japan) and, largely disjunct from the other Asian ones, *bianchii* (China: Gansu and Shaanxi) (Fig. 2.2).

Contrary to the situation for *C. familiaris*, I compare two disjunct subspecies of *C. discolor*, nominate *discolor* from the Himalayas and ssp. *manipurensis* from the borderlands of North-East India and Myanmar. Both clusters are well supported, whereas traditional *C. discolor* (including ssp. *manipurensis*) is not. The between-group mean distance of the two forms is 5.1%, similar to the two *familiaris* clusters and the *nipalensis/tianquanensis* species pair.

A comparably profound but shallower split exists in *C. brachydactyla*, separating central European and North African residents ( $2.9 \pm 0.7\%$ ); in this case, the species cluster and both subclusters are well supported. Within *C. americana*, the samples from Canada and the USA, all from the eastern part of the continent (ssp. *americana*; Table 2.1), are quite different

(within-group distance of 0.8%). I expect that larger sample sets may reveal more pronounced differentiation. The few samples of *C. himalayana*, a species inhabiting three disjunct areas in central Asia and China, largely east and west of the Himalayas, and in Myanmar (Natmataung in the southern Chin hills), respectively, cluster according to their geographical origin (Myanmar haplotype opposed to Sino-Himalayan haplotype cluster; not supported by BI). Between-group distance is low at  $0.5 \pm 0.3\%$ .



**Fig. 2.2:** Localities from which tissue samples of *Certhia familiaris* s.s. and *C. hodgsoni* from central and Southeast Asia were available for this study. The expected but still unknown zone of secondary contact between *C. familiaris* and *C. hodgsoni* is indicated by an arbitrarily drawn bar between the closest localities of c and d. – a) *C. h. hodgsoni* (Kashmir/India), b) *C. h. mandellii* (Nepal), c) *C. h. khamensis* (Sichuan/China), d) *C. f. bianchii* (Gansu, western China, and Shaanxi, eastern China), e) *C. f. tianschanica* (Kyrgyzstan), f) *C. f. daurica* (Tyva, Russia, western; Mongolia, eastern). No samples were available from the Caucasus/Alborz area (g, *C. f. caucasica*, western, and *C. f. persica*, eastern). Map drawn from various sources.

## 2.4 Discussion

### 2.4.1 Species in *Certhia*

The status of biospecies (Mayr 1942) is confirmed for all traditional *Certhia* species. Almost all of them occur sympatrically with at least one further species, and hybrid barriers are obvious in those cases. The exception is *C. americana*, which represents the sole species in the Nearctic. On morphological grounds, its originator C.L. Brehm (1857) believed his *C.*

*brachydactyla* to be present in North America, as did Hartert (1905) and Kleinschmidt (fide Kelm 1960) on the basis of markings of wing pattern and other morphological characters. However, in general, the American populations have been affiliated to *C. familiaris* (Vaurie 1957, Mayr & Short 1970). On acoustic grounds, Thielcke (1962) first ranked the American populations as separate species, and this is now generally accepted (AOU 1983, 1998, Harrap & Quinn 1996). Strong acoustic similarities between *C. americana* and western Palaearctic *C. brachydactyla* were stressed by Baptista & Krebs (2000). The molecular approach indeed assigns *C. americana* to *C. brachydactyla* as its closest relative (although the topology is only supported by ML). In view of the deep split between them, which is almost as deep as that between *C. familiaris* s.l. and *C. brachydactyla*, species rank of *C. brachydactyla* and *americana* is obvious.

A similar problem regarding uncertain but hitherto unrecognised species rank is posed by the extended populations of *C. familiaris* in northern Eurasia on the one hand, and in China and the Himalayas on the other. They are separated from each other by the deserts of Mongolia and northern China (Portenko & Stübs 1977; Fig. 2.2).

Some of the Sino-Himalayan populations of *C. familiaris* form a separate cluster, which is split from the northern population block by a between-group distance of 5.3%. This value is almost as high as that between allopatric *C. nipalensis* and *C. tianquanensis*, but lower than in sympatric species pairs. Although they are allopatrically distributed, the distance value indicates species rank of both subclusters of *C. familiaris*. This value is in accordance with those of many closely related and even sympatrically distributed species, e.g. the warblers of the *Seicercus burkii* complex (Olsson et al. 2004, Päckert et al. 2004). However, apart from character clines and more or less well-marked differences between subspecies, external morphology presents no reliable cues for the species status of northern and southern *C. "familiaris"* (Vaurie 1957, 1959). Although acoustic differences between the clusters are strongly developed, forming regiolect areas (Martens 1996), reciprocal "understanding" of alien songs in a territorial context in field experiments differs. Himalayan ssp. *mandellii* (southern *familiaris* group) did not recognise songs of *C. familiaris* s.s. from Germany (northern *familiaris* group), but individuals from Germany did react to various, also artificially altered, song types from Nepalese *mandellii* (Martens & Geduldig 1988). This is at least partly due to the "sreeh" note ("srieh" in German literature; cf. first note in sonagrams a, c–e and last note in f of Fig. 2.1),

which is present in most songs of all members of *C. familiaris* and related species, although it is differently shaped in various populations (Martens 1981).

The geographical situation within the *familiaris* complex is even more complicated. This molecular genetic split does not simply separate the two large disjunct population blocks; the geographical borderline separating northern and southern clusters runs through the Chinese population block. A part of this area, from the Qinling range northward, belongs to the northern taiga population block of *C. familiaris*, from which it is separated by a large belt uninhabited by treecreepers (Fig. 2.2). This biogeographically unexpected affiliation is well supported both by all phylogenetic trees (Fig. 2.1), and by morphology and acoustics (Vaurie 1957, Martens et al. 2002). Vaurie (1957) meticulously described a morphological cline within the northern population group and included the ssp. *bianchii* of northern China within this row of populations, although it is widely disjunct from the others (Fig. 2.2). This conclusion agrees fully with the molecular and acoustic results. Introgression and lineage sorting could be reasons for a misplacement of *bianchii* samples within the northern cluster instead of within *C. hodgsoni*, together with the other Chinese populations. But morphological and vocal differences within China reject these alternative explanations.

Consequently, I have to expect a zone of secondary contact between northern and southern populations of Chinese *C. "familiaris"* somewhere in the mountainous parts of western central China, probably in the northern parts of Sichuan. This zone is still unknown and may exist as a suture zone dividing the parapatric areas of the two species or even as an area of limited sympatry. In view of the similar ecology of the Chinese *C. "familiaris"* clusters, which are both confined to coniferous or mixed broad-leaved/coniferous forests at high altitudes above 2700 m (pers. obs.), I expect parapatry rather than a notable area of overlap. The species' interactions may even include local hybridisation but, given the amount of genetic and acoustic differences (Martens et al. 2002), only to a limited extent. The ssp. *khamensis* and *bianchii* are the taxonomic carriers of the population interactions concerned. The collecting localities closest to each other that represent the different acoustic and genetic characteristics are situated in northern Sichuan along the road between Jiuzhaigou and Sungpan (*C. hodgsoni*) and in southern Gansu near Zhuoni (*C. familiaris* s.s.), and are 165 km apart (Fig. 2.2).

A similar remarkable difference is obvious with the between-group distance of, again, slightly above 5% between the two branches of the *C. discolor* cluster. They represent allopatrically distributed subspecies, which are also characterised by striking morphological differences,

ssp. *discolor* in the Himalayas and ssp. *manipurensis* in Myanmar. This needs special emphasis, as treecreepers in general differ only slightly in external appearance, as mentioned above (see colour plates in Harrap & Quinn 1996).

In both cases a split at the species level is corroborated further by the fact that the traditional species *C. discolor* and *C. familiaris* are not well supported in all phylogenetic approaches.

#### 2.4.2 Phylogeny and bioacoustics

The phylogenetic tree (Fig. 2.1) quite clearly reflects the acoustic differentiation within *Certhia*, from simple to complex verse forms, from South Asia to high latitudes in the Palaearctic and Nearctic realms. *Certhia* species use single highly stereotyped songs, and only one of the available song types is ordinarily produced by an individual male (Thielcke 1970a, Martens 1981, Glutz von Blotzheim & Bauer 1993). Regarding territorial songs, two main song groups are obvious (Fig. 2.1). The species *C. discolor*, *C. manipurensis*, *C. nipalensis*, *C. himalayana* and *C. tianquanensis* use trills as territorial songs (Martens 1981, Martens et al. 2002). A series of identical or at least similar elements form the verse. These species inhabit the mountainous areas of Palaearctic Southeast Asia and, in addition, some of them have small to even relict-like areas even further south in Myanmar, Thailand, Laos and Viet Nam. The remaining species of the northern Palaearctic and of the Nearctic, *C. familiaris* s.s., *C. hodgsoni*, *C. americana* and *C. brachydactyla*, in general have much larger ranges, stretching even trans-continently in *C. familiaris* s.s. and *C. americana*. The songs of these species are considerably more complex and include a variety of highly differing notes. All notes typically differ from each other; pure trill songs alone do not exist. A typical song and call element for all of these species is the “sreeh” note, a high-frequency strongly modulated note. It is slightly modified in the single species and subspecies, but seems to be homologous to contact calls, which were integrated into songs during song evolution (Thielcke 1964a).

#### 2.4.3 Taxonomy

Until recently, the taxonomic situation in *Certhia* seemed straightforward. No problems were under discussion, although the discovery of a hitherto overlooked species, *C. tianquanensis*, was unexpected (Li 1995, Martens et al. 2002). Remarkable vocal differences in *C. familiaris* s.l., especially among Asian populations, which have long been known (Thielcke 1962, Martens 1981, Martens et al. 2002), underline the molecular genetic results and confirm their

taxonomic value. In the *Certhia* example presented here, the cytochrome-*b* distances between the presently accepted species are high (> 5.5%). One group requiring species rank is represented by the southern populations of *C. familiaris*, and was, apparently, hitherto placed incorrectly. The distance between its southern and northern subspecies blocks is almost of the same order as that between all other well-established species. The same holds true for the divergence of *C. d. discolor* and *C. d. manipurensis*, but acoustic differences are less striking and need further attention (sonagrams k and l in Fig. 2.1 and in Martens et al. 2002).

In the cases of allopatric populations that display genetic and acoustic differences, the biological species concept (Mayr 1942) fails because no interactions between carriers of different haplotypes or acoustic repertoire can be observed. Taxonomic decisions have to refer to inferences of various sets of characters of the populations in question, and consequently follow to a certain extent the phylogenetic species concept (Cracraft 1983), which is based on diagnosable “differences”. Taxonomists may concur with the split between *C. familiaris* s.s. and *C. hodgsoni* (strong genetic and acoustic differences) as well as between *C. discolor* s.s. and *C. manipurensis* (strong genetic, but less marked acoustic differences), probably hesitatingly that between European and African *C. brachydactyla* (less marked genetic, strong vocal difference), but are likely to reject a possible elevation of ssp. *hodgsoni* and ssp. *mandellii* within *C. hodgsoni* (genetic difference less marked, strong morphological, low acoustical, hybrids have never been found, contrary to Vaurie 1957, Martens & Eck 1995). In general, recently diverged taxa are more difficult to assign to rank than more anciently separated ones.

In both cases of relatively low molecular genetic differences between taxa pairs (*C. brachydactyla*, *C. himalayana*), biological species limits may exist, but are difficult to ascertain. However, it is evident that molecular genetic data even in combination with additional data sets (morphology, acoustics) may hardly determine, unequivocally, where species limits are to be drawn. Consequently, I recommend a promotion to species in only two cases, in which the cytochrome-*b* and, to a lesser extent, vocal differences between populations are straightforward.

According to the molecular approach, all species listed by Dickinson (2003) are valid entities under the various species concepts. For reasons explained above, I formally recommend that:

(1) *Certhia familiaris* Linné, 1758 be split into two species, *Certhia familiaris* s.s. (northern Eurasia including northern China) and *Certhia hodgsoni* Brooks, 1871 (China, Himalayas).

The latter species embraces the Sino-Himalayan subspecies *hodgsoni* Brooks, 1871 (western Himalayas), *mandellii* Brooks, 1874 (central Himalayas) and *khamensis* Bianchi, 1903 (south-western and western China), but the northernmost subspecies of the Sino-Himalayan population block in China, *bianchii* Hartert, 1905, is part of northern *C. familiaris* s.s. The relationships of the latter remain unresolved in this approach, which hints at a recent spreading from northern China via Siberia and Central Asia to Europe.

(2) *Certhia discolor* Blyth, 1845 be split into two species, *Certhia discolor* s.s. (Himalayas) and *Certhia manipurensis* Hume, 1881 (Manipur/India to Chin hills/Myanmar). The former species becomes monotypic, while all other subspecies of *C. discolor* may provisionally be assigned to *C. manipurensis*. Their territorial songs are, so far as is known, more similar to those of *C. manipurensis* than those of *C. discolor* (sonagrams k and l in Fig. 2.1; Martens et al. 2002). Furthermore, their distribution ranges form a mosaic of disjunct small areas in mountains of Southeast Asia similar to that of *manipurensis*: *shanensis* E.C.S. Baker, 1930 (northern Myanmar, Yunnan/China, Thailand), *laotiana* Delacour, 1951 (Laos), *meridionalis* Robinson & Kloss, 1919 (surroundings of Da Lat/Viet Nam). I regard this assignment as preliminary, until representatives of the taxa in question can be included in a molecular study. Morphological differences within *C. manipurensis*, as understood here, are striking, and I would not be surprised to find strong genetic differences between these taxa.

Martens et al. (2002) united *C. discolor* with *C. tianquanensis* to form a superspecies, *C. [discolor]*, but molecular genetics and a few morphological characters (Martens et al. 2002) now recognise *C. nipalensis* and *C. tianquanensis* as most closely related species. The latter two are allopatric, and even largely disjunct, and they may well qualify as a superspecies *C. [nipalensis]*. Similarly, *C. familiaris* and *C. americana* were thought to form a superspecies, *C. [familiaris]* (Glutz von Blotzheim & Bauer 1993: 922), after the status of the latter as a set of subspecies of the Old World *C. familiaris* had been abandoned (AOU 1983). But it is much more likely that *C. brachydactyla* and *C. americana* constitute a superspecies. Molecular genetics, acoustics and morphological characters underline their close relationships and, according to the concept of superspecies (Amadon 1966), their areas are allopatric as well. In addition, *C. familiaris* and *C. hodgsoni*, although their distributional limits in northern China are not yet fully known, apparently fulfil the requirements of the superspecies definition and may be combined as *C. [familiaris]*. *Certhia discolor* s.s. and *C. manipurensis* may make up a fur-

ther superspecies within *Certhia* for the same reasons. All recommended taxonomic changes are summarised in Table 2.3 and are introduced in Fig. 2.1.

**Table 2.3:** List of proposed species and superspecies in *Certhia* including the taxonomic changes.

Species	Included traditional taxa
<i>Certhia</i> [ <i>nipalensis</i> ] <i>nipalensis</i>	<i>Certhia nipalensis</i>
<i>Certhia</i> [ <i>nipalensis</i> ] <i>tianquanensis</i>	<i>Certhia</i> [ <i>discolor</i> ] <i>tianquanensis</i>
<i>Certhia</i> [ <i>discolor</i> ] <i>discolor</i>	<i>Certhia</i> [ <i>discolor</i> ] <i>discolor</i> <i>discolor</i>
<i>Certhia</i> [ <i>discolor</i> ] <i>manipurensis</i>	<i>Certhia</i> [ <i>discolor</i> ] <i>discolor</i> (all other ssp.)
<i>Certhia himalayana</i>	<i>Certhia himalayana</i>
<i>Certhia</i> [ <i>brachydactyla</i> ] <i>americana</i>	<i>Certhia</i> [ <i>familiaris</i> ] <i>americana</i>
<i>Certhia</i> [ <i>brachydactyla</i> ] <i>brachydactyla</i>	<i>Certhia brachydactyla</i>
<i>Certhia</i> [ <i>familiaris</i> ] <i>hodgsoni</i>	<i>Certhia</i> [ <i>familiaris</i> ] <i>familiaris</i> (ssp. <i>hodgsoni</i> , <i>mandellii</i> , <i>khamensis</i> )
<i>Certhia</i> [ <i>familiaris</i> ] <i>familiaris</i>	<i>Certhia</i> [ <i>familiaris</i> ] <i>familiaris</i> (all other ssp.)

## 2.5 Summary

I sequenced a part of the mitochondrial cytochrome-*b* gene from the seven treecreeper species, including 18 subspecies, to reconstruct the phylogeny of the genus *Certhia*. Species status of all seven species could be affirmed. *Certhia discolor*, *C. himalayana*, *C. nipalensis*, and *C. tianquanensis*, the species with relatively small distribution ranges in southeast Asia and simple territorial song, are found at the base of all phylogenetic trees, although without good support. A comparatively recent sister species of *C. tianquanensis* is *C. nipalensis*, replacing *C. discolor* as closest relative. *Certhia familiaris*, *C. brachydactyla* and *C. americana* form a derived set of species (again only weak support). The closest relative of *C. americana* is *C. brachydactyla*. The *C. familiaris* subtree is deeply split into two well-defined population groups: a Eurasian group including populations in northern China (Qinling range northward and all Eurasia) and a Sino-Himalayan group (Himalayas and China excluding northern China). In accordance with acoustic characters, the three subspecies *hodgsoni*, *mandellii* and *khamensis* of the Sino-Himalayan group are combined and elevated to species rank: *Certhia hodgsoni*. *Certhia discolor manipurensis* is deeply split from nominate *discolor* as well, and is also promoted to species level. Within *C. brachydactyla* (western Palaearctic) and within *C. hodgsoni* (Himalayas, China) several populations form well-supported separate lineages that diverged quite recently and represent subspecies level. In all other species, molecular-genetic and vocal characters support traditional species delimitation.

## 3 Evolutionary history of treecreeper vocalisations

### 3.1 Introduction

Treecreepers (*Certhia*) comprise a morphologically and genetically clearly defined group of passerine birds characterised by a suite of adaptations to foraging and nesting on and behind tree bark: long bill and hind claw, stiff rectrices and camouflaging plumage. Consequently, within-group differentiation in outer morphology is often slight (Harrap & Quinn 1996). Due to the lack of distinct morphological characters between taxa and despite the small number of species, the phylogenetic relationships within the genus had been difficult to ascertain.

I (Chapter 2) presented a comprehensive molecular phylogeny, which covered all described species and a number of subspecies (according to Dickinson 2003) from throughout the Holarctic range of the genus, and detected several levels of differentiation, thereby uncovering two cryptic species. The following nine species were recognised by me:

Superspecies *Certhia* [*familiaris*]

1. *Certhia* [*familiaris*] *familiaris* Linnaeus, 1758 with ten subspecies (from Britain and France east to the Pacific including Japan, southern distribution limit through Corsica, the Caucasus, Azerbaijan, the Tian Shan and the Qinling range in China)
2. *Certhia* [*familiaris*] *hodgsoni* Brooks, 1871 with three subspecies (Himalayas, W Chinese mountains south of the Qinling range), formerly included in Palearctic *C. familiaris* s.l.

Superspecies *Certhia* [*brachydactyla*]

3. *Certhia* [*brachydactyla*] *americana* Bonaparte, 1838 with 15 subspecies (N America from Alaska south to Nicaragua), American taxa formerly included in one of the Palearctic species, *C. brachydactyla* or *C. familiaris* s.l.
4. *Certhia* [*brachydactyla*] *brachydactyla* Brehm, 1820 with six subspecies (W Palearctic including NW Africa and the Caucasus)
5. Isospecies *Certhia himalayana* Vigors, 1832 with four subspecies (from the Tian Shan eastwards through the Himalayas to the W Chinese mountains, W Myanmar)

Superspecies *Certhia* [*nipalensis*]

6. *Certhia* [*nipalensis*] *tianquanensis* Li, 1995 (only few localities in the Chinese provinces of Sichuan and Shaanxi), treated as allospecies of *C. discolor* s.l. by Martens et al. (2002)
7. *Certhia* [*nipalensis*] *nipalensis* Blyth, 1845 (C and E Himalayas)

Superspecies *Certhia* [*discolor*]

8. *Certhia* [*discolor*] *discolor* Blyth, 1845 (C and E Himalayas)
9. *Certhia* [*discolor*] *manipurensis* Hume, 1881 with four disjunct subspecies (Assam/Myanmar, Shan Mountains, Laos, Dalat Plateau), formerly included in *C. discolor* s.l.

Treecreepers are restricted to the Holarctic realm with local extensions to the tropics. In the larger parts of the genus' range, there is only one species present, but in Europe *C. brachydactyla* and *C. familiaris* occur together. In the Himalayas, up to four species can be found sympatrically, but a tendency towards vertical segregation of species is obvious in all areas of sympatry (Martens 1981).

Because of the faint differences between *Certhia* taxa as regards outer morphology, there has been a long tradition of applying bioacoustics to their classification (Brehm 1820, Stresemann 1919, Mayr 1956, Thielcke 1961, 1962, 1964a, 1965a, Martens 1981, Martens & Geduldig 1988, Baptista & Krebs 2000), as Alström & Ranft (2003) demonstrated for several other bird taxa, too. This is facilitated by the fact that a single treecreeper male almost invariably utilises the same verse of song and that even across larger distributional areas territorial songs remain extremely uniform. The last time when *Certhia* vocalisations helped to discriminate two forms was the upgrading of *C. tianquanensis* to species level (Martens et al. 2002). All previous studies have in common that they compared the acoustic impressions or analysed the sonagrams of the calls and songs of different treecreeper forms, but did not undertake statistical comparisons of sonographic measurements or syntax parameters.

Here I want to test the hypotheses that (i) vocalisations as a behavioural trait are suitable to delimit taxonomic units (species groups and species) within *Certhia*, which underwent their own evolutionary history, and that (ii) there is a phylogenetic signal in treecreeper songs. Phylogenetically informative vocal characters should be least prone to homoplasy when mapped on a given phylogenetic tree. In this study, the degree of homoplasy was inferred from consis-

tency, retention and rescaled consistency indices. Given that the two hypotheses will be confirmed, treecreeper vocalisations should be helpful for a preliminary affiliation of taxa that were not incorporated into the recent phylogenetic reconstructions (Chapter 2). This study tries to reconstruct the evolution of the genus *Certhia* by opposing results from bioacoustics on the one hand and molecular systematics on the other hand. In addition, it questions whether inborn calls or partially learnt territorial songs are more suitable for taxonomic studies. Avian vocalisations have been tested for phylogenetic signal in the case of herons (McCracken & Sheldon 1997) and the passerine genera *Psarocolius* (Price & Lanyon 2002), *Regulus* and *Seicercus* (Päckert et al. 2003, 2004). Multivariate statistics have become a widespread means for the discrimination of closely related songbirds (e.g. Martens et al. 2004, Zhang et al. 2006), after Sparling & Williams (1978) recommended their application to the field of avian bioacoustics.

## 3.2 Methods

### 3.2.1 Definitions of terms

**Call:** Tends to be shorter and simpler than songs and is produced by both sexes throughout the year (Catchpole & Slater 1995: 10); innate vocalisation, given in various contexts including other than territorial significance. In this paper, “call” refers to aggression calls uttered in a territorial context.

**Song (territorial song):** Long and complex vocalisation mainly produced by males in the breeding season (Catchpole & Slater 1995: 10), composed of verses.

**Verse:** Unit of territorial song, discrete part of complex vocalisation of males consisting of different elements given within territorial song performance; verses are separated by pauses.

**Element:** Particular sound event, continuous line in a sonagram (Catchpole & Slater 1995: 10).

**“sreeh”:** Frequency-modulated song element at approx. 7 to 8 kHz and of ca. 0.3 s duration; typical call of *C. familiaris*, *C. hodgsoni* and most *C. americana* (in *C. brachydactyla* not in territorial context, but long-distance contact call as in *C. familiaris*), incorporated into territorial song of most *C. familiaris*, *C. hodgsoni*, *C. americana* and *C. brachydactyla* populations.

**“tyt”:** L-shaped song element of ca. 0.2 s duration, less modulated than the “sreeh” element, rather a pure whistle; typical call of *C. brachydactyla* (and sometimes also call of *C. americana*), used in various contexts, incorporated into territorial song of most *C. brachydactyla* and a few *C. americana* and *C. familiaris* populations.

**Syntax:** Denotes order of elements or element groups within territorial song.

**Trill:** Fast repetition of elements or element groups of the same element type; is given as a part of a verse or even makes up the whole verse.

**Trill speed:** Number of trill elements per time unit. Trill speed is higher the closer the elements are arranged to one another in each time unit.

**Repertoire:** Comprises the different verse types that are used by a given male or within a given population.

**Dialect:** Vocalisations which are limited to groups of individuals; they can be regarded as temporal or spatial variants of the acoustic system. Several dialects may occur in one population. Species-specific characters of dialects remain stable throughout the species’ area (Wickler 1986, Martens 1996).

**Regiolect:** Distinct song repertoire usually extending over a large distributional range of a given species. In contrast to dialects, there is no geographic overlap between regiolects (except in contact or hybrid zones), and song parameters used in species recognition differ markedly between regiolect populations (Martens 1996). Regiolects are close to species-specific songs and denote populations close to species rank (or hitherto misclassified biological species).

**Motif group:** Monophyletic group of *Certhia* species (*C. americana*, *C. brachydactyla*, *C. familiaris*, *C. hodgsoni*; Chapter 2) which use complex song types, mostly characterised by the “sreeh” element; for details see Results.

**Trill group:** Set of *Certhia* species (*C. discolor*, *C. himalayana*, *C. manipurensis*, *C. nipalensis*, *C. tianquanensis*) which use simple song types, mainly characterised by a trill; for details see Results.

### 3.2.2 Material

1155 song verses from 302 males and 758 calls produced by 176 different individuals were analysed (398 analysed recordings in total; see Table 3.1 for number of analysed individuals per taxon). Equipment used for field recordings up to 1998 is listed in Martens et al. (1999), that used until 2002 is given in Päckert et al. (2004). In 2003 and 2004, J. Martens used a NAGRA SN tape recorder with a Telinga Pro III microphone in a 60-cm plastic reflector, in 2005 a SONY WM-6DC stereo cassette recorder with a Sennheiser K6 directional microphone. In 2003 and 2004, I used a SONY MZ-N707 Portable Minidisc Recorder with a Sennheiser K6 directional microphone, in 2005 a SONY WM-6DC stereo cassette recorder with a Telinga Pro4 PIP microphone in a 60-cm plastic reflector and in 2006 a Marantz PMD660 solid-state recorder with a homemade microphone in a 60-cm plastic reflector. Equipment data for recordings other than those of J. Martens and me can be retrieved from the appropriate sound archive's database (if available).

**Table 3.1:** Number of males whose song verses have been analysed and number of individuals whose calls have been analysed per subspecies sensu Dickinson (2003) and species sensu Chapter 2. “Incorrect” sums are due to cases of uncertain subspecies affiliation.

Taxon	Singing males	Calling ind.
<i>C. f. britannica</i>	22	28
<i>C. f. macrodactyla</i>	4	3
<i>C. f. familiaris</i>	1	3
<i>C. f. corsa</i>	3	
<i>C. f. tianschanica</i>		3
<i>C. f. bianchii</i>	31	8
<i>C. f. daurica</i>	2	1
<b><i>C. familiaris</i></b>	<b>63</b>	<b>46</b>
<i>C. h. hodgsoni</i>	1	1
<i>C. h. mandellii</i>	16	13
<i>C. h. khamensis</i>	21	15
<b><i>C. hodgsoni</i></b>	<b>38</b>	<b>29</b>
<i>C. a. montana</i>	1	1
<i>C. a. occidentalis</i>	3	5
<i>C. a. zelotes</i>	11	10
<i>C. a. albescens</i>	2	2
<i>C. a. alticola</i>		2
<i>C. a. pernigra</i>		1
<i>C. a. americana</i>	20	13
<i>C. a. nigrescens</i>	1	1

Taxon	Singing males	Calling ind.
<b><i>C. americana</i></b>	<b>39</b>	<b>35</b>
<i>C. b. mauritanica</i>	9	1
<i>C. b. megarhynchos</i>	25	8
<i>C. b. brachydactyla</i>	1	2
<i>C. b. stresemanni</i>	1	1
<i>C. b. dorothaeae</i>	4	2
<b><i>C. brachydactyla</i></b>	<b>43</b>	<b>14</b>
<i>C. h. taeniura</i>	1	
<i>C. h. himalayana</i>	29	10
<i>C. h. yunnanensis</i>	16	9
<i>C. h. ripponi</i>	3	
<b><i>C. himalayana</i></b>	<b>49</b>	<b>19</b>
<b><i>C. tianquanensis</i></b>	<b>21</b>	<b>2</b>
<b><i>C. nipalensis</i></b>	<b>16</b>	<b>6</b>
<b><i>C. discolor</i></b>	<b>15</b>	<b>18</b>
<i>C. m. manipurensis</i>	12	4
<i>C. m. shanensis</i>	5	3
<i>C. m. meridionalis</i>	1	
<b><i>C. manipurensis</i></b>	<b>18</b>	<b>7</b>
<b>Genus <i>Certhia</i></b>	<b>302</b>	<b>176</b>

### 3.2.3 Sonographic analysis

For sonographic measurements, all recordings were converted to a sampling rate of 22.1 kHz/16 Bit. Avisoft SASLab Pro 4.36 (Specht 2005) was used to produce sonagrams. Since the repertoire of a single individual is mostly limited to one type of verse, a maximum of five

verses per bird were sonographically measured. The following verse parameters were taken: verse length ( $\Delta t$ ), minimum frequency ( $F_{\min}$ ), maximum frequency ( $F_{\max}$ ), frequency range ( $\Delta F$ ), mean frequency (arithmetic mean of minimum and maximum frequencies;  $F_{\text{mean}}$ ), number of elements and number of “sreeh” elements as well as (relevant taxa only) frequency increase/decrease of trill elements (frequency change per time), number of trill elements ( $n$ ), trill duration ( $t_1$ ) and trill speed ( $n/t_1$ ). The following parameters were taken from up to five call sonagrams per individual: call length ( $\Delta t$ ), minimum frequency ( $F_{\min}$ ), maximum frequency ( $F_{\max}$ ), frequency range ( $\Delta F$ ), mean frequency (arithmetic mean of minimum and maximum frequencies;  $F_{\text{mean}}$ ), number of “sreeh” elements and – in *C. tianquanensis* and *C. nipalensis* only – frequency increase of broadest call element. For all further analyses mean values per individual of all parameters were used. Acoustic differentiation between taxa was verified by pairwise Mann-Whitney U-tests (significance level of  $p < 0.05$ ), discriminant analyses (DA) and principal component analyses (PCA) with varimax rotation and Kaiser normalisation, performed in SPSS 13.

#### 3.2.4 Character tracing

Sixteen characters of *Certhia* song (verse, syntax or element features; data matrix in Table 3.2) were traced on the maximum-likelihood tree of *Certhia* species as presented by me (Chapter 2) with Mesquite 1.05 (Maddison & Maddison 2004). One branching that had only weak bootstrap support was collapsed and the outgroup was excluded. MacClade 3.0 (Maddison & Maddison 1992) was used in order to hypothesise ancestral states and to test for a presumed phylogenetic signal. Most traits have multiple states; for example, trill elements can be missing, falling, rising, first falling, then rising or alternately falling and rising (Tables 3.2 and 3.3). Whenever a trait was polymorphic for a single taxon, all states were included in the data matrix. As an estimate of acoustic homoplasy, I calculated the consistency index (CI, Kluge & Farris 1969), the retention index (RI, Farris 1989) and the rescaled consistency index ( $RC = CI \times RI$ , Farris 1989) for each character with MacClade 3.0 (Maddison & Maddison 1992). Low values of these indices imply that little phylogenetic information is derivable from an investigated character. Simulations with random datasets of ten taxa and 14 characters (which approximately equals the size of my study) yielded CI values between 0.350 and 0.438 (Klassen et al. 1991); thus, CI values for phylogenetically informative acoustic characters should notably exceed this range.

**Table 3.2:** Data matrix for 16 acoustic traits of *Certhia* song as used for character tracing with Mesquite/MacClade and estimates of mean character divergence; for polymorphic taxa multiple character states are separated by a comma.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
<i>C. americana</i>	2	1	1	2	2	0	0	1	2	0	1	1	0	1	1, 3	1
<i>C. brachydactyla</i>	2	2	3	1	2	0	0	1	2	0	1	1	0	1	3	2
<i>C. discolor</i>	3	0	2	1	1	2	1	3	1	0	1	0	0	0	0	0
<i>C. familiaris</i>	4	1	3	3	2	1	0	2	2	1	1	1	1	1	1, 2, 3	1
<i>C. himalayana</i>	3	0	2	1	1	2	4	2	1	1	1	0	1	0	0	0
<i>C. hodgsoni</i>	3	1	3	2	2	0	0	1	2	0	1	1	1	2	1	1
<i>C. manipurensis</i>	3	0	2	1	1	4	1	2	1	0	1	0	0	0	0	0
<i>C. nipalensis</i>	1	0	1	1	2	2	2	1	1	1	0	0	0	0	0	0
<i>C. tianquanensis</i>	2	1	1	1	2	3	3	3	1	1	1	0	0	0	0	0

Traits: A verse length: 1 0.5–1 s, 2 1–1.5 s, 3 1.5–2 s, 4 2–2.5 s; B verse increase: 0 no change, 1 negative (decrease), 2 positive; C frequency course: 1 narrow, 2 medium, 3 wide; D frequency range: 1 narrow, 2 medium, 3 wide; E mean frequency: 1 < 5 kHz; 2 > 5 kHz; F trill: 0 none, 1 rarely at end, 2 single elements repeated, 3 twice single elements repeated, 4 double elements repeated; G trill-element increase: 0 no trill, 1 falling, 2 rising, 3 rising, then falling, 4 alternating up- and downstrokes; H number of elements: 1 low, 2 medium, 3 high; I element types: 1 few, 2 many; J rising elements: 0 no, 1 yes; K falling elements: 0 no, 1 yes; L v-shaped elements: 0 no, 1 yes; M A-shaped elements: 0 no, 1 yes; N number of “sreeh” elements; O “sreeh” position: 0 no “sreeh”, 1 beginning, 2 middle, 3 end; P number of “tyt” elements: 0 none, 1 sometimes, 2 at least two.

**Table 3.3:** Character status of various acoustic traits. CI: consistency index; RI: retention index; RC: rescaled consistency index. Ontogeny of trait: i(nnate), l(earned), n(o information). Structure of trait: v(verse syntax), e(lement structure). States: number of character states of one trait. Steps: number of state changes of one trait. For details see Methods.

Acoustic trait	Ontogeny	Structure	States	Steps	CI	RI	RC
Verse length	l	v	4	4	0.75	0.50	0.38
Verse increase	l	v	3	3	0.67	0.67	0.44
Frequency course	n	v	3	3	0.67	0.75	0.50
Frequency range	n	v	3	3	0.67	0.00	0.00
Mean frequency	n	v	2	2	0.50	0.50	0.25
Trill	i	v	5	4	1.00	1.00	1.00
Trill-element increase	i	e	5	4	1.00	1.00	1.00
Number of elements	n	v	3	5	0.40	0.00	0.00
Element types	i	v	2	1	1.00	1.00	1.00
Rising elements	i	e	2	3	0.33	0.33	0.11
falling elements	i	e	2	1	1.00	0.00	0.00
V-shaped elements	i	e	2	1	1.00	1.00	1.00
A-shaped elements	i	e	2	2	0.50	0.50	0.25
Number of “sreeh” elements	i <sup>a</sup>	v	3	2	1.00	1.00	1.00
“sreeh” position	l	v	4	5	1.00	1.00	1.00
Number of “tyt” elements	i <sup>a</sup>	v	3	2	1.00	0.00	0.00

<sup>a</sup>Presence of “sreeh” and “tyt” elements is inborn since they stem from calls (Thielcke 1964a), but their exact number in a verse is due to learning.

A cluster analysis based on the sixteen discrete song parameters (Table 3.2) was performed with Mesquite 1.05 (Maddison & Maddison 2004). Both UPGMA and single linkage were alternatively chosen as clustering methods. The same character matrix was used in order to estimate the acoustic divergence between *Certhia* species. I calculated a mean character difference ( $D_{ac}$ ) between species with PAUP 4.0.1 (Swofford 2003) for unweighted characters and characters reweighted by CI, RI and RC. The correlation of mean acoustic character difference and genetic distances (uncorrected p-values as given in Table 2.2) was tested with SPSS 13.

### 3.3 Results

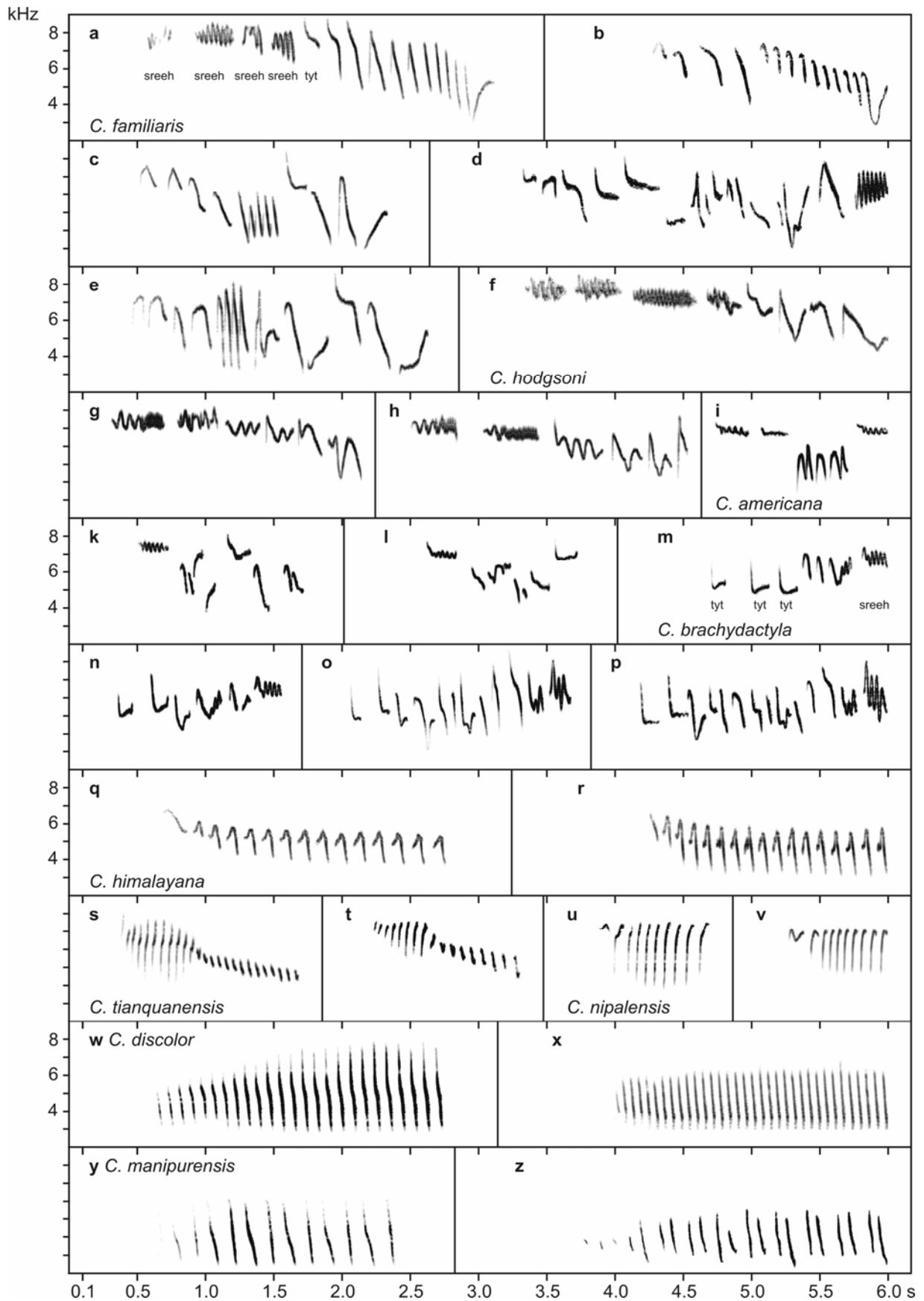
#### 3.3.1 Treecreeper songs

Territorial song in *Certhia* is organised in distinct verses. A single male almost invariably presents only one type of verse. Variation within the investigated populations is also relatively low. For mean values of all sonographic parameters see Table 3.4.

