

Intraspecific differentiation in Spotted Creepers, *Salpornis spilonotus* (Aves: Passeriformes: Certhiidae)

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> Abstract

Spotted Creepers (*Salpornis spilonotus*) occur in Africa and India. They are scarcely distributed in openly forested areas and little is known about them. The five currently accepted subspecies differ clearly from each other in morphological dimensions and vocal characters. Genetic divergence between the Indian and the single genetically investigated African subspecies is immense. Consequently, we propose to treat African and Indian populations as separate species, *Salpornis salvadori* and *Salpornis spilonotus*. This intercontinental split is corroborated by our morphometric data.

> Kurzfassung

Stammsteiger (*Salpornis spilonotus*) kommen in Afrika und Indien vor. Sie sind spärlich verbreitet, bewohnen offen bewaldete Gebiete und wenig ist über sie bekannt. Die fünf derzeit anerkannten Unterarten unterscheiden sich deutlich voneinander in Körpermaßen und stimmlichen Merkmalen. Der genetische Abstand zwischen der indischen und der einen genetisch untersuchten afrikanischen Unterart ist immens. Deshalb schlagen wir vor, die afrikanische und die indische Population als separate Arten, *Salpornis salvadori* und *Salpornis spilonotus*, zu führen. Diese interkontinentale Aufspaltung wird durch unsere morphometrischen Daten untermauert.

> Key words

Salpornis, systematics, morphometric analysis, vocalizations.

Introduction

The Spotted Creeper (*Salpornis spilonotus*) from tropical Africa and India resembles Holarctic treecreepers (*Certhia*) in numerous characters, and the species of both genera are thus united in the subfamily Certhiinae by SIBLEY & AHLQUIST (1990) which was adopted by HARRAP & QUINN (1996). With a long decurved bill, long hind claws and a bark-colored upper side *Certhia* and *Salpornis* species are adapted to a life on tree trunks. Stiffened rectrices which facilitate climbing in woodpeckers (Piciformes) and treecreepers are lacking in *Salpornis* as in other climbing birds in Certhioidea sensu CRACRAFT *et al.* (2004), namely nut-hatches (Sittinae) and Wallcreeper (Tichodromadinae).

Salpornis additionally differs from *Certhia* treecreepers in various behavioural traits. JOHANSSON *et al.* (2008) recently presented evidence from nuclear DNA sequences that *Certhia* and *Salpornis* are not sister taxa, but failed in providing a consistent alternative. Unfortunately, they had included all major lineages of Certhioidea except for the Wallcreeper *Tichodroma muraria* as the only representative of the Tichodromadinae, which we suggest as closest relative of *Salpornis* based on first morphological and acoustic data we presented (TIETZE & MARTENS, 2007). However, HARRAP (2008) put *Salpornis* into a subfamily of its own, Salpornithinae.

Tab. 1. Collections containing *Salpornis* specimens examined for this study.

Location	Name	Acronym	Specimens
Berlin (Germany)	Museum für Naturkunde der Humboldt-Universität	ZMB	2
Bonn (Germany)	Zoologisches Forschungsinstitut und Museum Alexander Koenig	ZFMK	5
Dresden (Germany)	Senckenberg Naturhistorische Sammlungen, Museum für Tierkunde	MTD	3
New York (USA)	American Museum of Natural History	AMNH	48
Stockholm (Sweden)	Naturhistoriska Riksmuseet	NRM	2
Tring (UK)	The Natural History Museum, Bird Group	NHM	35

In Africa the numerous populations, scattered across the savannah habitats, fall into four recognized subspecies (Tab. 1, HARRAP & QUINN, 1996; FRY *et al.*, 2000; DICKINSON, 2003; HARRAP, 2008). We consider all the populations with quite small distributional areas in East Africa north of the equator to belong to *Salpornis spilonotus erlangeri*, because subspecies affiliation has been previously undefined. For India, DICKINSON *et al.* (2006) synonymised *Salpornis spilonotus rajputanae* MEINERTZHAGEN & MEINERTZHAGEN, 1926 with *Salpornis spilonotus spilonotus* (FRANKLIN, 1831) resulting in a single subspecies for India, which is scarcely distributed in open dry woods of central India (RASMUSSEN & ANDERTON, 2005).

