

# A new subspecies of Eurasian Reed Warbler *Acrocephalus scirpaceus* in Egypt

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**SUMMARY.**—A new subspecies of European Reed Warbler *Acrocephalus scirpaceus* is described from the Egypt / Libya border region in the northern Sahara. Intensive studies revealed the new form to be clearly diagnosable within the Eurasian / African Reed Warbler superspecies, especially in biometrics, habitat, breeding biology and behaviour. The range of this sedentary form lies entirely below sea level, in the large depressions of the eastern Libyan Desert, in Qattara, Siwa, Sitra and Al Jaghub. The most important field characters are the short wings and tarsi, which are significantly different from closely related *A. s. scirpaceus*, *A. s. fuscus* and *A. s. avicenniae*, less so from *A. baeticatus cinnamomeus*, which is more clearly separated by behaviour / nest sites and toe length. Molecular genetic analyses determined that uncorrected distances to *A. s. scirpaceus* are 1.0–1.3%, to *avicenniae* 1.1–1.5% and to *fuscus* 0.3–1.2%. The song is similar to that of other Eurasian Reed Warbler taxa as well as that of African Reed Warbler *A. baeticatus*, but the succession of individual elements appears slower than in *A. s. scirpaceus* and therefore shows more resemblance to *A. s. avicenniae*. Among the new subspecies' unique traits are that its preferred breeding habitat in the Siwa Oasis complex, besides stands of reed, is date palms and olive trees. A breeding density of 107 territories per 10 ha was recorded in the cultivated area. Nest sites in trees, palms and shrubs are unique in the Eurasian and African Reed Warbler superspecies. Foraging in oasis gardens is mostly in the tree canopy. There are clear parallels in foraging behaviour and ecomorphology to oceanic island reed warblers. Finally, the biogeographic situation in North Africa, the newly revealed high ecological plasticity of *scirpaceus* taxa, the substantial spatial separation from other reed warbler taxa, and the reasons why these warblers remained undiscovered for so long are discussed.

In the course of comparative studies on the biology and taxonomy of African Reed Warbler *Acrocephalus baeticatus* and Eurasian Reed Warbler *A. scirpaceus* in Libya and Egypt (Hering *et al.* 2009, 2010a,b, 2011a,b, 2012, 2013), three reed warblers with conspicuously short wings were trapped in the Siwa Oasis, in the Egyptian Sahara, in November 2009. DNA analysis revealed that they belonged to the eastern *fuscus* population of the *scirpaceus* complex and were close to the *A. scirpaceus avicenniae* subgroup known as 'Mangrove Reed Warbler', which occurs along the Red Sea (for taxonomy see Leisler *et al.* 1997, Helbig & Seibold 1999, Fregin *et al.* 2009, Kennerley & Pearson 2010). In subsequent years, intensive field studies were undertaken on this reed warbler, which only occurs in the large desert depressions of the Libya / Egypt border region. The results showed several diagnostic characters within the reed warbler superspecies, suggesting that a new subspecies was involved, distinguished by biometrics, habitat, breeding biology and behaviour.

Eurasian Reed Warblers display a complex phylogeographic pattern that has not been completely resolved (Hering *et al.* 2009, Jiguet *et al.* 2010, Procházka *et al.* 2011, Hering *et al.* 2012, Stepniowska & Ożarowska 2012, Winkler *et al.* 2013, Arbabi *et al.* 2014, Winkler *et al.* in prep.). However, relationships among populations north of the Sahara are rather well understood. Two migratory groups occur, comprising nominate *scirpaceus* and eastern

*fuscus*, and largely sedentary populations currently united into *A. baeticatus*, which occur in Africa and in Iberia (Winkler *et al.* 2013, in prep.). Another form, *avicenniae*, described by Ash *et al.* (1989) and found along the Red Sea as well as in the eastern Sahara, is closest to *fuscus* (Hering *et al.* 2009, 2011a, 2012, 2015).

## Material and Methods

*Study period.*—The initial discovery was made at Siwa, Egypt, on 19–24 November 2009 (JH & H. Hering). From 30 December 2009 to 1 January 2010, and again on 27–28 December 2010, the area around Al Jaghub in Libya was searched for short-winged reed warblers (JH & H. Hering). Thereafter, further studies in the breeding period were conducted on 27 April–3 May 2011 at Siwa (JH, E. Fuchs). The Egyptian oases of Bahariya, Farafra, Dakhla, Kharga (Khārija) and Bāris were explored on 26 December 2011–10 January 2012 (JH & H. Hering). Winter presence in Siwa and the absence of reed warblers in Bahariya were confirmed on 26 December 2012–4 January 2013 (JH & H. Hering). A concluding visit in the breeding season was made to Siwa and Bahariya on 11–21 May 2014 (JH, E. Fuchs & W. Heim).

*Trapping.*—The necessary trapping to take biometrics and to collect blood samples was undertaken using mist-nets, with the permission of the Administration of the Siwa Protectorate (April/May 2011, May 2014). Measurements and ringing were made in accordance with recent guidelines (Deutsche Ornithologen-Gesellschaft 2011). To attract and trap birds, an acoustic lure was used with the voices of Eurasian and African Reed Warblers (recordings on Chappuis 2000, Schulze 2003), as well as recordings of the local reed warblers. The birds caught in May 2014 were fitted with Helgoland Observatory metal rings. One ringing casualty and one dried corpse are preserved as study skins at the Senckenberg Natural History Collections, Dresden, Germany.