**Table 3.4:** Number of investigated males and mean values ( $\pm$  s.d.) of several parameters taken from the sonograms of territorial song verses per *Certhia* species.

Species (n)	<i>C. familiaris</i> (63)	<i>C. hodgsoni</i> (38)	<i>C. americana</i> (39)	<i>C. brachydactyla</i> (43)	<i>C. himalayana</i> (49)	<i>C. tianquanensis</i> (21)	<i>C. nipalensis</i> (16)	<i>C. discolor</i> (15)	<i>C. manipurensis</i> (18)
Verse length [s]	2.2 $\pm$ 0.3	2.0 $\pm$ 0.2	1.3 $\pm$ 0.2	1.4 $\pm$ 0.2	1.7 $\pm$ 0.3	1.2 $\pm$ 0.2	0.7 $\pm$ 0.1	1.7 $\pm$ 0.3	1.8 $\pm$ 0.3
Minimum frequency [kHz]	3.2 $\pm$ 0.3	4.0 $\pm$ 0.4	3.8 $\pm$ 0.4	4.3 $\pm$ 0.4	3.2 $\pm$ 0.3	4.1 $\pm$ 0.2	4.8 $\pm$ 0.6	2.9 $\pm$ 0.2	2.5 $\pm$ 0.2
Maximum frequency [kHz]	8.2 $\pm$ 0.5	8.3 $\pm$ 0.4	7.8 $\pm$ 0.4	7.5 $\pm$ 0.5	6.6 $\pm$ 0.6	7.5 $\pm$ 0.4	7.7 $\pm$ 0.2	6.2 $\pm$ 0.8	5.9 $\pm$ 0.4
Frequency range [kHz]	5.0 $\pm$ 0.5	4.3 $\pm$ 0.5	4.0 $\pm$ 0.6	3.2 $\pm$ 0.8	3.4 $\pm$ 0.7	3.4 $\pm$ 0.4	2.9 $\pm$ 0.7	3.3 $\pm$ 0.8	3.5 $\pm$ 0.4
Mean frequency [kHz]	5.7 $\pm$ 0.3	6.1 $\pm$ 0.3	5.8 $\pm$ 0.3	5.9 $\pm$ 0.2	4.9 $\pm$ 0.3	5.8 $\pm$ 0.2	6.2 $\pm$ 0.3	4.6 $\pm$ 0.4	4.2 $\pm$ 0.2
Elements	13.8 $\pm$ 2.6	7.6 $\pm$ 1.3	7.4 $\pm$ 1.4	7.7 $\pm$ 2.4	12.6 $\pm$ 2.6	21.1 $\pm$ 3.3	9.1 $\pm$ 1.7	25.7 $\pm$ 5.7	16.5 $\pm$ 4.3
“sreeh” elements	1.2 $\pm$ 1.4	1.8 $\pm$ 0.8	1.3 $\pm$ 0.7	0.9 $\pm$ 0.3					
Increase [kHz/0.1 s]					3.9 $\pm$ 1.8	4.9 $\pm$ 1.4	5.0 $\pm$ 1.2		
Decrease [kHz/0.1 s]					4.8 $\pm$ 1.2	2.9 $\pm$ 1.1		4.8 $\pm$ 0.8	4.7 $\pm$ 0.9
Trill elements					10.9 $\pm$ 2.8	20.7 $\pm$ 3.3	7.2 $\pm$ 2.0	25.4 $\pm$ 5.5	16.0 $\pm$ 3.9
Trill duration [s]					1.5 $\pm$ 0.3	1.2 $\pm$ 0.2	0.5 $\pm$ 0.1	1.7 $\pm$ 0.3	1.8 $\pm$ 0.3
Trill speed [1/s]					7.3 $\pm$ 1.5	17.8 $\pm$ 2.5	14.4 $\pm$ 1.4	15.0 $\pm$ 2.6	8.9 $\pm$ 1.5

### 3 Evolutionary history of vocalisations



**Fig. 3.1:** See previous page. Territorial song of a) *C. familiaris britannica* (UK, Buckinghamshire; W. Pedley), b) *C. familiaris familiaris* (Russia, Ryazanskaya oblast; B.N. Veprintsev), c) *C. familiaris daurica* (Japan, Hokkaido; Voice of Hokkaido, vol. 6, Birds of Sapporo, Music Anton, AO-697S-20), d) *C. familiaris bianchii* (China, Shaanxi; J.M.), e) *C. familiaris bianchii* (China, Qinghai; J.M.), f) *C. hodgsoni khamensis* (China, Sichuan; J.M.), g) *C. hodgsoni mandellii* (Nepal; J.M.), h) *C. hodgsoni hodgsoni* (Pakistan, North-West Frontier Province; P. Alström), i) *C. americana zelotes* (USA, California; D.C. Moyer), k) *C. americana americana* (Canada, Ontario; T. Cosburn), l) *C. americana nigrescens* (USA, North Carolina; M.R. Plymire), m) *C. brachydactyla megarhynchos* (France, Dombes; J.C. Roché), n) *C. brachydactyla megarhynchos* (Germany, Rheinland-Pfalz; J.M.), o) *C. brachydactyla mauritanica* (Morocco, Middle Atlas, Dayet Hachlaff; J.C. Roché), p) *C. brachydactyla mauritanica* (Morocco, Middle Atlas, Ras el Ma; D.T.T.), q) *C. himalayana himalayana* (India, Kashmir; J.M.), r) *C. himalayana yunnanensis* (China, Yunnan; J.M.), s) *C. tianquanensis* (China, Sichuan; J.M.), t) *C. tianquanensis* (China, Shaanxi; J.M.), u–v) *C. nipalensis* (Nepal; J.M.), w) *C. discolor* (Bhutan; B.C.R. Bertram), x) *C. discolor* (India, Uttar Pradesh; P.I. Holt), y) *C. manipurensis manipurensis* (Myanmar, Chin State; D.T.T.), z) *C. manipurensis meridionalis* (Viet Nam, Lâm Đồng; C. Robson). – D.T.T. = D.T. Tietze, J.M. = J. Martens.

#### 3.3.1.1 Motif group

In general, the monophyletic group consisting of *C. familiaris*, *C. hodgsoni*, *C. americana* and *C. brachydactyla* is characterised by a “sreeh” element, by a larger number of different elements, by trills only in a few populations as a minor part of a verse, but v- and A-shaped elements (Table 3.2, Fig. 3.1). Most members display a larger frequency range within the song verse than the remaining species (Table 3.4).

##### 3.3.1.1.1 *C. familiaris*

Most verses start with one to four “sreeh” elements (first elements in Fig. 3.1a) and fall in frequency. Verses from individuals in the western Palaearctic end with a trill of descending notes, followed by a v-shaped element (Fig. 3.1a–b), whereas those from the eastern Palaearctic are terminated by a downstroke and an upstroke (Fig. 3.1c and e) or a “sreeh”-like element (Fig. 3.1d). Mostly falling elements with a wide frequency range are located in the central part of a verse.

Geographical variation: In some males of ssp. *britannica*, the first element is much less frequency-modulated than usual in a “sreeh” element, or the trill part at the end of the verse is reduced. A few individuals of W European ssp. *macroductyla* start the central part with a bend opening downwards. From the song verse of NE European individuals of ssp. *familiaris* and those further east, the initial “sreeh” part is omitted. The verse of ssp. *corsa* less clearly

falls and has a u-shaped element in the middle part. While one male of ssp. *daurica* from mainland Russian Far East does not utter the typical end part, another one from Hokkaido (Fig. 3.1c) sings similarly to Chinese males of ssp. *bianchii* (Fig. 3.1e). Acoustically, the latter is the most variable subspecies – without trill or with trill in the beginning or middle of the verse and even sometimes a “sreeh”(-like) element at the end (Fig. 3.1d). However, these variations are also population-bound.

#### **3.3.1.1.2 *C. hodgsoni***

Almost all verses start with one to three “sreeh” elements (first elements in Fig. 3.1f–h) or their equivalents, whistled “tseeh” notes, and gently fall in frequency. From the second “sreeh” onwards, the elements continuously decline in frequency and become less frequency-modulated, thus becoming simple up- and downstrokes.

Geographical variation: The song verses of all three subspecies (*hodgsoni*, *mandellii* and *khamensis*) are very similar to each other. It is hardly possible to assign a single sonagram correctly to the appropriate subspecies (Fig. 3.1f–h).

#### **3.3.1.1.3 *C. americana***

Almost all verses start with one (or rarely two) “sreeh” element (first elements in Fig. 3.1i–l) and gently descend in frequency. The remaining elements are short and diverse notes. Many element types are uniquely found in this species. Some are notably complex with several ascendant and descendant parts or steeply fall in the beginning and steeply rise at the end, connected by a frequency-constant part.

Geographical variation: A further “sreeh” element at the end of the verse is only found in ssp. *zelotes* from California (USA). The song of *C. americana* is highly variable, but further discrimination as to geographic origin is not possible at present.

#### **3.3.1.1.4 *C. brachydactyla***

All verses start with at least two “tyt” elements (first two to three elements in Fig. 3.1m–p), then rise and terminate with a “sreeh” element. Between one and several elements of wide frequency range, which are simple downstrokes or combined up- and downstrokes, are located in the middle part of a verse.

Geographical variation: Subspecies *mauritanica* from northern Africa (Fig. 3.1o–p) has a song clearly different from European ones (Fig. 3.1m–n): the last two elements differ in shape (both not typical “sreeh” elements), the frequency span is significantly larger (by 1.5 kHz), the verses last longer and consist of more elements. In European subspecies, the penultimate element (shank) ascends in frequency with frequency modulation. Within the NW European ssp. *megarhynchos*, a few males utter extraordinarily long verses, up to 1.7 s. However, the majority shares the typical European song with SE European ssp. *brachydactyla*, while that of Turkish *stresemanni* differs in the final elements. A downstroke of wide frequency range is inserted between the last two elements of most Cypriot ssp. *dorotheae* songs.

### 3.3.1.2 Trill group

This group consists of the remaining *Certhia* species (*C. himalayana*, *C. tianquanensis*, *C. nipalensis*, *C. discolor*, *C. manipurensis*) and is characterised by songs which are dominated by trill elements. Consequently, they have only a few element types and especially neither “sreeh”, “tyt” nor v-shaped elements (Table 3.2, Fig. 3.1). Rising trill elements can be found in *C. himalayana*, *C. tianquanensis* and *C. nipalensis*, falling elements in *C. himalayana*, *C. tianquanensis*, *C. discolor* and *C. manipurensis*. Except for *C. himalayana* and *C. tianquanensis* (its falling part) with less steep elements, ca. 5 kHz are covered within 0.1 s. The average number of trill elements per verse in a given species ranges from 7 to 25 (see species accounts). Since there are only a few cases of verse types with introductory notes, trill duration is mostly identical with verse length. *C. himalayana* and *C. manipurensis* utter slower trills (7 and 9 elements per second), the remaining species produce up to twice as many per time unit.

#### 3.3.1.2.1 *C. himalayana*

The verse consists of a trill of one single element (or rarely element pair), preceded by one (to three) introductory notes (Fig. 3.1q–r). The single element (pair) is composed of one (to two) ascending and one (to two) descending shanks.

Geographical variation: Constitution and frequency bandwidth slightly vary between males independent of their geographical origin.

#### **3.3.1.2.2 *C. tianquanensis***

The verse normally consists of a barbell-shaped double trill, often connected by an s-shaped element (Fig. 3.1s–t). In the first part, which mostly has the larger frequency range, only rising elements occur; in the second part, which often lasts longer, only falling ones are present.

Geographical variation: not found.

#### **3.3.1.2.3 *C. nipalensis***

The verse is a short trill at high frequency (Fig. 3.1u–v). All elements except the introductory note(s) are rising. They cover a wide frequency range and end up in a hook bent downwards.

Geographical variation: not found.

#### **3.3.1.2.4 *C. discolor***

The verse is quite a long trill at low frequency and high speed (12–21 elements/s; Fig. 3.1w–x). All elements besides the exceptional introductory notes are falling. They are all similarly formed and rarely have a slight “knee” in the centre of the individual element.

Geographical variation: not found.

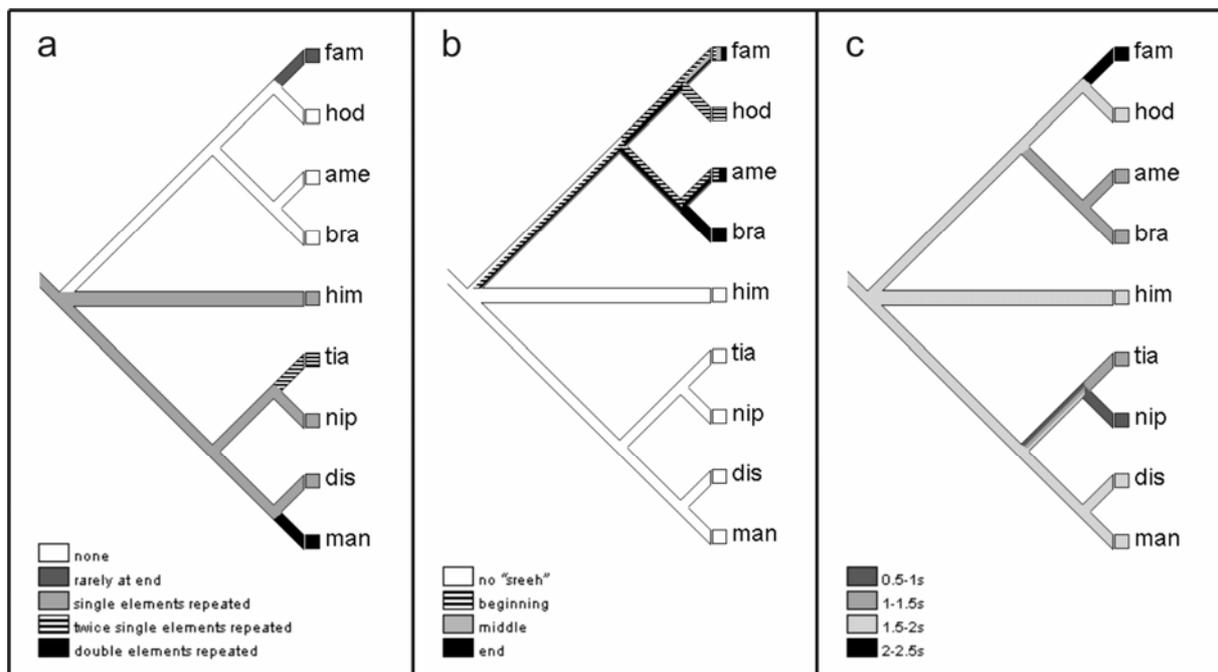
#### **3.3.1.2.5 *C. manipurensis***

The verse is quite a long trill at low frequency and low speed (6–12 elements/s; Fig. 3.1y–z). All elements besides the exceptional introductory notes are falling. They are alternately similarly formed: one element is even and the other has a slight “knee” and is less steep. This does not hold true for males of ssp. *shanensis* recorded in Yunnan (China), but for those recorded in Thailand.

Geographical variation: In the song of Vietnamese ssp. *meridionalis* (Fig. 3.1z), the elements vary in their frequency bandwidth and form element pairs more clearly than in the song of ssp. *manipurensis* from Myanmar (Fig. 3.1y). Song of ssp. *shanensis* either lacks the species-specific inhomogeneity of the trill elements (Yunnan, China) or it is even more pronounced than in the other subspecies (Thailand). There have been only few recordings available of this species; the song of ssp. *laotiana* from Laos is unknown.

### 3.3.1.3 Character tracing

Song syntax in most *Certhia* species is constant in and representative for all populations of a given species. In most cases, sonagrams from each species in Fig. 3.1 show the only taxon-wide song structure (for details see above). Several acoustic traits are highly consistent with the molecular data. The highest values of CI, RI and RC (1 or close to 1) indicate a strong phylogenetic signal (Table 3.3) and were calculated for presence/type of trill (Fig. 3.2a), increase of trill-elements, number of element types, presence of v-shaped elements, number of “sreeh” elements and “sreeh” position (Fig. 3.2b).

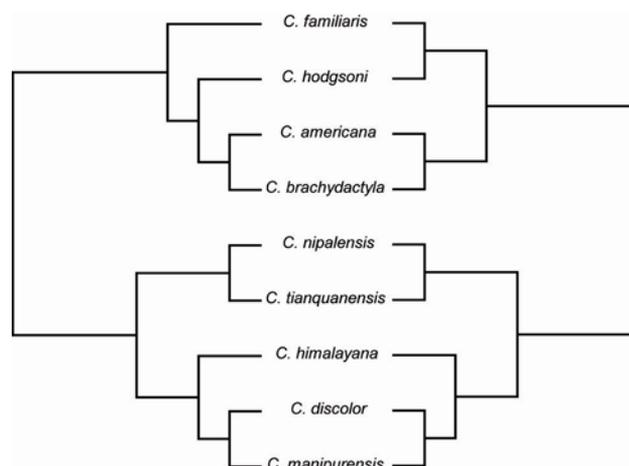


**Fig. 3.2:** Evolution of single acoustic traits mapped onto the molecular phylogeny in Chapter 2: a) presence/type of trill, b) presence/position of “sreeh” element and c) verse length.

These traits on the one hand clearly discriminate two major groups of *Certhia* species: trills are a constitutive part of the songs of the trill-group species, the motif-group species therefore have a higher number of element types, among which v-shaped and “sreeh” elements are unique for this species group (cf. Fig. 3.1). On the other hand, these traits allow for differentiation within these groups: the trill type and the inclination of trill elements (the frequency change per time unit) vary among species of the trill group. The number and position of “sreeh” elements in the song of motif-group members is likewise taxon-specific.

The numbers of falling elements and of “tyt” elements have a high CI but RI and RC of zero, and consequently indicate a low phylogenetic signal of these traits. Such conflicting values between homoplasy indices are typical for autapomorphic characters like “tyt” elements (only a compulsory part of *C. brachydactyla* song) or plesiomorphic characters like falling elements (only missing in *C. nipalensis*). Other song parameters are least consistent with the molecular tree according to CI and reach low values of RI and RC as well (Table 3.3, cf. Fig. 3.2c).

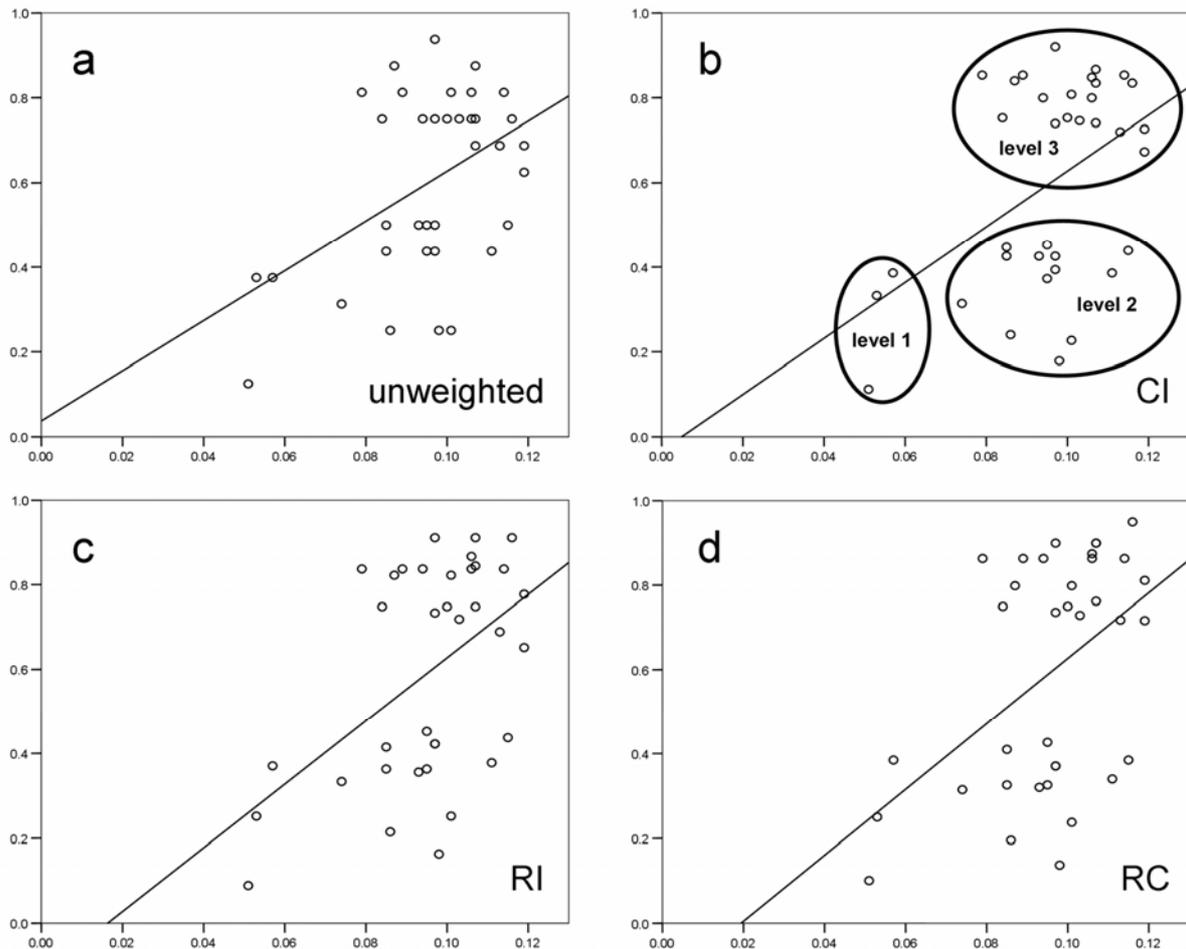
Cluster analysis of nine taxa and 16 acoustic characters resulted in two most parsimonious trees tracing all major splits between *Certhia* species according to the molecular phylogeny and additionally switches from a trichotomy to a topology in which *C. himalayana* is sister taxon to *C. discolor* and *C. manipurensis* (Fig. 3.3, length = 40, CI = 0.78, RI = 0.73, RC = 0.56). In one single-linkage topology, *C. familiaris* is sister taxon to all other motif-group members (Fig. 3.3 left).



**Fig. 3.3:** Cladograms inferred from cluster analysis (single linkage: both cladograms, UPGMA: right cladogram only) based on 16 acoustic characters of territorial songs of all nine *Certhia* species (Table 3.2).

Mean acoustic character difference ( $D_{ac}$ ) increases with genetic distances between *Certhia* species (Fig. 3.4). This correlation is as significant for unweighted characters as for characters reweighted by CI, RI and RC. Least acoustic difference ( $D_{ac} < 0.13$ ) and thus very similar song types are found between *C. discolor* and *C. manipurensis*. The highest acoustic divergence occurs between *C. americana* and *C. himalayana* ( $D_{ac} > 0.9$ ). A closer look at the four scatterplots (Fig. 3.4) reveals three agglomerations of dots (marked in Fig. 3.4b): on level 1 there are three species pairs with low genetic and low acoustic differentiation (*discolor/manipurensis*, *nipalensis/tianquanensis*, *familiaris/hodgsoni*), on level 2 there are 13 species pairs with high genetic and comparatively low acoustic differentiation (the remaining

species pairs within trill or motif groups, respectively) and on level 3 there are 20 species pairs with high genetic and high acoustic differentiation (pairs between trill- and motif-group species).

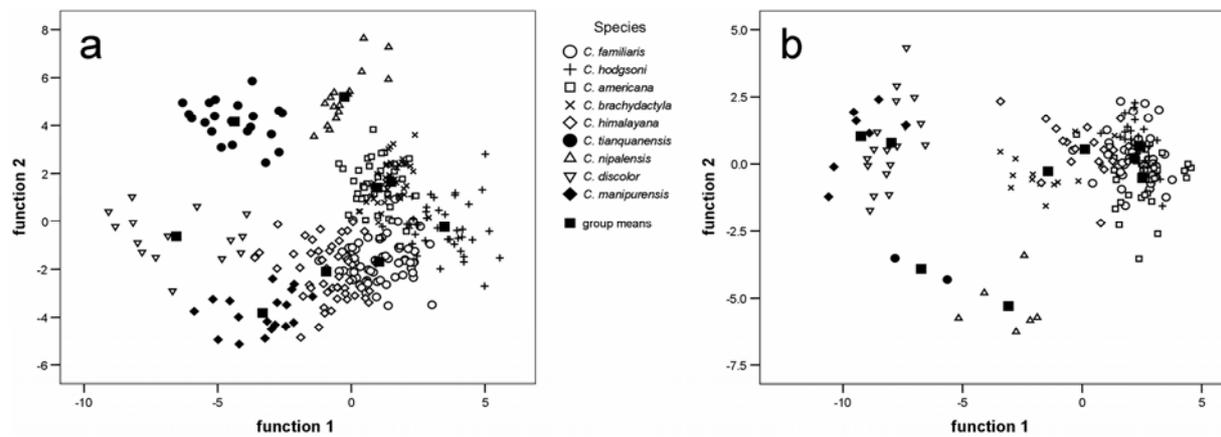


**Fig. 3.4:** Linear correlation of acoustic divergence ( $D_{ac}$ , y-axes) and genetic distances (cytochrome *b*, uncorrected p-values; x-axes) between taxon pairs of *Certhia*. Scatterplots for a) unweighted acoustic characters ( $r^2 = 0.22$ ,  $F = 9.40$ ,  $p < 0.01$ ) and characters reweighted by maximum values of b) CI ( $r^2 = 0.22$ ,  $F = 9.35$ ,  $p < 0.01$ ), c) RI ( $r^2 = 0.25$ ,  $F = 11.37$ ,  $p < 0.01$ ) and d) RC ( $r^2 = 0.24$ ,  $F = 10.54$ ,  $p < 0.01$ ).

### 3.3.1.4 Statistical analysis

Songs of the nine species can be distinguished from each other by DA 1 using the parameters verse length, minimum and maximum frequencies, frequency range, mean frequency, number of all and of “sreeh” elements (Fig. 3.5a). Frequency range and mean frequency failed the tolerance test. Five discriminant functions were used in the analysis (Table 3.5). The highest correlations occurred between number of elements and function 1, and between minimum frequency, mean frequency and function 2. For all functions,  $\chi^2$  was 1558, df was 40 and

Wilks' Lambda was 0.005 ( $p < 0.01$ ). 86.1% of all males could be correctly assigned to the appropriate species.



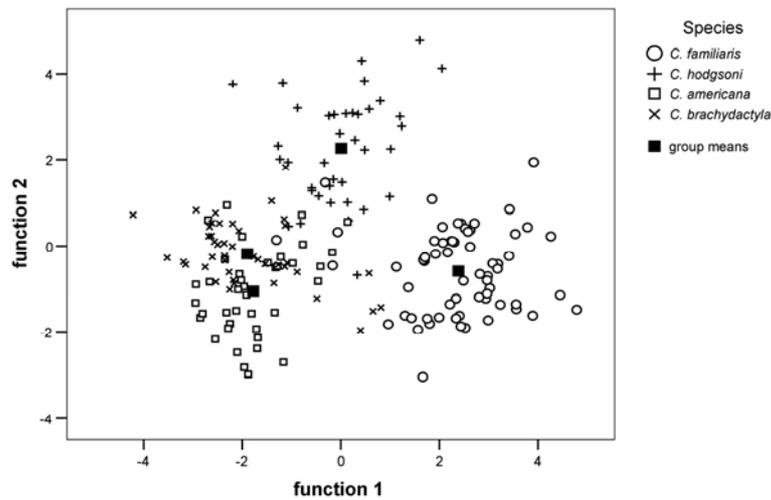
**Fig. 3.5:** Scatterplots of discriminant analyses incorporating all nine *Certhia* species and the parameters a) verse length, minimum, maximum frequencies, frequency range, mean frequency, number of elements and number of “sreeh” elements for song and b) call length, minimum, maximum frequencies, frequency range, mean frequency and number of “sreeh” elements for calls.

**Table 3.5:** Percentages of explained variance and eigenvalues of the three to five discriminant functions used in the five discriminant analyses (DA).

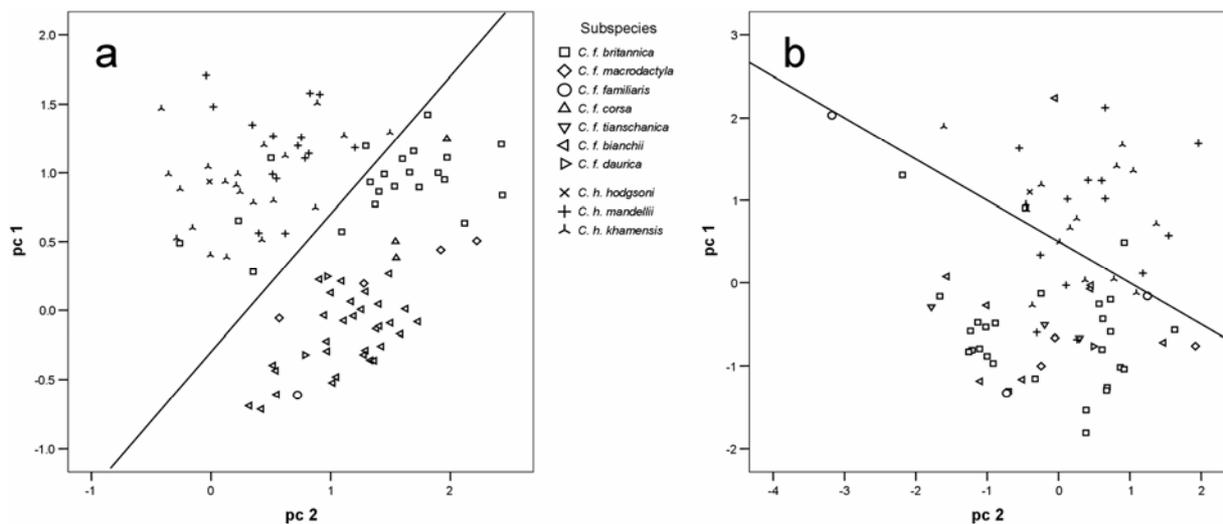
Function	DA 1		DA 2		DA 3		DA 4		DA 5	
	% of variance	eigenvalue								
1	46.2	6.654	66.4	3.556	68.5	12.555	87.5	15.130	81.6	14.082
2	39.3	5.652	27.2	1.459	28.1	5.145	8.6	1.494	18.1	3.127
3	11.3	1.628	6.4	0.342	2.9	0.531	3.8	0.658	0.3	0.049
4	2.5	0.353			0.6	0.110				
5	0.7	0.105								

### 3.3.1.4.1 Motif group

The four species can be distinguished from each other by DA 2 using the parameters verse length, minimum and maximum frequencies, frequency range, mean frequency, number of all and of “sreeh” elements (Fig. 3.6). Frequency range and mean frequency again failed the tolerance test. Three discriminant functions were used in the analysis (Table 3.5). The highest correlations occurred between verse length, number of elements, minimum frequency and function 1, mean frequency and function 2. For all functions,  $\chi^2$  was 481, df was 15 and Wilks' Lambda was 0.067 ( $p < 0.01$ ). 85.8% of all males could be correctly assigned to the appropriate species.



**Fig. 3.6:** Scatterplot of discriminant analysis incorporating the four species of the motif group and the parameters verse length, minimum, maximum frequencies, frequency range, mean frequency, number of elements and number of “sreeh” elements.



**Fig. 3.7:** Scatterplots of first two principal components of a) song and b) call parameters for the investigated subspecies of *C. familiaris* and *C. hodgsoni*. Arbitrary bars separate the two species.

The superspecies *Certhia [familiaris]* unites the closely related allopecies *C. familiaris* and *C. hodgsoni*. Song of these two species differs significantly in six out of seven parameters (Mann-Whitney U-test,  $p < 0.05$ ; Table 3.6). *C. familiaris* has the longer and lower-frequency song with wider frequency range, more elements in general, but fewer “sreeh” elements (Table 3.4, Fig. 3.1). 93.1% of all *C. familiaris* and *C. hodgsoni* males in DA 2 performed for the motif group could be correctly assigned to the appropriate species. In a PCA which incorporated the seven parameters used in DA 1 and 2 and all species, two principal components could be extracted which together explain 77.3% of the total variance. PC 1 is mainly loaded

by mean and maximum frequencies, PC 2 by verse length and frequency range. The scatterplots of the two species *C. familiaris* and *C. hodgsoni* are better separated from each other than are the scatterplots of the investigated subspecies (except some *C. f. britannica* dots within *C. hodgsoni*; Fig. 3.7a).

**Table 3.6:** Number of pairwise Mann-Whitney U-tests with significant ( $p < 0.05$ ) differences between two species each versus the total number of tested parameters between the two species. Left: test of verse parameters, right: test of call parameters.

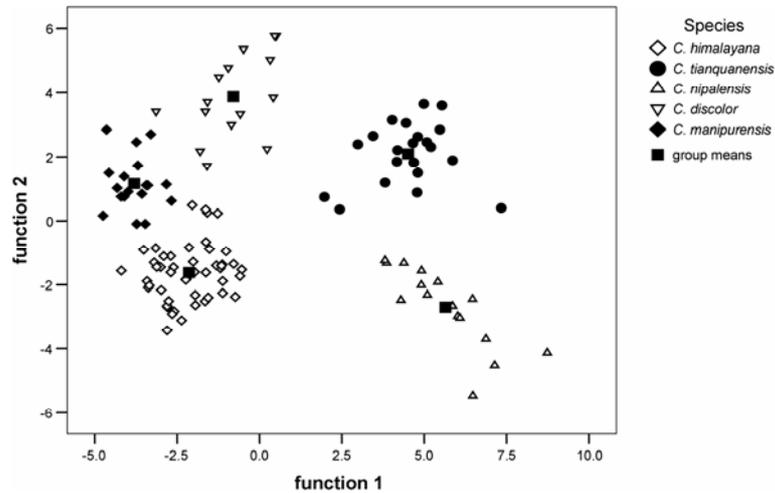
	<i>C. familiaris</i>	<i>C. hodgsoni</i>	<i>C. americana</i>	<i>C. brachydactyla</i>	<i>C. himalayana</i>	<i>C. tianquanensis</i>	<i>C. nipalensis</i>	<i>C. discolor</i>	<i>C. manipurensis</i>
<i>C. familiaris</i>	–	4/6	4/6	6/6	3/5	5/5	4/5	5/5	5/5
<i>C. hodgsoni</i>	6/7	–	4/6	5/6	5/5	4/5	4/5	5/5	5/5
<i>C. americana</i>	6/7	6/7	–	6/6	4/5	4/5	4/5	5/5	5/5
<i>C. brachydactyla</i>	6/7	6/7	5/7	–	4/5	4/5	4/5	4/5	3/5
<i>C. himalayana</i>	5/6	6/6	6/6	5/6	–	4/5	5/5	5/5	5/5
<i>C. tianquanensis</i>	5/6	6/6	4/6	4/6	10/11	–	2/6	3/5	4/5
<i>C. nipalensis</i>	6/6	5/6	5/6	5/6	11/11	9/11	–	4/5	4/5
<i>C. discolor</i>	6/6	6/6	6/6	5/6	7/11	10/11	9/11	–	2/5
<i>C. manipurensis</i>	6/6	5/6	6/6	6/6	8/11	10/11	11/11	6/11	–

### 3.3.1.4.2 Trill group

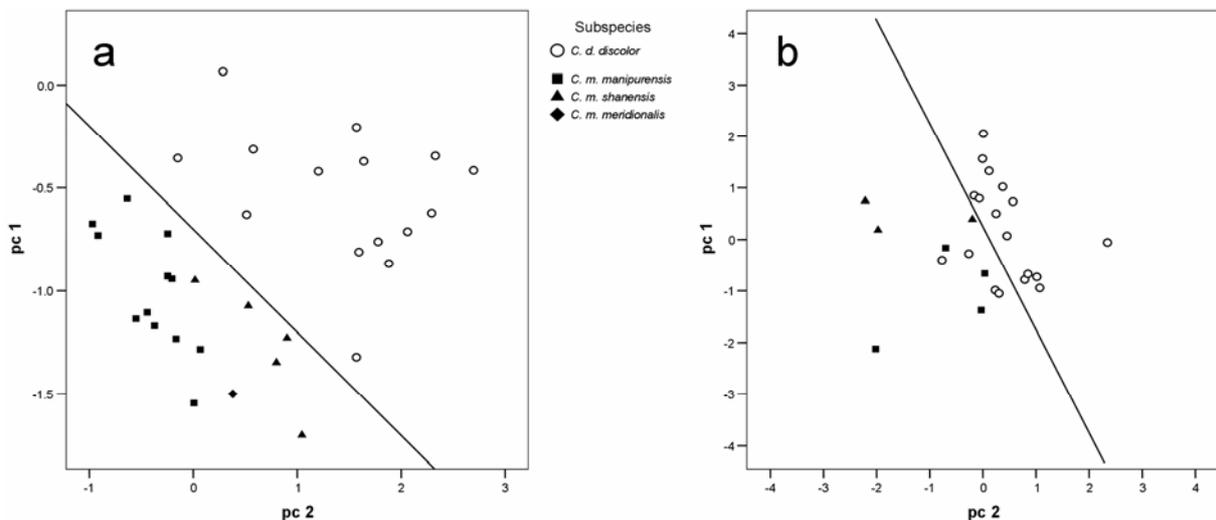
The five species can be distinguished from each other by DA 3 using the parameters verse length, minimum and maximum frequencies, frequency range, mean frequency, number of all and of trill elements, trill duration and trill speed (Fig. 3.8). Mean frequency failed the tolerance test. Four discriminant functions were used in the analysis (Table 3.5). The highest correlations occurred between minimum, mean frequencies and function 1, and between number of trill elements, number of elements, trill speed and function 2. For all functions,  $\chi^2$  was 552, df was 32 and Wilks' Lambda was 0.007 ( $p < 0.01$ ). 99.2% of all males could be correctly assigned to the appropriate species.