In this paper, we present a morphometric characterisation for four out of the five valid *Salpornis* subspecies, and we include sonographic analyses of all hitherto available song and call recordings. Combining these two datasets we intend to shed some light on the differentiation within *Salpornis*. We support our findings with first short mitochondrial DNA sequences for *Salpornis*.

Materials and methods

Morphometrics

We examined 95 *Salpornis* specimens from six different collections (Tab. 1), 70 of which could be affiliated to a current subspecies, identified as full grown, and used for measuring at least one of the following body dimensions (Tab. 2). We measured the lengths of wing, tail, hind claw, and bill, width and depth of the bill as well as the wing tip, as described in detail in TIETZE & MARTENS (2009).

Bioacoustics

For sonographic measurements, all recordings (Tab. 2) were converted to a sampling rate of 22.1 kHz/16 Bit. Avisoft SASLab Pro 4.36 (SPECHT, 2005) was used

to produce sonagrams. Duration of the vocalization, minimum (F_{\min}) and maximum frequencies (F_{\max}) were measured and number of elements was determined on the sonagrams and mean frequency ($(F_{\min} + F_{\max}) / 2$) and frequency range ($F_{\max} - F_{\min}$) were calculated (TIETZE *et al.*, 2008).

Molecular analysis

From few museum specimens (Tab. 3) we sampled small pieces of their toe pads in order to extract DNA and sequence a short fragment of the mitochondrial cytochrome-*b* gene following the methods described in TIETZE *et al.* (2006). As primers for PCR and cycle sequencing we used L14841 (5'-AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA-3') and H15149 (5'-AAA CTG CAG CCC CTC AGA ATG ATA TTT GTC CTC A-3') of KOCHER *et al.* (1989). Corrections and alignment of sequences and analyses were performed in MEGA version 4 (TAMURA *et al.*, 2007). Group-wise distances as well as phylogenetic reconstructions using neighbour joining and maximum parsimony algorithms were calculated with 2000 bootstrap replications each. GTR+ Γ distances were calculated in PAUP* 4.0b10 (SWOFFORD, 2003).

Statistical analysis

Measurements of body dimensions and sonographic parameters were evaluated and plotted in R 2.9.2 (R Development Core Team 2009). *t*-tests and discriminant analyses were used to test whether taxa can be separated according to morphometric parameters.

Results

Morphometrics

Mean values for each treated *Salpornis* taxon are presented together with standard deviations, ranges and

Tab. 2. Taxon-wise numbers of *Salpornis* specimens measured (males, females; differences due to unsexed birds), of samples for DNA analysis, of males analyzed for song verses, and of individuals analyzed for calls together with distributional data taken from DICKINSON (2003; except for the Indian and East African populations, see text details).

Taxon	Specimens	Samples	Males	Ind.	Distribution
<i>S. s. emini</i> HARTLAUB, 1884	16 (9,6)		3		Gambia to NE Zaire
<i>S. s. erlangeri</i> NEUMANN, 1907	13 (5,8)		1	1	W and S Ethiopia, NW Uganda, W Kenya
<i>S. s. salvadori</i> (BOCAGE, 1878)	21 (15,6)	3	3	1	Angola to S Tanzania and N Mozambique
<i>S. s. xylodromus</i> CLANCEY, 1975			1	1	E Zimbabwe, W Mozambique
<i>S. s. spilonotus</i> (FRANKLIN, 1831)	20 (12,6)	1	1	2	NW India
	70	5	9	5	

Tab. 3. Toe-pad samples used for DNA extraction, sequencing, and analysis, with corresponding tissue collection numbers from MAR series and GenBank accession numbers.

Specimen	Subspecies	Locality	Date	MAR	Accession no.
ZFMK 64.3519	<i>salvadori</i>	Mozambique, Sangea Distr.	27 May 1964	5497	FJ660919
ZFMK 64.3520			18 May 1964	5498	FJ660920
ZFMK 64.3518			19 May 1964	5500	FJ660921
ZFMK 75.189	<i>spilonotus</i>	India, Udaipur	4 December 1974	4341	FJ660918

Tab. 4. Measurements taken from *Salpornis* specimens summarized by taxon (all in mm): mean \pm s.d. (minimum – maximum, sample size). p-values are given for t-tests comparing the three African subspecies (pooled) to Indian *spilonotus*.