*Molecular analysis.*—Blood samples were taken from 49 reed warblers mist-netted at Siwa, of which ten were successfully sequenced. Genetic analyses were undertaken at the Konrad-Lorenz-Institut für vergleichende Verhaltensforschung [Institute of Ethology] in Vienna. Blood samples used to classify individual birds came from Lake Neusiedler (*A. s. scirpaceus*), or were made available by S. Fregin (see Leisler *et al.* 1997, Fregin *et al.* 2009) for *A. s. avicenniae* and *A. s. fuscus*, and by V. Salewski for *A. baeticatus guiersi* (Senegal) and *A. s. scirpaceus* (Germany, Lake Constance). We sequenced two sections of the mitochondrial genome, a 594-base section of the cytochrome-*b* gene and 543 bases of the mitochondrial control region II (Bensch & Hasselquist 1999, Singh *et al.* 2008) using standard methods and standard primers, and a primer (for CR II) developed by M. Kapun. BigDye chemistry (Applied Biosystems) was used for all sequencing reactions, and the products were sequenced on an ABI PRISM 3130 9 I automated sequencer (Applied Biosystems). Alignments were produced with MUSCLE version 3.8 (Edgar 2004) and optimised manually.

*Bioacoustic analysis.*—For recording songs and calls, digital audio recorders Swissonic MDR-2 and Olympus LS3 were used. Recordings were produced in uncompressed wav format with 44.1 kHz sampling and 16-bit resolution. Evaluation was performed in the Tierstimmenarchiv des Museums für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin [Animal Voice Archive at the Natural History Museum, Leibniz Institute, Humboldt University, Berlin] using the programme Avisoft SASLab Pro (Version 5.0.14). For all sonograms the following parameters were uniformly selected: sampling rate—22.05 kHz, FFT length—512 measuring points, Hamming Window, and 50% overlap. Recordings made in Siwa Oasis in April / May 2011 and May 2014 can be heard at: [www.tierstimmenarchiv.de](http://www.tierstimmenarchiv.de) (Reg. nos. TSA:

Acrocephalus\_scirpaceus\_DIG0135\_01–DIG0135\_10 and TSA: Acrocephalus\_scirpaceus\_DIG0190\_11–DIG0190\_23).

## Results and Diagnosis

Field observations of reed warblers in north-east Africa show that, alongside passage migrants (long-winged Eurasian Reed Warblers *A. s. scirpaceus* and *A. s. fuscus*), birds belonging to *fuscus* that breed in the wider region (Nile Delta and Valley), *A. s. avicenniae* (along the Red Sea), African Reed Warbler *A. baeticatus* (breeding in, e.g., Libya) and Clamorous Reed Warbler *A. stentoreus* (breeding in oases further east, and in the Nile Delta and Valley), there is also an undescribed, short-winged reed warbler taxon breeding in the desert depressions of the Egypt / Libya border region.

**Breeding range.**—The sedentary short-winged form is restricted to the depressions of Qattara, Siwa, Sitra and Al Jaghbub in the eastern Libyan and Egyptian desert, within just c.20,500 km<sup>2</sup> of suitable habitat. The stronghold is Siwa Oasis, where the birds nest in reedbeds, but also at high density in date palm and olive gardens. At other oases, inhabited by people like Qara and Al Jaghbub, or uninhabited like Sitra, only stands of reed are used. Nest sites are all 5–55 m below sea level. As all of the unexplored (and currently uninhabited) oases that could harbour reed warblers are in desert depressions, it can be assumed that the entire breeding range of the taxon is below sea level (Fig. 1, Table 2).

**Siwa Oasis (Egypt).**—Siwa Oasis, with its 18 lakes, 150 artesian springs and extensive oasis gardens, forms the core range (Fig. 2). In the c.28-km broad and 50-km long oasis, which is part of Siwa Protectorate, all large areas of reed as well as plantations of old date palms and olive trees have been occupied by the reed warbler. Nest sites are all 6–20 m below sea level. Qara oasis to the north-east is c.100 km distant, while Al Jaghbub oasis to the north-west is 110 km away and Sitra oasis to the south-east is c.150 km.

**Qara Oasis (Egypt).**—In this isolated oasis, on the western edge of the Qattara Depression, the reed warbler was found at 55 m below sea level in an extensive reedbed. There was no evidence of it in the few open oasis gardens.

**Al Jaghbub Oasis (Libya).**—The Al Jaghbub depression comprises several small areas below sea level, where several sight records of the reed warbler were made and nests were found in stands of reed c.5 m below sea level near the inhabited oasis. The oasis gardens of Al Jaghbub, which are only small in extent, do not fulfil its habitat requirements.

Further sight records of short-winged reed warblers were made in other reedbeds and oasis gardens in Siwa, in stands of reed in Sitra, as well as at Malfa salt lake near Al Jaghbub. As yet no field work has been undertaken at the very isolated El Moghra lake, Qattara Depression, which probably forms the north-east border of the reed warbler's range. There is, however, a record of a single dead 'reed warbler' there (Goodman & Ames 1983), but it appears that the specimen was not preserved, as it is not among the expedition material at the Field Museum of Natural History, Chicago (J. M. Bates *in litt.* 2015). Its real identity thus remains unknown.

It can be assumed that the range of this form is restricted to the large Libyan Desert depressions on the Libya / Egypt border. The evidence for this assumption is that a targeted search of the eastern oasis belt proved fruitless. In December 2011 and May 2014 no records were made during intensive work in the reedbeds and extensive oasis gardens of Bahariya. Negative evidence was also obtained at the other large Egyptian oases of Farafra, Dakhla, Kharga (Khārija), Bāris, and Wadi Natrun.

Breeding sites of closely related taxa (*A. s. scirpaceus*, *A. s. fuscus*, *A. s. avicenniae* and *A. baeticatus* ssp.) all lie several hundred kilometres away. To the west, African Reed Warbler breeds in Libya, in oases in the central Sahara and near the coast in Cyrenaica, where it is