The superspecies *Certhia [discolor]* unites the closely related allospecies *C. discolor* and *C. manipurensis*. Song of these two species differs significantly in six out of eleven parameters (Mann-Whitney U-test,  $p < 0.05$ ; Table 3.6). *C. discolor* has higher-frequency song with more (trill) elements, and the trill is faster (Table 3.4, Fig. 3.1). 97.0% of all *C. discolor* and *C. manipurensis* males in DA 3 performed for the trill group could be correctly assigned to the appropriate species. In a PCA incorporating the nine parameters used in DA 3 and all trill-group species, three principal components could be extracted which together explain 95.0% of the

total variance; the first two explain 78.9%. PC 1 is mainly loaded by mean and minimum frequencies and verse length, PC 2 by number of trill and all elements and PC 3 by frequency range. The scatterplots of the two species *C. discolor* and *C. manipurensis* are better separated from each other than are the scatterplots of the investigated subspecies (despite the larger scattering of *C. discolor*; Fig. 3.9a).



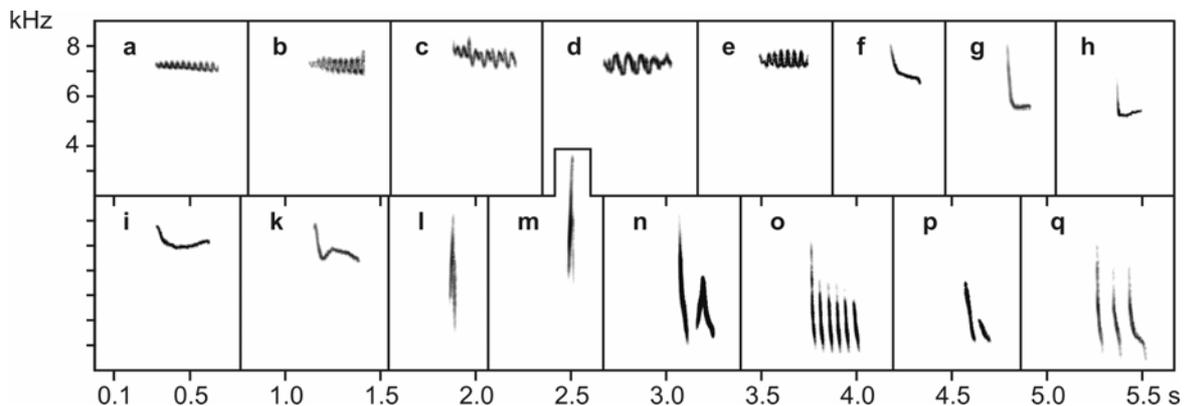
**Fig. 3.8:** Scatterplot of discriminant analysis incorporating the five species of the trill group and the parameters verse length, minimum, maximum frequencies, frequency range, mean frequency, number of elements, number of trill elements, trill duration and trill speed.



**Fig. 3.9:** Scatterplots of first two principal components of a) song and b) call parameters for the investigated subspecies of *C. discolor* and *C. manipurensis*. Arbitrary bars separate the two species.

### 3.3.2 Treecreeper calls

In territorial context, treecreepers normally use high-frequency calls like “sreeh”, “tyt” or a sharp upstroke (Fig. 3.10). Only *C. discolor* and *C. manipurensis* utter short trills. Variation within a given species is quite low (but see below). For mean values of all sonographic parameters see Table 3.7.



**Fig. 3.10:** “sreeh” calls of a) *C. familiaris britannica* (UK, Hampshire; P. Riddett), b) *C. familiaris macrodactyla* (Germany, Hessen; D.T.T.), c) *C. hodgsoni khamensis* (China, Sichuan; J.M.), d) *C. hodgsoni mandellii* (Nepal; J.M.) and e) *C. americana americana* (Canada, Ontario; T. Cosburn), “tyt” calls of f) *C. americana albescens* (USA, Arizona; M. Braun), g) *C. brachydactyla megarhynchos* (Germany, Rheinland-Pfalz; J.M.) and h) *C. brachydactyla dorotheae* (Cyprus; A. Knox), calls of i) *C. himalayana himalayana* (Nepal; J.M.), k) *C. himalayana yunnanensis* (China, Yunnan; J.M.), l) *C. tianquanensis* (China, Sichuan; P. Alström), m) *C. nipalensis* (Nepal; J.M.), n) *C. discolor* (Bhutan; P.I. Holt), o) *C. discolor* (Nepal; J.M.), p) *C. manipurensis manipurensis* (Myanmar, Chin State; D.T.T.) and q) *C. manipurensis shanensis* (China, Yunnan; P.I. Holt). – D.T.T. = D.T. Tietze, J.M. = J. Martens.

#### 3.3.2.1 Characterisation of the specific calls

*C. familiaris*, *C. hodgsoni* and most populations of *C. americana* share the “sreeh” call type. It is also used by *C. brachydactyla*, but the context differs. In the former three species these calls are homologous to “sreeh” elements, however with a constant frequency modulation in *C. familiaris* (Fig. 3.10a–b), with a rather irregular frequency modulation in *C. hodgsoni* (Fig. 3.10c–d herein, Fig. 11 in Martens 1981) and of slightly different shape in *C. americana* (Fig. 3.10e). Relatively wide frequency ranges are caused by several facts: “sreehs” can be found at slightly different frequencies or with different frequency bandwidths, and some calls are in the form of bends opening downwards.

**Table 3.7:** Number of investigated individuals and mean values ( $\pm$  s.d.) of several parameters taken from the sonagrams of calls for each *Certhia* species.

Species (n)	<i>C. familiaris</i> (46)	<i>C. hodgsoni</i> (29)	<i>C. americana</i> (35)	<i>C. brachydactyla</i> (14)	<i>C. himalayana</i> (19)	<i>C. tianquanensis</i> (2)	<i>C. nipalensis</i> (6)	<i>C. discolor</i> (18)	<i>C. manipurensis</i> (7)
Call length [s]	0.3 $\pm$ 0.1	0.3 $\pm$ 0.0	0.3 $\pm$ 0.1	0.2 $\pm$ 0.1	0.3 $\pm$ 0.0	0.0 $\pm$ 0.0 <sup>a</sup>	0.0 $\pm$ 0.0 <sup>a</sup>	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1
Minimum frequency [kHz]	6.7 $\pm$ 0.3	6.8 $\pm$ 0.2	6.9 $\pm$ 0.4	5.3 $\pm$ 0.6	6.0 $\pm$ 0.5	3.6 $\pm$ 0.6	5.0 $\pm$ 0.5	3.0 $\pm$ 0.2	2.4 $\pm$ 0.3
Maximum frequency [kHz]	7.7 $\pm$ 0.3	8.2 $\pm$ 0.3	8.0 $\pm$ 0.4	6.9 $\pm$ 0.5	7.6 $\pm$ 0.5	8.6 $\pm$ 0.4	9.5 $\pm$ 0.8	6.9 $\pm$ 0.9	6.4 $\pm$ 1.0
Frequency range [kHz]	1.0 $\pm$ 0.3	1.4 $\pm$ 0.3	1.2 $\pm$ 0.3	1.6 $\pm$ 0.4	1.6 $\pm$ 0.4	5.0 $\pm$ 0.2	4.5 $\pm$ 0.9	4.0 $\pm$ 1.1	3.9 $\pm$ 1.2
Mean frequency [kHz]	7.2 $\pm$ 0.2	7.5 $\pm$ 0.2	7.4 $\pm$ 0.4	6.1 $\pm$ 0.5	6.8 $\pm$ 0.5	6.1 $\pm$ 0.5	7.2 $\pm$ 0.5	4.9 $\pm$ 0.4	4.4 $\pm$ 0.4
Number of “sreeh” elements	1.0 $\pm$ 0.0	1.0 $\pm$ 0.0	0.8 $\pm$ 0.3	0.3 $\pm$ 0.4	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
Increase [kHz/0.1 s]						10.0 $\pm$ 0.5	11.6 $\pm$ 2.1		

<sup>a</sup>*C. tianquanensis* and *C. nipalensis* calls both last a little less than 0.05 s.

The “tyt” or L-shaped call type is characteristic for *C. brachydactyla*, but *C. americana* from NE, NW and Californian populations utter “tyt”-like calls (Fig. 3.10f) as well; *C. himalayana* calls also come close to this pattern. Most *C. brachydactyla* calls are “tyt” calls (Fig. 3.10g–h), some are “sreeh” calls. The mean frequency of a “tyt” call is not fixed – even within a single individual’s repertoire. *C. himalayana* calls are simple whistles which consist of a downstroke and an upstroke (Fig. 3.10i) and of a further downstroke (Fig. 3.10k). Some *C. himalayana* calls even tend to be almost constant in frequency.

*C. tianquanensis* and *C. nipalensis* share the click call type: their calls are sharp upstrokes, immediately followed by a weaker downstroke, and cover a wide frequency range. *C. nipalensis* (Fig. 3.10m) and *C. tianquanensis* calls (Fig. 3.10l) are separated mainly by a marked frequency shift, and the former are also slightly steeper.

Finally, a composite call type exists in *C. discolor* and *C. manipurensis*. *C. discolor* calls consist of at least two elements: the first is a downstroke with wide frequency range, followed either by a second element (hook-shaped or downstroke) or a fast series of up to eight downstrokes of smaller bandwidth (Fig. 3.10n–o). *C. manipurensis* calls consist of two to three elements similar to those of *C. discolor*: the first is a downstroke with medium frequency

range, followed either by a second element (hook-shaped or downstroke) or two trill-like downstrokes (Fig. 3.10p–q).

### 3.3.2.2 Statistical analysis

In general, call parameters separate closely related species from each other to a lesser degree than songs. The number of significantly different parameters per species pair is lower for calls than for songs (Table 3.6). Only the trill-group species can be distinguished from each other in DA 4 for all nine species using the parameters call length, minimum and maximum frequencies, frequency range, mean frequency and number of “sreeh” elements (Fig. 3.5b). Frequency range and mean frequency failed the tolerance test. Three discriminant functions were used in the analysis (Table 3.5). The highest correlations occurred between minimum frequency, mean frequency and function 1, and between call length and function 2. For all functions,  $\chi^2$  was 710, df was 24 and Wilks’ Lambda was 0.015 ( $p < 0.01$ ). Only 65.9% of all individuals could be correctly assigned to the appropriate species.

#### 3.3.2.2.1 Motif group

Only 62.9% of all motif-group individuals in DA 4 performed for all species could be correctly assigned to the appropriate species. This could only slightly be improved in a separate DA (thus not shown). Calls of *C. familiaris* and *C. hodgsoni* are very similar (Fig. 3.10). All differing parameters have slightly larger values in *C. hodgsoni* (Table 3.7). In a PCA incorporating the six parameters used in DA 4 except number of “sreeh” elements, two principal components could be extracted which together explain 83.2% of the total variance. PC 1 is mainly loaded by maximum and mean frequencies, PC 2 by frequency range and minimum frequency; after the rotation PC 1 is mainly loaded by frequency range and maximum frequency, PC 2 by minimum and mean frequencies. The scatterplots of the two species *C. familiaris* and *C. hodgsoni* are better separated from each other than are the scatterplots of the investigated subspecies (except for some *C. f. britannica* dots and one *C. f. bianchii* dot within *C. hodgsoni* and some *C. h. khamensis* and *mandellii* dots within *C. familiaris*; Fig. 3.7b).

#### 3.3.2.2.2 Trill group

73.1% of all trill-group individuals in DA 4 performed for all species could be correctly assigned to the appropriate species. This could be improved in a separate DA 5 without the

number of “sreeh” elements: frequency range and mean frequency again failed the tolerance test. Three discriminant functions were used in the analysis (Table 3.5). The highest correlations occurred between minimum frequency and function 1, and between call length and function 2. For all functions,  $\chi^2$  was 196, df was 12 and Wilks’ Lambda was 0.015 ( $p < 0.01$ ). 92.3% of all individuals could be correctly assigned to the appropriate species (only *C. discolor* and *C. manipurensis* overlap). Calls of *C. discolor* and *C. manipurensis* are very similar (Fig. 3.10). All differing parameters have slightly larger values in *C. discolor* (Table 3.7). In a PCA incorporating the five parameters used in DA 5 for the trill group, two principal components could be extracted which together explain 85.1% of the total variance. PC 1 is mainly loaded by maximum frequency, frequency range and mean frequency, PC 2 by minimum frequency and call length. The scatterplots of the two species *C. discolor* and *C. manipurensis* are well separated from each other (except some *C. discolor* dots within *C. manipurensis*; Fig. 3.9b).

## 3.4 Discussion

### 3.4.1 Species delimitation by acoustic methods

Work on treecreeper vocalisations of Old World species is quite abundant. However, most publications have focussed on the sibling species *C. familiaris* and *C. brachydactyla* in the western Palearctic (Bauer 1988, 1989, Bauer & Nagl 1992, Chappuis 1976, Gil 1997, Osiejuk & Kuczyński 1997, 2000a, 2000b, 2003, Thielcke 1961, 1964a, 1965a, 1965b, 1971, 1972, 1984a, 1984b, 1986, 1988, 1992, Thielcke & Thielcke 1986, Thielcke & Wüstenberg 1985). Only a few treated *C. americana* or even compared its vocalisations with those of its European congeners (Thielcke 1962, Baptista & Johnson 1982, Baptista & Krebs 2000). Löhrl & Thielcke (1969) presented the first sonagram of Afghan *C. himalayana* and proposed a closer relationship to *C. familiaris* rather than to *C. brachydactyla*. It was not until the 1980’s that the first analysis of the songs and calls of all treecreeper species from the genus’ diversity hotspot, the Himalayas, was published by J. Martens, who then extended his research to western Chinese mountains (Martens 1981, Martens & Geduldig 1988, Martens et al. 2002). Martens (1981) depicted the first *C. nipalensis* vocalisations and proposed an evolutionary history of *Certhia* based on vocal characters. Martens et al. (2002) described *tianquanensis* songs, the knowledge of which facilitated the revalidation of this taxon from a *C.*

*familiaris* subspecies to a distinct species, closely related to another East Asian species with trill song.

The results of PCA and DA confirm the taxonomic suggestions made by me (Chapter 2) on a molecular basis since each of the nine species is represented by a corresponding acoustic cluster. Correct assignment of males to the respective taxon is still relatively reliable among closely related taxa where the simple measured data or syntax characters of verses are similar or those of calls almost identical. Consequently, I support my hypothesis that vocalisations as a behavioural trait are suitable to delimit taxonomic units within *Certhia*. Another separation through DA for song and call measurements was much clearer than the one of the single species: there are two species groups within *Certhia*, which were already pointed out by Martens (1981) and me (Chapter 2): the monophyletic “motif group” and the exclusively southeast Asian “trill group”.

### 3.4.2 Acoustic species determination at a low taxonomic level

With respect to the results of his own ethological studies on treecreepers, Thielcke (1970a) discussed “learning of song as a pacemaker of evolution”. The tradition of song does not take place without copying errors. Although they occur only rarely, because learning also reduces the variability of song in order to maintain its effectiveness as a species-specific signal (Thielcke 1970a; Becker 1990), they create dialects and even regiolects through hundreds of thousand years. Dialects of *C. brachydactyla* changed remarkably within only twenty years (Thielcke 1992)! Geographic isolation of populations reinforces the diversification so that a pre-mating isolating mechanism might be established, although the regiolect carriers might still be genetically compatible (Martens 1996). Therefore it is worth taking a closer look at the three youngest species pairs, which diverged only recently: *C. nipalensis* and *C. tianquanensis* (ca. 2.9 million years ago), *C. familiaris* and *C. hodgsoni* (ca. 2.7 Mya), *C. discolor* and *C. manipurensis* (ca. 2.6 Mya) (according to the distance values in Tietze et al., 2006, and the “2% rule” discussed by Lovette, 2004).

As demonstrated on the species level, it is possible to separate genetically independent taxonomic units by means of multivariate statistics that are based on various mensural characters. This suggests that the same parameters can be used to assign single populations or even single males of uncertain status to the appropriate species. I performed principal-component analyses of sonographic measurements in order to affiliate subspecies of the allospecies pairs in

*Certhia [familiaris]* and *Certhia [discolor]* to the appropriate species. The vocalisations of a higher number of subspecies of the allospecies defined by me (Chapter 2) could be analysed in this study than had been incorporated into my molecular-systematic investigation.

### 3.4.2.1 *Certhia [nipalensis]*

Songs of *C. nipalensis* (Fig. 3.1u–v) and *C. tianquanensis* (Fig. 3.1s–t) are at first sight not very similar to each other. Nevertheless, they cover a similar frequency range and *C. nipalensis* song and the first part of *C. tianquanensis* song both consist of rising elements. One aggressive call series from *C. nipalensis* (Fig. 4n in Martens, 1981) was like a short verse, followed by elements whose frequency and frequency range were slightly reduced element by element – as in a *C. tianquanensis* song verse; however, those last elements were still upstrokes! Therefore *C. nipalensis* might have lost the second half of the trill, rather than *C. tianquanensis* elongating the verse by another element type. Calls of *C. nipalensis* (Fig. 3.10m) and *C. tianquanensis* (Fig. 3.10l), on the other hand, are very similar and justify the subsumption of both taxa under a common superspecies (Chapter 2). Due to the small number of call recordings, only a frequency shift can be postulated as evolutionary change.

### 3.4.2.2 *Certhia [familiaris]*

I (Chapter 2) did not analyse samples of ssp. *britannica* from Britain and Ireland or of ssp. *corsa* from Corsica (France). Both are island populations at the northwestern and southwestern limits of the superspecies' range, respectively. They are regarded as subspecies of *C. familiaris* on morphological grounds and also according to their song characteristics (Fig. 3.7a) and call parameters (Fig. 3.7b). The many outlying *britannica* dots in both scatterplots can be explained by a generally larger variability of island dialects. Thielcke (1986) explained the differences between British and Central European *C. familiaris* songs by copying errors during tradition. The few recordings of males from Corsica hint at the same phenomenon. Baptista & Johnson (1982) also found a larger individual variability in the isolated *C. americana* population of the Californian Angel Island. Thielcke & Wüstenberg (1985) explained the atypical *C. brachydactyla* songs from Cyprus and Morocco by founder effects. This phenomenon is also known from kinglets (genus *Regulus*) on the Azores (Päckert & Martens 2004), where cultural drift plays a crucial role beside founder effects.

The songs of the three *C. hodgsoni* subspecies are more similar to each other than are the *C. familiaris* subspecies to each other, although the genetic lineages of the former are more deeply split, whereas there is almost no genetic substructuring within *C. familiaris* (Chapter 2). A possible explanation is that the effective population sizes of the three Sino-Himalayan *C. hodgsoni* subspecies were quite stable during the last several hundred thousand years, whilst *C. familiaris* was subject to several range oscillations because of the ice ages within the last one hundred thousand years. Therefore, in *C. familiaris* dialects could develop on islands and in isolated areas that sometimes stabilised to regiolects, although genetic divergence of the carriers is low. *C. familiaris* also appears to be a more flexible learner than *C. brachydactyla*, because a larger number of the known mixed singers among Central European treecreepers turned out to be of this species (for review see Osiejuk & Kuczyński 2000b). Interestingly, Central European *C. familiaris* reacted to the playback of *C. hodgsoni mandellii*, but not vice versa (Martens & Geduldig 1988). The initial “sreeh” element (close to the call) as well as the rest of the verse are sufficient to provoke the territorial behaviour.

### 3.4.2.3 *Certhia [discolor]*

This superspecies has a patchy distribution in Southeast Asia. All allopatric forms are morphologically clearly distinct (Harrap & Quinn 1996, Martens & Tietze 2006), which is quite exceptional for *Certhia*. This should coincide with distinct regiolects. However, this is not the case: all males in the available recordings perform a more or less uniform simple trill of downstrokes (Fig. 3.1w–z). This is an indication of either a high constancy of learnt vocalisations or a small contribution of learning to the territorial song of these taxa. Becker et al. (1980) showed for chiffchaffs (*Phylloscopus collybita* s.l.) that the frequency course (the inclination) of a single element is crucial for species recognition. Although mean values for element increase in *C. discolor* and *C. manipurensis* are almost the same, element shape mostly differs and might – along with the clearly different element repetition rate – contribute to a (presumed) vocal isolation.

In spite of these similarities, the songs and calls of *C. discolor* and *C. manipurensis* can be affiliated to the appropriate species based on sonographic measurements. Subspecies *meridionalis* from Viet Nam and ssp. *shanensis* in the Shan Mountains in southern Yunnan (China), eastern Myanmar and northern Thailand, both not incorporated into my phylogenetic reconstructions (Chapter 2), can be regarded as subspecies of *C. manipurensis* because of their grouping of song (Fig. 3.9a) and call parameters (Fig. 3.9b). Nothing is known about the vo-

calisations of ssp. *laotiana* from Laos. I recommend keeping it preliminarily in *C. manipurensis* rather than *C. discolor* due to its distribution between *meridionalis* and *shanensis* – all at the forefront of *Certhia*'s overall range. More acoustic data from all *C. manipurensis* populations are desirable.

### 3.4.3 Phylogenetic signal in song characters

Besides the statistical support (see above), the obvious subdivision of *Certhia* into a trill and a motif group is corroborated by (i) the results of a cluster analysis based on 16 acoustic song characters (Fig. 3.3) and (ii) a high phylogenetic signal in the concerned characters (highest CI, RI and RC values for trill and trill-element increase). Character “trill” is a fundamental syntax trait of the verse and “trill-element increase” (frequency change per time unit) is an element trait. Syntax traits of the verse are also phylogenetically informative in *Regulus* and *Seicercus* (Päckert et al. 2003, 2004). On the other hand, it is not surprising that in the case of treecreepers – especially in trill singers that have only one element type in their verse – phylogenetic information can be found in single elements.

High phylogenetic signal is indicated by high homoplasy indices (CI, RI, RC). Thus, these phylogenetically informative characters underwent little or no parallel or convergent evolution on different clades of the molecular tree (homoplasy). This seems to contradict the fact that territorial song is learnt from a tutor (Thielcke 1977). However, treecreepers learn song within a narrow scope, so that one can expect that characters important for species recognition were retained. Existence of phylogenetic signal is only possible in the case of marked conservatism of the songs. This can be evaluated by the temporal axis according to the “2% rule”. In passerines, the mitochondrial cytochrome-*b* gene mutates somewhat more slowly, leading to greater ages than given in the following (Lovette 2004). The three most recent lineage separations (see above) took place 2.6 to 2.9 Mya, all others 4 to 6 Mya. Within these large periods, I can observe only relatively few changes in the acoustic traits under discussion.

Cluster analysis of the song characters lead to a tree topology that is in overall accordance with the molecular one and even resolves the only trichotomy of the cytochrome-*b* topology in a plausible way (Fig. 3.3): *C. himalayana* as a trill singer is now integrated into the trill group instead of being in an undefined position between the trill group and the motif group. The calls of *C. himalayana* are similar to those of *C. brachydactyla* (and other motif singers), but this might be a symplesiomorphy.

In addition, the acoustic divergence is significantly positively correlated with the mitochondrial DNA sequence divergence (Fig. 3.4). This holds true for unweighted acoustic characters as well as for those reweighted by one of the homoplasy indices. Unfortunately, the coefficient of determination never exceeds 0.25. This might originate from the fact that bird song is not only influenced by genetic predisposition (anatomy as well as behaviour) and cultural transmission (learning and errors), but also by selectional forces that habitat exerts on song evolution (McCracken & Sheldon 1997, Rheindt et al. 2004). Furthermore, one of the three agglomerations of dots (level 2 in Fig. 3.4b) is a little off the regression line, because these 13 species pairs have in common a high genetic and a comparatively low acoustic differentiation. They are all formed within one of the two species groups, which apparently means that the “decision” for one of these groups during acoustic differentiation retarded vocal diversification. Conversely, the contrast between trill group and motif group was thus even intensified. Together with the approximate age of these two groups, namely five million years, this speaks against a secondary character displacement and rejects the hypothesis that trill songs are derived (Bauer 1989).

#### 3.4.4 Impact of learning processes

In all analyses performed for both call and song parameters, it is striking that the taxa can be separated from each other more clearly in the case of verse than of call parameters. This holds true for DA (Fig. 3.5) as well as for PCA (Fig. 3.7, Fig. 3.9). Especially in the case of closely related species pairs (*C. nipalensis* – *C. tianquanensis*, *C. familiaris* – *C. hodgsoni*, *C. discolor* – *C. manipurensis*), more significant differences have been found in learnt songs than in innate calls (Table 3.6). It seems that inborn calls are less suitable for the study of (recent) differentiation processes than the more plastic territorial songs are. This might stem from the fact that these shorter and simpler vocalisations provide us with fewer characters. Nevertheless, the main reason evidently is that calls are fully innate vocalisations and therefore evolve more slowly than territorial songs, which are subject to various processes like learning errors, cultural drift or bottleneck effects such as founder effects (see above).

In *Certhia [discolor]*, also the songs of the two allospecies are quite difficult to separate statistically. Perhaps the percentage of inborn parts is very high in these enormously stereotypic songs. This has not yet been investigated. Becker (1990) reared Grasshopper Warblers (*Locustella naevia*) and demonstrated which parameters of their trill-like song are innate or

learnt. He concluded that the simplicity of a song type does not tell anything about the function of learning for passing the song on to the next generation.

Thielcke (1961, 1964a) showed that in the two western Palaearctic *Certhia* species inborn calls are integral components of the song. This has played a role in the evolution of song characters. Nevertheless, in many hitherto investigated oscine passerine birds (among them treecreepers) learning of song is necessary for the crystallisation of their species-specific song (Thielcke 1977). This seems to be done in order to achieve several advantages: learning of song is a good mechanism for the transmission of complex information and allows social, genetic and habitat adaptations (Catchpole & Slater 1995). On the other hand, learning can only take place within the limits of the morphological constraints provided by the vocal apparatus (Marler & Slabbekoorn 2004).

### 3.5 Summary

Since the vocalisations of passerine birds are in general a good means to separate taxa when external morphological differences are few, song and call recordings of 33 treecreeper (*Certhia*) taxa were sonagraphed and their parameters analysed. The vocalisations show low intra-individual and intra-population variation. Phylogenetic evolutionary units at the population level were delimited by time, frequency and syntax parameters by means of principal-component and discriminant analyses. Traits of territorial song were traced on a phylogenetic tree based on cytochrome-*b* sequences, and a mean acoustic character difference was calculated. All presently recognised nine species could clearly be distinguished from one another by their vocalisations. Subspecies not included in the molecular phylogeny are affiliated with the correct species based on statistical analysis. The obvious subdivision of *Certhia* species into two groups, trill and motif singers, is corroborated by different findings: a high phylogenetic signal in the characters concerned (highest homoplasy index values for trill characters), discriminant analyses for song and call measurements and a cluster analysis. Innate calls turned out to be less suitable for studies at a low taxonomic level than learnt territorial songs, which need social interactions for their species-specific formation.

## 4 Song-playback experiments on Central European *Certhia familiaris*

### 4.1 Introduction

Vocalisations play an important role in every part of birds' lives. They use songs for mate attraction and territory defence. Therefore these songs are highly species-specific. Nevertheless, songs of passerine birds can vary considerably with respect to geography. On the one hand, there are “dialects”, which are limited to groups of individuals and transmitted to the next generation by learning. Dialects can overlap, resulting in a geographic mosaic (Wickler 1986). On the other hand, there are “regiolects”, which are distinct song repertoires usually extending over a large distributional range of a given species with no overlap. Song parameters used in species recognition differ markedly between regiolect populations; hence regiolects are practically species-specific songs and denote populations close to species rank or hitherto misclassified biological species (Martens 1996).

The genus *Certhia* consists of nine species with mainly Holarctic distribution (Table 2.3) which are hard to distinguish by outer appearance because they all are adapted to a narrowly circumscribed habitat, the bark of trees. A single treecreeper male almost invariably utilises the same verse of song, and even across larger distributional areas territorial songs remain extremely uniform (Harrap & Quinn 1996). The genus can be subdivided into two groups on the basis of the type of song: the monophyletic “motif group” with *C. familiaris*, *C. hodgsoni*, *C. americana* and *C. brachydactyla* and the “trill group”, comprising all other species which are restricted to Southeast Asia (Martens 1981, Chapter 3).

Two allospecies, *C. familiaris* s.s. (northern Eurasia and northern China) and *C. hodgsoni* (Sino-Himalayas), were formerly treated as a single species, *C. familiaris* s.l., until I (Chapter 2) detected a marked genetic differentiation between the two taxa. I had been motivated to perform this analysis by the results of playback experiments demonstrating acoustic barriers between populations from the two assemblages (Martens & Geduldig 1988), one of several such experiments with *Certhia* treecreepers (Thielcke 1962, 1971, Thielcke & Wüstenberg 1985, Bauer 1988, Gil 1997, Osiejuk & Kuczyński 2003) which also searched for species limits, geographic song variability and species-specific features in the songs or other aspects of the communication among these birds.

By further series of playback experiments, I wanted to find out the extent to which Central European Eurasian Treecreepers (*Certhia familiaris macrodactyla*) recognise song of – hitherto not tested (Martens & Geduldig 1988) – allopatric taxa of the motif group as conspecific. This should also give deeper insight into which components of the song carry species-specific signals.

## 4.2 Methods

### 4.2.1 Definition of terms

**Call:** Tends to be shorter and simpler than songs and is produced by both sexes throughout the year (Catchpole & Slater 1995: 10); innate vocalisation, given in various contexts including other than territorial significance.

**Song (territorial song):** Long and complex vocalisation mainly produced by males in the breeding season (Catchpole & Slater 1995: 10), composed of verses.

**Verse:** Unit of territorial song, discrete part of complex vocalisation of males consisting of different elements given within territorial song performance; verses are separated by pauses.

**Element:** Particular sound event, continuous line in a sonagram (Catchpole & Slater 1995: 10).

**“sreeh”:** Frequency-modulated song element at approx. 7 to 8 kHz and of ca. 0.3 s duration; typical call of *C. familiaris*, *C. hodgsoni* and most *C. americana* (in *C. brachydactyla* not in territorial context, but long-distance contact call as in *C. familiaris*), incorporated into territorial song of most *C. familiaris*, *C. hodgsoni*, *C. americana* and *C. brachydactyla* populations.

**“tyt”:** L-shaped song element of ca. 0.2 s duration, less modulated than the “sreeh” element, rather a pure whistle; typical call of *C. brachydactyla* (and sometimes also call of *C. americana*), used in various contexts, incorporated into territorial song of most *C. brachydactyla* and a few *C. americana* and *C. familiaris* populations.

**Syntax:** Denotes order of elements or element groups within territorial song.

**Trill:** Fast repetition of elements or element groups of the same element type; is given as a part of a verse or even makes up the whole verse.

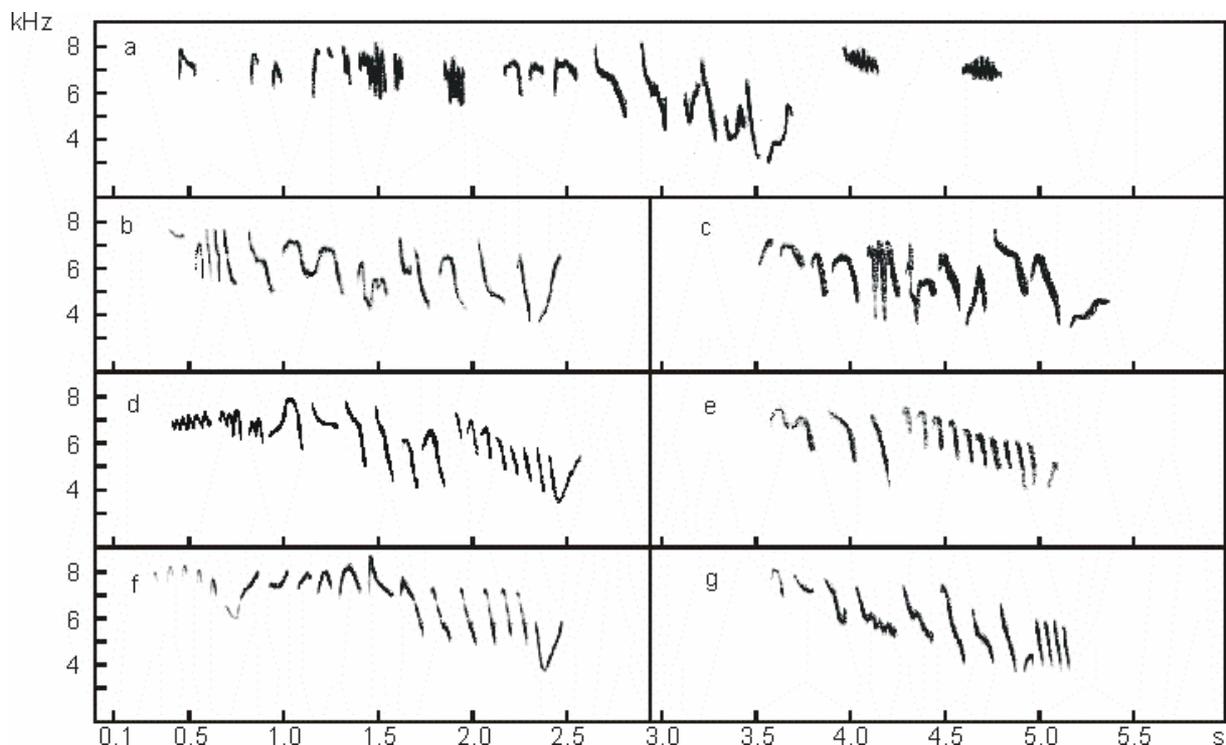
**Repertoire:** Comprises the different verse types that are used by a given male or within a given population.

**Motif group:** Monophyletic group of *Certhia* species (*C. americana*, *C. brachydactyla*, *C. familiaris*, *C. hodgsoni*; Chapter 2) which use complex song types, mostly characterised by the “sreeh” element.

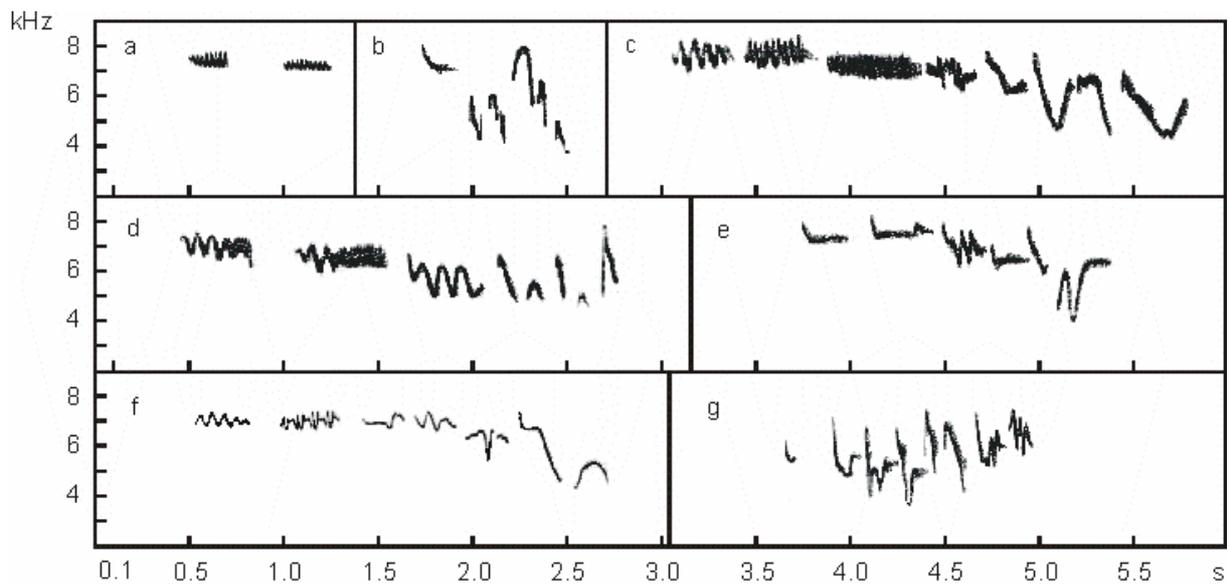
**Trill group:** Set of *Certhia* species (*C. discolor*, *C. himalayana*, *C. manipurensis*, *C. nipalensis*, *C. tianquanensis*) which use simple song types, mainly characterised by a trill.

## 4.2.2 Material

The sound recordings were taken from J. Martens’ collection (Table 4.1). Avisoft SASLab Pro 4.36 (Specht 2005) was used to copy a representative song verse from the original recording and to paste it into the playback ten times with a break of six seconds between each verse, resulting in test playbacks with durations from 71 up to 113 s opposed to the control playback of 85 s duration. Sonograms of the played verses (and calls) are given in Figs. 4.1 and 4.2.



**Fig. 4.1:** Sonogram plate with songs of *C. familiaris* ssp. a) *tianschanica*, b) *bianchii* (Gansu), c) *bianchii* (Qinghai), d) *macroductyla* (control playback), e) *familiaris*, f) *corsa*, g) *daurica* (for details on the recordings see Table 4.1).



**Fig. 4.2** Sonagram plate with a) calls of *C. familiaris* and songs of b) *C. americana albescens*, c) *C. hodgsoni khamensis*, d) *C. h. hodgsoni*, e) *C. h. mandellii* (India), f) *C. h. mandellii* (Nepal), g) *C. brachydactyla mauritanica* (for details on the recordings see Table 4.1).

**Table 4.1:** Recorded song verses used in the playback experiments (for sonagrams see Figs. 4.1 and 4.2) and p-values of Wilcoxon test on different intensity of reaction of Central European *C. familiaris macrodactyla* to the test and the control playbacks (No 0), respectively (p-values < 0.05 in bold).