Taxon	<i>emini</i>	<i>erlangeri</i>	<i>salvadori</i>	<i>spilonotus</i>	p-value
Hind claw	8.5 \pm 0.33 (8.0–9.1, 16)	9.3 \pm 0.46 (8.7–10.2, 13)	8.8 \pm 0.53 (7.3–9.8, 21)	8.9 \pm 0.48 (8.2–9.9, 19)	0.511
Bill length	23.9 \pm 0.86 (22.0–25.1, 16)	20.6 \pm 0.86 (19.4–22.6, 13)	21.7 \pm 1.03 (20.3–24.1, 20)	25.9 \pm 1.29 (23.0–28.7, 20)	< 0.0001
Bill depth	3.2 \pm 0.17 (3.0–3.6, 16)	2.9 \pm 0.11 (2.8–3.1, 13)	3.1 \pm 0.21 (2.8–3.6, 16)	3.4 \pm 0.17 (3.2–3.8, 18)	< 0.0001
Bill width	3.2 \pm 0.24 (2.7–3.6, 16)	2.8 \pm 0.14 (2.6–3.0, 13)	3.0 \pm 0.19 (2.7–3.4, 20)	2.9 \pm 0.16 (2.7–3.3, 18)	0.012
Wing length	92.0 \pm 2.40 (87.5–96.5, 16)	92.7 \pm 1.39 (90.5–95.0, 13)	92.1 \pm 2.72 (87.5–97.5, 21)	88.5 \pm 2.76 (83.5–94.0, 20)	< 0.0001
Wing tip	26.7 \pm 2.24 (22.0–31.0, 16)	28.5 \pm 1.63 (26.0–31.0, 11)	28.2 \pm 2.03 (24.0–31.0, 19)	25.8 \pm 1.87 (22.0–29.0, 19)	0.001
Tail length	52.4 \pm 1.80 (49.0–55.0, 15)	54.4 \pm 1.62 (53.0–58.0, 12)	55.8 \pm 1.87 (53.0–59.0, 16)	53.8 \pm 2.05 (50.0–57.0, 17)	0.280

sample sizes in Tab. 4. Male specimens were on average slightly larger in all dimensions than female ones, but these differences were never significant (p-values between 0.058 and 0.976); thus we present all morphometric results pooled for sexes.

African Spotted Creepers have shorter and flatter bills, but longer wings than Indian representatives (see Tab. 4 for p-values). In particular, hind claws are slightly shorter in *ssp. emini*, but longer in *ssp. erlangeri* than in the other two subspecies. The bill is much longer in Indian *spilonotus* and somewhat longer in *ssp. emini* than in the other two African subspecies. The bill depth follows the same pattern whereas bill width is outstandingly larger only in *ssp. emini*. The

wing length only slightly varies among African subspecies, the wing is a little shorter in Indian specimens. Therefore the wing tip is shorter in *ssp. emini* and much shorter in *ssp. spilonotus* than in the other two subspecies. The tail length varies within each subspecies to almost the same extent as does the wing length, but there are only minor differences between the taxa.

Specimens of the four analyzed subspecies could be distinguished from each other by a discriminant analysis using all measurements (Fig. 1). Three discriminant functions were used in the analysis, the first one explaining 77.3 % of the variance (Eigen value: 10.5), the second one 17.0 % (Eigen value: 4.9), the