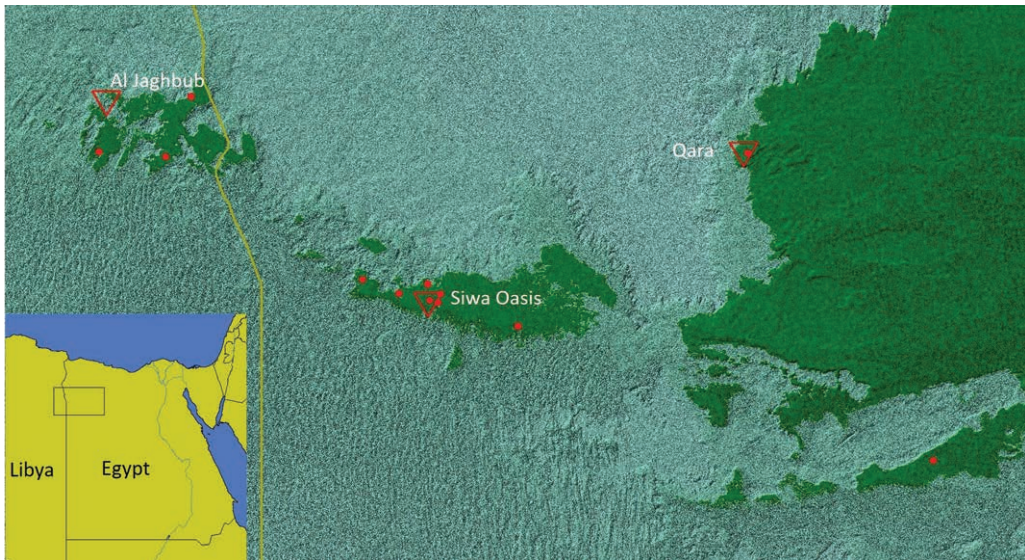


Figure 1. Relief map of the study area with records of the newly discovered taxon shown as red dots. Areas below sea level shown in green. Map constructed from NASA SRTM1 elevation data using the Behrmann cylindrical equal-area projection.



Figure 2. Oasis gardens of Siwa with the Amun Temple, the core breeding range of the newly discovered taxon, Siwa, Egypt, 20 November 2009 (Jens Hering)

sympatric with Eurasian Reed Warbler (Hering *et al.* 2009, 2010a,b, 2011b). It is probable that *Acrocephalus* breeding in isolated oases in south and south-east Libya are also African Reed Warblers (Hering *et al.* 2011a). To the east, Eurasian Reed Warbler breeds in the Nile Delta alongside Clamorous Reed Warbler (Meininger *et al.* 1986, Goodman & Meininger 1989, Ożarowska *et al.* 2011). Recent work has confirmed breeding of *A. s. fuscus* there (JH pers. obs.). Two trapped Eurasian Reed Warblers (wing 64 mm) with brood patches, in Wadi El Rayan south-west of Al Fayyūm, require further investigation (Stępniewska & Ożarowska 2012), but were probably also *fuscus* breeding on the Nile. Recent studies in Egypt have also revealed that ‘Mangrove Reed Warbler’ (*avicenniae*) nests on the Red Sea coast (Hering *et al.* 2012, 2013).

Based on morphological, molecular and ecological differences, as well as in behaviour and song types (see below), when compared with all known taxa in the *scirpaceus / baeticatus*

complex, we consider the population of the great Egyptian depression to represent an undescribed subspecies of Eurasian Reed Warbler, which we name:

***Acrocephalus scirpaceus ammon*, subsp. nov., Siwa Reed Warbler**

**Holotype.**—Adult (sex unknown), Senckenberg Natural History Collections, Dresden, Germany (SNSD) no. 2014/64, dried corpse found near nest site at start of breeding season, Siwa Oasis, Egypt (29°13'16.58"N, 25°25'43.33"E, 16 m below sea level), 12 May 2014, collected by JH, W. Heim & E. Fuchs. Cause of death: assumed exhaustion / dehydration.

**Paratype.**—Adult female (egg in ovary), SNSD 2014/69, at the same locality and on same date as the holotype, by the same collectors. Ringing casualty due to predation (ring no. Helgoland, Germany [B] 90362139).

**Description of holotype.**—Forehead, crown (large parts missing), nape and mantle Raw Umber (Smithe 1975, no. 123), merging into more Cinnamon (123A) back to uppertail-coverts. Eye-ring not visible. Lores, ear-coverts and sides of breast Buff (124), contrasting with whitish / off-white chin, throat and upper breast. Lower breast and belly Buff (124), flanks varying slightly between Yellow Ocher (123C), Clay Color (123B) and Pale Pinkish Buff (121D). Thighs Clay Color (123B) with a rusty hue. Vent not well preserved but single feathers have whitish-cream (off 54) tinge. Undertail-coverts (few remaining in holotype) whitish. Scapulars, marginal coverts and centres of median and greater wing-coverts pure Raw Umber (123), fringes of median and greater wing-coverts Clay Colour (123B). Alula as greater wing-coverts but Tawny Olive (223D) fringe. Primaries and secondaries Hair Brown (119A) with Tawny Olive (223D) outer fringes. Proximate half of pp2–7 (counted ascendently) with inner webs diffusely margined whitish grey. Pp8–10 and secondaries have their inner webs entirely fringed whitish grey. Tertiaries Dark Drab (119B, i.e. paler than secondaries) with Tawny Olive (223D) fringes. Leading edge Buff (124), lesser and greater underwing-coverts off-white. Ventral coloration of primaries and secondaries as in dorsal view. Shafts of flight feathers same colour as feather centres, but fractionally darker. Outer rectrix (fresh) off-white on inner web and tip, with Drab (27) centre, shaft darker; growth bars obvious. Remaining rectrices (worn) Dark Drab (119B) with very narrow Tawny Olive (223D) fringes and tips. Underside identical. Bare part coloration (in specimen): maxilla Sepia (119), cutting edges and mandible Drab-Grey (119D). Gape not visible. Tarsometatarsus Brownish Olive horn (29), toes and claws Vandyke Brown horn (121), soles paler (yellowish). For measurements see Table 1.

**Variation.**—Single paratype very similar to holotype, but upperparts slightly more bleached, breast and belly visibly paler, and flanks Tawny (38) instead of Pale Pinkish Buff (121D) as in holotype. Remiges (except pp2–3, numbered ascendently, and secondaries) and rectrices heavily worn.