No	Playback	recorded in	on	by	p [%]
0	<i>C. familiaris macrodactyla</i>	Germany (Hessen, Ruppertshain)	1981-04-20	J. Martens	91.5
1	<i>C. f. corsa</i>	France (Corsica, Col de Bavella)	1982-06-10	J. Martens	<b>0.7</b>
2	<i>C. f. familiaris</i>	Russia (Ryazanskaya oblast)	1984-04-03	B. Veprintsev	10.6
3	<i>C. f. tianschanica</i>	Kyrgyzstan (Ysyk Köl basin)	1993-06-18	J. Martens	7.0
4	<i>C. f. daurica</i>	Russia (Primorskiy kray, Kunashir Island)	1984-06-10	B. Veprintsev	75.7
5	<i>C. f. bianchii</i> (Qinghai)	China (Qinghai, Bei Shan)	1996-05-28	J. Martens	<b>4.8</b>
6	<i>C. f. bianchii</i> (Gansu)	China (Gansu, Lianhua Shan)	1999-04-16	J. Martens	11.7
7	<i>C. hodgsoni khamensis</i>	China (Sichuan, Wawu Shan)	2002-05-13	J. Martens	<b>4.5</b>
8	<i>C. h. mandellii</i> (Nepal)	Nepal (Thak, Thaksang above Tukche)	1980-04-28	J. Martens	33.9
9	<i>C. h. mandellii</i> (India)	India	1999-04-24	P. Singh	13.3
10	<i>C. h. hodgsoni</i>	Pakistan (Kaghan valley)	1998-06-15	P. Alström	<b>1.0</b>
11	<i>C. americana albescens</i>	USA (Arizona, Oak Creek Canyon)	1999-10-04	D. Von Gausig	25.8
12	<i>C. brachydactyla mauritanica</i>	Tunisia	2001-03-16	S. Eck	<b>4.2</b>

### 4.2.3 Field experiments

In each single experiment, the loudspeaker was placed at the foot of a tree trunk no less than 20 m away from the bird and positioned in such a way that its sound was directed towards the crown. The experimenters hid at least 10 m away from the speaker and observed the bird's reactions. In one playback experiment, the bird was confronted with two playbacks, first the actual test and then the control playback. When the test playbacks were presented, the bird's

behaviour was observed for further two minutes. Immediately afterwards, the control playback was handled the same way. A given male was never tested twice a day or twice with the same test playback.

In total, 169 complete experiments (13 per test playback) were performed: 24 in Šumava (Czech Republic), May 7–12 2003, 80 and 57 in the Dahner Felsenland (Rheinland-Pfalz, Germany), April 3–15 2004 and March 30 – April 8 2005, and 8 in the Black Forest (Baden-Württemberg, Germany), May 9–11 2004. Although in 84% of the experiments the tree-creeper was searched for and attracted by playback of *Certhia familiaris* calls (Fig. 4.2a), it took approximately 1.5 h in the field per successful experiment on average. This is a consequence of low breeding-pair density of *C. familiaris* in the area of investigation. Field work took place between 07:00 and 21:00.

#### 4.2.4 Statistics

The bird's reaction was quantified according to Table 4.2, assessing only approach, song and call activity. It was not possible to register other behavioural traits for each experiment. Statistical evaluation was done with SPSS 14 following Kroodsmas's (1989) recommendations: the intensity of the reaction to the test playbacks was compared to the reaction to the control playback for each playback by Wilcoxon tests. For (groupwise) comparisons between males and years Mann-Whitney U-tests were performed.

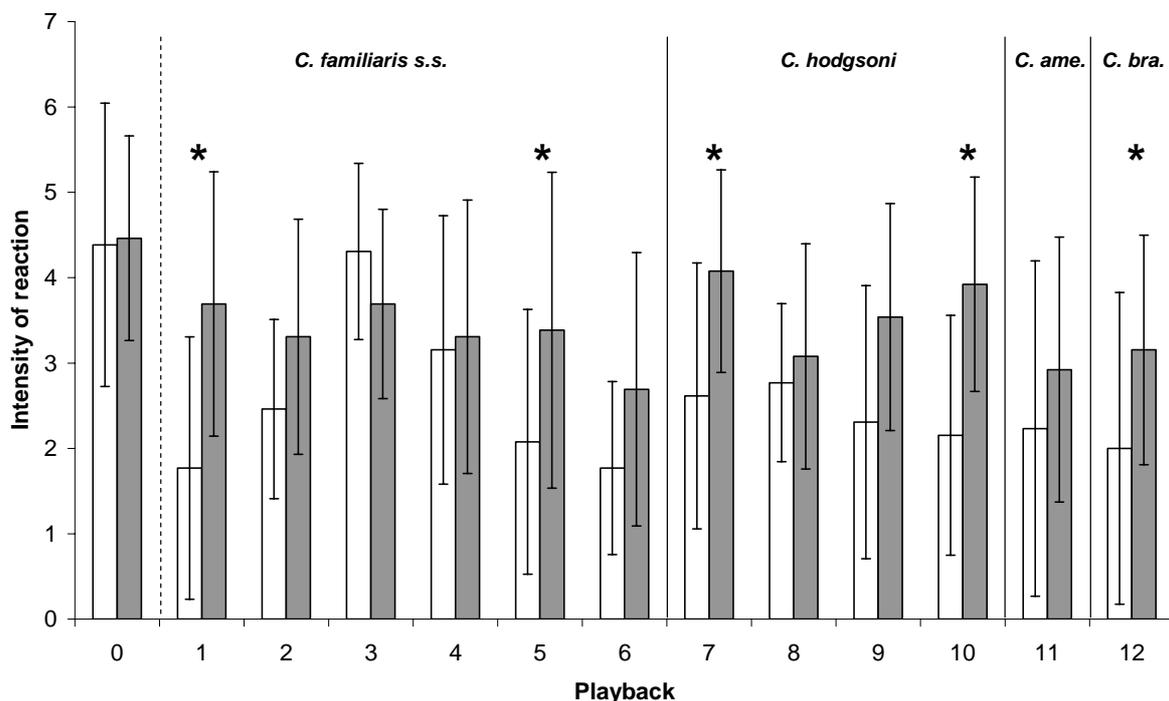
**Table 4.2:** Quantification of the intensity of reaction to playbacks.

Behavioural aspect	Points
<b>Approach</b> (no approach = 0; > 10 m = 1; 1–10 m = 2)	2
<b>Vocalisations</b>	4
Calls (no calls = 0; calls = 2)	2
Song (no song = 0; 1–10 verses = 1; > 10 verses = 2)	2
<b>Maximum score</b>	<b>6</b>

### 4.3 Results

The intensity of the reaction to the control playback is significantly negatively correlated with the time of the year ( $p < 0.01$ ,  $R^2 = 0.063$ ) and thus increases significantly by year of investigation (Mann-Whitney U-test,  $p < 0.05$ ) because the experiments were performed at different times of the breeding cycles in the different years, earlier in the last two years. The time of day had only a slight influence on the reaction.

In the double-control experiments, both presentations of the control playback were on average answered with the same intensity. In all other series of playbacks (except the one with *C. f. tianschanica* song), the reaction to the foreign song was less intensive than that to the control playback, but differences were significant only in nearly half of the experimental series (Fig. 4.3, Table 4.1). Central European Eurasian Treecreepers also reacted to the heterospecific playbacks. These reactions were on the whole no less intensive than those to conspecific playbacks; there is a significant difference only in the reaction to the song of the Short-toed Tree-creeper (*C. brachydactyla mauritanica*) from North Africa (Fig. 4.3, Tables 4.1 and 4.3).



**Fig. 4.3:** Mean intensity of reaction to test (white bars) and control playbacks (grey bars) with s.d. (error bars). \* = significant difference due to Wilcoxon test ( $p < 0.05$ ). Playback experiments: 0 = *C. familiaris macrodactyla* (control experiment), 1 = *C. f. corsa*, 2 = *C. f. familiaris*, 3 = *C. f. tianschanica*, 4 = *C. f. daurica*, 5 = *C. f. bianchii* (Qinghai), 6 = *C. f. bianchii* (Gansu), 7 = *C. hodgsoni khamensis*, 8 = *C. h. mandellii* (Nepal), 9 = *C. h. mandellii* (India), 10 = *C. h. hodgsoni*, 11 = *C. americana albescens*, 12 = *C. brachydactyla mauritanica*.

## 4.4 Discussion

The experiments were performed under more or less constant conditions, although – because of the low abundance of Eurasian Treecreepers in Central Europe – they were carried out in three years, by different field assistants, in three study areas and at various times of year and day. The reaction to the control playback became less intensive during the seasons, but overall

the double-control experiments yielded similar results, demonstrating the applicability of the chosen approach.

In general, Central European Eurasian Treecreepers reacted more intensively to the control playback than to foreign playbacks. This does not imply an intensification by the second stimulus because otherwise this pattern would be also observable in the double-control experiments. The more reasonable explanation is that the playback verses do not contain all components necessary to elicit full territorial response, typically given to conspecific intruders. However, the song of *C. f. tianschanica* must have more of those characters because its playback provoked a stronger response than the playback of the Central European regiolect.

Unexpectedly, there was not a single playback to which on average there was no reaction at all. Not only songs of representatives of the allospecies *C. hodgsoni*, but even those from less closely related species *C. americana* and *C. brachydactyla* (though not the sympatric regiolect) were answered. Consequently, also the songs of the closest relatives – at least in certain regiolects – can contain features that provoke territorial behaviour.

**Table 4.3:** p-values (in %) of Mann-Whitney U-test on differences in the intensities of reaction of Central European *C. familiaris macrodactyla* to the playback of song verses from two given species (playbacks pooled). Intensity: absolute values compared, Ratio: reaction to playback in relation to that to the control playback compared.

	Intensity			Ratio		
	hod.	ame.	bra.	hod.	ame.	bra.
<i>Certhia familiaris</i> s.s. (playbacks 0–6)	15.5	22.7	6.2	30.4	71.5	22.5
<i>Certhia hodgsoni</i> (playbacks 7–10)	–	49.3	22.4	–	98.0	58.0
<i>Certhia americana</i> (playback 11)	–	–	75.4	–	–	62.3
<i>Certhia brachydactyla</i> (playback 12)	–	–	–	–	–	–

#### 4.4.1 The single playbacks

Response to the Corsican song was less than half the intensity of that to the control playback (Fig. 4.3) – a significant difference. This is not surprising since *C. f. corsa* is an island population at the south-western limit of the species' range, and on islands miscopied variants of songs have often been found in treecreepers (Baptista & Johnson 1982, Thielcke 1986) as well as in other species like kinglets (genus *Regulus*) on the Azores (Päckert & Martens 2004). But the song of *C. f. corsa* (Fig. 4.1f) is extremely similar to that of the control playback (Fig. 4.1d). Only the introductory notes are rather like begging calls (Thielcke 1965b)

and not the typical “sreeh” element, which is homologous to a call that serves as begging call in older chicks and for intersexual or long-distance contact (Thielcke 1964a, 1970b).

A more intensive reaction that was not significantly different from that to the control playback was observed in the playback series with songs of *C. f. familiaris* (Fig. 4.1e), *C. f. daurica* (Fig. 4.1g) and *C. f. bianchii* from Gansu (Fig. 4.1b). Interestingly, these verses are less similar to the control playback than is the Corsican song verse, and all of them also lack a “sreeh” element. Therefore, they share the overall falling verse frequency and either a trill in the second half of the verse (*familiaris*, *daurica*) or the final v-shaped structure (*bianchii* from Gansu, reaction to playback almost as strong as to control playback!). The other *C. f. bianchii* song type from Qinghai (Fig. 4.1c) provoked a response significantly reduced by 40% compared to that to the control playback, although all important characters are shared with the first *C. f. bianchii* song type.

The song of the disjunct Central Asian subspecies *tianschanica* was the only playback that was more strongly answered than the corresponding control playbacks. It is the longest verse used in playback (almost double the duration of the control-playback verse), has a falling, but not trilling central part, ending in the v-structure, but has two “sreeh”-like elements in the middle and two real “sreehs” at the very end. Thus, this playback was a kind of overexcitement for the bird and not really comparable to the other experimental series with playback verses of similar length.

Response to *C. hodgsoni* songs (Fig. 4.2c–f), which are at first glance quite similar to those of *C. familiaris* (Fig. 4.1b–g), had already been tested by Martens & Geduldig (1988). Again, *mandellii* song was quite well understood, the song type from Nepal (Fig. 4.2f) with two introductory “sreeh” elements and a final v-structure even gained 90% of the control response. Response to the other *mandellii* playback (Fig. 4.2e) was also strong because the unmodulated introductory elements resemble *C. familiaris* rivalry calls. The intensity of the reaction to the songs of *C. hodgsoni* subspecies *khamensis* (Fig. 4.2c) and *hodgsoni* (Fig. 4.2d) was significantly smaller than that of the reaction to the control playback. This is difficult to explain, since both verses start with two or four “sreeh”-like elements and that of *khamensis* even ends in a v-element.

*Certhia americana* has the most variable song of all motif-group species (Chapter 3). The single verse type used in these experiments is less than half as long as the verse of the control

playback and lacks “sreeh” elements as well as a v-structure. Features that could explain the relatively strong response are the introductory “tyt” element (fifth element in Fig. 4.1d) and the second half of the verse, which could be interpreted as a (short) descending trill. Thielcke (1962) reported limited approaching behaviour of both *C. familiaris* and *C. brachydactyla* when playing back a *C. americana* verse, which in contrast to my test playback had an introductory “sreeh” element.

Song verses of *C. brachydactyla* are shorter and overall rather ascending in frequency, they start with “tyt” and end with “sreeh” elements; in North African *mauritanica*, they are longer and their frequency span is significantly larger, almost as in *C. familiaris* (Chapter 3). Nevertheless, response of *C. familiaris macrodactyla* to the *C. b. mauritanica* playback was significantly weaker. Central European *C. brachydactyla* also showed limited territorial behaviour following the playback of its African conspecific (Thielcke & Wüstenberg 1985).

#### 4.4.2 Outlook

Altogether, the results of Martens & Geduldig (1988) could be confirmed. Central European *C. familiaris* vividly reacts to song of *C. hodgsoni mandellii* from Nepal (and India). The “sreeh” element, a homologous feature in most songs of all motif-group species, seems to play a major role. But in my experiments, (*mandellii*) songs without that component evoked notable territoriality as well. I also have to follow my predecessors in stating that in most cases of intensive reaction to the playbacks the stimulating features of the verses concerned remain unclear. In the Goldcrest (*Regulus regulus*), Martens et al. (1998) also found that response-eliciting parameters can be altered from one subspecies to another.

Territorial reaction in Central European *C. familiaris* is not limited to conspecific song, since several species-specific features are also present in the song of closely related species (but not in all of their subspecies). This may be a phenomenon only found in *C. familiaris*, since *C. hodgsoni* in Nepal did not react to the playback of *C. familiaris* song from Central Europe (Martens & Geduldig 1988); furthermore, a relatively large number of the known mixed singers among Central European treecreepers turned out to be *C. familiaris* (for review see Osiejuk & Kuczyński 2000b) and proportions of mixed singers seem to remain constant during decades (Thielcke & Thielcke 1986). Additionally, *C. familiaris* reacts with similar intensity to the playback of typical, mixed and shortened song (Osiejuk & Kuczyński 2000b). It appears strange that *C. familiaris* does not have more contrasting song in areas of sympatry

(Thielcke 1986, 1988) to avoid territorial conflict with heterospecific males. At least, Gil (1997) found increased territorial behaviour of *C. brachydactyla* in areas of sympatry to the playback of *C. familiaris* song. This *Certhia* species also showed reduced reaction to foreign dialects, however less pronounced than to foreign regiolects (Bauer 1988).

It appears that the applicability of playback experiments to testing of species limits and to the search for species-specific song features depends on the passerine taxa investigated: Central European Reed Buntings (*Emberiza schoeniclus*) understood their Mediterranean conspecifics only slightly less while they showed hardly any reaction to Yellowhammer (*E. citrinella*) song (Matessi et al. 2000). Chinese allospecies of the *Phylloscopus proregulus* complex did not react at all to the playback of the song of other allospecies (Alström & Olsson 1990), although they are genetically less differentiated from each other than are *C. familiaris* and *C. hodgsoni* (Martens et al. 2004, Chapter 2). However, Central European Common Chiffchaffs (*Phylloscopus collybita*) only faintly answered Siberian *tristis* song (Martens & Meincke 1989), although *tristis* can still be regarded as conspecific on molecular-genetic grounds (Helbig et al. 1996).

## 4.5 Summary

Series of playback experiments were performed in order to test the extent to which Central European Eurasian Treecreepers (*Certhia familiaris macrodactyla*) recognise song of allopatric taxa of the “motif group” as conspecific, since earlier playback experiments suggest imperfect acoustic isolation of *C. familiaris* – at least in comparison with allopatric populations. *Certhia* treecreepers of the “motif group” (*C. americana*, *C. brachydactyla*, *C. familiaris*, *C. hodgsoni*) display the most variable songs of the species of that genus but share several song features. Reaction to the song of *C. familiaris* subspecies *corsa*, *familiaris*, *daurica* and *bianchii* was limited, that to the extraordinary *tianschanica* song stronger than that to *macrodactyla* control playback. Song of the allospecies *C. hodgsoni* produced a significantly less intensive reaction in the case of the subspecies *hodgsoni* and *khamensis*, but not in that of subspecies *mandellii*. There was also strong territorial response to the very different songs of *C. americana albescens* and *C. brachydactyla mauritanica*. Song features that possibly cause the (limited) recognition and complementary papers are discussed.

## 5 Morphometric characterisation of treecreepers

### 5.1 Introduction

The genus *Certhia* (treecreepers) unites small passerine birds of uniform outer appearance. The combination of long, curved pincer-like bills and stiff woodpecker-like tail feathers makes treecreepers unique and unmistakable among all Holarctic small passerines. Climbing with tail support is accompanied by derived modifications of the hind-limb musculature (Moreno 1991). Since few species have distinctive morphological characters, the relationships within the genus have been difficult to ascertain, despite the small number of species concerned. Treecreepers are restricted to the Holarctic with local extensions to the tropics. In the larger parts of the genus' range, there is only one species present, but in Europe two species occur together. In the Himalayas up to four species can be found sympatrically, but a tendency towards vertical segregation of species is obvious in all areas of sympatry (Martens 1981).

By performing a molecular analysis of all accepted treecreeper species and a selection of currently accepted subspecies, I (Chapter 2) was able to show that there is cryptic diversity in *Certhia* and that two populations have to be upgraded to species level. Calls and verses of territorial song of the respective taxa can also be clearly told apart, using general sonagram parameters and multivariate-statistical methods (Chapter 3). In the present, final step of the revision of this genus, I returned to traditional morphological methods, since not only the upgraded taxa needed to be characterised by external criteria which will be of use both in the field and in museum collections.

#### 5.1.1 Study species

The following nine species were recognised by me (Chapter 2) on mainly phylogenetic grounds (“phylopecies”). Subspecies follow Dickinson (2003) and Webster (1986). Due to the type of song, two species groups are distinguished: the “motif group” comprising *C. familiaris*, *C. hodgsoni*, *C. americana* and *C. brachydactyla* and the “trill group” with the remaining species (Martens 1981, Chapter 3).

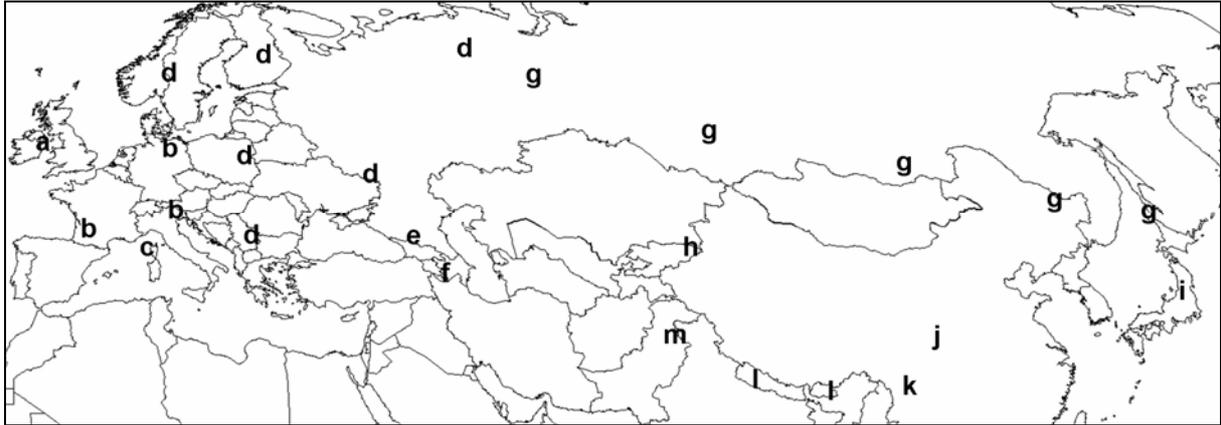
Motif group

Superspecies *Certhia* [*familiaris*] (Fig. 5.1)

1. *Certhia* [*familiaris*] *familiaris* Linnaeus, 1758 with ten subspecies (*britannica* in Britain and Ireland, *macrodactyla* in W and C Europe to N Spain, Italy and W Croatia, *corsa* on Corsica, *familiaris* in N and E Europe to the Balkan countries, *caucasica* in N Turkey and the Caucasus area, *persica* in SE Azerbaijan and N Iran, *daurica* in S Siberia from the Urals to Sakhalin, NE China, on the S Kurils and Hokkaido, *tianschanica* from S and E Tian Shan to the Hami area in E Xinjiang, *japonica* on Honshu and Shikoku, *bianchii* from E and NE Qinghai to C Gansu and S Shaanxi)
2. *Certhia* [*familiaris*] *hodgsoni* Brooks, 1871 with three subspecies (*khamensis* including “*waschanensis*” and “*kwanhsienensis*” in SE and E Xizang, N Myanmar, N Yunnan, W Sichuan and S Gansu, *mandellii* in the Himalayas from NW India to NW Assam, *hodgsoni* in N Pakistan and Kashmir), formerly included in Palearctic *C. familiaris* s.l.

Superspecies *Certhia* [*brachydactyla*]

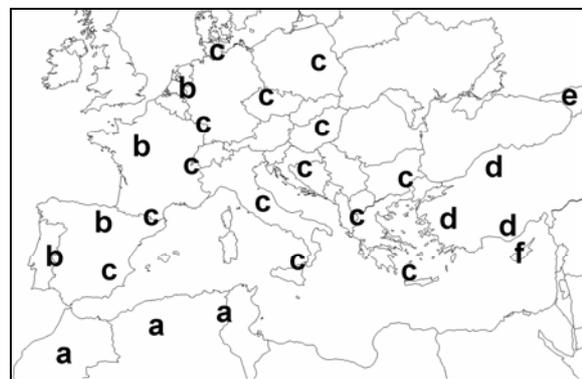
3. *Certhia* [*brachydactyla*] *americana* Bonaparte, 1838 (Fig. 5.2) with 15 subspecies (*montana* in the mountains of SW Canada and W USA, *occidentalis* along the coasts of W Canada and NW USA, *alascensis* in Alaska, *stewarti* on British Columbian islands, *zelotes* in Californian hinterland, *phillipsi* along the C Californian coast, *leucosticta* in S Nevada and Utah, *albescens* in SW USA and NW Mexico, *jaliscensis* in WC Mexico, *guerrerensis* in SW Mexico, *alticola* in C and SE Mexico, *pernigra* in S Mexico and W Guatemala, *extima* from E Guatemala to Nicaragua, *americana* in C and E Canada, EC and NE USA, *nigrescens* in CE USA), American taxa formerly included in one of the Palearctic species, *C. brachydactyla* or *C. familiaris* s.l.
4. *Certhia* [*brachydactyla*] *brachydactyla* Brehm, 1820 (Fig. 5.3) with six subspecies (*mauritanica* in NW Africa, *megarhynchos* in Portugal, W Spain, W and N France to W Germany, *brachydactyla* in E Spain, Italy, Sicily to C and SE Europe and NW Turkey, *stresemanni* in Asia Minor, *rossocaucasica* in the SW Caucasus, *dorotheae* on Cyprus)



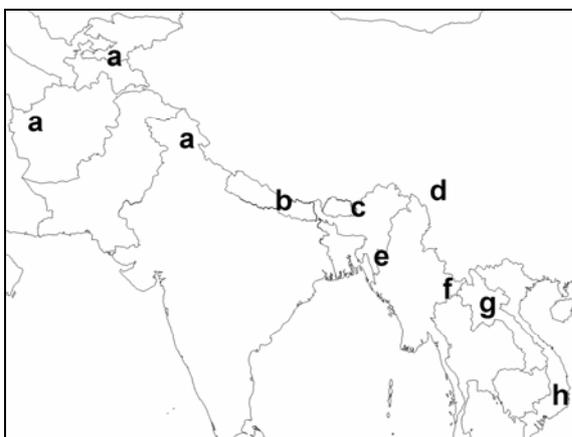
**Fig. 5.1:** Relative distribution of *C. [familiaris]* taxa: *C. familiaris* spp. a) *britannica*, b) *macroductyla*, c) *corsa*, d) *familiaris*, e) *caucasica*, f) *persica*, g) *daurica*, h) *tianschanica*, i) *japonica*, j) *bianchii*, *C. hodgsoni* spp. k) *khamensis*, l) *mandellii*, m) *hodgsoni*. For details see section Study species in the Introduction.



**Fig. 5.2:** Relative distribution of *C. americana* spp. a) *montana*, b) *occidentalis*, c) *alascensis*, d) *stewarti*, e) *zelotes*, f) *phillipsi*, g) *leucosticta*, h) *albescens*, i) *jaliscensis*, j) *guerrerenensis*, k) *alticola*, l) *pernigra*, m) *extima*, n) *americana*, o) *nigrescens*. For details see section Study species in the Introduction.



**Fig. 5.3:** Relative distribution of *C. brachydactyla* spp. a) *mauritanica*, b) *megarhynchos*, c) *brachydactyla*, d) *stresemanni*, e) *rossocaucasica*, f) *dorotheae*. For details see section Study species in the Introduction.



**Fig. 5.4:** Relative distribution of *C. himalayana* and *C. [discolor]* taxa: a) *C. h. taeniura*, b) *C. h. himalayana* and *C. [d.] discolor*, c) *C. [d.] discolor*, d) *C. h. yunnanensis*, e) *C. h. ripponi* and *C. [d.] ma. manipurensis*, f) *C. [d.] ma. shanensis*, g) *C. [d.] ma. laotiana*, h) *C. [d.] ma. meridionalis*. For details see section Study species in the Introduction.

Trill group

5. Isospecies *Certhia himalayana* Vigors, 1832 (Fig. 5.4) with four subspecies (*taeniura* in W Tian Shan, E Uzbekistan, W Tajikistan and N Afghanistan, *himalayana* in SE Afghanistan, N and W Pakistan east to W Nepal, *yunnanensis* in E Assam, N and NE Myanmar, SE Xizang and N Yunnan to W Sichuan, S Shaanxi and SW Guizhou, *ripponi* in W Myanmar)

Superspecies *Certhia* [*nipalensis*]

6. *Certhia* [*nipalensis*] *tianquanensis* Li, 1995 (only a few localities in the Chinese provinces of Sichuan and Shaanxi), treated as allospecies of *C. discolor* s.l. by Martens et al. (2002)
7. *Certhia* [*nipalensis*] *nipalensis* Blyth, 1845 (C and E Himalayas)

Superspecies *Certhia* [*discolor*] (Fig. 5.4)

8. *Certhia* [*discolor*] *discolor* Blyth, 1845 (C and E Himalayas)
9. *Certhia* [*discolor*] *manipurensis* Hume, 1881 with four disjunct subspecies (*manipurensis* in S and SE Assam, W and SW Myanmar, *shanensis* in N Myanmar, W Yunnan, W and N Thailand, NW Viet Nam, *laotiana* in N and C Laos, *meridionalis* on the Da Lat Plateau in Viet Nam), formerly included in *C. discolor* s.l.

### 5.1.2 Hypotheses

I intended to compare large series of specimens in order to find morphological features that unequivocally characterise the recently unravelled cryptic species. The approach was a statistical analysis of morphometric data rather than descriptive comparison of colorations. Several recent studies also succeeded in morphologically distinguishing species that had been established on molecular-systematic or bioacoustic grounds from closely related congeners with similar outer morphology (Martens et al. 1999: *Seicercus burkii* complex, LeCroy & Barker 2006: *Cettia haddeni*, Martens et al. 2006: *Parus ater eckodedicatus*).

I wanted to reveal evolutionary trends or at least discover trends in certain morphometric parameters within the (super)species. Continuous clines could give hints regarding the evolutionary history of a taxon. Breaks within a trend – especially in superspecies – might support (possible) species splits.

I finally focussed on two areas of sympatric occurrence of *Certhia* species and competition avoidance of the sexes in order to work out the decisive parameters for coexistence. In all cases, the aim was to determine whether lengths of the bill and the hind claw were valuable morphometric parameters in order to compare the occupation of ecological niches by *Certhia* treecreepers (breeding behind protruding bark, feeding on arthropods in bark chinks).

## 5.2 Methods

### 5.2.1 Material

I studied 1891 specimens from almost all valid taxa of *Certhia* according to the list above; only for *C. brachydactyla rossocaucasica* and *C. manipurensis laotiana* no material was available. *Certhia americana* specimens were affiliated to subspecies according to Webster (1986), Unitt & Rea (1997) and Hejl et al. (2002). In areas where representatives of other subspecies are known to occur during migration and winter only specimens collected from May to August are evaluated on the subspecific level. Due to a large range overlap in *C. a. americana* and *C. a. nigrescens* (Webster 1986), their data are presented in a combined manner. Material was examined at or was borrowed from the museums listed in Table 5.1. I am well aware that museum specimens may be wrongly labelled as regards locality, subspecies, age and sex (Rasmussen & Prÿs-Jones 2003). But in the case of treecreepers with their similar outer appearance, only a minority of the material seemed to be affected. All doubtful specimens were excluded from the data analysis. Finally, I analysed only data of 1614 full-grown specimens of known sex.

**Table 5.1:** Collections containing *Certhia* specimens examined for this study.

Location	Name	Acronym	Specimens
Ann Arbor (USA)	Museum of Zoology, University of Michigan	UMMZ	10
Berkeley (USA)	Museum of Vertebrate Zoology, University of California	MVZ	23
Berlin (Germany)	Museum für Naturkunde der Humboldt-Universität	ZMB	21
Bonn (Germany)	Zoologisches Forschungsinstitut und Museum Alexander Koenig	ZFMK	196
Dresden (Germany)	Staatliches Museum für Tierkunde	MTD	211
Hamburg (Germany)	Zoologisches Institut und Zoologisches Museum der Universität	ZMH	18
Mainz (Germany)	private collection of Jochen Martens	MAR	15
München (Germany)	Zoologische Staatssammlung	ZSM	2
New York (USA)	American Museum of Natural History	AMNH	560
Stockholm (Sweden)	Naturhistoriska Riksmuseet	NRM	45
Tring (UK)	The Natural History Museum, Bird Group	NHM	499
Wien (Austria)	Naturhistorisches Museum	NMW	4
Wiesbaden (Germany)	Landesmuseum, Naturwissenschaftliche Sammlung	MWHN	10

### 5.2.2 Measurements

The following measurements (description, accuracy, measuring instrument) were taken from all specimens in which the corresponding part of the body appendages was in good condition: claw length (chord length between emergence of claw from hind toe to tip of claw of the right leg measured from above, 0.1 mm, callipers), bill length (from tip of bill to the angle between bill and skull, 0.1 mm, callipers; Fig. 16 in Svensson, 1992), bill depth (at distal end of nostrils, 0.1 mm, callipers), bill width (at distal end of nostrils, 0.1 mm, callipers), wing length (maximum chord of left wing according to Kelm, 1970; 0.5 mm; flat ruler with stop at zero), wing tip (distance between tip of secondary 1 and tip of left wing according to Stegmann, 1940, and Kipp, 1959; 1 mm; flat ruler), tail length (from emergence of central rectrix pair to tip of longest tail feather of tail in natural shape, 1 mm, dividers and ruler with stop at zero; Fig. 12 in Svensson, 1992), tail tip (distance between tips of shortest and longest rectrices, 1 mm, flat ruler) and – in only a few specimens – tarsus length (distance between intertarsal joint and the joint between tarsus and middle toe of the right leg according to Leisler & Winkler, 1991; 0.1 mm, callipers). Tail length and tail tip were only evaluated when the tail state was fresh or only slightly abraded and neither growing nor broken.

### 5.2.3 Statistics

Sexes were treated separately since there is a marked dimorphism (e.g. Stepanyan 1965, Inozemtsev & Stepanyan 1967, Dornbusch 1980, Markovets 1991, Suhonen & Kuitunen 1991, Martens & Eck 1995; see also Results).

I calculated the following indices (acronym, description): wing-tip index (WTI, wing tip as % of wing length), tail-wing index (TWI, tail length as % of wing length), bill-wing index (BWI, bill length as % of wing length), claw-wing index (CWI, claw length as % of wing length), claw-bill index (CBI, claw length as % of bill length) and tail-tip index (TTI, tail tip as % of tail length).

Morphometric differentiation between taxa (and sexes) was investigated with the help of pairwise Mann-Whitney U-tests (significance level of  $p < 0.05$ , if no other values indicated) and discriminant analyses (DA) performed in SPSS 14. A cluster analysis based on all eight measurements except tarsus was also done in SPSS; UPGMA was chosen as clustering method and different measures were tested.

## 5 Morphometric characterisation

**Table 5.2:** Measurements taken from male specimens summarised by taxon (all in mm): mean ± s.d. (minimum – maximum, sample size).