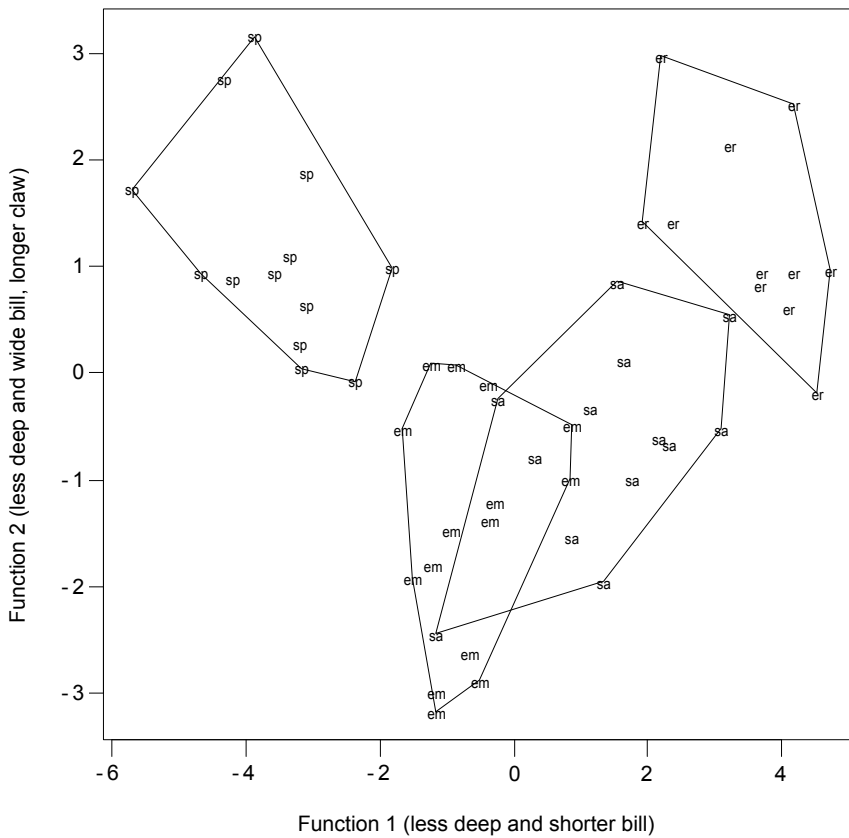


Fig. 1. Scatterplot of a discriminant analysis separating 52 specimens of four *Salpornis* taxa by morphometric parameters.

em = emini
 er = erlangeri
 sa = salvadori
 sp = spilonotus.

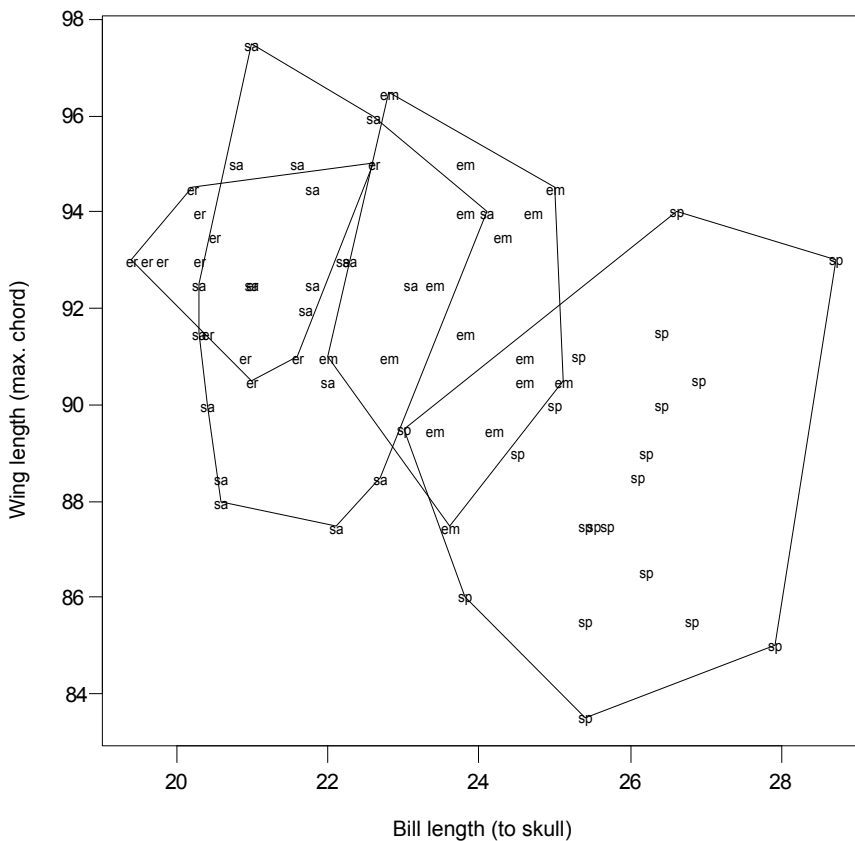


Fig. 2. Scatterplot of bill and wing lengths (measured in mm) of 69 specimens of four *Salpornis* taxa.

em = emini
 er = erlangeri
 sa = salvadori
 sp = spilonotus

last one 5.8 % (Eigen value: 2.9). The highest correlations occurred between and function 1, bill depth, bill length, claw length and function 2. 69 % of the incor-

porated 52 specimens could be correctly assigned to the appropriate taxon. While the scatterplot of Indian *spilonotus* in Fig. 1 is completely separated from all

Tab. 5. Means \pm s.d. of several parameters taken from sonagrams of territorial song verses in *Salpornis* taxa (n = number of males investigated).