**Diagnosis.**—In the field, the new taxon appears rather small (visibly so vs. *A. s. scirpaceus*, *A. s. fuscus*; shorter winged than *A. palustris*), with brown upperparts, cinnamon rump and uppertail-coverts, yellowish-brown flanks and whitish underparts. Overall coloration, as in other reed warbler taxa, individually variable (Harvey & Porter 1984, Schulze-Hagen 1991). The upperparts can be heavily affected by UV-light / sun exposure and appear bleached to hay colour. Juveniles, like other reed warblers, easily identified by their fresh dark brown plumage, which limits contrast with the cinnamon rump. Song similar to other taxa of the *scirpaceus* / *baeticatus* superspecies and only distinguishable using sonograms (see below). Most conspicuous are the short wings and toes (similar to *A. s. avicenniae*, *A. baeticatus* spp., but see Table 1 for diagnostic differences in measurements; Figs. 12–13). Identification of the live bird in the hand relies—apart from small size and short wings, compared to *A. s. scirpaceus*, *A. s. fuscus* and *A. palustris*—on distinguishable emargination on inner web of

TABLE 1

Standard measurements of two specimens of *A. s. amnon* compared to closely related taxa, using museum specimens (SNSD = Senckenberg Naturkundliche Sammlungen Dresden; ZMB = Museum für Naturkunde Berlin; ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig Bonn; IZH-V = Zentralmagazin Naturwissenschaftlicher Sammlungen der Martin-Luther-Universität Halle-Wittenberg; SMNS = Staatliches Museum für Naturkunde Stuttgart; NHMUK = Natural History Museum Tring). \* = weakly developed; abbreviations follow Deutsche Ornithologen-Gesellschaft (2011): Wmax = wing from carpal joint to tip of longest primary (max. chord); tail T1 = from the two innermost rectrices, where their bases emerge from the skin to the tip of the longest feather; bill BSk = from the angle at the front of the skull to the tip; bill BF length of exposed culmen from foremost feathers to tip; bill width BWD = at distal edge of nostrils; bill width BWF = at feathering; Tarsus Tar2 = from back of intertarsal joint to front edge of last undivided scale; hind toe vToeh = taken ventrally, notches of separation of foot from toe-pads to base of claws; central toe vToec = central toe, otherwise as previous; vClh = taken ventrally, claw of hind toe from base to tip; vClc = central toe, otherwise as previous; P1 to P10 = pp1–10 (counted from outer edge of wing, p1 being smallest feather); WT = wingtip; PC = primary-coverts; Kipp index = distance between tip of s1 and tip of longest primary in naturally folded wing; R1 to R6 = rr1 (outer) to 6 (inner); shape of bill = measured against millimetre paper, distance of bill tip to horizontal gape of bill; all measurements in mm.

**Author:** 1 = auct.; 2 = Ash *et al.* 1989; 3 = (Ehrenberg, 1833); 4 = (Hermann, 1804); 5 = Reichenow, 1908; 6 = (Bechstein, 1798). **Status:** h = holotype; p = paratype; s = syntype; div = detached wing. **Age:** ad = adult; br = adult (breeding); ju = juvenile; ? = not given. **Sex:** f = female; m = male; ? = not given. **Collected by / Measured by:** AM = A. F. v. Mecklenburg; B = Berg; BA = B. Alexander; BM = BMNH staff; BS = B. Sergeevic; CE = C.G. Ehrenberg; DH = D. Heldecke; DP = D. Pearson; EF = E. Fuchs; ES = E. Stresemann; FH = F.W. Hemprich; GN = G. Nikolaus; HB = H. v. Bötticher; HL = H. Lynes; HS = H. Schubotz; JH = J. Hering; RP = R. Piechocki; WH = W. Heim; Z = Zsch. (Mr. Zschorn); ZN = ZNS staff; ? = not given. **Measurements:** [b] = broken; [l] = [lacking]; [m] = [moult]; [n] = [not taken]; [w] = [worn].

Genus	Specific epithet	Author	Status	Age	Sex	Locality	Date	Collected by	Measured by	Wmax left	Wmax right	Tail T1	Bill BSk	Bill BF	Tarsus Tar2 left	Tarsus Tar2 right	Bill width BWD	Bill width BWF	Hind toe vToeh	Hind toe claw vClh	Central toe vToec	Central toe claw vClc	Length P1	P1/PC	P2/WT	P3/WT	P4/WT	P5/WT	P6/WT	P7/WT	P8/WT	P9/WT	P10/WT	Kipp index	Emargination inner web P2	Emargination inner web P3	Notch outer web P3	Notch outer web P4	Tail feather R1/R6	Bristles	Shape of bill
<i>Acrocephalus</i>	<i>scirpaceus</i>	1 h	SNSD 2014/64	ad	?	Siwa, Egypt	12 May 2014	JH, EF, WH	JH	56.3	56.1	48.2	14.9	12.0	20.8	20.9	3.8	4.7	7.8	6.5	7.2	5.0	7.4	-1.2	-0.8	0.0	-0.5	-2.2	-3.4	-5.0	-5.8	-8.0	-8.8	11.0	14.0	16.5*	16.8	0.0	6.8	6.8	0.2
		1 p	SNSD 2014/69	ad	?	Siwa, Egypt	12 May 2014	JH, EF, WH	JH	52.3	52.9	47.8	14.2	10.3	20.0	19.4	2.4	4.4	7.7	7.6	9.8	6.0	6.0	-3.0	-3.8	-1.0	0.0	-1.1	-2.3	-3.9	-4.8	-6.7	-8.0	10.7	11.8	9.2*	15.4	0.0	8.3	4.9	1.7
<i>Acrocephalus</i>	<i>avcaninae</i>	2	ZMB 2002/95	ju	m	Tokhoshi, Awdal, Somalia	16 Oct 2002	GN	GN	57.1	55.0	49.3	16.0	11.2	21.0	20.9	3.0	5.3	8.8	7.7	10.2	5.0	7.4	-4.1	[m]	0.0	0.0	0.0	-3.0	-4.0	-5.3	-7.1	-8.4	10.0	[m]	[m]	11.5*	7.7	5.3	1.1	
		2	ZFMK 76.818	br	m	Suakin, NE Sudan	11 Mar 1976	GN	GN	57.0	59.2	58.0	15.4	11.3	19.8	18.8	3.2	6.1	8.2	6.9	10.2	4.9	8.3	-3.0	-4.7	0.0	0.0	-1.4	-2.8	-5.0	-6.2	-7.0	-9.2	11.0	13.7	10.8	17.0	11.0*	5.3	5.7	1.4
<i>Acrocephalus</i>	<i>avcaninae</i>	2	ZFMK 76.819	br	m	Suakin, NE Sudan	10 Mar 1976	GN	GN	56.2	56.0	49.2	15.4	9.6	20.0	19.7	3.3	5.9	8.4	6.7	9.0	5.2	7.2	-3.1	-3.0	0.0	-0.5	-1.0	-3.2	-4.8	-5.2	-7.5	-9.0	10.5	13.4	10.7	13.0	9.3*	5.1	5.4	1.5
		2	ZFMK 76.820	br	m	Suakin, NE Sudan	10 Mar 1976	GN	GN	56.6	58.0	50.0	15.3	10.6	19.4	19.0	3.4	6.3	8.3	6.0	10.0	5.0	6.7	-2.9	-4.2	0.0	-0.3	-1.9	-3.7	-6.0	-7.3	-8.0	-10.0	10.4	13.1	10.7	13.5	9.6*	6.5	6.7	1.3