Taxon	Hind claw	Bill length (skull)	Bill depth	Bill width	Wing length (max chord)	Wing tip	Tail length	Tail tip	Tarsus
<i>C. f. britannica</i>	9.0 ± 0.52 (7.7–10.4, 72)	16.8 ± 1.22 (13.9–19.1, 71)	2.5 ± 0.14 (2.2–2.9, 65)	1.9 ± 0.11 (1.6–2.2, 69)	63.6 ± 1.87 (59.0–67.0, 70)	12 ± 0.9 (10–14, 65)	59 ± 3.3 (53–65, 63)	14 ± 2.8 (6–23, 58)	14.5 ± 0.57 (13.9–15.1, 4)
<i>C. f. macrodactyla</i>	9.3 ± 0.63 (7.5–10.7, 73)	17.3 ± 1.28 (14.5–20.8, 70)	2.6 ± 0.12 (2.3–2.9, 65)	1.8 ± 0.14 (1.5–2.1, 65)	65.0 ± 2.02 (58.5–69.5, 79)	12 ± 0.7 (10–13, 74)	62 ± 3.0 (55–68, 61)	14 ± 2.0 (9–19, 57)	14.3 ± 0.93 (13.3–16.4, 9)
<i>C. f. corsa</i>	9.1 ± 0.41 (8.3–9.8, 14)	20.1 ± 1.14 (17.4–21.6, 12)	2.6 ± 0.11 (2.5–2.8, 13)	2.0 ± 0.12 (1.8–2.2, 13)	67.4 ± 1.97 (63.5–70.0, 14)	13 ± 0.8 (12–14, 11)	67 ± 2.2 (61–68, 11)	16 ± 2.4 (12–21, 10)	13.2 ± 1.36 (11.6–14.0, 3)
<i>C. f. familiaris</i>	9.2 ± 0.59 (7.6–11.6, 105)	17.2 ± 0.99 (13.8–20.5, 103)	2.6 ± 0.15 (2.3–3.0, 87)	1.8 ± 0.14 (1.6–2.2, 88)	65.4 ± 1.71 (59.5–69.5, 106)	12 ± 0.9 (10–14, 96)	63 ± 3.1 (57–70, 78)	15 ± 2.0 (11–20, 67)	14.9 ± 0.23 (14.5–15.1, 5)
<i>C. f. caucasica</i>	9.1 ± 0.50 (8.3–10.0, 16)	16.9 ± 1.19 (15.1–19.2, 15)	2.5 ± 0.14 (2.3–2.8, 16)	1.9 ± 0.07 (1.8–2.0, 15)	64.6 ± 2.12 (60.0–69.5, 16)	12 ± 1.0 (10–14, 14)	64 ± 2.7 (60–68, 14)	16 ± 1.7 (13–19, 14)	14.4 ± 0.48 (13.8–15.0, 5)
<i>C. f. persica</i>	10.1 ± 0.31 (9.6–10.3, 4)	19.2 ± 0.61 (18.4–19.7, 4)	2.6 ± 0.21 (2.4–2.7, 2)	2.2 ± 0.07 (2.1–2.2, 2)	63.3 ± 2.18 (61.5–66.0, 4)	12 (3)	61 ± 2.6 (58–63, 3)	14 (1)	–
<i>C. f. daurica</i>	9.1 ± 0.63 (8.0–10.4, 19)	16.8 ± 1.43 (13.9–19.6, 19)	2.7 ± 0.18 (2.4–3.0, 15)	2.0 ± 0.16 (1.7–2.3, 16)	64.7 ± 2.40 (60.0–68.0, 19)	12 ± 0.9 (11–14, 17)	61 ± 2.9 (55–66, 16)	14 ± 2.1 (10–18, 15)	12.7 ± 0.58 (11.9–13.8, 7)
<i>C. f. tianshanica</i>	9.5 ± 0.55 (8.6–10.4, 19)	18.7 ± 1.70 (16.1–23.0, 18)	2.6 ± 0.12 (2.5–2.9, 17)	1.9 ± 0.15 (1.6–2.1, 18)	67.5 ± 1.76 (62.5–70.0, 19)	12 ± 1.1 (10–14, 17)	67 ± 3.2 (62–73, 16)	14 ± 1.4 (12–17, 13)	13.8 ± 0.67 (13.3–14.7, 4)
<i>C. f. japonica</i>	9.2 ± 0.29 (8.8–9.5, 5)	15.7 ± 0.82 (15.0–16.6, 5)	2.7 ± 0.14 (2.5–2.8, 4)	1.9 ± 0.23 (1.7–2.2, 5)	62.3 ± 2.08 (60.5–65.5, 5)	12 ± 1.0 (11–13, 5)	57 ± 5.4 (49–62, 5)	13 ± 2.6 (8–14, 5)	12.1 ± 2.40 (10.4–13.8, 2)
<i>C. f. bianchii</i>	9.9 ± 0.64 (8.9–11.3, 17)	18.6 ± 1.07 (16.7–21.5, 17)	2.5 ± 0.13 (2.3–2.7, 16)	1.9 ± 0.18 (1.7–2.3, 16)	66.5 ± 1.56 (64.0–70.5, 17)	12 ± 1.0 (10–14, 17)	63 ± 3.7 (57–70, 16)	15 ± 3.5 (6–21, 15)	12.5 ± 1.65 (10.6–13.5, 3)
<b><i>C. familiaris</i></b>	<b>9.2 ± 0.61 (7.5–11.6, 344)</b>	<b>17.3 ± 1.41 (13.8–23.0, 334)</b>	<b>2.6 ± 0.15 (2.2–3.0, 300)</b>	<b>1.9 ± 0.14 (1.5–2.3, 307)</b>	<b>65.1 ± 2.18 (58.5–70.5, 349)</b>	<b>12 ± 0.9 (10–14, 319)</b>	<b>62 ± 3.8 (49–73, 283)</b>	<b>15 ± 2.4 (6–23, 255)</b>	<b>13.8 ± 1.21 (10.4–16.4, 42)</b>
<i>C. ho. "waschanensis"</i>	9.4 ± 0.31 (9.1–9.7, 3)	17.3 ± 0.44 (16.8–17.6, 3)	2.9 ± 0.21 (2.7–3.1, 3)	2.1 ± 0.12 (2.0–2.2, 3)	66.2 ± 0.29 (66.0–66.5, 3)	11 ± 0.6 (11–12, 3)	58 (2)	12 ± 0.7 (11–12, 2)	13.5 (1)
<i>C. ho. "kwanhsienensis"</i>	9.0 (1)	15.3 (1)	2.6 (1)	2.0 (1)	63.0 (1)	11 (1)	62 (1)	12 (1)	–
<i>C. ho. khamensis</i>	9.4 ± 0.61 (8.0–10.5, 28)	18.0 ± 1.38 (14.5–20.4, 23)	2.8 ± 0.15 (2.5–3.0, 22)	2.0 ± 0.17 (1.7–2.3, 23)	68.7 ± 2.48 (64.0–73.0, 28)	12 ± 1.1 (11–15, 21)	65 ± 4.8 (50–72, 22)	18 ± 2.8 (12–22, 17)	14.8 ± 0.52 (14.5–15.4, 3)
<i>C. ho. mandellii</i>	9.7 ± 0.60 (8.3–10.7, 23)	16.5 ± 0.97 (14.5–18.1, 25)	2.8 ± 0.16 (2.5–3.1, 20)	2.0 ± 0.19 (1.7–2.6, 21)	67.8 ± 1.90 (64.0–71.5, 26)	12 ± 0.9 (11–14, 24)	65 ± 3.0 (60–70, 13)	20 ± 1.4 (17–22, 12)	15.7 ± 0.07 (15.6–15.7, 2)
<i>C. ho. hodgsoni</i>	8.8 ± 0.53 (7.7–9.7, 15)	19.5 ± 1.73 (15.3–21.9, 15)	2.6 ± 0.21 (2.2–3.1, 14)	1.9 ± 0.25 (1.7–2.7, 15)	65.4 ± 1.78 (62.0–68.5, 15)	11 ± 0.9 (10–13, 12)	60 ± 2.5 (58–64, 5)	13 ± 1.9 (11–16, 5)	15.7 (1)
<b><i>C. hodgsoni</i></b>	<b>9.4 ± 0.65 (7.7–10.7, 70)</b>	<b>17.7 ± 1.75 (14.5–21.9, 67)</b>	<b>2.7 ± 0.18 (2.2–3.1, 60)</b>	<b>2.0 ± 0.20 (1.7–2.7, 63)</b>	<b>67.5 ± 2.46 (62.0–73.0, 73)</b>	<b>12 ± 1.0 (10–15, 61)</b>	<b>64 ± 4.4 (50–72, 43)</b>	<b>17 ± 3.3 (11–22, 37)</b>	<b>15.0 ± 0.84 (13.5–15.7, 7)</b>
<i>C. a. montana</i>	8.1 ± 0.37 (7.6–8.8, 11)	18.7 ± 1.08 (16.5–20.3, 11)	2.4 ± 0.11 (2.3–2.6, 10)	1.9 ± 0.12 (1.7–2.1, 10)	66.4 ± 2.39 (61.0–69.0, 11)	13 ± 0.8 (12–14, 10)	58 ± 3.0 (53–62, 8)	14 ± 2.0 (12–17, 8)	13.8 (1)
<i>C. a. occidentalis</i>	8.3 (1)	16.9 (1)	2.6 (1)	2.1 (1)	65.5 (1)	12 (1)	54 (1)	12 (1)	–
<i>C. a. alascensis</i>	8.5 ± 0.28 (8.1–8.8, 6)	17.0 ± 0.84 (15.7–17.7, 6)	2.4 ± 0.15 (2.2–2.6, 6)	1.8 ± 0.16 (1.7–2.1, 6)	64.2 ± 1.75 (62.5–67.0, 6)	13 ± 0.8 (12–14, 5)	54 (1)	12 (1)	–
<i>C. a. stewarti</i>	–	–	–	–	–	–	–	–	–
<i>C. a. zelotes</i>	7.9 ± 0.35 (7.2–8.5, 11)	18.1 ± 1.62 (14.8–19.4, 10)	2.4 ± 0.10 (2.2–2.5, 11)	2.0 ± 0.13 (1.8–2.2, 11)	64.4 ± 1.95 (60.0–66.5, 11)	12 ± 1.0 (11–14, 9)	57 ± 3.3 (52–61, 7)	12 ± 2.9 (6–15, 7)	13.1 ± 0.42 (12.8–13.4, 2)
<i>C. a. phillipsi</i>	7.6 ± 0.34 (7.3–8.2, 6)	18.2 ± 2.00 (15.9–20.4, 5)	2.4 ± 0.08 (2.3–2.5, 5)	2.2 ± 0.22 (1.9–2.4, 5)	62.7 ± 1.91 (60.0–65.5, 6)	12 ± 0.8 (11–13, 4)	59 ± 4.6 (54–63, 3)	16 ± 4.0 (11–18, 3)	13.6 ± 0.14 (13.5–13.7, 2)
<i>C. a. leucosticta</i>	7.8 ± 0.23 (7.4–8.1, 9)	18.5 ± 1.36 (15.7–20.4, 9)	2.4 ± 0.12 (2.2–2.6, 9)	1.8 ± 0.09 (1.7–1.9, 9)	66.5 ± 1.71 (64.5–70.0, 9)	12 ± 0.7 (11–13, 7)	60 ± 1.0 (59–61, 3)	14 ± 4.9 (10–17, 2)	–
<i>C. a. albescens</i>	7.6 ± 0.26 (7.4–8.3, 9)	16.7 ± 0.48 (15.9–17.3, 10)	2.4 ± 0.10 (2.2–2.5, 6)	1.9 ± 0.20 (1.6–2.2, 6)	63.8 ± 1.89 (61.5–67.0, 10)	11 ± 1.1 (9–12, 7)	61 ± 1.9 (58–63, 6)	15 ± 1.8 (12–16, 6)	–
<i>C. a. jaliscensis</i>	8.0 ± 0.41 (7.6–8.5, 4)	16.3 ± 1.61 (14.9–18.5, 4)	2.4 ± 0.10 (2.3–2.5, 4)	2.1 ± 0.13 (1.9–2.2, 4)	62.6 ± 1.65 (61.0–64.5, 4)	11 ± 0.6 (11–12, 3)	60 ± 4.7 (53–63, 4)	15 ± 3.0 (11–18, 4)	12.6 ± 0.85 (12.0–13.2, 2)
<i>C. a. guerrensis</i>	7.9 ± 0.72 (7.4–8.7, 3)	16.4 ± 1.46 (14.7–17.4, 3)	2.6 ± 0.21 (2.4–2.7, 2)	2.1 ± 0.14 (2.0–2.2, 2)	62.3 ± 2.84 (60.0–65.5, 3)	9 (2)	61 ± 4.4 (58–66, 3)	14 ± 3.5 (11–16, 2)	–
<i>C. a. alticola</i>	8.7 ± 0.40 (8.1–9.6, 17)	17.3 ± 0.99 (15.1–18.7, 17)	2.5 ± 0.23 (2.1–2.9, 15)	2.1 ± 0.15 (1.8–2.4, 17)	67.0 ± 2.37 (63.0–70.0, 14)	11 ± 1.3 (9–14, 13)	65 ± 3.4 (58–70, 10)	15 ± 2.9 (11–20, 10)	13.5 (1)
<i>C. a. pennigra</i>	8.5 ± 0.31 (8.0–8.8, 7)	16.7 ± 0.93 (15.4–17.8, 6)	2.6 ± 0.15 (2.4–2.8, 5)	2.1 ± 0.18 (2.0–2.5, 7)	66.8 ± 1.85 (63.0–68.5, 7)	12 ± 0.5 (11–12, 6)	63 ± 2.5 (60–65, 3)	14 ± 2.8 (12–16, 2)	–
<i>C. a. extima</i>	7.8 ± 0.41 (7.0–8.8, 20)	18.8 ± 0.96 (16.8–20.6, 20)	2.7 ± 0.19 (2.4–3.1, 18)	2.1 ± 0.13 (1.9–2.4, 18)	62.3 ± 2.08 (59.0–66.0, 21)	12 ± 1.0 (10–14, 20)	58 ± 2.7 (54–64, 18)	16 ± 1.9 (13–19, 16)	12.6 ± 0.31 (12.3–13.0, 4)
<i>C. a. americana/nigrescens</i>	8.0 ± 0.38 (6.8–9.1, 74)	16.9 ± 1.02 (14.4–19.1, 76)	2.5 ± 0.12 (2.2–2.8, 69)	1.9 ± 0.17 (1.3–2.3, 71)	66.2 ± 1.92 (61.0–70.0, 78)	14 ± 1.2 (11–16, 75)	62 ± 3.9 (54–69, 67)	16 ± 2.8 (6–22, 67)	13.4 ± 0.86 (12.2–14.8, 12)
<b><i>C. americana</i></b>	<b>8.0 ± 0.48 (6.8–9.6, 231)</b>	<b>17.4 ± 1.33 (14.4–20.6, 227)</b>	<b>2.5 ± 0.17 (2.1–3.1, 207)</b>	<b>2.0 ± 0.19 (1.3–2.6, 213)</b>	<b>65.0 ± 2.56 (59.0–72.0, 238)</b>	<b>13 ± 1.5 (9–16, 216)</b>	<b>60 ± 4.0 (51–70, 181)</b>	<b>15 ± 2.8 (6–24, 175)</b>	<b>13.2 ± 0.87 (11.1–14.8, 34)</b>
<i>C. b. mauritanica</i>	7.7 ± 0.46 (6.8–8.6, 27)	18.8 ± 1.31 (15.8–20.9, 25)	2.6 ± 0.13 (2.3–2.8, 24)	2.1 ± 0.17 (1.9–2.5, 25)	65.2 ± 2.22 (59.0–68.5, 27)	11 ± 0.9 (9–13, 27)	59 ± 2.0 (55–62, 15)	14 ± 2.5 (8–17, 15)	14.5 ± 0.81 (12.9–16.0, 15)
<i>C. b. megarhynchos</i>	7.7 ± 0.37 (6.8–8.6, 50)	18.7 ± 1.26 (14.6–21.0, 49)	2.6 ± 0.15 (2.3–3.1, 44)	2.0 ± 0.17 (1.7–2.5, 44)	63.0 ± 1.62 (59.0–66.5, 50)	11 ± 1.0 (9–14, 48)	59 ± 3.1 (53–65, 41)	14 ± 2.5 (9–18, 39)	15.1 ± 0.07 (15.0–15.1, 2)
<i>C. b. brachydactyla</i>	7.7 ± 0.38 (6.6–9.2, 111)	19.3 ± 1.21 (15.5–22.9, 111)	2.6 ± 0.14 (2.3–2.9, 98)	2.0 ± 0.12 (1.7–2.3, 98)	63.1 ± 1.85 (55.5–68.0, 117)	11 ± 0.9 (7–13, 106)	59 ± 3.1 (52–65, 80)	15 ± 2.8 (6–21, 69)	12.8 ± 1.43 (11.0–14.9, 8)
<i>C. b. stresemanni</i>	7.8 ± 0.47 (7.0–8.3, 6)	17.9 ± 1.20 (16.3–19.5, 5)	2.4 ± 0.25 (2.1–2.7, 4)	2.1 ± 0.23 (1.9–2.3, 4)	61.5 ± 1.84 (59.5–64.0, 6)	11 ± 0.5 (10–11, 4)	58 ± 1.0 (57–59, 3)	15 ± 1.4 (14–16, 2)	–
<i>C. b. dorothaeae</i>	7.6 ± 0.48 (6.3–8.2, 14)	18.9 ± 1.24 (17.2–21.0, 14)	2.6 ± 0.21 (2.4–2.9, 9)	2.0 ± 0.19 (1.8–2.4, 11)	62.8 ± 1.50 (60.5–65.0, 14)	11 ± 1.1 (9–13, 9)	60 ± 1.5 (58–63, 14)	16 ± 2.8 (8–19, 14)	13.1 ± 0.62 (12.4–14.1, 9)
<i>C. d. discolor</i>	9.4 ± 0.33 (8.7–9.7, 13)	17.8 ± 0.87 (16.0–19.2, 13)	2.6 ± 0.12 (2.5–2.9, 13)	2.5 ± 0.20 (2.2–3.0, 13)	69.6 ± 2.37 (64.0–74.0, 13)	12 ± 0.8 (11–13, 13)	75 ± 4.8 (67–81, 13)	26 ± 3.9 (20–31, 13)	–
<b><i>C. brachydactyla</i></b>	<b>7.7 ± 0.40 (6.3–9.2, 210)</b>	<b>19.0 ± 1.27 (14.6–22.9, 206)</b>	<b>2.6 ± 0.15 (2.1–3.1, 181)</b>	<b>2.0 ± 0.15 (1.7–2.5, 184)</b>	<b>63.3 ± 1.98 (55.5–68.5, 216)</b>	<b>11 ± 1.0 (7–14, 196)</b>	<b>59 ± 2.8 (52–65, 155)</b>	<b>15 ± 2.7 (6–21, 141)</b>	<b>13.8 ± 1.22 (11.0–16.0, 34)</b>
<i>C. hi. taeniura</i>	9.4 ± 0.79 (8.4–10.5, 11)	24.4 ± 2.35 (18.8–27.0, 12)	2.6 ± 0.23 (2.3–3.0, 12)	2.0 ± 0.24 (1.8–2.6, 12)	71.7 ± 2.23 (67.5–75.0, 13)	14 ± 0.8 (13–16, 12)	67 ± 2.7 (63–71, 11)	13 ± 1.6 (11–16, 10)	13.6 ± 0.14 (13.5–13.7, 2)
<i>C. hi. himalayana</i>	9.3 ± 0.47 (8.5–10.5, 32)	21.4 ± 1.38 (18.8–23.5, 27)	2.6 ± 0.16 (2.3–3.0, 29)	2.1 ± 0.13 (1.9–2.4, 29)	70.7 ± 2.02 (66.5–74.0, 33)	14 ± 1.2 (11–16, 25)	64 ± 3.5 (57–70, 30)	14 ± 3.2 (7–21, 29)	12.6 ± 1.03 (11.7–14.5, 8)
<i>C. hi. yunnanensis</i>	9.3 ± 0.90 (7.6–10.5, 9)	21.6 ± 2.97 (16.7–25.3, 9)	2.6 ± 0.18 (2.3–2.8, 9)	1.9 ± 0.11 (1.8–2.1, 9)	73.2 ± 3.67 (68.0–78.0, 9)	15 ± 1.5 (13–18, 9)	65 ± 3.3 (62–70, 7)	13 ± 1.6 (11–16, 7)	13.5 (1)
<i>C. hi. ripponi</i>	9.3 ± 0.76 (8.2–10.1, 5)	22.5 ± 0.92 (21.6–24.0, 5)	2.7 ± 0.09 (2.6–2.8, 5)	2.0 ± 0.19 (1.8–2.2, 5)	68.3 ± 2.11 (66.0–71.0, 5)	12 (3)	–	–	13.2 ± 0.92 (12.5–13.8, 2)
<b><i>C. himalayana</i></b>	<b>9.3 ± 0.62 (7.6–10.5, 57)</b>	<b>22.2 ± 2.25 (16.7–27.0, 53)</b>	<b>2.6 ± 0.17 (2.3–3.0, 55)</b>	<b>2.1 ± 0.17 (1.8–2.6, 55)</b>	<b>71.1 ± 2.62 (66.0–78.0, 60)</b>	<b>14 ± 1.3 (11–18, 49)</b>	<b>65 ± 3.5 (57–71, 48)</b>	<b>13 ± 2.7 (7–21, 46)</b>	<b>12.9 ± 0.93 (11.7–14.5, 13)</b>
<i>C. tianquanensis</i>	<b>10.0 ± 0.43 (9.1–10.4, 8)</b>	<b>15.1 ± 0.66 (14.5–16.3, 8)</b>	<b>2.5 ± 0.15 (2.4–2.8, 8)</b>	<b>2.3 ± 0.17 (2.0–2.5, 8)</b>	<b>71.2 ± 1.96 (69.0–74.0, 8)</b>	<b>13 ± 0.7 (13–15, 8)</b>	<b>71 ± 6.3 (64–80, 6)</b>	<b>28 ± 4.2 (22–33, 5)</b>	–
<i>C. nipalensis</i>	<b>10.2 ± 0.48 (9.3–11.6, 25)</b>	<b>16.1 ± 0.71 (15.0–17.4, 24)</b>	<b>2.7 ± 0.16 (2.5–3.0, 23)</b>	<b>2.4 ± 0.19 (2.0–2.7, 24)</b>	<b>72.1 ± 2.12 (69.0–76.0, 25)</b>	<b>13 ± 1.2 (12–16, 24)</b>	<b>76 ± 5.6 (60–85, 24)</b>	<b>35 ± 5.4 (23–43, 24)</b>	<b>17.0 ± 0.10 (16.9–17.1, 4)</b>
<b><i>C. discolor</i></b>	<b>9.4 ± 0.33 (8.7–9.7, 13)</b>	<b>17.8 ± 0.87 (16.0–19.2, 13)</b>	<b>2.6 ± 0.12 (2.5–2.9, 13)</b>	<b>2.5 ± 0.20 (2.2–3.0, 13)</b>	<b>69.6 ± 2.37 (64.0–74.0, 13)</b>	<b>12 ± 0.8 (11–13, 13)</b>	<b>75 ± 4.8 (67–81, 13)</b>	<b>26 ± 3.9 (20–31, 13)</b>	–
<i>C. m. manipurensis</i>	9.1 ± 0.39 (8.6–9.6, 7)	19.3 ± 1.21 (18.2–21.6, 7)	2.8 ± 0.18 (2.6–3.0, 6)	2.4 ± 0.14 (2.3–2.7, 7)	70.0 ± 1.91 (68.0–74.0, 7)	12 ± 0.4 (12–13, 6)	77 ± 3.2 (71–80, 6)	26 ± 2.7 (21–29, 6)	14.2 ± 0.35 (13.9–14.4, 2)
<i>C. m. shanensis</i>	9.5 ± 0.27 (9.1–9.8, 8)	18.6 ± 1.64 (15.7–20.7, 8)	2.7 ± 0.21 (2.4–3.0, 8)	2.6 ± 0.31 (2.2–3.1, 9)	69.4 ± 1.54 (67.5–72.5, 9)	12 ± 1.3 (10–14, 8)	73 ± 4.7 (67–81, 8)	25 ± 3.0 (22–30, 7)	14.3 ± 0.07 (

## 5 Morphometric characterisation

**Table 5.3:** Measurements taken from female specimens summarised by taxon (all in mm): mean ± s.d. (minimum – maximum, sample size).

Taxon	Hind claw	Bill length (skull)	Bill depth	Bill width	Wing length (max chord)	Wing tip	Tail length	Tail tip	Tarsus
<i>C. f. britannica</i>	8.9 ± 0.48 (7.6–10.0, 48)	15.9 ± 1.22 (13.7–19.0, 48)	2.5 ± 0.14 (2.2–2.8, 40)	1.9 ± 0.13 (1.6–2.2, 40)	61.9 ± 1.73 (58.5–67.5, 49)	11 ± 0.9 (9–13, 48)	58 ± 2.7 (52–64, 38)	14 ± 2.6 (9–21, 36)	14.6 ± 0.53 (14.1–15.3, 4)
<i>C. f. macrodactyla</i>	9.0 ± 0.44 (8.1–9.8, 43)	15.9 ± 0.98 (13.9–18.4, 42)	2.5 ± 0.14 (2.3–2.9, 37)	1.8 ± 0.14 (1.5–2.1, 37)	62.8 ± 2.14 (58.5–67.0, 48)	11 ± 0.9 (10–13, 42)	60 ± 3.9 (53–67, 37)	14 ± 2.3 (9–18, 36)	13.8 ± 0.59 (13.4–14.5, 3)
<i>C. f. corsa</i>	9.1 ± 0.35 (8.3–9.6, 14)	18.1 ± 0.98 (16.2–20.5, 14)	2.6 ± 0.12 (2.4–2.8, 12)	2.0 ± 0.08 (1.9–2.1, 12)	64.5 ± 0.99 (63.0–66.5, 14)	12 ± 1.1 (11–14, 13)	62 ± 2.1 (57–65, 14)	14 ± 1.3 (11–16, 13)	13.8 ± 0.25 (13.5–14.1, 4)
<i>C. f. familiaris</i>	9.0 ± 0.59 (7.1–10.2, 55)	15.7 ± 1.20 (13.5–18.3, 50)	2.6 ± 0.13 (2.2–2.8, 41)	1.9 ± 0.13 (1.6–2.1, 43)	62.9 ± 2.04 (59.0–68.5, 57)	12 ± 0.8 (10–13, 52)	62 ± 2.7 (56–68, 41)	14 ± 2.2 (8–19, 34)	13.3 ± 0.89 (12.3–14.0, 3)
<i>C. f. caucasica</i>	9.1 ± 0.60 (8.0–9.6, 6)	16.2 ± 1.52 (13.6–17.9, 6)	2.5 ± 0.17 (2.3–2.7, 6)	1.9 ± 0.10 (1.7–2.0, 6)	64.0 ± 2.28 (61.0–66.0, 6)	12 ± 0.8 (11–13, 6)	62 ± 4.8 (55–68, 6)	16 ± 3.1 (11–19, 6)	14.5 ± 0.50 (13.8–15.0, 4)
<i>C. f. persica</i>	9.1 (1)	16.6 (1)	2.5 (1)	1.9 (1)	60.0 (1)	11 (1)	56 (1)	12 (1)	–
<i>C. f. daurica</i>	8.7 ± 0.64 (7.8–9.8, 7)	15.8 ± 1.47 (13.9–17.8, 8)	2.6 ± 0.19 (2.4–2.9, 8)	1.8 ± 0.15 (1.6–2.1, 8)	62.6 ± 3.43 (57.0–66.0, 8)	13 ± 1.5 (11–15, 5)	61 ± 3.2 (57–64, 6)	14 ± 1.7 (12–16, 4)	12.6 ± 0.64 (12.1–13.0, 2)
<i>C. f. tianshanica</i>	9.7 ± 1.18 (8.5–11.8, 7)	17.6 ± 1.55 (16.0–19.9, 7)	2.5 ± 0.13 (2.4–2.7, 7)	2.0 ± 0.13 (1.7–2.1, 7)	64.4 ± 2.48 (61.0–67.0, 7)	12 ± 0.8 (11–13, 7)	63 ± 4.3 (56–68, 7)	14 ± 2.1 (12–18, 7)	13.6 ± 0.51 (13.0–14.2, 4)
<i>C. f. japonica</i>	9.1 ± 0.52 (8.6–9.5, 4)	15.5 ± 0.17 (15.2–15.6, 4)	2.7 ± 0.10 (2.6–2.8, 3)	2.1 ± 0.15 (1.9–2.2, 3)	64.1 ± 3.17 (61.0–68.5, 4)	11 ± 1.1 (10–12, 3)	58 ± 5.0 (54–65, 4)	14 ± 1.0 (13–15, 4)	12.9 (1)
<i>C. f. bianchii</i>	10.0 ± 0.32 (9.7–10.3, 4)	17.3 ± 1.38 (15.5–18.4, 4)	2.5 ± 0.17 (2.3–2.7, 4)	1.8 ± 0.10 (1.6–1.8, 4)	66.0 ± 1.78 (64.0–67.5, 4)	12 ± 1.0 (11–13, 4)	61 ± 2.6 (59–64, 3)	15 ± 3.5 (12–19, 3)	11.9 (1)
<b><i>C. familiaris</i></b>	<b>9.0 ± 0.57 (7.1–11.8, 189)</b>	<b>16.1 ± 1.34 (13.5–20.5, 184)</b>	<b>2.5 ± 0.14 (2.2–2.9, 159)</b>	<b>1.9 ± 0.14 (1.5–2.2, 161)</b>	<b>62.9 ± 2.20 (57.0–68.5, 198)</b>	<b>11 ± 0.9 (9–15, 181)</b>	<b>60 ± 3.5 (52–68, 157)</b>	<b>14 ± 2.3 (8–21, 144)</b>	<b>13.7 ± 0.84 (11.9–15.3, 26)</b>
<i>C. ho. "waschanensis"</i>	9.0 ± 0.21 (8.8–9.1, 2)	16.0 ± 0.00 (16.0–16.0, 2)	2.7 (1)	1.9 (1)	62.8 ± 0.35 (62.5–63.0, 2)	11 ± 0.7 (10–11, 2)	58 ± 2.1 (56–59, 2)	17 ± 0.0 (17–17, 2)	–
<i>C. ho. "kwanhsienensis"</i>	10.0 (1)	14.9 (1)	2.4 (1)	1.5 (1)	63.5 (1)	11 (1)	60 (1)	14 (1)	–
<i>C. ho. khamensis</i>	9.2 ± 0.35 (8.7–9.7, 7)	16.9 ± 1.21 (15.6–18.9, 7)	2.7 ± 0.11 (2.5–2.8, 7)	2.0 ± 0.13 (1.7–2.1, 7)	65.0 ± 3.64 (61.0–70.0, 7)	12 ± 0.5 (11–12, 6)	61 ± 4.2 (58–66, 3)	14 ± 0.0 (14–14, 2)	–
<i>C. ho. mandellii</i>	8.9 ± 0.36 (8.3–9.4, 13)	14.5 ± 0.45 (14.0–15.4, 11)	2.6 ± 0.10 (2.4–2.7, 10)	2.0 ± 0.19 (1.6–2.2, 10)	65.2 ± 1.81 (62.0–69.0, 12)	12 ± 0.4 (11–12, 9)	61 ± 1.8 (60–64, 6)	18 ± 1.5 (17–21, 6)	–
<i>C. ho. hodgsoni</i>	8.6 ± 0.39 (8.2–9.3, 8)	17.0 ± 0.61 (16.0–18.1, 8)	2.5 ± 0.11 (2.3–2.6, 8)	1.9 ± 0.11 (1.7–2.0, 8)	62.4 ± 1.74 (59.5–65.0, 8)	11 ± 0.8 (10–12, 7)	56 ± 1.5 (55–58, 3)	13 ± 1.7 (12–15, 3)	–
<b><i>C. hodgsoni</i></b>	<b>8.9 ± 0.45 (8.2–10.0, 31)</b>	<b>15.9 ± 1.36 (14.0–18.9, 29)</b>	<b>2.6 ± 0.14 (2.3–2.8, 27)</b>	<b>1.9 ± 0.17 (1.5–2.2, 27)</b>	<b>64.2 ± 2.51 (59.5–70.0, 30)</b>	<b>11 ± 0.7 (10–12, 25)</b>	<b>60 ± 3.0 (55–66, 15)</b>	<b>16 ± 2.6 (12–21, 14)</b>	–
<i>C. a. montana</i>	8.0 ± 0.51 (7.2–8.7, 9)	16.9 ± 0.87 (15.9–18.9, 9)	2.4 ± 0.10 (2.3–2.5, 8)	2.0 ± 0.25 (1.6–2.3, 8)	63.2 ± 2.26 (59.0–66.0, 9)	12 ± 1.1 (11–14, 7)	56 ± 3.5 (51–62, 7)	14 ± 3.0 (10–18, 6)	11.8 (1)
<i>C. a. occidentalis</i>	9.4 (1)	16.4 (1)	2.7 (1)	1.8 (1)	64.5 (1)	12 (1)	53 (1)	11 (1)	–
<i>C. a. alascensis</i>	8.3 (1)	15.6 (1)	2.4 (1)	2.0 (1)	63.0 (1)	13 (1)	63 (1)	14 (1)	–
<i>C. a. stewarti</i>	8.4 ± 0.42 (8.1–8.7, 2)	15.5 ± 0.57 (15.1–15.9, 2)	2.3 (1)	2.1 (1)	60.3 ± 0.35 (60.0–60.5, 2)	12 ± 0.7 (11–12, 2)	56 ± 0.7 (55–56, 2)	15 ± 1.4 (14–16, 2)	15.0 (1)
<i>C. a. zelates</i>	7.7 ± 0.58 (7.0–8.4, 6)	17.0 ± 1.71 (15.1–19.6, 6)	2.4 ± 0.21 (2.2–2.7, 5)	2.1 ± 0.16 (1.8–2.3, 6)	62.1 ± 1.91 (60.0–65.0, 6)	12 ± 0.9 (11–13, 5)	60 ± 10.6 (52–67, 2)	13 ± 2.1 (11–14, 2)	12.2 ± 0.57 (11.8–12.6, 2)
<i>C. a. phillipsi</i>	7.8 (1)	18.1 (1)	2.7 (1)	2.2 (1)	59.0 (1)	11 (1)	48 (1)	9 (1)	–
<i>C. a. leucosticta</i>	7.5 (1)	15.8 (1)	2.5 (1)	1.9 (1)	62.0 (1)	11 (1)	–	–	–
<i>C. a. albescens</i>	8.2 ± 0.70 (7.5–8.9, 3)	16.4 ± 1.11 (15.0–17.7, 4)	2.5 ± 0.10 (2.4–2.6, 3)	1.9 ± 0.25 (1.7–2.2, 3)	63.4 ± 2.93 (61.0–67.0, 4)	12 ± 0.6 (11–12, 3)	61 ± 2.8 (59–63, 2)	13 ± 3.5 (10–15, 2)	13.7 (1)
<i>C. a. jaliscensis</i>	8.4 ± 0.21 (8.2–8.6, 3)	17.3 ± 0.66 (16.7–18.0, 3)	2.5 ± 0.15 (2.4–2.7, 3)	2.0 ± 0.06 (2.0–2.1, 3)	63.2 ± 2.52 (60.5–65.5, 3)	11 ± 1.4 (10–12, 2)	61 ± 2.1 (59–63, 3)	15 ± 2.1 (13–17, 3)	13.8 (1)
<i>C. a. guerrerensis</i>	8.3 ± 0.74 (7.5–9.4, 5)	16.6 ± 0.77 (15.6–17.6, 6)	2.7 ± 0.14 (2.5–2.8, 5)	2.0 ± 0.12 (1.8–2.1, 6)	64.8 ± 2.42 (62.0–68.0, 6)	12 ± 1.7 (10–14, 4)	62 ± 3.3 (57–65, 4)	15 ± 2.2 (13–18, 4)	–
<i>C. a. alticola</i>	8.3 ± 0.57 (7.5–9.2, 9)	15.7 ± 0.63 (14.7–16.9, 9)	2.5 ± 0.10 (2.4–2.6, 7)	2.0 ± 0.06 (1.9–2.1, 8)	63.0 ± 1.32 (61.5–65.5, 9)	11 ± 0.5 (10–11, 7)	61 ± 2.6 (58–65, 6)	14 ± 4.1 (11–21, 5)	13.6 (1)
<i>C. a. pennigra</i>	8.1 ± 0.28 (8.0–8.3, 4)	16.0 ± 0.45 (15.4–16.5, 4)	2.6 ± 0.25 (2.4–2.9, 3)	2.3 ± 0.07 (2.0–2.3, 2)	64.4 ± 0.85 (63.0–65.5, 4)	11 ± 1.3 (11–12, 4)	61 ± 1.9 (60–63, 4)	15 ± 1.7 (12–16, 4)	–
<i>C. a. extima</i>	7.4 ± 0.33 (7.0–7.8, 4)	16.4 ± 1.07 (16.8–17.3, 4)	2.5 ± 0.21 (2.4–2.6, 2)	2.1 ± 0.15 (1.9–2.3, 3)	59.6 ± 0.48 (59.0–60.0, 4)	11 ± 0.5 (10–11, 4)	57 ± 2.4 (54–60, 4)	15 ± 2.2 (13–18, 4)	12.5 ± (12.3–12.5, 1)
<i>C. a. americana/nigrescens</i>	7.8 ± 0.41 (6.7–8.8, 38)	15.5 ± 0.96 (13.7–17.6, 38)	2.5 ± 0.14 (2.3–2.9, 33)	1.9 ± 0.16 (1.5–2.3, 34)	64.4 ± 2.10 (60.5–69.0, 40)	13 ± 1.0 (11–16, 39)	59 ± 4.7 (49–66, 31)	14 ± 3.1 (8–19, 31)	13.6 ± 0.54 (12.9–14.5, 13)
<b><i>C. americana</i></b>	<b>7.9 ± 0.55 (6.5–9.4, 122)</b>	<b>16.1 ± 1.19 (13.6–20.1, 126)</b>	<b>2.5 ± 0.14 (2.2–2.9, 109)</b>	<b>2.0 ± 0.17 (1.5–2.3, 113)</b>	<b>63.4 ± 2.19 (59.0–69.0, 129)</b>	<b>12 ± 1.3 (9–16, 117)</b>	<b>59 ± 4.5 (48–68, 97)</b>	<b>14 ± 3.0 (8–24, 94)</b>	<b>13.4 ± 0.72 (11.8–15.0, 27)</b>
<i>C. b. mauritanica</i>	7.4 ± 0.32 (6.6–7.7, 14)	17.8 ± 1.14 (16.1–20.7, 13)	2.5 ± 0.11 (2.3–2.6, 11)	2.1 ± 0.14 (1.8–2.3, 12)	63.8 ± 3.54 (60.0–70.0, 13)	11 ± 1.1 (9–12, 13)	57 ± 4.5 (51–64, 11)	14 ± 3.2 (11–21, 11)	14.1 ± 0.29 (13.9–14.5, 4)
<i>C. b. megarhynchos</i>	7.5 ± 0.35 (6.7–8.2, 33)	17.4 ± 1.02 (15.8–19.2, 32)	2.5 ± 0.13 (2.3–2.9, 30)	2.1 ± 0.15 (1.7–2.3, 30)	60.6 ± 1.82 (57.0–65.0, 33)	11 ± 0.9 (9–13, 30)	57 ± 3.3 (50–62, 28)	14 ± 1.9 (11–17, 24)	13.7 (1)
<i>C. b. brachydactyla</i>	7.4 ± 0.39 (6.6–9.0, 80)	17.5 ± 1.19 (14.5–21.6, 81)	2.5 ± 0.10 (2.3–2.8, 74)	1.9 ± 0.15 (1.6–2.3, 75)	60.7 ± 1.68 (57.0–65.0, 86)	11 ± 0.9 (9–13, 83)	57 ± 2.9 (52–65, 60)	15 ± 2.5 (10–21, 55)	13.9 ± 1.33 (11.6–15.0, 5)
<i>C. b. stresemanni</i>	7.7 ± 0.31 (7.4–8.0, 3)	17.6 ± 0.53 (17.0–18.0, 3)	2.4 (1)	2.0 ± 0.17 (1.9–2.2, 3)	61.2 ± 1.04 (60.0–62.0, 3)	10 ± 0.0 (10–10, 2)	57 ± 1.2 (56–58, 3)	15 ± 1.5 (13–16, 3)	–
<i>C. b. dorotheae</i>	7.4 ± 0.27 (7.1–7.9, 7)	17.9 ± 0.65 (17.2–18.7, 7)	2.6 ± 0.16 (2.3–2.8, 6)	2.1 ± 0.23 (1.7–2.3, 7)	61.1 ± 1.54 (59.0–64.0, 7)	11 ± 0.6 (10–12, 7)	57 ± 2.8 (52–59, 5)	16 ± 0.8 (15–17, 4)	13.3 ± 0.69 (12.5–14.4, 5)
<b><i>C. brachydactyla</i></b>	<b>7.5 ± 0.37 (6.6–9.0, 139)</b>	<b>17.5 ± 1.12 (14.5–21.6, 138)</b>	<b>2.5 ± 0.11 (2.3–2.9, 123)</b>	<b>2.0 ± 0.17 (1.6–2.3, 128)</b>	<b>61.0 ± 2.09 (57.0–70.0, 145)</b>	<b>11 ± 0.9 (9–13, 138)</b>	<b>57 ± 3.1 (50–65, 110)</b>	<b>15 ± 2.4 (9–21, 100)</b>	<b>13.8 ± 0.88 (11.6–15.0, 15)</b>
<i>C. hi. taeniura</i>	9.1 ± 0.50 (8.2–9.8, 8)	20.8 ± 1.77 (19.1–25.2, 9)	2.5 ± 0.17 (2.2–2.7, 8)	1.9 ± 0.13 (1.7–2.1, 8)	68.3 ± 1.95 (65.5–71.0, 9)	13 ± 1.1 (12–15, 8)	60 ± 3.5 (56–64, 4)	11 ± 1.7 (9–13, 4)	11.8 ± 1.61 (10.0–13.1, 3)
<i>C. hi. himalayana</i>	9.0 ± 0.50 (7.8–9.9, 30)	19.3 ± 1.53 (17.4–25.6, 30)	2.6 ± 0.17 (2.2–2.9, 28)	2.1 ± 0.16 (1.8–2.4, 28)	67.7 ± 2.08 (64.5–74.0, 31)	13 ± 1.3 (9–16, 26)	62 ± 4.1 (53–72, 24)	12 ± 2.0 (8–17, 22)	12.8 ± 0.42 (12.2–13.3, 5)
<i>C. hi. yunnanensis</i>	8.4 ± 0.10 (8.3–8.5, 3)	18.5 ± 1.25 (17.3–19.8, 3)	2.5 ± 0.10 (2.4–2.6, 3)	2.3 ± 0.15 (2.1–2.4, 3)	68.3 ± 2.89 (65.0–70.0, 3)	13 ± 0.6 (13–14, 3)	57 ± 11.3 (49–65, 2)	12 ± 2.8 (10–14, 2)	12.9 (1)
<i>C. hi. ripponi</i>	8.9 (1)	19.1 (1)	2.5 (1)	2.2 (1)	65.0 (1)	12 (1)	60 (1)	17 (1)	–
<b><i>C. himalayana</i></b>	<b>9.0 ± 0.49 (7.8–9.9, 43)</b>	<b>19.5 ± 1.66 (17.3–25.6, 43)</b>	<b>2.6 ± 0.17 (2.2–2.9, 40)</b>	<b>2.1 ± 0.18 (1.7–2.4, 40)</b>	<b>67.8 ± 2.07 (64.5–74.0, 45)</b>	<b>13 ± 1.2 (9–16, 39)</b>	<b>61 ± 4.4 (49–72, 32)</b>	<b>12 ± 2.1 (8–17, 30)</b>	<b>12.5 ± 0.99 (10.0–13.3, 9)</b>
<i>C. tianquanensis</i>	–	–	–	–	–	–	–	–	–
<b><i>C. nipalensis</i></b>	<b>9.5 ± 0.59 (8.6–10.7, 13)</b>	<b>14.9 ± 0.80 (13.5–15.9, 11)</b>	<b>2.6 ± 0.13 (2.3–2.7, 10)</b>	<b>2.4 ± 0.18 (2.1–2.6, 11)</b>	<b>67.8 ± 1.63 (65.0–70.5, 13)</b>	<b>12 ± 0.9 (11–14, 13)</b>	<b>74 ± 4.2 (65–80, 12)</b>	<b>34 ± 6.4 (22–41, 12)</b>	<b>16.1 ± 1.27 (15.2–17.0, 2)</b>
<b><i>C. discolor</i></b>	<b>9.2 ± 0.36 (8.5–9.8, 15)</b>	<b>16.8 ± 1.10 (15.0–19.1, 14)</b>	<b>2.6 ± 0.14 (2.3–2.8, 14)</b>	<b>2.5 ± 0.20 (2.2–2.8, 14)</b>	<b>67.6 ± 1.64 (64.5–70.5, 15)</b>	<b>12 ± 0.7 (11–13, 15)</b>	<b>74 ± 3.7 (68–83, 14)</b>	<b>28 ± 2.7 (22–34, 13)</b>	<b>13.5 ± 1.08 (12.3–14.3, 3)</b>
<i>C. m. manipurensis</i>	8.8 ± 0.48 (8.1–9.6, 8)	18.2 ± 1.15 (16.4–20.0, 8)	2.7 ± 0.21 (2.5–3.1, 6)	2.5 ± 0.28 (2.2–3.0, 7)	66.6 ± 0.69 (66.0–68.0, 8)	12 ± 0.6 (11–13, 6)	69 ± 3.1 (63–72, 8)	21 ± 2.4 (19–25, 7)	13.6 ± 0.28 (13.4–13.8, 2)
<i>C. m. shanensis</i>	9.0 ± 0.51 (8.4–10.0, 9)	17.0 ± 1.44 (15.5–19.4, 7)	2.6 ± 0.18 (2.4–2.9, 8)	2.5 ± 0.07 (2.4–2.6, 9)	67.1 ± 1.12 (66.0–68.5, 8)	11 ± 0.5 (11–12, 7)	72 ± 2.9 (68–74, 4)	25 ± 2.1 (22–27, 4)	14.0 (1)
<i>C. m. meridionalis</i>	8.6 ± 0.19 (8.3–8.7, 4)	18.5 ± 1.03 (17.3–19.8, 4)	2.8 ± 0.21 (2.6–3.0, 3)	2.6 ± 0.13 (2.4–2.7, 4)	70.1 ± 1.89 (68.5–72.0, 4)	13 ± 1.0 (12–14, 4)	74 ± 1.5 (73–76, 3)	25 ± 2.6 (22–27, 3)	14.8 (1)
<b><i>C. manipurensis</i></b>	<b>8.8 ± 0.46 (8.1–10.0, 21)</b>	<b>17.8 ± 1.35 (15.5–20.0, 19)</b>	<b>2.7 ± 0.20 (2.4–3.1, 17)</b>	<b>2.5 ± 0.17 (2.2–3.0, 20)</b>	<b>67.5 ± 1.75 (66.0–72.0, 20)</b>	<b>12 ± 0.8 (11–14, 17)</b>	<b>71 ± 3.4 (63–76, 15)</b>	<b>23 ± 2.8 (19–27, 14)</b>	<b>14.0 ± 0.59 (13.4–14.8, 4)</b>

## 5.3 Results

Mean values for each treated taxon are presented together with standard deviations, spans and sample sizes in Tables 5.2 (males) and 5.3 (females). Index values are given in the same fashion in Tables 5.4 (males) and 5.5 (females). In the following sections, at first, differences and trends, respectively, in the single parameters are summarised parameter by parameter, and then the results of further analyses are given if any were performed.