Taxon (n)	<i>emini</i> (3)	<i>erlangeri</i> (1)	<i>salvadori</i> (3)	<i>xylodromus</i> (1)	<i>sylonotus</i> (1)
Verse length [s]	1.5 \pm 0.1	2.0	3.3 \pm 0.5	2.9	3.0
Minimum frequency [kHz]	2.6 \pm 0.2	5.3	5.7 \pm 0.7	5.0	4.1
Maximum frequency [kHz]	6.3 \pm 0.3	8.8	8.4 \pm 0.5	7.9	7.1
Frequency range [kHz]	3.7 \pm 0.4	3.4	2.7 \pm 0.4	2.9	3.0
Mean frequency [kHz]	4.5 \pm 0.2	7.1	7.0 \pm 0.5	6.5	5.6
Elements	4.0 \pm 0.6	5.6	9.8 \pm 1.5	9.6	10.4

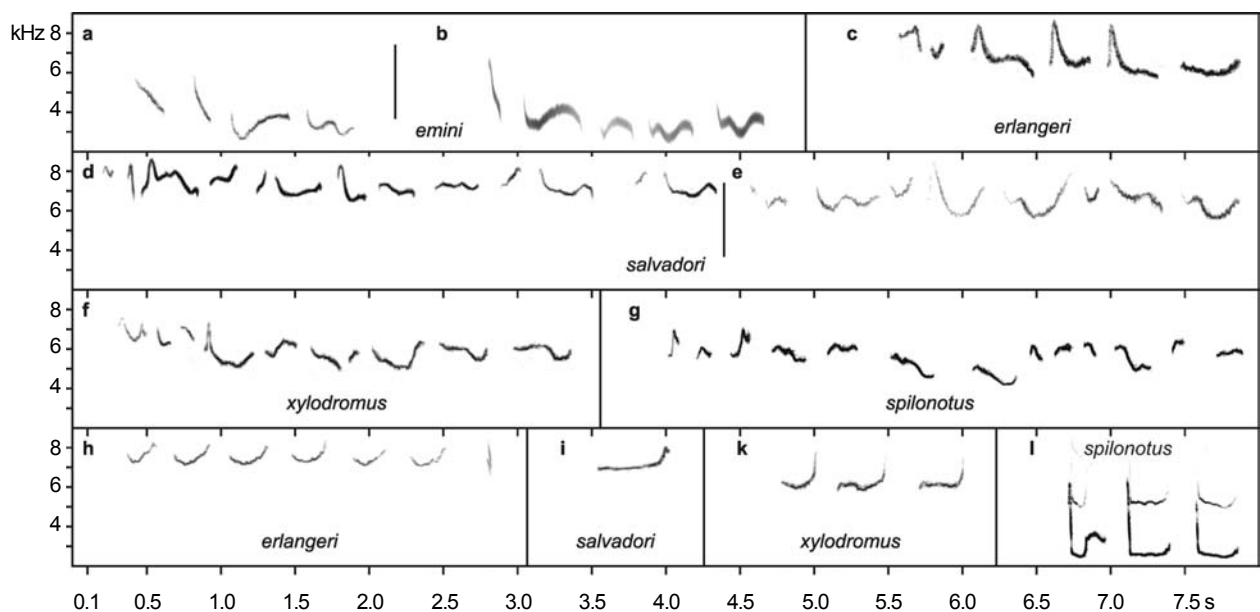


Fig. 3. Sonagrams of territorial songs and calls in *Salpornis sylonotus*: Song of ssp. *emini* from a) Côte d'Ivoire (F. Rheindt) and b) Benin (C. Chappuis), of c) ssp. *erlangeri* from Kenya (R. McVicker), of ssp. *salvadori* from d) Malawi (C. Chappuis) and e) Zambia (C. Carter), f) of ssp. *xylodromus* from Zimbabwe (A.C. Kemp), and of g) ssp. *sylonotus* from India (P.I. Holt); calls of h) ssp. *erlangeri* from Kenya (R. McVicker), i) ssp. *salvadori* from Zambia (R. Stjernstedt), k) ssp. *xylodromus* from Zimbabwe (A.C. Kemp), and l) ssp. *sylonotus* from India (P.I. Holt).

others (by function 1 alone!), those of the three African subspecies partially overlap.