TABLE 1 cont.

**Author:** 1 = auct.; 2 = Ash et al. 1989; 3 = (Ehrenberg, 1833); 4 = (Hermann, 1804); 5 = Reichenow, 1908; 6 = (Beckstein, 1798). **Status:** h = holotype; p = paratype; s = syntype; div = detached wing. **Age:** ad = adult; br = adult (breeding); ju = juvenile; ? = not given. **Sex:** f = female; m = male; ? = not given. **Collected by / Measured by:** AM = A. F. v. Mecklenburg; B = Berg; BA = B. Alexander; BM = BMNH staff; BS = B. Sergeev; CE = C.G. Ehrenberg; DH = D. Heidecke; DP = D. Pearson; EF = E. Fuchs; ES = E. Sremsmann; FH = F.W. Hemprich; GN = G. Nikolaus; HB = H. v. Böttcher; HL = H. Lynes; HS = H. Schubotz; JH = J. Hering; RP = R. Prechock; WH = W. Helm; Z = Zsch. (Mr Zschorn); ZN = ZNS staff; ? = not given. **Measurements:** [bl] = broken; [l] = [lacking]; [m] = [moult]; [nt] = [not taken]; [w] = [worn].

Genus	Subspecific epithet	Author	Status	Inventry number	Age	Sex	Locality	Date	Collected by	Measured by	Wmax left	Tail T1	Bill BSK	Bill BF	Tarsus Tar2 right	Tarsus Tar2 left	Bill width BWD	Bill width BWF	Hind toe Vtoeh	Hind toe claw Vch	Central toe Vtoec	Central toe claw Vclc	Length P1	P1/PC	P2/WT	P3/WT	P4/WT	P5/WT	P6/WT	P7/WT	P8/WT	P9/WT	P10/WT	Kipp index	Emergination inner web P2	Emergination inner web P3	Notch outer web P3	Notch outer web P4	Tail feather R1/R6	Bristles	Shape of bill		
Acrocephalus	sarcocollis	2	ZFMK	76821	br	f	Suakin, NE Sudan	10 Mar 1976	GN	GN	56.3	52.1	15.0	10.1	19.3	19.8	2.9	5.2	8.5	6.1	10.1	5.2	7.8	-3.3	-3.7	0.0	-0.8	-2.6	-3.5	-4.9	-5.3	-8.0	-9.1	10.5	13.3	10.0	15.0	9.7*	3.4	6.0	2.4		
							Suakin, NE Sudan	11 Mar 1976	GN	GN	58.4	48.0	15.2	9.3	19.6	19.9	3.0	5.7	7.8	6.8	9.9	5.1	7.3	-2.0	-3.9	0.0	-0.5	-2.3	-3.8	-5.7	-7.5	-8.2	-10.8	11.9	13.3	11.5	16.5	11.0*	5.5	5.0	1.3		
Acrocephalus	sarcocollis	2	ZFMK	76823	br	f	Suakin, NE Sudan	11 Mar 1976	GN	GN	59.2	51.3	16.1	10.3	18.1	19.4	3.9	5.3	9.1	6.8	9.3	5.2	10.0	-2.1	-3.8	0.0	-0.1	-1.8	-3.7	-4.9	-6.7	-8.2	-10.0	11.3	13.5	10.7	14.1	10.1*	4.2	4.8	1.2		
							Suakin, NE Sudan	11 Mar 1976	GN	GN	57.0	57.5	15.0	9.6	19.3	18.6	3.3	5.2	8.0	6.8	9.4	5.0	7.7	-1.8	-5.0	-0.1	0.0	-2.3	-3.1	-3.9	-5.0	-7.6	-8.1	11.3	13.3	10.0	15.8	10.0*	5.8	5.0	0.8		
Acrocephalus	sarcocollis	2	ZFMK	76825	?	f	Suakin, NE Sudan	11 Mar 1976	GN	GN	55.9	56.0	14.4	10.1	19.1	18.9	3.9	5.8	7.7	6.1	9.2	5.7	7.8	-2.0	-3.6	0.0	-0.4	-1.8	-2.4	-3.2	-6.1	-6.9	-8.2	10.0	12.7	8.4	16.3	9.2*	6.2	5.5	1.7		
							30km N Suakin, NE Sudan	3 Aug 1981	GN	DP	57.0	57.0	15.8	9.1	19.2	20.5	3.0	5.1	9.2	7.2	10.6	5.4	9.1	0.0	-3.7	0.0	-1.1	-2.7	-4.2	-5.3	-6.4	-7.6	-8.0	9.4	12.8	[nt]	13.0*	[nt]	13.0*	[nt]	7.0	6.3	1.1
Acrocephalus	sarcocollis	2	SMNS	59306	ad	f	Suakin, NE Sudan	3 Aug 1981	GN	DP	55.0	55.4	16.2	11.6	21.0	20.3	3.3	6.2	8.8	7.1	10.7	5.4	[w]	[w]	-3.3	0.0	-1.1	-2.2	-4.0	-5.1	-6.7	-8.0	-9.2	9.8	12.7	[nt]	15.0*	[nt]	15.0*	[nt]	6.2	1.2	
							30km N Suakin, NE Sudan	18 Mar 1983	GN	DP	56.0	55.4	15.1	15.2	9.9	21.3	21.4	3.2	6.5	8.3	6.0	11.5	5.2	6.5	-2.8	-4.2	0.0	-0.2	-1.7	-2.3	-4.8	-6.6	-7.3	-9.9	11.1	12.7	[nt]	14.5*	[nt]	14.5*	[nt]	6.0	5.8
Acrocephalus	sarcocollis	2	SMNS	59910	ad	f	Suakin, NE Sudan	18 Mar 1983	GN	DP	56.2	50.9	14.8	9.5	20.3	19.9	2.9	5.9	8.4	6.3	10.4	5.1	6.4	-3.8	-4.7	0.0	-0.5	-3.0	-4.9	-6.0	-8.3	-9.2	-9.7	11.2	13.2	[nt]	16.2*	[nt]	16.2*	[nt]	5.5	5.9	1.0
							30km N Suakin, NE Sudan	18 Mar 1983	GN	DP	56.0	55.0	16.2	10.3	20.5	20.6	3.0	6.3	8.2	6.7	10.2	5.9	7.7	-2.6	-5.0	0.0	-0.4	-1.2	-4.2	-6.7	-7.8	-9.2	-10.5	10.8	12.8	[nt]	16.8*	[nt]	16.8*	[nt]	7.1	5.9	1.3