**Table 5.4:** Indices of measurements taken from male specimens summarised by taxon: mean  $\pm$  s.d. (minimum – maximum, sample size).

Taxon	Wing-tip index [%]	Tail-wing index [%]	Bill-wing index [%]	Claw-wing index [%]	Claw-bill index [%]	Tail-tip index [%]
<i>C. f. britannica</i>	18 $\pm$ 1.3 (16–21, 65)	93 $\pm$ 4.4 (82–100, 60)	27 $\pm$ 1.6 (23–30, 67)	14 $\pm$ 0.8 (12–16, 68)	53 $\pm$ 4.3 (46–66, 70)	24 $\pm$ 4.1 (11–38, 56)
<i>C. f. macrodactyla</i>	18 $\pm$ 1.0 (15–21, 74)	95 $\pm$ 4.4 (82–102, 61)	27 $\pm$ 1.7 (23–31, 70)	14 $\pm$ 0.9 (12–17, 73)	54 $\pm$ 4.6 (41–63, 64)	23 $\pm$ 2.5 (16–28, 57)
<i>C. f. corsa</i>	19 $\pm$ 1.1 (17–21, 11)	98 $\pm$ 2.1 (94–101, 11)	30 $\pm$ 1.3 (27–32, 12)	14 $\pm$ 0.4 (13–14, 14)	45 $\pm$ 2.1 (42–49, 12)	24 $\pm$ 3.5 (18–31, 10)
<i>C. f. familiaris</i>	18 $\pm$ 1.3 (15–22, 96)	97 $\pm$ 3.9 (86–104, 77)	26 $\pm$ 1.4 (21–32, 102)	14 $\pm$ 0.9 (12–18, 104)	54 $\pm$ 3.8 (45–70, 101)	24 $\pm$ 2.7 (18–32, 67)
<i>C. f. caucasica</i>	18 $\pm$ 1.7 (15–22, 14)	100 $\pm$ 2.8 (94–105, 14)	26 $\pm$ 1.3 (25–29, 15)	14 $\pm$ 0.8 (13–15, 16)	54 $\pm$ 4.0 (47–61, 15)	25 $\pm$ 2.6 (21–30, 14)
<i>C. f. persica</i>	19 $\pm$ 0.8 (18–20, 3)	96 $\pm$ 1.3 (94–97, 3)	30 $\pm$ 1.4 (29–32, 4)	16 $\pm$ 0.6 (15–17, 4)	53 $\pm$ 3.1 (49–56, 4)	23 (1)
<i>C. f. daurica</i>	19 $\pm$ 1.1 (17–21, 17)	95 $\pm$ 5.0 (81–103, 16)	26 $\pm$ 2.2 (23–31, 19)	14 $\pm$ 0.8 (12–16, 19)	54 $\pm$ 5.7 (42–63, 19)	22 $\pm$ 3.8 (16–31, 15)
<i>C. f. tianschanica</i>	18 $\pm$ 1.6 (15–21, 17)	100 $\pm$ 4.5 (90–106, 16)	28 $\pm$ 2.1 (24–33, 18)	14 $\pm$ 0.8 (13–16, 19)	51 $\pm$ 5.1 (41–64, 18)	21 $\pm$ 1.5 (19–24, 13)
<i>C. f. japonica</i>	19 $\pm$ 1.2 (18–21, 5)	92 $\pm$ 6.6 (81–97, 5)	25 $\pm$ 1.0 (24–27, 5)	15 $\pm$ 0.5 (14–15, 5)	59 $\pm$ 1.5 (57–61, 5)	22 $\pm$ 3.1 (16–24, 5)
<i>C. f. bianchii</i>	18 $\pm$ 1.5 (16–21, 17)	95 $\pm$ 4.7 (89–104, 16)	28 $\pm$ 1.4 (26–33, 17)	15 $\pm$ 1.0 (13–17, 17)	53 $\pm$ 3.2 (47–59, 17)	24 $\pm$ 4.7 (10–30, 15)
<b><i>C. familiaris</i></b>	<b>18 <math>\pm</math> 1.3 (15–22, 319)</b>	<b>96 <math>\pm</math> 4.6 (81–106, 279)</b>	<b>27 <math>\pm</math> 1.8 (21–33, 329)</b>	<b>14 <math>\pm</math> 0.9 (12–18, 339)</b>	<b>53 <math>\pm</math> 4.5 (41–70, 325)</b>	<b>23 <math>\pm</math> 3.3 (10–38, 253)</b>
<i>C. ho. "waschanensis"</i>	17 $\pm$ 0.8 (17–18, 3)	88 (2)	26 $\pm$ 0.6 (25–27, 3)	14 $\pm$ 0.5 (14–15, 3)	54 $\pm$ 1.3 (53–55, 3)	20 $\pm$ 1.2 (19–21, 2)
<i>C. ho. "kwanhsienensis"</i>	17 (1)	98 (1)	24 (1)	14 (1)	59 (1)	19 (1)
<i>C. ho. khamensis</i>	17 $\pm$ 1.3 (16–21, 21)	94 $\pm$ 5.7 (75–102, 22)	26 $\pm$ 1.5 (23–29, 23)	14 $\pm$ 0.8 (12–15, 28)	52 $\pm$ 3.1 (48–58, 23)	27 $\pm$ 3.1 (21–31, 17)
<i>C. ho. mandellii</i>	18 $\pm$ 1.2 (16–20, 24)	96 $\pm$ 4.0 (89–101, 13)	24 $\pm$ 1.3 (22–27, 25)	14 $\pm$ 0.9 (13–16, 23)	58 $\pm$ 3.8 (53–64, 22)	30 $\pm$ 2.4 (27–34, 12)
<i>C. ho. hodgsoni</i>	17 $\pm$ 1.3 (15–20, 12)	92 $\pm$ 4.3 (89–97, 5)	30 $\pm$ 2.1 (25–33, 15)	13 $\pm$ 0.8 (12–15, 15)	45 $\pm$ 4.7 (41–61, 15)	22 $\pm$ 2.6 (19–25, 5)
<b><i>C. hodgsoni</i></b>	<b>18 <math>\pm</math> 1.2 (15–21, 61)</b>	<b>94 <math>\pm</math> 5.1 (75–102, 43)</b>	<b>26 <math>\pm</math> 2.6 (22–33, 67)</b>	<b>14 <math>\pm</math> 0.9 (12–16, 70)</b>	<b>53 <math>\pm</math> 6.2 (41–64, 64)</b>	<b>27 <math>\pm</math> 4.1 (19–34, 37)</b>
<i>C. a. montana</i>	20 $\pm$ 1.3 (18–21, 10)	86 $\pm$ 4.3 (79–93, 8)	28 $\pm$ 1.3 (27–31, 11)	12 $\pm$ 0.8 (11–14, 11)	44 $\pm$ 3.0 (38–47, 11)	24 $\pm$ 3.6 (20–29, 8)
<i>C. a. occidentalis</i>	18 (1)	82 (1)	26 (1)	13 (1)	49 (1)	22 (1)
<i>C. a. alascensis</i>	20 $\pm$ 0.8 (19–21, 5)	86 (1)	26 $\pm$ 1.5 (24–28, 6)	13 $\pm$ 0.5 (13–14, 6)	50 $\pm$ 2.1 (47–54, 6)	22 (1)
<i>C. a. stewarti</i>	–	–	–	–	–	–
<i>C. a. zelotes</i>	19 $\pm$ 1.4 (17–21, 9)	90 $\pm$ 4.7 (81–95, 7)	28 $\pm$ 1.9 (25–30, 10)	12 $\pm$ 0.6 (11–13, 11)	43 $\pm$ 4.7 (39–52, 10)	21 $\pm$ 4.3 (12–25, 7)
<i>C. a. phillipsi</i>	19 $\pm$ 0.6 (18–20, 4)	92 $\pm$ 8.2 (84–101, 3)	29 $\pm$ 3.0 (26–32, 5)	12 $\pm$ 0.4 (12–13, 6)	42 $\pm$ 4.1 (39–47, 5)	26 $\pm$ 5.2 (20–30, 3)
<i>C. a. leucosticta</i>	18 $\pm$ 1.3 (16–20, 7)	88 $\pm$ 1.5 (87–90, 3)	28 $\pm$ 2.2 (24–31, 9)	12 $\pm$ 0.4 (11–12, 9)	42 $\pm$ 3.0 (38–48, 9)	22 $\pm$ 8.4 (16–28, 2)
<i>C. a. albescens</i>	17 $\pm$ 1.7 (14–19, 7)	95 $\pm$ 5.1 (89–101, 6)	26 $\pm$ 1.1 (25–28, 10)	12 $\pm$ 0.6 (11–13, 9)	46 $\pm$ 2.5 (43–51, 9)	24 $\pm$ 2.6 (21–27, 6)
<i>C. a. jalascensis</i>	18 $\pm$ 0.6 (17–19, 3)	95 $\pm$ 5.9 (86–99, 4)	26 $\pm$ 1.9 (24–29, 4)	13 $\pm$ 0.6 (12–13, 4)	49 $\pm$ 3.8 (46–54, 4)	25 $\pm$ 3.3 (21–29, 4)
<i>C. a. guerrerensis</i>	15 $\pm$ 0.3 (15–15, 2)	98 $\pm$ 2.6 (96–101, 3)	26 $\pm$ 2.6 (24–29, 3)	13 $\pm$ 0.6 (12–13, 3)	48 $\pm$ 4.9 (43–51, 3)	22 $\pm$ 3.7 (19–24, 2)
<i>C. a. alticola</i>	16 $\pm$ 1.6 (14–20, 13)	95 $\pm$ 5.4 (83–100, 7)	26 $\pm$ 1.3 (24–28, 14)	13 $\pm$ 0.6 (12–14, 14)	51 $\pm$ 2.9 (46–56, 17)	23 $\pm$ 3.8 (17–30, 10)
<i>C. a. pernigra</i>	17 $\pm$ 1.1 (16–19, 6)	92 $\pm$ 3.4 (88–95, 3)	25 $\pm$ 1.2 (23–27, 6)	13 $\pm$ 0.5 (12–13, 7)	50 $\pm$ 2.3 (48–54, 6)	23 $\pm$ 3.8 (20–25, 2)
<i>C. a. extima</i>	19 $\pm$ 1.6 (16–23, 20)	93 $\pm$ 3.1 (87–97, 18)	30 $\pm$ 1.5 (28–33, 20)	13 $\pm$ 0.7 (11–14, 20)	42 $\pm$ 3.1 (35–47, 19)	27 $\pm$ 2.9 (22–33, 16)
<i>C. a. americana/nigrescens</i>	21 $\pm$ 1.6 (16–24, 75)	93 $\pm$ 5.3 (80–102, 67)	25 $\pm$ 1.5 (22–30, 76)	12 $\pm$ 0.6 (11–14, 74)	48 $\pm$ 2.9 (40–55, 72)	25 $\pm$ 3.8 (11–34, 67)
<b><i>C. americana</i></b>	<b>19 <math>\pm</math> 2.1 (14–25, 216)</b>	<b>93 <math>\pm</math> 5.2 (79–102, 178)</b>	<b>27 <math>\pm</math> 2.2 (22–33, 224)</b>	<b>12 <math>\pm</math> 0.7 (11–15, 228)</b>	<b>46 <math>\pm</math> 4.0 (35–56, 217)</b>	<b>24 <math>\pm</math> 4.1 (10–38, 175)</b>
<i>C. b. mauritanica</i>	17 $\pm$ 1.3 (14–20, 27)	90 $\pm$ 3.7 (84–96, 15)	29 $\pm$ 1.7 (26–32, 25)	12 $\pm$ 0.7 (10–13, 27)	41 $\pm$ 2.6 (35–47, 25)	23 $\pm$ 3.7 (15–27, 15)
<i>C. b. megarhynchos</i>	18 $\pm$ 1.5 (14–22, 48)	94 $\pm$ 4.0 (83–101, 41)	30 $\pm$ 1.9 (23–33, 48)	12 $\pm$ 0.6 (11–14, 49)	42 $\pm$ 2.9 (36–49, 48)	24 $\pm$ 3.5 (16–30, 39)
<i>C. b. brachydactyla</i>	18 $\pm$ 1.5 (11–22, 106)	93 $\pm$ 4.4 (83–108, 80)	31 $\pm$ 1.9 (26–39, 110)	12 $\pm$ 0.7 (10–15, 110)	40 $\pm$ 2.8 (34–53, 104)	25 $\pm$ 4.0 (11–34, 68)
<i>C. b. stresemanni</i>	17 $\pm$ 0.7 (17–18, 4)	96 $\pm$ 0.8 (95–97, 3)	29 $\pm$ 1.3 (27–31, 5)	13 $\pm$ 0.9 (11–13, 6)	44 $\pm$ 2.6 (42–48, 5)	26 $\pm$ 2.1 (25–28, 2)
<i>C. b. dorothaeae</i>	17 $\pm$ 1.6 (15–20, 9)	95 $\pm$ 2.6 (89–99, 14)	30 $\pm$ 1.7 (28–33, 14)	12 $\pm$ 0.8 (10–13, 14)	40 $\pm$ 3.6 (33–47, 14)	26 $\pm$ 4.6 (14–32, 14)
<b><i>C. brachydactyla</i></b>	<b>18 <math>\pm</math> 1.5 (11–22, 196)</b>	<b>93 <math>\pm</math> 4.2 (83–108, 155)</b>	<b>30 <math>\pm</math> 1.9 (23–39, 204)</b>	<b>12 <math>\pm</math> 0.7 (10–15, 208)</b>	<b>41 <math>\pm</math> 3.0 (33–53, 198)</b>	<b>25 <math>\pm</math> 3.9 (11–34, 140)</b>
<i>C. hi. taeniura</i>	20 $\pm$ 1.0 (18–22, 12)	94 $\pm$ 2.6 (87–96, 11)	34 $\pm$ 2.5 (28–37, 12)	13 $\pm$ 0.9 (12–14, 11)	39 $\pm$ 4.0 (31–45, 11)	19 $\pm$ 2.4 (16–24, 10)
<i>C. hi. himalayana</i>	20 $\pm$ 1.6 (16–23, 25)	91 $\pm$ 5.2 (78–98, 30)	30 $\pm$ 1.6 (27–34, 27)	13 $\pm$ 0.7 (12–14, 32)	44 $\pm$ 3.0 (38–51, 26)	21 $\pm$ 4.4 (12–32, 29)
<i>C. hi. yunnanensis</i>	20 $\pm$ 1.4 (19–23, 9)	89 $\pm$ 3.4 (82–93, 7)	29 $\pm$ 2.8 (25–33, 9)	13 $\pm$ 0.9 (11–14, 9)	43 $\pm$ 3.1 (39–47, 9)	19 $\pm$ 2.5 (17–24, 7)
<i>C. hi. ripponi</i>	18 $\pm$ 0.4 (17–18, 3)	–	33 $\pm$ 0.6 (32–34, 5)	14 $\pm$ 1.0 (12–15, 5)	41 $\pm$ 2.6 (38–45, 5)	–
<b><i>C. himalayana</i></b>	<b>20 <math>\pm</math> 1.5 (16–23, 49)</b>	<b>91 <math>\pm</math> 4.6 (78–98, 48)</b>	<b>31 <math>\pm</math> 2.6 (25–37, 53)</b>	<b>13 <math>\pm</math> 0.8 (11–15, 57)</b>	<b>42 <math>\pm</math> 3.8 (31–51, 51)</b>	<b>20 <math>\pm</math> 3.8 (12–32, 46)</b>
<b><i>C. tianquanensis</i></b>	<b>19 <math>\pm</math> 0.7 (18–20, 8)</b>	<b>100 <math>\pm</math> 7.2 (91–111, 6)</b>	<b>21 <math>\pm</math> 1.2 (20–23, 8)</b>	<b>14 <math>\pm</math> 0.7 (13–15, 8)</b>	<b>66 <math>\pm</math> 3.0 (63–70, 8)</b>	<b>40 <math>\pm</math> 3.3 (34–43, 5)</b>
<b><i>C. nipalensis</i></b>	<b>18 <math>\pm</math> 1.5 (16–22, 24)</b>	<b>105 <math>\pm</math> 7.4 (85–114, 24)</b>	<b>22 <math>\pm</math> 0.9 (20–24, 24)</b>	<b>14 <math>\pm</math> 0.7 (13–16, 25)</b>	<b>63 <math>\pm</math> 3.0 (57–68, 24)</b>	<b>45 <math>\pm</math> 4.9 (34–51, 24)</b>
<b><i>C. discolor</i></b>	<b>17 <math>\pm</math> 1.1 (15–19, 13)</b>	<b>108 <math>\pm</math> 4.9 (99–113, 13)</b>	<b>26 <math>\pm</math> 1.0 (24–27, 13)</b>	<b>13 <math>\pm</math> 0.5 (12–14, 13)</b>	<b>53 <math>\pm</math> 2.6 (48–57, 13)</b>	<b>35 <math>\pm</math> 4.3 (26–41, 13)</b>
<i>C. m. manipurensis</i>	17 $\pm$ 0.8 (16–19, 6)	109 $\pm$ 4.4 (101–114, 6)	28 $\pm$ 2.0 (25–31, 7)	13 $\pm$ 0.7 (12–14, 7)	47 $\pm$ 3.5 (42–52, 7)	33 $\pm$ 2.3 (30–37, 6)
<i>C. m. shanensis</i>	18 $\pm$ 1.7 (14–20, 8)	106 $\pm$ 5.4 (98–112, 8)	27 $\pm$ 2.7 (22–30, 8)	14 $\pm$ 0.3 (13–14, 8)	50 $\pm$ 4.1 (46–58, 7)	34 $\pm$ 2.4 (32–38, 7)
<i>C. m. meridionalis</i>	18 $\pm$ 2.3 (14–20, 6)	110 $\pm$ 2.9 (107–114, 5)	28 $\pm$ 1.2 (27–30, 6)	13 $\pm$ 0.2 (12–13, 6)	45 $\pm$ 1.6 (42–46, 6)	34 $\pm$ 2.1 (32–37, 5)
<b><i>C. manipurensis</i></b>	<b>18 <math>\pm</math> 1.6 (14–20, 20)</b>	<b>108 <math>\pm</math> 4.7 (98–114, 19)</b>	<b>27 <math>\pm</math> 2.1 (22–31, 21)</b>	<b>13 <math>\pm</math> 0.6 (12–14, 21)</b>	<b>48 <math>\pm</math> 3.8 (42–58, 20)</b>	<b>34 <math>\pm</math> 2.2 (30–38, 18)</b>

**Table 5.5:** Indices of measurements taken from female specimens summarised by taxon: mean  $\pm$  s.d. (minimum – maximum, sample size).

Taxon	Wing-tip index [%]	Tail-wing index [%]	Bill-wing index [%]	Claw-wing index [%]	Claw-bill index [%]	Tail-tip index [%]
<i>C. f. britannica</i>	18 $\pm$ 1.4 (15–21, 48)	94 $\pm$ 3.8 (85–102, 38)	26 $\pm$ 1.6 (22–29, 48)	14 $\pm$ 0.8 (12–16, 48)	56 $\pm$ 3.9 (45–66, 47)	24 $\pm$ 3.9 (16–34, 36)
<i>C. f. macrodactyla</i>	18 $\pm$ 1.1 (16–21, 42)	95 $\pm$ 4.1 (88–102, 37)	25 $\pm$ 1.2 (23–28, 41)	14 $\pm$ 0.7 (12–16, 43)	56 $\pm$ 4.2 (48–68, 39)	23 $\pm$ 2.9 (17–30, 36)
<i>C. f. corsa</i>	19 $\pm$ 1.5 (17–21, 13)	97 $\pm$ 2.9 (90–102, 14)	28 $\pm$ 1.2 (26–31, 14)	14 $\pm$ 0.7 (13–15, 14)	51 $\pm$ 3.5 (42–56, 14)	22 $\pm$ 2.1 (17–25, 13)
<i>C. f. familiaris</i>	18 $\pm$ 1.1 (16–21, 52)	98 $\pm$ 4.0 (86–108, 40)	25 $\pm$ 1.6 (22–29, 49)	14 $\pm$ 0.9 (12–16, 54)	58 $\pm$ 4.5 (42–68, 48)	23 $\pm$ 3.2 (14–31, 34)
<i>C. f. caucasica</i>	19 $\pm$ 1.1 (18–21, 6)	97 $\pm$ 4.9 (90–103, 6)	25 $\pm$ 1.8 (22–27, 6)	14 $\pm$ 0.8 (13–15, 6)	56 $\pm$ 2.1 (53–59, 6)	26 $\pm$ 3.5 (20–29, 6)
<i>C. f. persica</i>	18 (1)	93 (1)	28 (1)	15 (1)	55 (1)	21 (1)
<i>C. f. daurica</i>	20 $\pm$ 1.7 (18–23, 5)	97 $\pm$ 3.1 (92–100, 6)	25 $\pm$ 1.2 (24–27, 8)	14 $\pm$ 1.1 (13–16, 7)	56 $\pm$ 5.0 (49–63, 7)	23 $\pm$ 3.2 (19–27, 4)
<i>C. f. tianschanica</i>	18 $\pm$ 1.4 (17–20, 7)	98 $\pm$ 4.0 (91–104, 7)	27 $\pm$ 1.8 (25–30, 7)	15 $\pm$ 1.7 (13–18, 7)	55 $\pm$ 4.2 (50–62, 7)	23 $\pm$ 2.7 (18–27, 7)
<i>C. f. japonica</i>	18 $\pm$ 1.8 (16–19, 3)	91 $\pm$ 4.2 (86–95, 4)	24 $\pm$ 1.2 (23–25, 4)	14 $\pm$ 1.0 (13–16, 4)	59 $\pm$ 3.2 (55–61, 4)	24 $\pm$ 1.6 (22–25, 4)
<i>C. f. bianchii</i>	18 $\pm$ 1.9 (16–20, 4)	92 $\pm$ 6.9 (87–100, 3)	26 $\pm$ 2.2 (24–29, 4)	15 $\pm$ 0.7 (14–16, 4)	58 $\pm$ 3.2 (55–63, 4)	25 $\pm$ 4.7 (20–30, 3)
<i>C. familiaris</i>	<b>18 <math>\pm</math> 1.3 (15–23, 181)</b>	<b>96 <math>\pm</math> 4.3 (85–108, 156)</b>	<b>26 <math>\pm</math> 1.7 (22–31, 182)</b>	<b>14 <math>\pm</math> 0.9 (12–18, 188)</b>	<b>56 <math>\pm</math> 4.4 (42–68, 177)</b>	<b>23 <math>\pm</math> 3.2 (14–34, 144)</b>
<i>C. ho. "waschanensis"</i>	17 $\pm$ 1.2 (16–18, 2)	92 $\pm$ 3.9 (89–94, 2)	25 $\pm$ 0.1 (25–26, 2)	14 $\pm$ 0.3 (14–14, 2)	56 $\pm$ 1.3 (55–57, 2)	30 $\pm$ 1.1 (29–30, 2)
<i>C. ho. "kwanhsienensis"</i>	17 (1)	94 (1)	23 (1)	16 (1)	67 (1)	23 (1)
<i>C. ho. khamensis</i>	18 $\pm$ 0.4 (17–18, 6)	92 $\pm$ 1.7 (91–94, 3)	26 $\pm$ 0.6 (25–27, 7)	14 $\pm$ 0.7 (13–15, 7)	55 $\pm$ 3.3 (49–58, 7)	23 $\pm$ 2.1 (21–24, 2)
<i>C. ho. mandellii</i>	18 $\pm$ 0.7 (17–19, 9)	94 $\pm$ 2.6 (91–98, 6)	22 $\pm$ 0.7 (21–23, 10)	14 $\pm$ 0.6 (13–14, 12)	61 $\pm$ 3.5 (56–66, 11)	30 $\pm$ 2.0 (28–33, 6)
<i>C. ho. hodgsoni</i>	18 $\pm$ 1.3 (16–20, 7)	89 $\pm$ 1.3 (88–91, 3)	27 $\pm$ 1.0 (26–29, 8)	14 $\pm$ 0.4 (13–14, 8)	51 $\pm$ 2.6 (46–55, 8)	23 $\pm$ 3.6 (21–27, 3)
<i>C. hodgsoni</i>	<b>18 <math>\pm</math> 0.9 (16–20, 25)</b>	<b>92 <math>\pm</math> 2.8 (88–98, 15)</b>	<b>25 <math>\pm</math> 2.2 (21–29, 28)</b>	<b>14 <math>\pm</math> 0.7 (13–16, 30)</b>	<b>57 <math>\pm</math> 5.5 (46–67, 29)</b>	<b>27 <math>\pm</math> 3.9 (21–33, 14)</b>
<i>C. a. montana</i>	19 $\pm$ 1.5 (17–22, 7)	88 $\pm$ 5.3 (80–96, 7)	27 $\pm$ 1.1 (25–29, 9)	13 $\pm$ 0.8 (11–13, 9)	47 $\pm$ 2.5 (44–51, 9)	25 $\pm$ 5.0 (17–32, 6)
<i>C. a. occidentalis</i>	19 (1)	82 (1)	25 (1)	15 (1)	57 (1)	21 (1)
<i>C. a. alascensis</i>	21 (1)	100 (1)	25 (1)	13 (1)	53 (1)	22 (1)
<i>C. a. stewarti</i>	–	92 $\pm$ 1.7 (91–93, 2)	26 $\pm$ 1.1 (25–27, 2)	14 $\pm$ 0.8 (13–15, 2)	54 $\pm$ 0.8 (54–55, 2)	27 $\pm$ 2.2 (25–29, 2)
<i>C. a. zelotes</i>	19 $\pm$ 1.5 (17–21, 5)	95 $\pm$ 11.6 (87–103, 2)	27 $\pm$ 2.5 (24–31, 6)	12 $\pm$ 0.6 (12–13, 6)	46 $\pm$ 5.3 (40–56, 6)	21 $\pm$ 0.2 (21–21, 2)
<i>C. a. phillipsi</i>	19 (1)	81 (1)	31 (1)	13 (1)	43 (1)	19 (1)
<i>C. a. leucosticta</i>	18 (1)	–	25 (1)	12 (1)	47 (1)	–
<i>C. a. albescens</i>	19 $\pm$ 1.0 (18–20, 3)	97 $\pm$ 0.7 (97–98, 2)	26 $\pm$ 1.2 (25–27, 4)	13 $\pm$ 0.9 (12–14, 3)	49 $\pm$ 5.3 (45–55, 3)	20 $\pm$ 4.9 (17–24, 2)
<i>C. a. jaliscensis</i>	17 $\pm$ 1.8 (16–18, 2)	97 $\pm$ 0.8 (96–98, 3)	27 $\pm$ 1.7 (25–28, 3)	13 $\pm$ 0.2 (13–14, 3)	49 $\pm$ 2.3 (47–51, 3)	24 $\pm$ 3.1 (22–27, 3)
<i>C. a. guerrerensis</i>	18 $\pm$ 2.3 (16–22, 4)	95 $\pm$ 2.4 (92–98, 4)	26 $\pm$ 0.5 (25–26, 6)	13 $\pm$ 0.6 (12–14, 5)	50 $\pm$ 3.1 (47–55, 5)	25 $\pm$ 3.0 (23–29, 4)
<i>C. a. alticola</i>	17 $\pm$ 1.0 (15–18, 7)	97 $\pm$ 2.3 (94–99, 6)	25 $\pm$ 1.1 (24–27, 9)	13 $\pm$ 0.9 (12–15, 9)	53 $\pm$ 3.8 (48–60, 9)	23 $\pm$ 5.8 (17–32, 5)
<i>C. a. pernigra</i>	17 $\pm$ 2.0 (16–19, 4)	94 $\pm$ 3.5 (88–98, 4)	25 $\pm$ 0.4 (23–25, 4)	13 $\pm$ 0.4 (12–13, 4)	51 $\pm$ 2.4 (48–54, 4)	24 $\pm$ 2.8 (20–27, 4)
<i>C. a. extima</i>	18 $\pm$ 0.9 (16–19, 4)	95 $\pm$ 3.8 (87–100, 4)	28 $\pm$ 1.7 (28–29, 4)	12 $\pm$ 0.5 (11–13, 4)	45 $\pm$ 1.7 (35–47, 4)	26 $\pm$ 2.9 (22–30, 4)
<i>C. a. americana/nigrescens</i>	21 $\pm$ 1.2 (18–23, 39)	91 $\pm$ 5.8 (78–100, 31)	24 $\pm$ 1.3 (22–27, 38)	12 $\pm$ 0.7 (11–14, 38)	50 $\pm$ 3.3 (43–56, 36)	24 $\pm$ 4.1 (14–30, 31)
<i>C. americana</i>	<b>19 <math>\pm</math> 1.8 (14–23, 117)</b>	<b>92 <math>\pm</math> 5.8 (78–104, 97)</b>	<b>25 <math>\pm</math> 1.9 (22–31, 126)</b>	<b>13 <math>\pm</math> 0.8 (10–15, 122)</b>	<b>49 <math>\pm</math> 3.9 (40–60, 119)</b>	<b>24 <math>\pm</math> 4.2 (14–39, 94)</b>
<i>C. b. mauritanica</i>	16 $\pm$ 1.1 (14–18, 12)	90 $\pm$ 3.1 (85–94, 10)	28 $\pm$ 1.0 (26–30, 12)	12 $\pm$ 0.8 (11–13, 13)	42 $\pm$ 2.7 (37–45, 13)	25 $\pm$ 4.2 (20–34, 11)
<i>C. b. megarhynchus</i>	18 $\pm$ 1.3 (15–21, 30)	93 $\pm$ 4.5 (82–99, 28)	29 $\pm$ 1.5 (26–32, 32)	12 $\pm$ 0.5 (11–13, 33)	43 $\pm$ 2.6 (36–47, 32)	25 $\pm$ 3.0 (20–31, 24)
<i>C. b. brachydactyla</i>	17 $\pm$ 1.3 (15–21, 83)	93 $\pm$ 3.9 (86–102, 60)	29 $\pm$ 1.7 (25–34, 81)	12 $\pm$ 0.7 (10–14, 80)	43 $\pm$ 2.9 (35–53, 75)	26 $\pm$ 3.7 (18–32, 55)
<i>C. b. stresmanni</i>	16 $\pm$ 0.4 (16–17, 2)	94 $\pm$ 2.8 (91–97, 3)	29 $\pm$ 1.2 (27–30, 3)	13 $\pm$ 0.7 (12–13, 3)	44 $\pm$ 0.9 (43–45, 3)	26 $\pm$ 3.1 (22–29, 3)
<i>C. b. dorotheae</i>	18 $\pm$ 0.5 (17–19, 7)	94 $\pm$ 5.0 (85–98, 5)	29 $\pm$ 0.7 (29–31, 7)	12 $\pm$ 0.4 (12–13, 7)	42 $\pm$ 1.9 (38–44, 7)	27 $\pm$ 1.6 (25–29, 4)
<i>C. brachydactyla</i>	<b>17 <math>\pm</math> 1.3 (14–21, 137)</b>	<b>93 <math>\pm</math> 4.1 (82–102, 109)</b>	<b>29 <math>\pm</math> 1.6 (25–34, 137)</b>	<b>12 <math>\pm</math> 0.7 (10–14, 138)</b>	<b>43 <math>\pm</math> 2.8 (35–53, 131)</b>	<b>26 <math>\pm</math> 3.5 (17–34, 100)</b>
<i>C. hi. taeniura</i>	19 $\pm$ 1.5 (17–21, 8)	88 $\pm$ 4.4 (83–93, 4)	30 $\pm$ 2.0 (29–35, 9)	13 $\pm$ 0.4 (13–14, 8)	44 $\pm$ 2.5 (39–47, 8)	19 $\pm$ 2.0 (16–21, 4)
<i>C. hi. himalayana</i>	19 $\pm$ 1.9 (13–24, 26)	91 $\pm$ 5.3 (78–99, 24)	28 $\pm$ 1.9 (26–36, 30)	13 $\pm$ 0.7 (12–15, 30)	47 $\pm$ 3.3 (39–57, 30)	20 $\pm$ 2.7 (15–27, 22)
<i>C. hi. yunnanensis</i>	20 $\pm$ 0.8 (19–20, 3)	84 $\pm$ 12.4 (75–93, 2)	27 $\pm$ 1.1 (26–28, 3)	12 $\pm$ 0.7 (12–13, 3)	46 $\pm$ 3.4 (42–49, 3)	21 $\pm$ 0.8 (20–22, 2)
<i>C. hi. ripponi</i>	18 (1)	92 (1)	29 (1)	14 (1)	47 (1)	28 (1)
<i>C. himalayana</i>	<b>19 <math>\pm</math> 1.8 (13–24, 39)</b>	<b>90 <math>\pm</math> 5.5 (75–99, 32)</b>	<b>29 <math>\pm</math> 2.0 (26–36, 43)</b>	<b>13 <math>\pm</math> 0.7 (12–15, 43)</b>	<b>46 <math>\pm</math> 3.3 (39–57, 42)</b>	<b>20 <math>\pm</math> 2.9 (15–28, 30)</b>
<i>C. tianquanensis</i>	–	–	–	–	–	–
<i>C. nipalensis</i>	<b>18 <math>\pm</math> 1.2 (16–21, 13)</b>	<b>109 <math>\pm</math> 5.7 (97–115, 12)</b>	<b>22 <math>\pm</math> 0.9 (20–23, 11)</b>	<b>14 <math>\pm</math> 0.8 (13–15, 13)</b>	<b>63 <math>\pm</math> 4.2 (58–70, 11)</b>	<b>45 <math>\pm</math> 7.2 (31–53, 12)</b>
<i>C. discolor</i>	<b>18 <math>\pm</math> 0.9 (17–20, 15)</b>	<b>110 <math>\pm</math> 4.2 (104–120, 14)</b>	<b>25 <math>\pm</math> 1.5 (22–28, 14)</b>	<b>14 <math>\pm</math> 0.5 (13–14, 15)</b>	<b>55 <math>\pm</math> 3.7 (46–61, 14)</b>	<b>37 <math>\pm</math> 2.2 (32–41, 13)</b>
<i>C. m. manipurensis</i>	18 $\pm$ 0.9 (16–19, 6)	104 $\pm$ 4.5 (94–108, 8)	27 $\pm$ 1.5 (25–30, 8)	13 $\pm$ 0.6 (12–14, 8)	48 $\pm$ 2.7 (46–54, 8)	31 $\pm$ 2.6 (29–36, 7)
<i>C. m. shanensis</i>	17 $\pm$ 0.8 (16–18, 7)	106 $\pm$ 3.7 (103–110, 4)	25 $\pm$ 2.4 (23–29, 6)	13 $\pm$ 1.0 (12–15, 8)	53 $\pm$ 4.1 (46–59, 7)	34 $\pm$ 2.1 (32–36, 4)
<i>C. m. meridionalis</i>	18 $\pm$ 1.3 (17–20, 4)	107 $\pm$ 4.5 (102–111, 3)	26 $\pm$ 1.2 (25–28, 4)	12 $\pm$ 0.3 (12–13, 4)	46 $\pm$ 2.9 (44–50, 4)	34 $\pm$ 3.7 (30–37, 3)
<i>C. manipurensis</i>	<b>18 <math>\pm</math> 1.1 (16–20, 17)</b>	<b>105 <math>\pm</math> 4.3 (94–111, 15)</b>	<b>26 <math>\pm</math> 1.9 (23–30, 18)</b>	<b>13 <math>\pm</math> 0.8 (12–15, 20)</b>	<b>50 <math>\pm</math> 4.0 (44–59, 19)</b>	<b>33 <math>\pm</math> 2.8 (29–37, 14)</b>

### 5.3.1 Morphometric delimitation of phylospecies

#### 5.3.1.1 All species

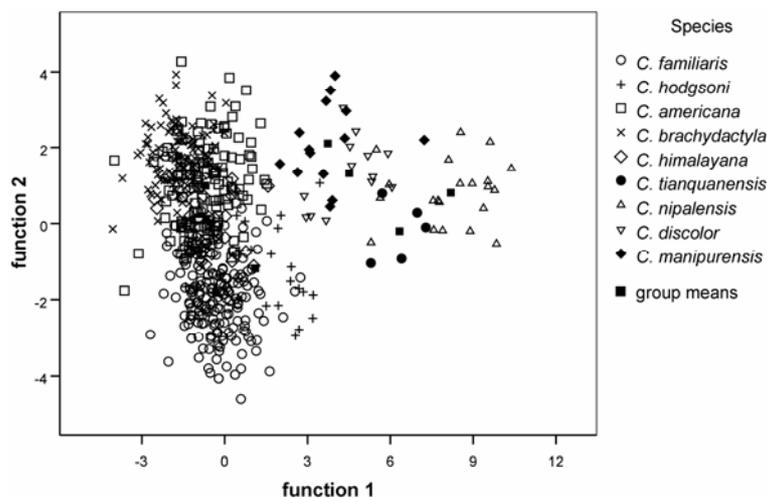
Hind claws are longer in males; species pairs of similar size are *familiaris/hodgsoni*, *americana/brachydactyla* and *tianquanensis/nipalensis*; *discolor* has longer claws than *manipurensis*. Bills are longer in males; *familiaris* and *hodgsoni* have similar size; *brachydactyla* has the longest bill of all motif-group species, *himalayana* the longest one of all species; size within trill-group species increases from *tianquanensis* via *nipalensis* and *discolor* to *manipurensis*. Bills are deeper in males; *familiaris* has smaller values than *hodgsoni*, *discolor* than *manipurensis*, *tianquanensis* than *nipalensis*. Bill width in general does not discriminate sexes; values are each slightly smaller in *familiaris* than in *hodgsoni*, in *discolor* than in *manipurensis*.