When simply wing length is plotted against bill length, another diagram results (Fig. 2) in which dots of the African subspecies overlap and only few of these with *sylonotus* dots. *Salpornis sylonotus emini* from western Africa is the African subspecies whose dots lie closest to those of the Indian one in both figures.

Bioacoustics

Territorial song

Salpornis sylonotus song verses consist of 3–13 mostly whistling elements of different shape, fre-

quency, and frequency range which are loosely strung together (Fig. 3 a–g, Tab. 5). The elements of a single verse all differ from one another and thus shape “uneasy” verses. Contrastingly, different verses of the same male are almost indistinguishable. We do not know of any male using a second verse type; however this might be due to the low number of recordings available. Variation among males of the same taxon is larger, but still follows a restricted pattern:

Songs in West Africa (ssp. *emini*, Fig. 3 a, b) are the shortest ones and of the lowest frequency, but with the largest frequency range due to one or two steeply falling introductory notes. Songs in East Africa (ssp. *erlangeri*, Fig. 3 c) are slightly longer than the former ones, reach the highest frequencies in *Salpornis*, and have the elements with largest frequency range within the verse. Southern African subspecies *salvadori* and *xylodromus* utter much longer song verses at medium to high frequency with about double the number of

Tab. 6. Means \pm s.d. of several parameters from sonagrams of calls of *Salpornis* taxa (n = number of individuals investigated).

Taxon (n)	<i>emini</i> (0)	<i>erlangeri</i> (1)	<i>salvadori</i> (1)	<i>xylodromus</i> (1)	<i>spilonotus</i> (2)
Call length [s]		0.2	0.3	0.3	0.3 \pm 0.0
Minimum frequency [kHz]		6.5	6.8	5.6	2.6 \pm 0.0
Maximum frequency [kHz]		8.2	8.2	7.2	5.1 \pm 1.2
Frequency range [kHz]		1.7	1.4	1.7	2.5 \pm 1.2
Mean frequency [kHz]		7.4	7.5	6.4	3.9 \pm 0.6

elements compared to the other two African subspecies (Fig. 3 d-f). Indian Spotted Creeper songs (Fig. 3 g) finally are similar to the latter, but with more and shorter elements, longer pauses between several of the notes and at lower frequencies than all other subspecies except *emini*.

Calls

We are not certain about the behavioural context in which the calls depicted here (Fig. 3 h–l, Tab. 6) were used. But since at least all African calls on-hand are all of similar shape, they might be comparable between the taxa, although some individuals used single calls whereas others uttered call series with different numbers of notes. One such series in East Africa (ssp. *erlangeri*, Fig. 3 h) consisted of more or less u-shaped notes at a high frequency similar to the one of this taxon's song (Fig. 3 c). Calls of the southern African subspecies *salvadori* and *xylodromus* (Fig. 3 i, k) also correspond to their songs in frequency, but the single call note differs in its shape. In both subspecies the calls are longer than in ssp. *erlangeri* and end in a marked upstroke. In ssp. *salvadori* the main part of the call is constant in frequency (Fig. 3 i), while in ssp. *xylodromus* this part is frequency-modulated (Fig. 3 k). Calls of Indian *spilonotus* are completely different (Fig. 3 l): They are very low-pitched, with an initial rapid downstroke, and noticeable harmonics. We lack the recording of an *emini* call.

Molecular analysis

Cytochrome-*b* fragments we achieved range from 263 to 268 bp with an overlap of 224 bp in all samples. All *Salpornis* samples represent unique cytochrome-*b* haplotypes. They proved to be one monophyletic lineage when aligned with and compared to cytochrome-*b* sequences from other Certhioidea. The African haplotypes cluster with full bootstrap support in neighbour joining and maximum parsimony. African (*salvadori*) and Indian samples (*spilonotus*) represent two sister lineages diverging by 12.1 % \pm 2.1 % (between groups mean in the overlapping part of the alignment of un-

corrected pairwise distances; mean GTR+ Γ distance of 17.9 %). There is a within groups mean distance of 0.9 % \pm 0.5 % in *salvadori* (uncorrected pairwise distances; mean GTR+ Γ distance of 0.9 %).

Discussion

Intraspecific differentiation

Morphometrics

Additional data from HARRAP & QUINN (1996) for the fourth African subspecies does not change our result that the Indian Spotted Creeper is clearly differentiated from all African populations based on external body dimensions (particularly the bill-wing ratio: 29 % opposed to 22–26 %) while the latter overlap to a large extent in all collected measurements.