TABLE 1 cont.

**Author:** 1 = auct.; 2 = Ash et al. 1989; 3 = (Ehrenberg, 1833); 4 = (Hermann, 1804); 5 = Reichenow, 1908; 6 = (Beckstein, 1738). **Status:** h = holotype; p = paratype; s = syntype; div = detached wing. **Age:** ad = adult; br = adult (breeding); ju = juvenile; ? = not given. **Sex:** f = female; m = male; ? = not given. **Collected by / Measured by:** AM = A. F. v. Mecklenburg; B = Berg; BA = B. Alexander; BM = BMNH staff; BS = B. Sergeevic; CE = C.G. Ehrenberg; DH = D. Heidecke; DP = D. Pearson; EF = E. Fucius; ES = E. Stresmann; FH = F.W. Hemprich; GN = G. Nikolaus; HB = H. v. Böttcher; HL = H. Lynes; HS = H. Schubotz; JH = J. Hering; RP = R. Piechocki; WH = W. Helm; Z = Zsch. (Mr Zschorn); ZN = ZNS staff; ? = not given. **Measurements:** [b] = [lacking]; [m] = [moult]; [nt] = [not taken]; [w] = [worn].

Genus	Specific epithet	Author	Status	Inventory number	Age	Sex	Locality	Date	Collected by	Measured by	Wmax right	Wmax left	Tail T1	Bill BSK	Bill BF	Tarsus Tar2 right	Tarsus Tar2 left	Bill Width BWD	Bill Width BWF	Hind toe to Vtoeh	Hind toe to claw VCh	Central toe to Vtoec	Central toe to claw VCic	Length P1	P1/PC	P2MT	P3MT	P4MT	P5MT	P6MT	P7MT	P8MT	P9MT	P10MT	Kipp index	Emargination inner web P2	Emargination inner web P3	Notch outer web P3	Notch outer web P4	Tail feather R1/R6	Bristles	Shape of bill
<i>fuscus</i>	3 s	ZMB 260	? ?	N Arabia	not given				FH, CE	66.0	64.8	49.8	16.7	14.0	22.7	23.2	3.4	6.0	10.1	7.0	11.6	5.8	11.0	1.7	-1.7	0.0	-1.2	-3.5	-6.0	-7.1	[m]	-8.9	[m]	14.7	10.7	0.0	11.3*	0.0	6.1	4.8	0.8	
	3 s	ZMB 3958	? ?	[Nubia]	not given				FH, ES	65.9	65.4	53.8	15.9	11.5	21.3	22.7	3.0	5.6	10.2	7.0	11.0	4.9	11.1	0.0	-1.7	0.0	-1.3	-5.1	-7.3	[m]	-10.2	-11.4	-13.7	17.2	12.9	0.0	12.8*	0.0	7.4	[w]	1.3	
	3	ZMB 2000/40590	ju ?	Yeloten, Murgap R., Turkmenistan	24 Jul 1939				BS, ES	63.3	63.9	51.3	15.8	11.4	23.2	22.6	3.3	5.9	10.1	7.2	11.4	6.7	10.0	-0.1	-2.8	0.0	-2.1	-4.9	-7.6	[b]	-11.8	[m]	-13.7	16.8	11.0	0.0	14.4*	0.0	8.2	5.1	0.4	
<i>Acrocephalus</i>	4	IZH-V 7749	? ?	Halae [Halte/ Saale, Germany]	1816 [acqu.]				Z, HB	64.0	64.3	55.6	15.2	11.1	23.3	[b]	3.3	5.5	9.4	7.1	11.7	5.2	8.2	-3.0	-1.7	0.0	-1.8	-4.6	-8.0	-9.7	-10.8	-11.5	-13.1	16.2	11.7	6.8*	14.2	0.0	5.8	5.1	1.3	
	4	IZH-V 7751	? ?	Halae [Halte/ Saale, Germany]	not given				?, HB	65.0	64.2	53.2	14.9	9.6	22.6	21.9	3.2	5.3	9.0	7.0	11.4	5.2	8.9	-1.3	-1.2	0.0	-2.7	-5.2	-8.1	-10.7	-12.4	-14.7	-16.8	18.7	13.0	7.5*	11.0	0.0	7.7	5.0	1.0	
	4	IZH-V 7735	? ?	Halae [Halte/ Saale, Germany]	[< 1830]				Z, HB	62.4	62.8	50.5	14.5	10.7	22.8	21.5	3.2	6.1	9.1	7.2	12.0	6.6	9.4	-1.0	-2.5	0.0	-2.8	-6.6	-8.3	-9.5	-10.4	-12.0	-14.0	16.2	10.7	6.3*	14.4	0.0	5.5	5.1	0.8	
	4	IZH-V 4303	ad f	Faule Ort, Müritz, Germany	20 May 1969				?, ZN	64.0	65.0	54.4	15.6	11.7	20.8	21.6	3.2	5.3	9.6	7.3	11.1	6.3	9.7	-1.7	-1.7	-1.2	0.0	-1.7	-3.8	-6.4	-8.7	-10.7	-13.1	-13.7	16.4	12.9	7.5*	14.0	0.0	5.3	5.0	1.2
<i>scirpaceus</i>	4	IZH-V 4297	ad m	Faule Ort, Müritz, Germany	20 May 1968				?, ZN	67.9	68.1	54.5	16.3	10.8	22.5	22.7	3.3	5.2	9.2	7.3	11.4	6.2	10.5	0.8	-1.7	0.0	-2.6	-6.3	-8.7	-10.2	-14.2	-14.6	-15.3	18.3	13.2	7.6*	17.2	0.0	4.8	6.4	1.7	
	4	IZH-V 4294	ad m	Faule Ort, Müritz, Germany	29 May 1966				B, RP	64.8	65.7	54.6	15.1	10.8	22.2	22.2	3.2	5.4	8.4	7.6	11.3	7.0	8.7	-3.4	-2.7	0.0	-2.7	-5.0	-8.1	-10.2	-12.1	-14.3	-16.7	18.0	12.7	7.7*	13.5	0.0	2.4	6.0	1.2	
4	IZH-V 4874	ju f	Faule Ort, Müritz, Germany	7 Aug 1960				RP, RP	65.4	64.8	52.8	14.8	9.6	23.5	22.7	3.2	5.3	9.7	7.9	12.6	7.2	10.5	[m]	-1.3	0.0	-2.4	-5.4	-8.3	-10.8	-12.8	-14.0	-16.6	17.8	11.3	8.3*	13.1	0.0	3.2	5.0	0.7		