*sis*, in *tianquanensis* than in *nipalensis*, but larger in trill-group species except *himalayana* than in the more uniform motif-group species. Wings are longer in males; trill-group species have longer wings than motif-group species; *familiaris* has shorter wings than *hodgsoni*, *americana* longer wings than *brachydactyla* and *discolor* slightly longer wings than *manipurensis*. Wing tips are only slightly longer in males than in females and in trill-group than in motif-group species; values are similar in *familiaris* and *hodgsoni*, *tianquanensis* and *nipalensis*, *discolor* and *manipurensis*, but larger in *americana* than in *brachydactyla*. Tails are longer in males; motif-group species and *himalayana* have shorter tails than the other species; tails of *familiaris* and *hodgsoni* are of similar length, those in *americana* are a little longer than in *brachydactyla* and those in *discolor* a little longer than in *manipurensis*, but *tianquanensis* tails are shorter than *nipalensis* tails. Tail tips are slightly larger in males, smaller in motif-group species and *himalayana* than in the remaining species, shorter in *familiaris* than in *hodgsoni* and in *tianquanensis* than in *nipalensis*, but longer in *discolor* than in *manipurensis* and of similar size in *americana* and *brachydactyla*. Tarsi are slightly longer in males; the values of the four *nipalensis* specimens are highest; *familiaris* has shorter tarsi than *hodgsoni*, *americana* shorter than *brachydactyla*, *discolor* and *manipurensis* are of similar size (no measurements from *discolor* males, *hodgsoni* females and *tianquanensis*).

WTI is similar in both sexes; values are larger in *familiaris* than in *hodgsoni*, in *americana* than in *brachydactyla*, slightly larger in *tianquanensis* than in *nipalensis* and similar in *discolor* and *manipurensis*. TWI is slightly larger in males; values are higher in (*tianquanensis*), *nipalensis*, *discolor* and *manipurensis* than in all other species and are slightly larger in *familiaris* than in *hodgsoni*, in *discolor* than in *manipurensis*, smaller in *tianquanensis* than in *nipalensis* and similar in *americana* and *brachydactyla*. BWI is larger in males; it is about 25% in *familiaris*, *hodgsoni* and *americana* and about 30% in *brachydactyla* and *himalayana*, the remaining species vary between 20% and 27%; values are larger for *familiaris* than for *hodgsoni*, smaller for *americana* than for *brachydactyla*, smaller for *tianquanensis* than for *nipalensis* and smaller for *discolor* than for *manipurensis*. CWI is larger in males of motif-group species and *himalayana* and vice versa for the rest; *familiaris* has slightly larger values than *hodgsoni*, both are above the average; *americana* and *brachydactyla* have similar values and are below the average; CWI for *tianquanensis* and *nipalensis* is similar, for *discolor* larger than for *manipurensis*. CBI is smaller for males (exception: *nipalensis*); *familiaris* has slightly smaller values than *hodgsoni*, *americana* larger values than *brachydactyla*, *tianquanensis* than *nipalensis* and *discolor* than *manipurensis*. TTI does not differ between sexes

and is on a similarly low level in the motif-group species and *himalayana*; values are lower in *familiaris* than in *hodgsoni*, slightly lower in *americana* than in *brachydactyla*, lower in *tianquanensis* than in *nipalensis* and slightly higher in *discolor* than in *manipurensis*.

Males of the nine species could be distinguished from each other by DA 1 using all measurements except tarsus (Fig. 5.5). Eight discriminant functions were used in the analysis (Table 5.6). The highest correlations occurred between tail tip and function 1, hind claw and function 2. For all functions,  $\chi^2$  was 2293, df was 64 and Wilks' Lambda was 0.013 ( $p = 0$ ). 82.8% of all males could be correctly assigned to the appropriate species. DA 2 for females yielded similar results: seven discriminant functions were used in the analysis (Table 5.6). The highest correlations occurred between tail tip, tail length and function 1, hind claw and function 2. For all functions,  $\chi^2$  was 1359, df was 56 and Wilks' Lambda was 0.013 ( $p < 0.001$ ). 83.3% of all females could be correctly assigned to the appropriate species. In both sexes, the clusters of *familiaris*, *hodgsoni*, *americana*, *brachydactyla* and *himalayana* are close together. No better separation was obtained by another DA which only incorporated these five species.

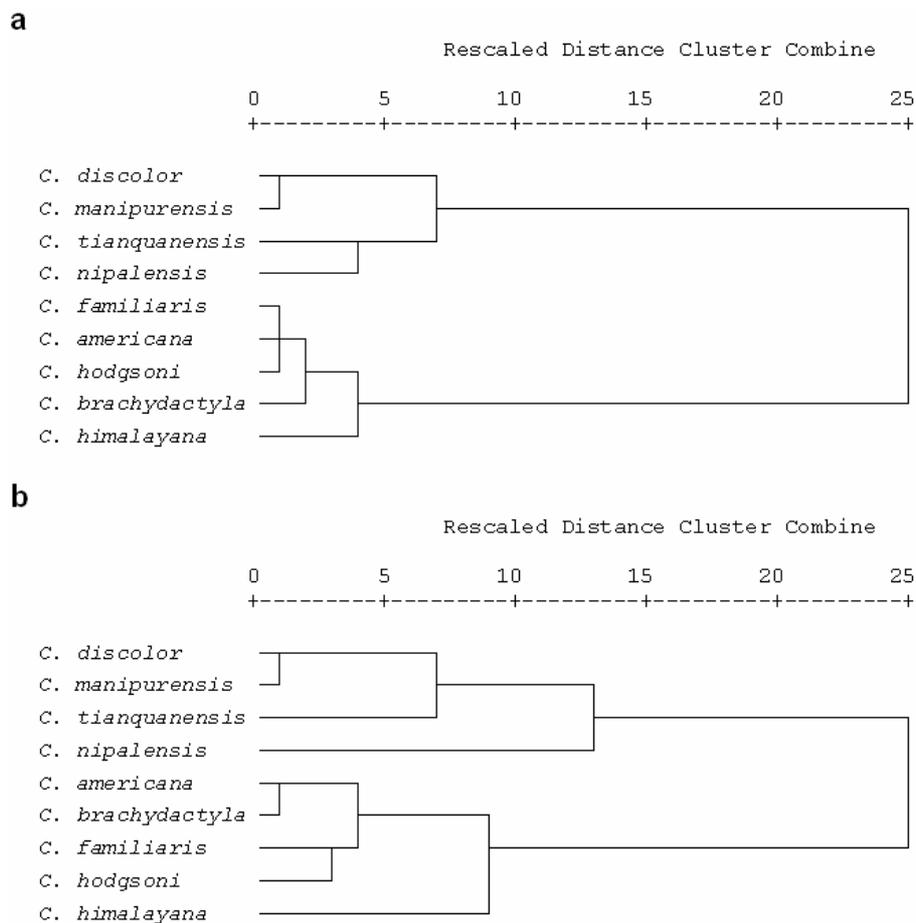


**Fig. 5.5:** Scatterplot of DA 1 separating 534 males of all nine species by claw length, bill length, bill depth, bill width, wing length, wing tip, tail length and tail tip.

Cluster analysis of all nine species and eight measurements resulted in two trees which come close to the molecular phylogeny (Fig. 5.6). In one of them, the sister relationship between *americana* and *brachydactyla* was not confirmed, in the other, the one between *tianquanensis* and *nipalensis* failed. Both show the high similarity between *himalayana* and the motif-group species.

**Table 5.6:** Percentages of explained variance and eigenvalues of the two to eight discriminant functions used in the six discriminant analyses (DA) with more than one function (for the others see text).

DA	Function	1	2	3	4	5	6	7	8
1	% of variance	53.2	26.0	9.5	7.9	2.2	1.1	0.2	0.0
	eigenvalue	4.735	2.313	0.846	0.700	0.195	0.094	0.016	0.000
2	% of variance	53.4	26.9	11.9	4.9	2.1	0.6	0.1	
	eigenvalue	4.798	2.417	1.071	0.443	0.190	0.051	0.008	
4	% of variance	82.5	17.5						
	eigenvalue	3.672	0.777						
5	% of variance	74.9	14.2	10.8					
	eigenvalue	3.644	0.693	0.527					
6	% of variance	48.2	26.0	10.4	5.7	4.5	2.7	2.0	0.5
	eigenvalue	2.165	1.167	0.469	0.258	0.202	0.120	0.088	0.022
9	% of variance	84.7	10.4	4.9					
	eigenvalue	12.202	1.498	0.711					

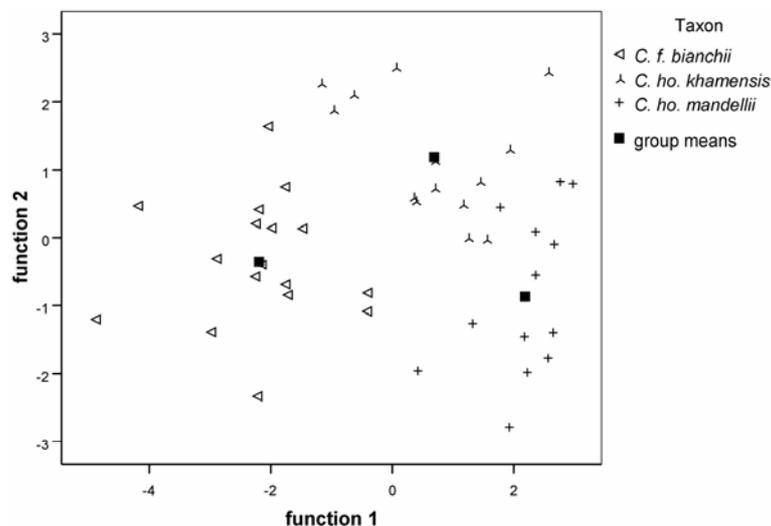


**Fig. 5.6:** Dendrograms inferred from two cluster analyses based on all eight measurements except tarsus taken from all nine *Certhia* species, matching the phylogenetic relationships best, using average linkage between groups (UPGMA): a) cosine of vectors of values, b) Chebychev distance metric.

### 5.3.1.2 *Certhia [familiaris]*

*Certhia familiaris bianchii* and *C. hodgsoni khamensis* differ significantly in bill depth and width, wing length, tail tip, BWI, CWI and TTI (males) and in claw length and bill depth (females). In DA 3, all 31 specimens from which all measurements except tarsus were available could be correctly assigned to the appropriate taxon. The highest correlations occurred between the discriminant function and bill depth, claw length and bill length. The eigenvalue was 3.337,  $\chi^2$  was 37, df was 8 and Wilks' Lambda was 0.231 ( $p < 0.001$ ).

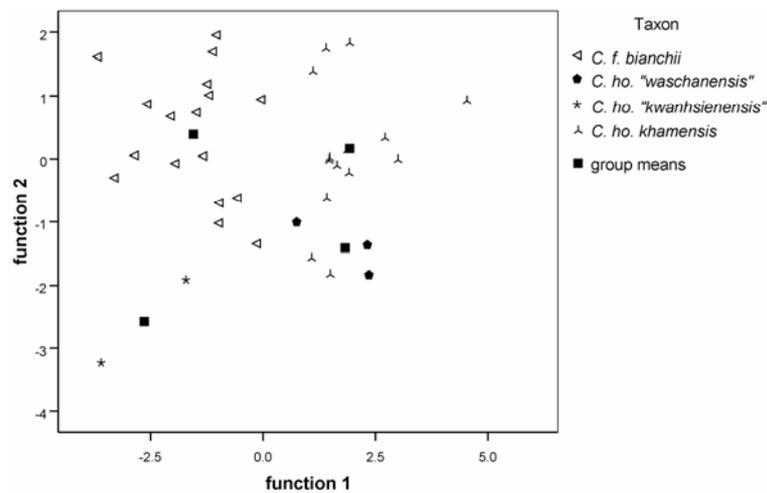
In DA 4 including *C. hodgsoni mandellii* from the Himalayas with the same parameters, 93% of 44 specimens were assigned to the correct taxon (Fig. 5.7). Two discriminant functions were used in the analysis (Table 5.6). The highest correlations occurred between bill length and function 1, bill depth and function 2. For all functions,  $\chi^2$  was 79, df was 16 and Wilks' Lambda was 0.120 ( $p < 0.001$ ). The clusters of conspecific sspp. *khamensis* and *mandellii* were less well separated from each other than either of them was from the *C. familiaris bianchii* cluster.



**Fig. 5.7:** Scatterplot of DA 4 separating 44 specimens of neighbouring taxa of superspecies *C. [familiaris]* in the Sino-Himalayas by claw length, bill length, bill depth, bill width, wing length, wing tip, tail length and tail tip.

When *C. hodgsoni* “*waschanensis*” and *C. hodgsoni* “*kwanhsienensis*” specimens were added to the two valid western Chinese subspecies, specimens of “*kwanhsienensis*” were grouped independently, while those of “*waschanensis*” fell into the *C. hodgsoni khamensis* cluster (DA 5, Fig. 5.8). Three discriminant functions were used in the analysis (Table 5.6). The highest

correlations occurred between bill depth and function 1, bill length, wing length and function 2. For all functions,  $\chi^2$  was 72, df was 24 and Wilks' Lambda was 0.083 ( $p < 0.001$ ). 91.7% of all 36 specimens could be correctly assigned to the appropriate taxon.



**Fig. 5.8:** Scatterplot of DA 5 separating 36 specimens of west Chinese *Certhia [familiaris]* populations by claw length, bill length, bill depth, bill width, wing length, wing tip, tail length and tail tip.

### 5.3.1.3 *Certhia [discolor]*

Claws are shorter in *C. manipurensis* than in *C. discolor*, but in *C. manipurensis shanensis* they reach *C. discolor* level. Bills are shorter in *C. discolor* than in *C. manipurensis*, but in the females of *C. manipurensis shanensis* they are almost as short as in *C. discolor*. Bills of *C. m. manipurensis* and *C. m. meridionalis* are slightly deeper than average. Bill width is increasing eastwards. Wing length has large sexual dimorphism, the wing being longer in males (*vice versa* in ssp. *meridionalis*). Only females of ssp. *manipurensis* have tails and tail tips shorter than average.

*Certhia discolor* females and *C. manipurensis meridionalis* males have slightly higher TWI. BWI is smaller in *C. discolor* and females of ssp. *shanensis* than in other *C. manipurensis*. CWI is slightly smaller in ssp. *meridionalis* than in the rest of the taxa. *Certhia discolor* has larger CBI and TTI than *C. manipurensis*.

Discriminant analyses were not suitable for separating the four available taxa of this super-species. Either *C. manipurensis* ssp. *manipurensis* and *meridionalis* cluster together (females) or even *C. discolor* and *C. manipurensis shanensis* do this (males).

## 5.3.2 Geographic trends in morphometric parameters

### 5.3.2.1 *Certhia [familiaris]*

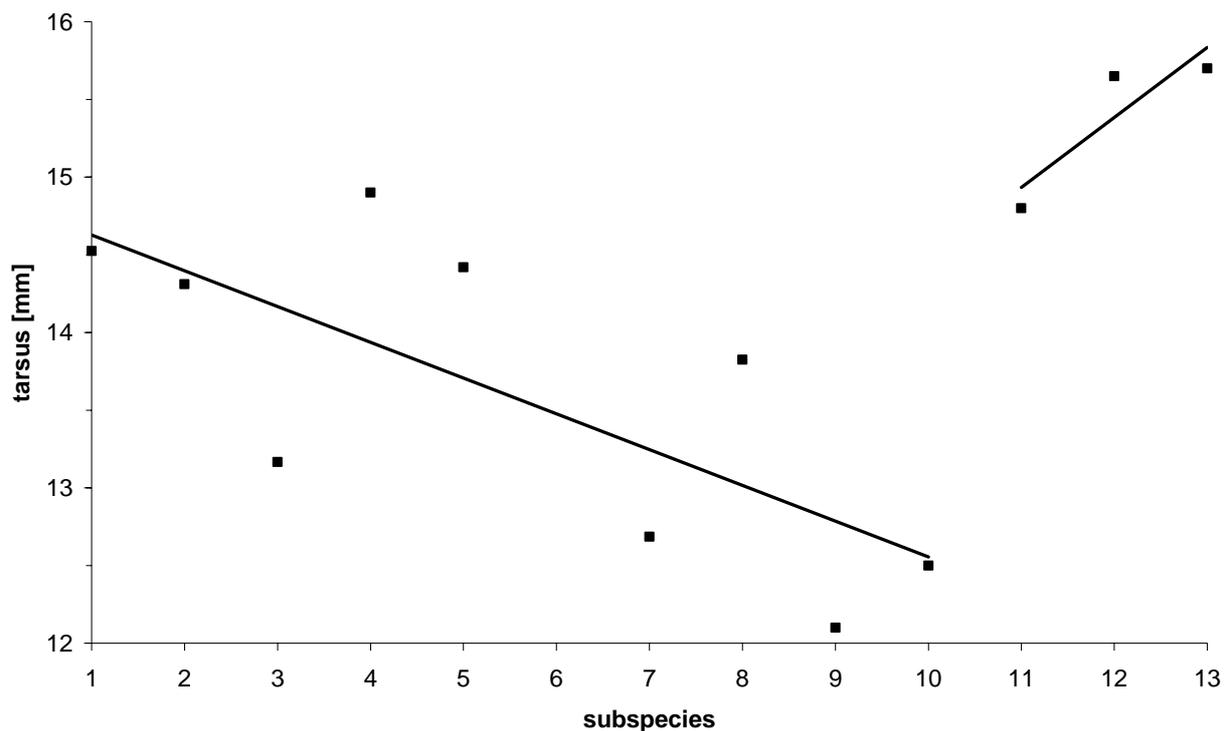
Claws are extraordinarily long in sspp. *persica* and *bianchii*. Bill length varies greatly with respect to subspecies and sex; sspp. *corsa*, *persica*, *tianschanica*, *bianchii* and especially *hodgsoni* are longer-billed than the rest of the subspecies. *Certhia hodgsoni* and *C. familiaris japonica* have deeper bills than all other subspecies. *Certhia hodgsoni* except ssp. *hodgsoni* and *C. familiaris persica* have wider bills than the other taxa. Wing length in general strongly varies between subspecies; sspp. *corsa*, *tianschanica* and *khamensis* have extraordinarily long wings. Wing tip is slightly shorter in ssp. *hodgsoni* than in other taxa. Tail length is overall very variable; sspp. *corsa* and *tianschanica* have longer and ssp. *japonica* and *hodgsoni* shorter tails than the rest. Tail tip is slightly larger in *C. familiaris* ssp. *caucasica* and *bianchii* and also larger in *C. hodgsoni* except for ssp. *hodgsoni* than in other forms. In tarsus length (only a few specimens measured!), there is a trend in *C. familiaris*, becoming shorter from Europe east to the Pacific and furthermore to the disjunct Chinese ssp. *bianchii* (but tarsus in ssp. *bianchii* slightly larger than in *japonica*) and another one in *C. hodgsoni* (with generally higher values) becoming longer from east to west, beginning with Chinese ssp. *khamensis* (Fig. 5.9).

There is less variability in WTI in *C. hodgsoni* than in *C. familiaris*; in *C. hodgsoni* all index values are about as low as in *C. familiaris bianchii*. TWI increases eastward in *C. familiaris* up to (male) sspp. *caucasica* and *tianschanica*; but easternmost subspecies have lower values than *C. hodgsoni*. BWI is higher in sspp. *corsa*, *persica* and *hodgsoni* than in the remaining subspecies. Subspecies *persica* has the largest CWI within *C. familiaris*, whilst values in *C. hodgsoni* are somewhat smaller and more uniform than in *C. familiaris*. In CBI, *C. familiaris corsa* and *C. h. hodgsoni* have smaller and *C. hodgsoni mandellii* has slightly higher values than the average. TTI is variable; only ssp. *mandellii* has higher values than the rest.

### 5.3.2.2 *Certhia americana*

Hind claw in general is longer in males, longest in sspp. *alascensis*, *alticola* and *pernigra*. Bill in general is longer in males, longest in sspp. *montana*, *zelotes*, *phillipsi*, *leucosticta* and *extima*, shortest in ssp. *stewarti* (and other northerly forms). Bills are deepest and widest in sspp. *jaliscensis* (width only), *guerrerensis*, *alticola*, *pernigra* and *extima*. Wings are longer

in males; they are shortest in ssp. *extima* and longest in ssp. *montana* and few southerly subspecies. Wing tip is longest in ssp. *montana*, *alascensis* and *americana/nigrescens* and shortest in the southernmost subspecies. Tails are on average longer in males; they are shortest in ssp. *montana*, *zelotes* and *extima* and longest in ssp. *alticola*; and Central American subspecies have in general longer tails than North American ones. Tail tip is in general longer in males.



**Fig. 5.9:** Geographic trend in tarsus length of male *Certhia [familiaris]*: *C. familiaris* subspecies (1–10) from the British Isles eastward to the Pacific, then Chinese ssp. *bianchii*, *C. hodgsoni* subspecies (11–13) from Chinese ssp. *khamensis* westward to the western Himalayas.

WTI is generally larger in males, and is largest in *americana/nigrescens*; furthermore, there is a clear decline southwards, only slightly reversed in the southernmost ssp. *pernigra* and *extima*. TWI is in general larger in more southerly than northerly subspecies. BWI is in general larger in males; there is a southward decline, but largest values occurred in the southernmost subspecies *extima* and the values of north-eastern *americana/nigrescens* are among the smallest. There are no clear trends in CWI and CBI, but the southernmost subspecies (except ssp. *extima*) have on average larger values than the rest. There is no obvious trend in TTI.

Western populations have longer and wider bills, but shorter wings, wing tips, tails and tail tips than eastern populations. WTI, CBI and TTI are smaller and BWI and CWI are larger in western than in eastern populations. All differences are significant except for tail measurements and CBI in females and TTI in both sexes.

In DA 6 for all *C. americana* subspecies, the difference between western and eastern populations was confirmed (Fig. 5.10). Eight discriminant functions were used in the analysis (Table 5.6). The highest correlations occurred between wing tip, bill width and function 1, wing tip, hind claw and function 2. For all functions,  $\chi^2$  was 391, df was 104 and Wilks' Lambda was 0.053 ( $p < 0.001$ ). Only 66.9% of the specimens could be correctly assigned to the appropriate taxon. Besides, dots of ssp. *extima* are situated in another part of the scatterplot than are those of the remaining Central American subspecies. Especially, ssp. *extima* possesses clearly shorter claws and wings than its closest neighbours, sspp. *pernigra* and *alticola* (Fig. 5.11).

### 5.3.2.3 *Certhia brachydactyla*

Bill is slightly longer in ssp. *brachydactyla* than in ssp. *megarhynchos*. Bill width is smaller in ssp. *brachydactyla* than in other subspecies. Wing is longer in ssp. *mauritanica* than in the rest. Tail tip increases eastwards.

WTI is slightly larger in sspp. *megarhynchos* and *brachydactyla* than in the rest. TWI is smaller in ssp. *mauritanica* than in European subspecies. BWI slightly, TTI clearly increase eastwards.

### 5.3.2.4 *Certhia himalayana*

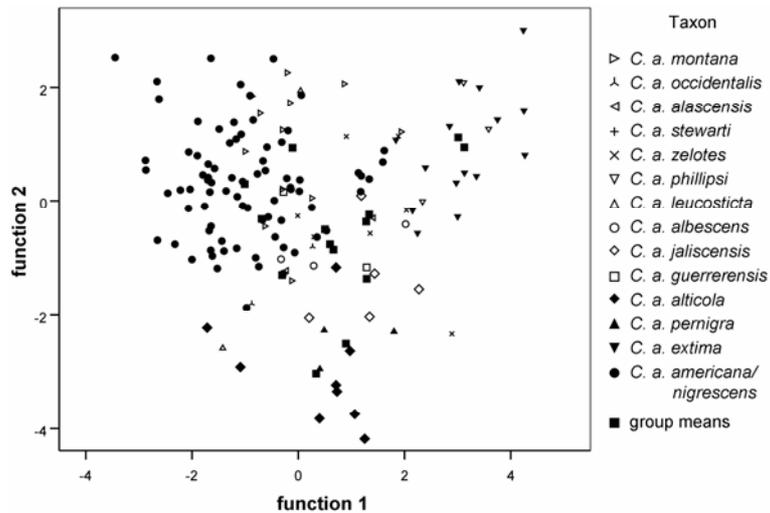
Claws are a little longer and bill is longer in ssp. *taeniura* than in other subspecies. Bill width is slightly smaller in ssp. *taeniura*, but larger in females of ssp. *yunnanensis* – compared to the remaining subspecies. Wing length decreases eastwards in the Himalayas, is longest in disjunct Chinese ssp. *yunnanensis* and shortest in also disjunct ssp. *ripponi*. Tail length also decreases eastwards in the Himalayas.

WTI is smaller in ssp. *ripponi* than in all other subspecies. There is an eastward decrease in TWI of males. BWI very clearly decreases eastwards in the Sino-Himalayas and is largest in ssp. *ripponi*. CWI is smaller in females of ssp. *yunnanensis* than in females of all other sub-

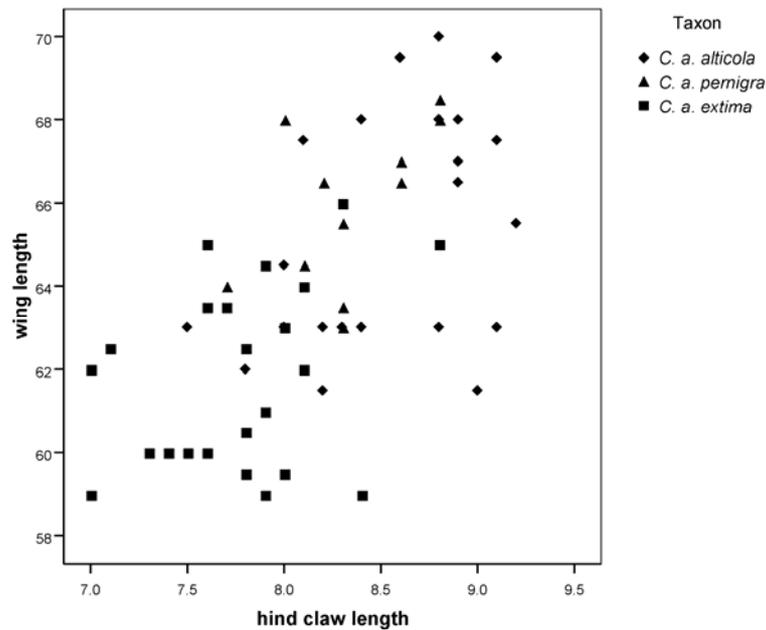
species, but slightly larger in ssp. *ripponi* than in other subspecies. CBI is smaller in ssp. *taeniura* than in the remainder of subspecies.

### 5.3.2.5 *Certhia tianquanensis*

In Shaanxi bill is shorter and wider, wing (almost significantly) longer, tail longer, TWI and CBI larger, BWI (significantly), CWI and TTI are smaller than in Sichuan.



**Fig. 5.10:** Scatterplot of DA 6 separating 145 *C. americana* specimens by claw length, bill length, bill depth, bill width, wing length, wing tip, tail length and tail tip.

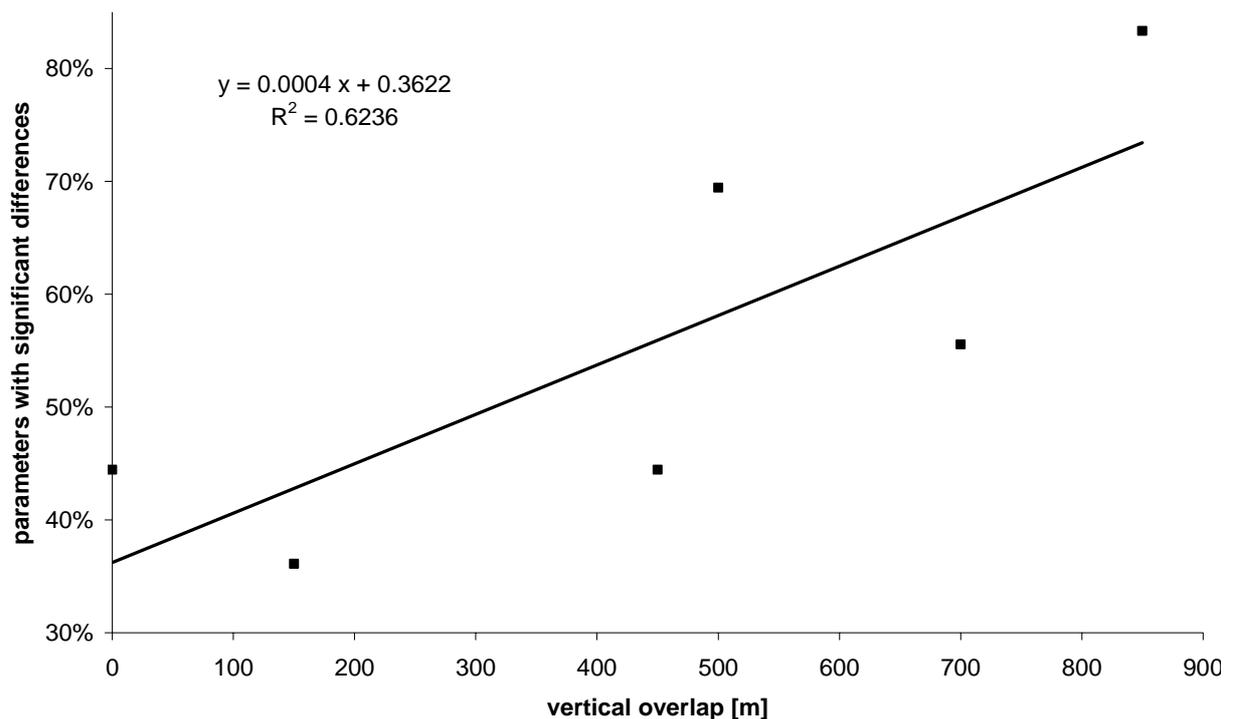


**Fig. 5.11:** Relation of wing and claw lengths in the three southernmost *C. americana* subspecies (measurements in mm).

### 5.3.3 Competition avoidance in sympatry

#### 5.3.3.1 Central Europe

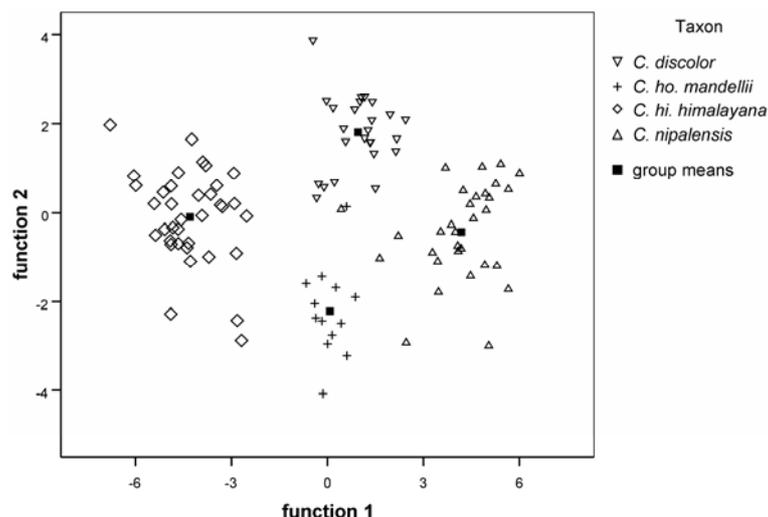
*Certhia familiaris macrodactyla* and *C. brachydactyla brachydactyla* differ significantly in all parameters except for tail tip and wing tip in males and bill depth, tail tip, tarsus and TWI in females. In DA 7, 97% of 157 specimens from which all measurements except tarsus were available could be correctly assigned to the appropriate species. The highest correlations occurred between the discriminant function and claw length. The eigenvalue was 4.730,  $\chi^2$  was 263, df was 8 and Wilks' Lambda was 0.175 ( $p < 0.001$ ). In DA 8 with only the parameters claw length and bill length, only 8 out of 282 specimens (2.8%) were incorrectly classified. The highest correlations occurred between the discriminant function and claw length. The eigenvalue was 4.104,  $\chi^2$  was 455, df was 2 and Wilks' Lambda was 0.196 ( $p < 0.001$ ).



**Fig. 5.12:** Relationship between amount of overlap in vertical distribution and percentage of measurements and indices with significant differences in both sexes (Mann-Whitney U-test) in the Himalayan species pairs (left to right) *C. discolor* – *C. hodgsoni* (no overlap), *C. discolor* – *C. nipalensis* (2550–2700 m), *C. nipalensis* – *C. hodgsoni* (2950–3400 m), *C. discolor* – *C. himalayana* (2200–2700 m), *C. himalayana* – *C. hodgsoni* (2950–3650 m) and *C. nipalensis* – *C. himalayana* (2550–3400 m).

### 5.3.3.2 Himalayas

Species pairs of the sympatric Himalayan treecreeper taxa *C. discolor*, *C. hi. himalayana*, *C. hodgsoni mandellii* and *C. nipalensis* can be discriminated as follows: *Certhia discolor* and *C. hodgsoni mandellii* differ significantly in bill length and width, wing and tail lengths, tail tip, WTI (males only), TWI, CWI (males only), CBI (males only) and TTI. *Certhia discolor* and *C. nipalensis* differ significantly in claw length (males only), bill length, wing length (males only), wing tip (males only), tail tip, WTI (males only), BWI, CWI (males only), CBI and TTI. *C. nipalensis* and *C. hodgsoni mandellii* differ significantly in claw length, bill width, wing length, wing tip (males only), tail length, tail tip, TWI, BWI (males only), CBI (males only) and TTI. *Certhia discolor* and *C. hi. himalayana* differ significantly in bill length and width, wing tip, tail length and tip and all six indices except CWI. *Certhia hi. himalayana* and *C. hodgsoni mandellii* differ significantly in claw length (males only), bill length, bill depth (males only), bill width (males only), wing length, wing tip, tail tip, tarsus length (males only measured) and all six indices (TWI and CWI in males only). *Certhia nipalensis* and *C. hi. himalayana* differ significantly in claw length, bill length, bill width, wing length (males only), tarsus length (males only), wing tip, tail length, tail tip and in all six indices. The number of significantly differing parameters is positively correlated with the vertical overlap of a syntopic species pair (Fig. 5.12).



**Fig. 5.13:** Scatterplot of DA 9 separating 105 specimens of all four taxa occurring sympatrically in Nepal by claw length, bill length, bill depth, bill width, wing length, wing tip, tail length and tail tip.

Specimens of the four taxa could be distinguished from each other by DA 9 using all measurements except tarsus (Fig. 5.13). Three discriminant functions were used in the analysis

(Table 5.6). The highest correlations occurred between tail tip and function 1, bill width, tail length and function 2. For all functions,  $\chi^2$  was 395, df was 24 and Wilks' Lambda was 0.018 ( $p < 0.001$ ). 97.1% of 105 specimens could be correctly assigned to the appropriate species.