Vocalizations

CHAPPUIS (2000) split *Salpornis spilonotus* in his CD collection of African bird vocalizations because of “the considerable acoustic differences”. West African *emini* remained in *Salpornis spilonotus*, but “for the eastern and southern African populations, with much shriller tones, the old denomination ‘*salvadori*’” was applied. After this introduction he presented one song and calls of *salvadori* from Malawi and Zambia, respectively, and another song of *emini* from Benin. A comparison with Indian representatives was not presented. Since we doubt this hypothesis that an African population is closer related to a disjunct Indian population, we propose the alternative hypothesis instead that all African populations – despite the differences between them – are more closely related to each other than each of them to Indian nominate *Salpornis spilonotus spilonotus*.

We agree with CHAPPUIS (2000) in that there are “considerable acoustic differences” between African ssp. *emini* and the other African subspecies – at least in songs. But we cannot support his statement that

Indian and West African “tones” are “identical”. The British Library Sound Archive (BLSA) recording he refers to is the only one in that archive from an Indian Spotted Creeper. PAUL I. HOLT who is the only one to our knowledge to have recorded Indian Spotted Creepers defines the vocalization on his 1994 recording (the one deposited in the BLSA) as a call when recording it again in 1998 (Fig. 3 I). The superficial similarity between this call series and an *emini* song verse (Fig. 3 a, b) might have lead CHAPPUIS (2000) to his misinterpretation. HOLT (pers. comm.) attempted to playback African Spotted Creepers to birds at Bharatpur, Rajasthan, India (27° 13' N, 77° 29' E), in 1998. The recordings that he used were from C. CHAPPUIS's set of African CDs (probably an older collection with only recordings from East Africa). *Salpornis spilonotus spilonotus* did not react at all to that, but the same individuals responded very strongly to playback of Indian birds (i.e. his call recording from 1994).

Molecular marker

Unfortunately, we could only sample one out of the four African taxa and only one specimen of the Indian subspecies. But the degree of genetic divergence between two haplotypes of African ssp. *salvadori* on the hand and one of these and the Indian one on the other is so strikingly high that we consider it worth mentioning here all the same. If we apply the “2.1 % rule” (WEIR & SCHLUTER, 2008) rather to the GTR+ Γ distance of 17.9 % than to the uncorrected distance values we provided for *Certhia treecreepers* (TIETZE *et al.*, 2006), we estimate up to nine million years since the two taxa last shared a common ancestor.

Synthesis and taxonomic recommendations

Mitochondrial sequence divergence is much lower in many other Certhioidea species pairs of the *Sitta* nuthatches (PASQUET, 1998) and *Certhia treecreepers* (TIETZE *et al.*, 2006) – even in sympatry – than it is between south-east African *salvadori* and Indian *spilonotus*. They hence most probably diverged over several million years, which is clearly enough time to become reproductively isolated (PRICE & BOUVIER, 2002).

This seems to be proven by the unanswered playback which simulated a possible secondary contact of actually allopatrically distributed taxa (P.I. HOLT, pers. comm.). However the songs of these two populations differ less than do the songs between *Salpornis* subspecies within Africa. Therefore calls more clearly diverged between Indian and (eastern) African subspecies. At least in *Certhia treecreepers* (TIETZE *et al.*,

2008) and other passerines calls are the more conservative vocal trait than songs, because calls are mostly innate and not modified through learning processes. Our morphometric data on the other hand seem to support an intercontinental split quite clearly. Although in *Certhia treecreepers* (TIETZE & MARTENS, 2009) morphometric differences are accumulated with increasing extent of sympatry, there is no constraint prohibiting the divergence in morphological traits observed in these allopatric *Salpornis* taxa.

In conclusion, we consider African and Indian Spotted Creeper populations as not conspecific. Despite the fact that *emini* song differs so much from other African *Salpornis* songs, we recommend to preliminarily keep all African subspecies in one species, before there is more molecular information for *Salpornis*, or at least further bioacoustic evidence. According to the priority rule the African Spotted Creeper is named *Salpornis salvadori* (BOCAGE, 1878) and the Indian Spotted Creeper *Salpornis spilonotus* (FRANKLIN, 1831) s. str.