TABLE 2  
Records of the new taxon in desert depressions in the Egypt / Libya border region (captures, nests, and selected sight and song records).

Site	Coordinates	Metres below sea level	Type of record
Siwa Oasis, Ain Safi spring	29°08'03.71"N, 25°47'57.33"E	8	Capture
Siwa Oasis, Lake Zaytun	29°13'12.28"N, 25°33'32.48"E	20	Sight record
Siwa Oasis, Lake Siwa	29°13'17.74"N, 25°25'44.06"E	18	Capture, nests
Siwa Oasis, Lake Maraqi	29°15'29.24"N, 25°18'55.30"E	16	Capture, nests
Siwa Oasis, sewage ponds	29°14'46.52"N, 25°31'06.81"E	6	Capture, nests
Siwa Oasis, Cleopatra's Spring gardens	29°11'49.43"N, 25°33'02.09"E	9	Capture, nests
Siwa Oasis, gardens near Shali	29°12'10.13"N, 25°31'31.87"E	10	Capture, nests
Qara oasis	29°35'49.78"N, 26°30'51.69"E	56	Capture
Sitra oasis, Haisha spring marsh	28°46'30.35"N, 27° 5'36.67"E	18	Sight record
Al Jaghbub oasis, Freja salt lake	29°36'02.81"N, 24°29'37.22"E	11	Nest, sight record
Al Jaghbub oasis, Abuzed salt lake	29°35'14.05"N, 24°42'05.37"E	5	Nest
Al Jaghbub oasis, Malfa salt lake	29°44'57.57"N, 24°46'51.44"E	5	Sight record

p2 and p3 (numbered ascendently) and emargination / notches on outer web of p3 (partly lacking in other taxa—see below), rather short toes (central toe <10 mm long) and slender bill (width at base <5 mm, length nearly identical to other taxa).

**Bare-part colours.**—Iris (in live bird) dark olive in juveniles and pale olive in adults. Gape reddish orange, tongue red with yellow tip; nestlings and juveniles have two dark spots on tongue.

**Geographic distribution.**—Large Libyan Desert depressions on the Libya / Egypt border (Qattara, Siwa, Sitra and Al Jaghbub).

**Specimens studied.**—For museum acronyms, see Table 1. *A. s. ammon* ( $n = 2$ ): SNSD 2014/64, 2014/69. *A. s. fuscus* ( $n = 3$ ): ZMB 260, 3958 (syntypes of *Curruca fusca* Hemprich & Ehrenberg, 1833), 2000/40590. *A. s. avicenniae* ( $n = 15$ ): ZMB 2002/95, ZFMK 76.818–76.825, SMNS 59305–59306, 59909–59911, NHMUK 1952.25.23 (holotype of *Acrocephalus baeticatus avicenniae* Ash *et al.*, 1989, photographs). *A. s. scirpaceus* ( $n = 31$ ): ZMB 43/1503, 54/81, 1995/42, 76/65, IZH-V 3510, 3528a–b, 4292–4303, 4865–4867, 4869–4874, 4877–4879. *A. b. cinnamomeus* ( $n = 5$ ): ZMB 48/9 (holotype of *Acrocephalus cinnamomeus* Reichenow, 1908), NHMUK 1922.12.8.1015–1017, 1911.12.23.2289. *A. r. rufescens* ( $n = 2$ ): ZMB 30843, 59/1. *A. g. gracilirostris* ( $n = 2$ ): ZMB 31158, 31159. *A. g. jacksoni* ( $n = 2$ ): ZMB 2000/40602–603. *A. s. stentoreus* ( $n = 2$ ): ZMB 3942 (syntype of *Curruca stentorea* Hemprich & Ehrenberg, 1833), 2000/40631. *A. palustris* ( $n = 9$ ): ZMB 2000/40573, 2000/40575, 54/82, 44/243, IZH-V 3526–3527, 4288–4290.