### 5.3.3.3 Sexual niche differentiation

In general, all measurements for males are on average larger than those for females (Table 5.7). This holds true for most of the investigated taxa (for further details see also sections under "Trends"). Exceptions occur mostly in taxa with low sample sizes. Differences are largest and most common in bill, wing and tail lengths. They are most significant in these parameters and claw length. Bill-related indices differ most strikingly: in 95% of all taxa males have on average 4% larger BWI and in 93% of all taxa females have on average 5% smaller CBI.

## 5.4 Discussion

The measurements presented in this study are more or less similar to *Certhia* data presented in other studies which applied the same measuring methods: Svensson's (1992) measurements of European treecreepers are within the range of mine except for a few *C. brachydactyla* with longer bills. The few morphometric data in Harrap & Quinn (1996) also largely fit, but in some cases spans are larger there. The same holds true for Schönfeld's (2003, 2006) intensive studies on Central European treecreepers because he had larger sample sizes, but from smaller areas. Very good accordance exists with Dutch (Osieck 1975) and Spanish *C. brachydactyla* (Rodriguez de los Santos 1985).

### 5.4.1 Morphometric delimitation of phylopecies

#### 5.4.1.1 All species

None of the single measurements or even indices can separate all nine current species from one another. But the combination of them makes discrimination possible. All trill-group species differ in tail length and graduation combined with claw length. As stated above, treecreepers use their tail as support for climbing. The primary difference between species thus lies in the way this tool is shaped. Unexpectedly, all motif-group species have a tail similar to that of *C. himalayana*, so that these five species must instead be told apart from each other by claw (and bill) length. Discrimination, i.e. niche differentiation, here focuses on a fine-scale habitat exploitation (foraging surface and food hides).

## 5 Morphometric characterisation

**Table 5.7:** Sexual dimorphism in the investigated taxa expressed by male divided by female mean values (number of males, females).

Significance of differences from Mann-Whitney U-tests: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.005$ .

Taxon	hind claw	bill length (skull)	bill depth	bill width	wing length (max chord)	wing tip	tail length	tail tip	tarsus
<i>C. f. britannica</i>	100% (72,48)	106% (71,48)***	102% (65,40)	99% (69,40)	103% (70,49)***	103% (65,48)	102% (63,38)	101% (58,36)	100% (4,4)
<i>C. f. macrodactyla</i>	104% (73,43)***	108% (70,42)***	102% (65,37)*	100% (65,37)	104% (79,48)***	103% (74,42)*	103% (61,37)*	103% (57,36)	103% (9,3)
<i>C. f. corsa</i>	100% (14,14)	111% (12,14)***	102% (13,12)	97% (13,12)	104% (14,14)***	107% (11,13)*	107% (11,14)***	118% (10,13)**	96% (3,4)
<i>C. f. familiaris</i>	103% (105,55)*	109% (103,50)***	103% (87,41)***	99% (88,43)	104% (106,57)***	105% (96,52)***	103% (78,41)***	104% (67,34)	112% (5,3)*
<i>C. f. caucasica</i>	100% (16,6)	104% (15,6)	102% (16,6)	104% (15,6)	101% (16,6)	96% (14,6)	103% (14,6)	100% (14,6)	100% (5,4)
<i>C. f. persica</i>	110% (4,1)	115% (4,1)	102% (2,1)	113% (2,1)	105% (4,1)	109% (3,1)	109% (3,1)	117% (1,1)	n.d. (0,0)
<i>C. f. daurica</i>	105% (19,7)*	106% (19,8)***	104% (15,8)***	109% (16,8)	103% (19,8)***	97% (17,5)***	101% (16,6)***	101% (15,4)	101% (7,2)*
<i>C. f. tianschanica</i>	98% (19,7)	106% (18,7)	104% (17,7)	95% (18,7)	105% (19,7)***	104% (17,7)	106% (16,7)*	101% (13,7)	101% (4,4)
<i>C. f. japonica</i>	101% (5,4)	101% (5,4)	100% (4,3)	92% (5,4)	97% (5,4)	107% (5,3)	99% (5,4)	92% (5,4)	94% (2,1)
<i>C. f. bianchii</i>	99% (17,4)	108% (17,4)	100% (16,4)	108% (16,4)	101% (17,4)	99% (17,4)	104% (16,3)	98% (15,3)	105% (3,1)
<i>C. ho. "waschanensis"</i>	105% (3,2)	108% (3,2)	109% (3,1)	109% (3,1)	105% (3,2)	108% (3,2)	101% (2,2)	68% (2,2)	n.d. (1,0)
<i>C. ho. "kwanhsienensis"</i>	90% (1,1)	103% (1,1)	108% (1,1)	133% (1,1)	99% (1,1)	100% (1,1)	103% (1,1)	86% (1,1)	n.d. (0,0)
<i>C. ho. khamensis</i>	102% (28,7)	106% (23,7)*	103% (22,7)	101% (23,7)	106% (28,7)*	104% (21,6)	106% (22,3)	126% (17,2)	n.d. (3,0)
<i>C. ho. mandellii</i>	109% (23,13)***	114% (25,11)***	106% (20,10)***	103% (21,10)	104% (26,12)***	103% (24,9)	106% (13,6)*	108% (12,6)	n.d. (2,0)
<i>C. ho. hodgsoni</i>	102% (15,8)	115% (15,8)***	107% (14,8)*	101% (15,8)	105% (15,8)***	103% (12,7)	106% (5,3)*	103% (5,3)	n.d. (1,0)
<i>C. a. montana</i>	102% (11,9)	111% (11,9)***	100% (10,8)	97% (10,8)	105% (11,9)**	107% (10,7)	103% (8,7)	101% (8,6)	117% (1,1)
<i>C. a. occidentalis</i>	88% (1,1)	103% (1,1)	96% (1,1)	117% (1,1)	102% (1,1)	100% (1,1)	102% (1,1)	109% (1,1)	n.d. (0,0)
<i>C. a. alascensis</i>	102% (6,1)	109% (6,1)	99% (6,1)	92% (6,1)	102% (6,1)	98% (5,1)	86% (1,1)	86% (1,1)	n.d. (0,0)
<i>C. a. stewarti</i>	n.d. (0,2)	n.d. (0,2)	n.d. (0,1)	n.d. (0,1)	n.d. (0,2)	n.d. (0,2)	n.d. (0,2)	n.d. (0,2)	n.d. (0,1)
<i>C. a. zelotes</i>	102% (11,6)	107% (10,6)	99% (11,5)	100% (11,6)	104% (11,6)*	106% (9,5)	97% (7,2)	96% (7,2)	107% (2,2)
<i>C. a. phillipsi</i>	98% (6,1)	101% (5,1)	90% (5,1)	99% (5,1)	106% (6,1)	109% (4,1)	123% (3,1)	174% (3,1)	n.d. (2,0)
<i>C. a. leucosticta</i>	104% (9,1)	117% (9,1)	96% (9,1)	95% (9,1)	107% (9,1)	110% (7,1)	n.d. (3,0)	n.d. (2,0)	n.d. (0,0)
<i>C. a. albescens</i>	93% (9,3)	102% (10,4)	94% (6,3)	97% (6,3)	101% (10,4)	92% (7,3)	100% (6,2)	117% (6,2)	n.d. (0,1)
<i>C. a. jaliscensis</i>	95% (4,3)	94% (4,3)	94% (4,3)	101% (4,3)	99% (4,3)	103% (3,2)	97% (4,3)	101% (4,3)	91% (2,1)
<i>C. a. guerrerensis</i>	95% (3,5)	98% (3,6)	94% (2,5)	107% (2,6)	96% (3,6)	77% (2,4)	99% (3,4)	89% (2,4)	n.d. (0,0)
<i>C. a. alticola</i>	105% (17,9)	110% (17,9)***	102% (15,7)	104% (17,8)	106% (14,9)***	102% (13,7)	106% (10,6)*	106% (10,5)	99% (1,1)
<i>C. a. pernigra</i>	105% (7,4)	105% (6,4)	97% (5,3)	95% (7,2)	104% (7,4)	109% (6,4)	104% (3,4)	97% (2,4)	n.d. (0,0)
<i>C. a. extima</i>	106% (20,4)*	115% (20,4)***	108% (18,2)	101% (18,3)	104% (21,4)*	109% (20,4)*	102% (18,4)	104% (16,4)	101% (4,1)
<i>C. a. americana/nigrescens</i>	103% (74,38)***	109% (76,38)***	100% (69,33)	100% (71,34)	103% (78,40)***	104% (75,39)*	105% (67,31)**	108% (67,31)	98% (12,13)
<i>C. b. mauritanica</i>	105% (27,14)*	106% (25,13)*	103% (24,11)	100% (25,12)	102% (27,13)	103% (27,13)	104% (15,11)	95% (15,11)	103% (15,4)
<i>C. b. megarhynchos</i>	103% (50,33)***	107% (49,32)***	103% (44,30)*	99% (44,30)	104% (50,33)***	104% (48,30)	105% (41,28)***	100% (39,24)	110% (2,1)
<i>C. b. brachydactyla</i>	104% (111,80)***	110% (111,81)***	104% (98,74)***	103% (98,75)***	104% (117,86)***	107% (106,83)***	104% (80,60)***	101% (69,55)	92% (8,5)
<i>C. b. stresemanni</i>	100% (6,3)	102% (5,3)	101% (4,1)	105% (4,3)	101% (6,3)	108% (4,2)	101% (3,3)	102% (2,3)	n.d. (0,0)
<i>C. b. dorotheae</i>	102% (14,7)	105% (14,7)	102% (9,6)	96% (11,7)	103% (14,7)*	97% (9,7)	105% (14,5)*	97% (14,4)	98% (9,5)
<i>C. hi. taeniura</i>	103% (11,8)	117% (12,9)***	105% (12,8)	108% (12,8)	105% (13,9)***	106% (12,8)	112% (11,4)**	116% (10,4)	115% (2,3)
<i>C. hi. himalayana</i>	104% (32,30)*	111% (27,30)***	102% (29,28)	101% (29,28)	104% (33,31)***	107% (25,26)*	104% (30,24)**	110% (29,22)	99% (8,5)
<i>C. hi. yunnanensis</i>	110% (9,3)	117% (9,3)	104% (9,3)	86% (9,3)*	107% (9,3)	109% (9,3)	114% (7,2)	105% (7,2)	105% (1,1)
<i>C. hi. ripponi</i>	104% (5,1)	118% (5,1)	106% (5,1)	91% (5,1)	105% (5,1)	100% (3,1)	n.d. (0,1)	n.d. (0,1)	n.d. (2,0)
<i>C. tianquanensis</i>	n.d. (8,0)	n.d. (8,0)	n.d. (8,0)	n.d. (8,0)	n.d. (8,0)	n.d. (8,0)	n.d. (6,0)	n.d. (5,0)	n.d. (0,0)
<i>C. nipalensis</i>	108% (25,13)***	108% (24,11)***	104% (23,10)	99% (24,11)	106% (25,13)***	108% (24,13)**	103% (24,12)	103% (24,12)	106% (4,2)
<i>C. d. discolor</i>	102% (13,15)	106% (13,14)*	103% (13,14)	100% (13,14)	103% (13,15)***	98% (13,15)	101% (13,14)	94% (13,13)	n.d. (0,3)
<i>C. m. manipurensis</i>	104% (7,8)	106% (7,8)	102% (6,6)	96% (7,7)	105% (7,8)***	101% (6,6)	111% (6,8)***	120% (6,7)*	104% (2,2)
<i>C. m. shanensis</i>	105% (8,9)*	109% (8,7)	102% (8,8)	103% (9,9)	103% (9,8)***	108% (8,7)	102% (8,4)	103% (7,4)	102% (2,1)
<i>C. m. meridionalis</i>	101% (6,4)	104% (6,4)	102% (5,3)	104% (5,4)	98% (6,4)	95% (6,4)	102% (5,3)	102% (5,3)	105% (1,1)
<b>males larger</b>	76%	95%	71%	57%	88%	71%	85%	73%	62%
<b>females larger</b>	24%	5%	26%	43%	12%	21%	15%	28%	38%

Apart from the exception of *C. himalayana*, the presented dendrograms of morphometric similarity resemble the current phylogram (Chapter 2). On the other hand, morphometric similarity in a group of sympatric tit species in western China, investigated by McCallum et al. (2001), was not in accordance with the degree of taxonomic relationship of the relevant taxa. This could be an indication of lower intrageneric morphometric differentiation in tree-creepers.

#### 5.4.1.2 *Certhia [familiaris]*

Although there is much overlap in morphometric values between the two allospecies *C. familiaris* and *C. hodgsoni*, a closer look at subspecies in western China (and the Himalayas) where they could most possibly come into contact reveals a remarkable morphometric contrast. Mainly bill measurements (length and depth) separate the two species in that area. This would avoid competition for food in the case of a secondary contact in the mountains of the Qinling range (border between Sichuan and Gansu provinces) where the two taxa are expected to meet (Fig. 2.2).

*Certhia hodgsoni* “*waschanensis*” and *C. hodgsoni* “*kwanhsienensis*”, both synonymised with *C. hodgsoni khamensis* by Vaurie (1957) and Hartert & Steinbacher (1933), respectively, were worth examining separately in that western Chinese assemblage from where, as recently as 1995, a hitherto overlooked treecreeper taxon was described (Li 1995). *Certhia hodgsoni* “*waschanensis*”, which also resembles true *C. hodgsoni khamensis* very much in coloration, could not be separated morphometrically from the latter (Fig. 5.8). *Certhia hodgsoni* “*kwanhsienensis*”, on the other hand, which is even more strongly differentiated from true *C. hodgsoni khamensis* than is *C. hodgsoni* “*waschanensis*” (Martens et al. 2002), was clearly separated from *C. hodgsoni khamensis* by DA. Its cluster was even closer to that of *C. familiaris bianchii*, but coloration is instead as in *C. hodgsoni*.

I thus revalidate *Certhia hodgsoni kwanhsienensis* Kleinschmidt & Weigold, 1922. It is only known from the type locality, Kwanhsien (= Dujiangyan, NW of Chengdu), Sichuan province, P.R. of China, where the only specimens were collected in winter 1914/1915. I define MTD C23908 (male) as the lectotype, while MTD C25159 (unsexed) and MTD C25160 (female) remain syntypes; the unsexed syntype MTD C23909 got lost during World War II (Eck & Quaiser 2004). *Certhia hodgsoni kwanhsienensis* was not re-collected after its description. Eck & Quaiser (2004) mention a newly collected specimen in the mountains close to Dujian-

gyan (the former Kwanhsien), which seems to be similar to *kwanhsienensis*, but is quite large and less grey below. *Certhia hodgsoni kwanhsienensis* thus has conservation status data deficient (DD) according to the IUCN criteria (IUCN 2001). – For *C. hodgsoni* “*waschanensis*”, I define MTD C25163 (male) as the lectotype; AMNH 684673, MTD C25162 (males), MTD C23913 and MTD C25161 (females) remain syntypes, and the male syntype MTD C23912 was likewise lost during World War II (Eck & Quaisser 2004).

#### 5.4.1.3 *Certhia* [*discolor*]

*Certhia discolor* and *C. manipurensis* are two phylogenetically separated species. It is impossible to affiliate the four investigated disjunct populations completely to one of them by the applied measurements. *Certhia manipurensis* ssp. *shanensis* shows some similarity to heterospecific *C. discolor*. All of the populations within *C. [discolor]* differ more strikingly from one another in coloration than is the fact in other treecreeper taxa (Harrap & Quinn 1996). Given that and quite a large genetic distance, I (Chapter 2) consequently gave species rank to the two forms which were analysed in their phylogenetic study, and preliminarily made all other described taxa subspecies of the geographically closer *C. manipurensis*. Based on the measurements presented here, I can neither refute nor support this suggestion. The observed morphometric similarity between *discolor* and *shanensis* could be due to a plesiomorphic character state, since *shanensis* vocalisations are more like those of other *C. manipurensis* subspecies than like those of *C. discolor* (Chapter 3). I regard those isolate forms as old relicts which differentiated only slightly in body measurements.

### 5.4.2 Geographic trends in morphometric parameters

#### 5.4.2.1 *Certhia* [*familiaris*]

Two extraordinarily clear discontinuities can be observed: first, bills and in some cases wings are longer in more southerly distributed and mostly disjunct subspecies. Vaurie (1957) already mentioned a very long bill in ssp. *persica* and called ssp. *tianschanica* the largest *C. familiaris* subspecies. I must now add *C. familiaris* ssp. *corsa* and *bianchii* and *C. h. hodgsoni* (cf. Martens & Eck 1995: 355). All of these taxa have furthermore in common that their isolate areas are relatively small. Up to now there is no reasonable explanation for this north-south trend. Do southern Palaearctic trees in general have thicker bark with deeper chinks, which would make longer bills a prerequisite in order to exploit the bark for food? Anyhow,

this morphological differentiation does not coincide with relative ages: while I (Chapter 2) found only a little genetic substructuring in *C. familiaris* (sspp. *tianschanica* and *bianchii* had been analysed, but not *corsa* and *persica*), *C. h. hodgsoni* had been differentiated from other *C. hodgsoni* subspecies for about two million years.

As the second discontinuity, Vaurie (1957) described a cline of increasing paleness from nominate *familiaris* eastward to *japonica* and then southwestward to *bianchii* in the Chinese province of Gansu, where the latter meets “the well-differentiated *khamensis*” which is “conspicuously darker”. These findings can be supported by the west-east decline in tarsus length that I observed (Fig. 5.9). The shift between neighbouring *C. f. bianchii* and *C. h. khamensis* in combination with a reversal of the trend within the ring of *C. [familiaris]* taxa supports the species split between *C. familiaris* and *C. hodgsoni*.

#### **5.4.2.2 *Certhia americana***

The north-to-south decline in wing measurements and WTI is something typical for migratory bird species (Kipp 1959) and follows Bergmann’s rule. A reversal of this cline in Central American taxa might suggest an unrevealed hidden diversity (see below).

The north and centre of eastern North America is inhabited by only one more or less invariable population of treecreepers (yet split into the two subspecies *americana* and *nigrescens*). Contrastingly, along the western coast and mountain chain of North America from Alaska south to Nicaragua, there is a variety of subspecies that are mostly well defined by coloration and morphometrics. Nevertheless, all western populations pooled differ significantly from the eastern one. I expect the latter to have quite a long independent evolutionary history.

*Certhia americana extima* from east and south of eastern Guatemala proves to be much more different from neighbouring forms than are other *C. americana* subspecies. Perhaps this form reached this southerly outpost of treecreeper distribution in tropical America much earlier than did adjacent populations.

#### **5.4.2.3 *Certhia brachydactyla***

Only the North African subspecies *mauritanica* differs obviously from other – European – subspecies. This corresponds with the fact that it is also represented by a distinct cytochrome-*b* lineage, separate from Western European and Cypriote samples, (Chapter 2) and sings in a

remarkably different way (Chappuis 1976, Thielcke & Wüstenberg 1985). The eastward trend towards a more graduated tail might reflect the species' range extension.

#### **5.4.2.4 *Certhia himalayana***

Vaurie (1950) described ssp. *taeniura* as less saturated in coloration and having a longer bill than nominate *himalayana*, the latter supported by me. In contrast, I (Chapter 2) found that those two subspecies do not belong to separate cytochrome-*b* clusters. Chinese *yunnanensis*, in contrast to that, and more clearly disjunct *ripponi* from Myanmar are represented by their own mitochondrial lineages and have also body measurements in which they differ from the two other subspecies.

#### **5.4.2.5 *Certhia tianquanensis***

There are relatively clear differences between the few investigated males of the two *C. tianquanensis* populations, which are larger than those between some of the accepted subspecies in other species. But it remains unclear whether they represent different subspecies, because – besides the low sample size in this study – there is no difference in cytochrome *b* (Chapter 2) and only minor ones in territorial song (Chapter 3), and furthermore it is not yet proven that the populations are really separated by an uninhabited area and females have not been compared.

### **5.4.3 Competition avoidance in sympatry**

#### **5.4.3.1 Central Europe**

My results confirm the findings of Mead & Wallace (1976) and Svensson (1992). Svensson's own ratio identifies 96.6% of my *Certhia [familiaris]* as *C. familiaris* and 92.7% of my *C. brachydactyla* correctly; the formula presented in Mead & Wallace (1976) identifies 98.4% of my *Certhia [familiaris]* as *C. familiaris* and 95.1% of my *C. brachydactyla* correctly. All three authors admitted that their formulae were not sufficient to assign all individuals; I might – in spite of all diligence – also have overlooked a few wrongly identified specimens in the collections.

Discrimination of the two sympatric species thus is mainly based on the lengths of hind claw and bill. Claw length is associated with the surface structure of the tree bark the bird creeps

on. *Certhia brachydactyla* prefers relatively roughly chapped bark and thus tree species like oaks (*Quercus sp.*), whereas *C. familiaris* inhabits smoother tree trunks as in spruce (*Picea sp.*) and beech (*Fagus sp.*; Glutz von Blotzheim & Bauer 1993). Bill length seems to be influenced by the preferred foraging technique. Osiejuk (1998) observed that *C. brachydactyla* creeps more slowly than *C. familiaris* because it has a longer bill and therefore prefers probing to gleaning.

### 5.4.3.2 Himalayas

The highest number of sympatric *Certhia* species can be found in the Himalayas. But due to a partial vertical separation (Martens 1981), only three species have been seen syntopically (*himalayana*, *hodgsoni*, *nipalensis* at Dhorpatan, 2950 m, Martens & Eck 1995: 351). All of the five species pairs in syntopy differ significantly in a number of measurements and indices (Fig. 5.12). Landmann & Winding (1995) also reported a high degree of morphometric divergence between seven Himalayan rosefinch (*Carpodacus*) species. Separation there was based on parameters linked to locomotion rather than to feeding. All of my four species pairs differ significantly in tail graduation, which was also the most important parameter in the DA (but claw length the least important one!). Insofar as the tail supports climbing, a locomotion parameter is most important for the occupation of niches by species in treecreepers, too. However, all dimensions of the bill are also important factors for the separation of the four Himalayan treecreeper species. Thus specialisation in foraging techniques plays a larger role in *Certhia* than in the finches, because no other birds share this extraordinary feeding behaviour.

### 5.4.3.3 Sexual niche differentiation

Males are larger than females – on average. Schönfeld (1983, 2003, 2006) also found this intersexual size ratio in almost all the breeding pairs he investigated. The most relevant part of the treecreeper's body for sexual dimorphism is the length of the bill. The sexes are disproportionately different in this measurement. So I can support the results of Geduldig (1986) and extend them to almost all currently accepted treecreeper taxa. Such a striking sexual difference in bill morphology (mainly length) of *Certhia* treecreepers is something unusual in (passerine) birds. Another passerine with even more extremely differently shaped bills in males and females was the extinct Huia (*Heteralocha acutirostris*) from northern New Zealand (Campbell & Lack 1985).

Suhonen & Kuitunen (1991) explained the intersexual niche differentiation as a consequence of sexual dimorphism caused by sexual selection. I question the biological consequences of this hypothesis and follow another explanation: sexual dimorphism, especially in bill length, is mainly due to food limitation in the bark of trees and competition avoidance in feeding.

#### 5.4.4 Low morphometric diversity among treecreepers

Treecreepers are the only species in the Holarctic belonging to the so-called trunk-foraging guild, apart from nuthatches (also passerines, but additionally feeding on seeds) and the more strongly billed woodpeckers (order Piciformes) with other foraging strategies and hence different morphological adaptations. Since there are many more nuthatch and woodpecker species, the question arises what treecreepers have brought about morphologically.

No other Holarctic birds combine stiffened rectrices and a pincer-like bill with mottled brownish upper- and lighter underside. Even the few other “tree creeper” species found in the tropics, Spotted Creeper (*Salpornis spilonotus*) in India and Africa, the Australo-Papuan treecreepers (*Climacteris*, *Cormobates*), the Philippine creepers (*Rhabdornis*) and South American woodcreepers (Dendrocolaptidae), do not share all the morphological and ethological peculiarities of *Certhia* treecreepers (Campbell & Lack 1985, Harrap & Quinn 1996).

All known *Certhia* taxa exhibit little variation of the basic morphological pattern. Simultaneously, the maximum number of species of this type of bird seems already to have been reached. Also, the unique ecological niche that treecreepers occupied seems to be so narrow that not more than four species could live sympatrically and not more than three syntopically. The tree bark provides only a limited resource for feeding and nesting. It remains unclear why the radiation of this genus was that limited. In Nepal, for example, the lowest 2000 altitudinal meters are uninhabited by *Certhia* species (Martens 1981). Other genera with rather uniform outer characteristics developed much larger species numbers in the Holarctic: rosefinches of genus *Carpodacus* differentiated into 21 (Dickinson 2003), leaf warblers of genus *Phylloscopus* into more than 50 species (Hoyo et al. 2006). In both cases up to ten species have been found breeding sympatrically – again in the Himalayas (Martens 1980, Trautmann 2007).

## 5.5 Summary

Lengths of claw, tarsus, bill, wing and tail plus bill depth and width, wing tip and tail tip were measured in nearly 2000 specimens from all nine currently accepted *Certhia* species and most subspecies to provide morphometric characterisation. In a discriminant analysis for all species, only *C. [discolor]*, *C. nipalensis* and *C. tianquanensis* were clearly separated from each other and from the remaining set of five species. Nevertheless, a cluster analysis produced dendrograms approximating the current molecular phylogeny of the genus. Thus, there is an overall relatively low morphometric diversity among *Certhia* treecreepers. Recently split allospecies can only partly be distinguished: the disjunct *C. [discolor]* taxa exhibit no clear affiliation to either allospecies, *C. discolor* or *C. manipurensis*, while in *C. [familiaris]* the species split is corroborated on one hand by a break in geographical trends and on the other by clear separability of neighbouring heterospecific populations. Also, in areas of sympatry, *Certhia* species differ markedly in body measurements related to the peculiar adaptations of treecreepers to their habitat (tree bark): i.e., bill, claw and tail measurements. The same applies to sexual dimorphism: males, on average larger in all body measurements, have, in particular, longer bills, possibly in order to better exploit the limited food and partition it between the two sexes. *Certhia hodgsoni kwanhsienensis* Kleinschmidt & Weigold, 1922 is revalidated, because it clearly differs morphologically from *C. h. khamensis* with which it was synonymised. Lectotypes are designated for *C. h. kwanhsienensis* and *C. h. "waschanensis"* Kleinschmidt & Weigold, 1922.

## 6 General conclusions: *Certhia* systematics

Due to the overall similar outer appearance of *Certhia* treecreepers it was necessary to clarify the taxonomic relationships on the basis of DNA-sequence comparisons. Against this background, it was possible to study vocal and morphometric intra-generic differentiation and to test how suitable song and call parameters on the one hand and body measurements on the other hand are as a means of delimiting evolutionary units between the taxonomic levels of subspecies and genus.

In a first approach (Chapter 2), I sequenced a part of the mitochondrial cytochrome-*b* gene from the seven treecreeper species, including 18 subspecies, to reconstruct the phylogeny of the genus *Certhia*. Species status of all seven species could be affirmed. *Certhia discolor*, *C. himalayana*, *C. nipalensis*, and *C. tianquanensis*, the species with relatively small distribution ranges in southeast Asia and simple territorial song, are found at the base of all phylogenetic trees, although without good support. A comparatively recent sister species of *C. tianquanensis* is *C. nipalensis*, replacing *C. discolor* as closest relative. *Certhia familiaris*, *C. brachydactyla* and *C. americana* form a derived set of species (again only weak support). The closest relative of *C. americana* is *C. brachydactyla*. The *C. familiaris* subtree is deeply split into two well-defined population groups: (i) a Eurasian group including populations in northern China (Qinling range northward and all Eurasia) and (ii) a Sino-Himalayan group (Himalayas and China excluding northern China). In accordance with acoustic characters, the three subspecies *hodgsoni*, *mandellii* and *khamensis* of the Sino-Himalayan group are combined and elevated to species rank: *Certhia hodgsoni*. *Certhia discolor manipurensis* is deeply split from nominate *discolor* as well, and is also promoted to species level. Within *C. brachydactyla* (western Palearctic) and within *C. hodgsoni* (Himalayas, China) several populations form well-supported separate lineages that diverged quite recently and represent subspecies level. In all other species, molecular-genetic and vocal characters support traditional species delimitation.

In a second approach (Chapter 3), I sonagraphed song and call recordings of 33 treecreeper (*Certhia*) taxa and analysed their parameters, since the vocalisations of passerine birds are in general a good means to separate taxa when external morphological differences are few. The vocalisations show low intra-individual and intra-population variation. Phylogenetic evolutionary units at the population level were delimited by time, frequency and syntax parameters by means of principal-component and discriminant analyses. Traits of territorial song were traced on the phylogenetic tree from Chapter 2, and a mean acoustic character difference was

calculated. All currently recognised nine species could clearly be distinguished from one another by their vocalisations. Subspecies not included in the molecular phylogeny are affiliated with the correct species based on statistical analysis. The obvious subdivision of *Certhia* species into two groups, “trill singers” and “motif singers”, is corroborated by various findings: a high phylogenetic signal in the characters concerned (highest homoplasy index values for trill characters), discriminant analyses for song and call measurements and a cluster analysis. Innate calls turned out to be less suitable for studies at a low taxonomic level than learnt territorial songs, which need social interactions for their final species-specific formation.

In a third approach (Chapter 4), I performed series of playback experiments, in order to test the extent to which Central European Eurasian Treecreepers (*Certhia familiaris macrodactyla*) recognise song of allopatric taxa of the motif group as conspecific. For *Certhia* treecreepers of the motif group (*C. americana*, *C. brachydactyla*, *C. familiaris*, *C. hodgsoni*) share several song features, although they display the most variable songs of all the species of that genus. Former playback experiments suggest imperfect acoustic isolation of *C. familiaris* – at least in comparison with allopatric populations. Reaction to the song of *C. familiaris* subspecies *corsa*, *familiaris*, *daurica* and *bianchii* was limited, that to the extraordinary *tianshanica* song more intensive than that to *macrodactyla* control playback. Song of the allospecies *C. hodgsoni* elicited a significantly less intensive reaction in the cases of the subspecies *hodgsoni* and *khamensis*, but not in that of subspecies *mandellii*. There was also strong territorial response to the very different songs of *C. americana albescens* and *C. brachydactyla mauritanica*. Song features that possibly cause the (limited) recognition, e.g. “sreeh” and “tyt” elements and trill-like structure, were discussed.

In a fourth approach (Chapter 5), I measured claw and tarsus lengths, bill length, bill depth and bill width, wing length and wing tip, tail length and tail tip in nearly 2000 specimens from all nine *Certhia* species and almost all subspecies in order to characterise them morphometrically. In a discriminant analysis for all species, only *C. [discolor]*, *C. nipalensis* and *C. tianquanensis* could be clearly separated from each other and from an agglomeration of the remaining five species. Nevertheless, a cluster analysis resulted in dendrograms similar to the molecular phylogeny of the genus. Thus, there is an overall relatively low morphometric diversity among *Certhia* treecreepers. Allospecies splits can only partly be supported: the disjunct taxa within the superspecies *C. [discolor]* do not exhibit a clear affiliation to one of the allospecies, *C. discolor* and *C. manipurensis*, while in *C. [familiaris]* the species split is cor-

roborated on the one hand by a break in geographical trends and on the other hand by a clear separability of neighbouring heterospecific populations by discriminant analysis. Also, in areas of sympatry, *Certhia* species differ markedly in body measurements that are related to the peculiar adaptations of treecreepers to their habitat, the tree bark, i.e. bill, claw and tail measurements. The same holds true for sexual dimorphism: males, on average, are larger in all body measurements and have, in particular, longer bills, possibly in order to better exploit the limited food resource and to partition it between the two sexes.

I drew the following taxonomic conclusions from my molecular systematic investigations, which are largely supported by my bioacoustical and morphological findings (see also Table 2.3): *C. familiaris* s.l. was split into the allospecies *C. familiaris* s.s. and *C. hodgsoni*. *Certhia brachydactyla* is sister species of *C. americana*. Both make up a second superspecies within the derived monophyletic motif group. The remaining five species are united in a paraphyletic trill group due to their song characteristics: isospecies *C. himalayana* is in an unresolved position between motif group and a presumably monophyletic group of the remaining trill-group species. The latter consists of two further superspecies with two allospecies each, on the one hand *C. nipalensis* and *C. tianquanensis* and on the other hand *C. manipurensis* (split from *C. discolor* s.l.) and *C. discolor* s.s. For a preliminary review of Asian treecreeper species see Martens & Tietze (2006). Furthermore, *Certhia hodgsoni kwanhsienensis* Kleinschmidt & Weigold, 1922 is revalidated, because it clearly differs morphologically from *C. h. khamensis* with which it was synonymised. Lectotypes are designated for *C. h. kwanhsienensis* and *C. h. "waschanensis"* Kleinschmidt & Weigold, 1922.

In order to complete the studies of evolutionary processes in *Certhia*, one should focus on the following aspects: *C. americana* is the – morphologically and vocally – most diverse species; therefore intensive phylogenetic and more detailed bioacoustic studies should supplement my detailed morphometric investigation. Little material was available from the populations of the Middle East (Turkey, Caucasus, Iran), so that their phylogenetic position remains to be determined and their vocalisations analysed. Our knowledge of the differentiation in *C. [discolor]* is still far from complete; due to the marked differences in plumage coloration – unusual in *Certhia* – more cryptic species might be uncovered. Finally, an extended molecular approach employing a combination of several marker genes with different resolution abilities and incorporating (almost) all known populations would shed more light on the fine-scale evolutionary history and phylogeography of northern treecreepers of the genus *Certhia*.

## 7 Summary

Evolutionary processes within the bird genus *Certhia* (treecreepers) are investigated and taxonomic uncertainties clarified. The original seven species of the genus have Holarctic distribution, are uniform morphologically and hence difficult to distinguish. I employed four methodological approaches. 1. Molecular phylogeny using the mitochondrial cytochrome-*b* gene largely established relationships and revealed two cryptic species. 2. Call and song recordings from all species and many subspecies were evaluated sonographically. The nine phylospecies outlined in Part 1 were clearly delimited from one another by time and frequency parameters. They comprise a monophyletic group of “motif singers” and a purely southeast Asian group of “trill singers”. Song-character differences were generally consistent with molecular phylogeny (strong phylogenetic signals). 3. Central European *Certhia familiaris* in the field responded territorially to playback of verses of allopatric “motif singer” taxa, but usually more weakly than to their own subsequently presented songs. No song characters were unambiguously recognised as species-specific. 4. Standard body dimensions of nearly 2000 museum specimens characterise species and subspecies biometrically and reveal geographic trends. Lengths of bill and hind claw proved important parameters to explain the treecreeper lifestyle (climbing and feeding on tree trunks). In the Himalayas (highest species density) tail dimensions are also significant.

## 8 Zusammenfassung

### **Differenzierungsprozesse bei Baumläufern (Aves: *Certhia*): Phylogenie, Lautäußerungen, Biometrie**

Die Dissertation untersucht evolutive Prozesse innerhalb der Vogelgattung *Certhia* (Baumläufer) und klärt taxonomische Unsicherheiten. Die ursprünglich sieben Arten der Gattung sind holarktisch verbreitet. Sie sind morphologisch einheitlich organisiert und damit schwer zu unterscheiden. Ich verfolgte vier methodische Ansätze: 1. Eine molekulare Phylogenie anhand des mitochondrialen Cytochrom-*b*-Gens klärte die meisten Verwandtschaftsbeziehungen und deckte zwei kryptische Arten auf. 2. Ruf- und Gesangsaufnahmen aller Arten und vieler Unterarten wurden sonagraphisch ausgewertet. Die im ersten Teil umrissenen neun Phylospecies ließen sich anhand der Zeit- und Frequenzparameter eindeutig gegeneinander abgrenzen. Sie verteilen sich auf eine monophyletische Gruppe von „Motivsängern“ und eine rein südostasiatische Gruppe von „Trillersängern“. Änderungen in Gesangsmerkmalen stimmten generell gut mit der molekularen Phylogenie überein (starke phylogenetische Signale). 3. Mitteleuropäische Waldbaumläufer reagierten im Freiland auf Vorspiel von Gesangstrophen allopatrischer Taxa aus der Gruppe der Motivsänger territorial, allerdings meist schwächer als auf anschließendes Vorspiel formeigenen Gesangs. Gesangsmerkmale, die eine eindeutige Arterkennung bewirken, ließen sich nicht erarbeiten. 4. Standardkörpermaße von knapp 2000 Museumsbälgen charakterisieren die Arten und Unterarten biometrisch und zeigen geographische Trends auf. Schnabel- und Hinterkrallenlänge bestätigten sich als wichtige Parameter, die die Einnischung von Baumläufern erklären (Klettern und Nahrungserwerb an Baumstämmen). Im Himalaja (höchste Artendichte) sind auch Maße am Stütزشwanz von Bedeutung.

## 9 Acknowledgements

...

... accompanied ... me on our collecting trip in the Chinese provinces of Yunnan and Sichuan in 2002. ... accompanied me to Morocco in 2004, ... to Myanmar in 2005, and ... to Cyprus in 2005 and ... to Corsica (France) in 2006.

... gave me invaluable help in performing the field experiments in Central Europe.

Additional tissue samples were provided by ...

Additional recordings were provided by ..., The British Library Sound Archive, London, and The Macaulay Library at the Cornell Lab of Ornithology, Ithaca, New York.

The following persons made collection material available for this study (for museum acronyms see Table 5.1): ... (AMNH), ... (MTD), ... (MVZ), ... (MWHN), ... (NHM), ... (NMW), ... (NRM), ... (UMMZ), ... (ZFMK), ... (ZMB), ... (ZMH), ... (ZSM).

The staff of the university libraries of Mainz and in particular Frankfurt am Main and of the museum libraries at the AMNH, MTD, NHM, NMW, ZFMK and ZMB provided friendly help especially to check the original descriptions of *Certhia* treecreepers from 1758 up to 2000.

... lent me a laptop, a desktop computer and a laser printer.

The Evangelisches Studienwerk Villigst supported my graduation and financed my journey to SE Asia and my stay at the AMNH in New York. European Commission's Research Infrastructure Action via the SYNTHESYS Project funded the stay at the NHM in Tring.

This work on *Certhia* treecreepers is part of a Sino-German co-operation project supported also by the National Natural Science Foundation of China (NSFC). Authorities of the Chinese Academy of Sciences helped to organise travel within China.

My family, my partner and all other good friends gave me the emotional support I needed, and lent me an ear in difficult times.

## *9 Acknowledgements*

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To all the people and institutions that have contributed to the success of this undertaking, I give my heartfelt thanks.

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## **11 Electronic appendix**

Supplementary short sound recordings corresponding to Figs. 3.1 and 3.10 can be found in electronic form in the second file.