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Literature

- CHAPPUIS, C. (2000): African Bird Sounds. Birds of North, West and Central Africa, 15 CDs. Paris.
- CRACRAFT, J., BARKER, F.K., BRAUN, M.J., HARSHMAN, J., DYKE, G., FEINSTEIN, J., STANLEY, S., CIBOIS, A., SCHIKLER, P., BERESFORD, P., GARCÍA-MORENO, J., SORENSON, M.D., YURI, T. & MINDELL, D.P. (2004):

- Phylogenetic relationships among modern birds (Neornithes): Toward an avian tree of life. In: CRACRAFT, J. & DONOGHUE, M.J. (edit.): *Assembling the tree of life*. New York: 468–489.
- DICKINSON, E.C. (edit.) (2003): *The Howard & Moore Complete Checklist of the Birds of the World*, 3rd ed. London.
- DICKINSON, E.C., LOSKOT, V.M., MORIOKA, H., SOMADIKARTA, S. & VAN DEN ELZEN, R. (2006): Systematic notes on Asian birds. 66. Types of the families Sittidae and Certhiidae. – *Zoologische Mededelingen (Leiden)*, **80-5**: 287–310.
- FRY, C.H., KEITH, S. & URBAN, E.K. (2000): *The Birds of Africa*, Vol. 6. London.
- HARRAP, S. (2008): Family Certhiidae (Treecreepers). In: DEL HOYO, J., ELLIOTT, A. & CHRISTIE, D.A. (Edit.): *Handbook of the birds of the world*. Vol. 13. *Pendulines to shrikes*. Barcelona: 166–195.
- HARRAP, S. & QUINN, D. (1996): *Tits, Nuthatches & Treecreepers*. London.
- JOHANSSON, U.S., FIELDSÅ, J. & BOWIE, R.C.K. (2008): Phylogenetic relationships within Passerida (Aves: Passeriformes): A review and a new molecular phylogeny based on three nuclear intron markers. – *Molecular Phylogenetics and Evolution*, **48**: 858–876.
- KOCHER, T.D., THOMAS, W.K., MEYER, A., EDWARDS, S.V., PÄÄBO, S., VILLABLANCA, F.X. & WILSON, A.C. (1989): Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. – *Proceedings of the National Academy of Sciences of the United States of America*, **86**: 6196–6200.
- PASQUET, E. (1998): Phylogeny of the nuthatches of the *Sitta canadensis* group and its evolutionary and biogeographic implications. – *Ibis*, **140**: 150–156.
- PRICE, T.D. & BOUVIER, M.M. (2002): Evolution of F_1 postzygotic incompatibilities in birds. – *Evolution*, **56**: 2083–2089.
- R Development Core Team (2009): *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>.
- RASMUSSEN, P.C. & ANDERTON, J.C. (2005): *Birds of South Asia. The Ripley Guide*. Vol. 1 and 2. Washington, D. C., & Barcelona.
- SIBLEY, C.G. & AHLQUIST, J.E. (1990): *Phylogeny and classification of birds. A study in molecular evolution*. New Haven & London.
- SPECHT, R. (2005): *Avisoft-SASLab Pro (Sound Analysis and Synthesis Laboratory)*, version 4.36. Berlin.
- SWOFFORD, D.L. (2003): *Phylogenetic Analysis Using Parsimony (and Other Methods)*, Version 4. Sunderland, MA.
- TAMURA, K., DUDLEY, J., NEI, M. & KUMAR, S. (2007): *MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0*. – *Molecular biology and evolution*, **24**: 1596–1599.
- TIETZE, D.T. & MARTENS, J. (2007): Stammbaum und Stimme des Stammsteigers, *Salpornis sibilans*. – *Vogelwarte*, **45**: 347.
- TIETZE, D.T. & MARTENS, J. (2009): Morphometric characterisation of treecreepers (genus *Certhia*). – *Journal of Ornithology*, **150**: 431–457.
- TIETZE, D.T., MARTENS, J. & SUN, Y.-H. (2006): Molecular phylogeny of treecreepers (*Certhia*) detects hidden diversity. – *Ibis*, **148**: 477–488.
- TIETZE, D.T., MARTENS, J., SUN, Y.-H. & PÄCKERT, M. (2008): Evolutionary history of treecreeper vocalisations (Aves: *Certhia*). – *Organisms, diversity & evolution*, **8**: 305–324.
- WEIR, J.T. & SCHLUTER, D. (2008): Calibrating the avian molecular clock. – *Molecular Ecology*, **17**: 2321–2328.