**Etymology.**—The epithet *ammon*, a noun in apposition (*cf.* Art. 11, 31.2.1., 31.2.3., ICZN 1999) derives from the ancient Egyptian sun god *Ammon-Re* (or *Amun-Re*) who was deified by the local people of the Siwa Oasis and its environs. Siwa was known by the names *Ammonion* and *Ammonium* during ancient times as the site of an oracle consulted by Bedouins. The ruins of the sun temple are centred in the gardens of Siwa Oasis (Fig. 2), the distribution hotspot of Siwa Reed Warbler. The English vernacular name refers to this locality.

### Comparisons with other *Acrocephalus* in the region

*A. scirpaceus avicenniae* Ash *et al.* 1989 (Figs. 3, 8–9), breeding in coastal mangroves in Egypt and nearby Sudan and Somalia (Ash *et al.* 1989, Dyrce 2006, Hering *et al.* 2012, 2013),

has grey-olive upperparts and whitish underparts with a yellow tinge towards vent, flanks equally pale, emargination on inner web of p2 and, sometimes albeit poorly developed, on p3, and emarginations on outer web of p3 and, hardly visible or even lacking, on p4. In comparison, *ammon* has a prominent cinnamon tinge to lower upperparts and more intense coloration (not whitish, but yellow ochre to pale pinkish buff) on flanks and lower belly. Emarginations on inner webs of primaries and emarginations on outer webs similar, especially compared to a series collected 30 km north of Suakin, north-east Sudan, with rather pointed wings. A first-year *avicenniae* from Somalia (ZMB 2002/95) is quite close in coloration to adult *ammon*, but the dorsal tone is olive-brown/grey in the former, not cinnamon. The overall size and eco-morphological measurements (wing shape and foot morphology) are similar in these taxa and reflect similarities in their ecological niches, such as non-migratory and tree-dwelling behaviour (*cf.* Table 1).

*A. s. fuscus* (Hemprich & Ehrenberg, 1833) (Figs. 4–5), known to migrate through Egypt at least (Goodman & Meininger 1989), differs in the following characters: strongly olive upperparts (fresh juveniles have rufous-tinged rump; in *ammon* cinnamon), more whitish underparts (rather buff in *ammon*), flanks only slightly washed clay colour, and thighs off-white (strongly clay with rusty hue in *ammon*). Fringes of primaries and secondaries less tawny olive and rather inconspicuous. In specimens, bill, legs and claws horn, thus much paler than *ammon*. Overall size visibly larger, especially wings, tarsi less so; slight emargination on outer web of p3, no notch / emargination on outer web of p4 in those specimens studied, but for populations in Arabia, Israel and presumably those in Nile Delta emarginations are occasionally recorded on p4 (D. J. Pearson *in litt.* 2015), no emargination on inner web of p3; primary projection indicates a migrant (*cf.* Table 1). Toes in *fuscus* considerably longer than *ammon* (central and hind toe >10 mm).

*A. s. scirpaceus* (Hermann, 1804) (Figs. 6–7), a common migrant in the region (Schulze-Hagen 1991, Pearson 1997, Dyrz 2006), is a rather uniformly coloured taxon with hair-brown (*cf.* Smithe 1975) upperparts (lacking cinnamon tinge of *ammon*), primaries, secondaries and wing-coverts lacking clay and tawny-olive fringes of *ammon*, underparts very similar or nearly indistinguishable from *ammon*, but on average with less prominent yellowish-ochre/pale pinkish-buff flanks. Larger than *ammon* with considerable differences in wing length and proportions (migratory vs. sedentary), with a rather slight but proximal emargination on inner web of p3 and considerably longer toes, with central toe >11 mm (in *ammon*, but statistically weak with two specimens <10 mm), indicating better adaptation to reedbed environment than in *ammon*, which is a more tree-dwelling bird.

*A. baeticatus cinnamomeus* Reichenow, 1908 (Figs. 8–9), also resident in region, breeding in Chad, western Sudan, South Sudan (Pearson 1997, Dyrz 2006) and nearby Libya (Hering *et al.* 2010a); similar to both *avicenniae* and *ammon*. Field data indicate that due to colour variation within *A. b. cinnamomeus*, differentiation between it and *ammon* is difficult (Hering *et al.* 2009, 2010a). The holotype of *cinnamomeus* (ZMB 48/9) is dorsally and ventrally unambiguously cinnamon (adult *ammon* is only cinnamon on upperparts while the underparts vary between pale buff, yellowish ochre and clay), but due to its being 'juvenile' this is not diagnostic. Adult *cinnamomeus* is similar to *ammon* on belly and flanks, but less whitish on throat and upper breast (also rather buff). Upperparts, especially forehead, crown, mantle and upper back, visibly less cinnamon than *ammon*, more olive-brown; cinnamon tinge only on vent and uppertail-coverts. However, these differences are probably due to UV bleaching and moult cycle, respectively, rather than a diagnostic character. Bill more amber to yellowish ochre in *cinnamomeus*, rather than pale grey as in *ammon* according to both label / field data and specimens. Overall size is similar in *ammon* with a slightly broader bill and shorter tail. Divergence in eco-morphological characters is



Figure 3 (left). Holotype of *Acrocephalus scirpaceus avicenniae* NHMUK 1952.25.23, lateral, ventral, lateral, dorsal views (© Harry Taylor, Natural History Museum, London)

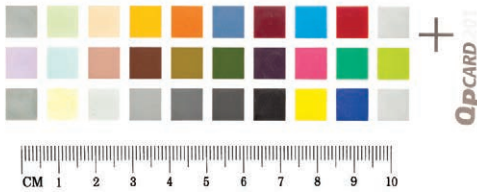


Figure 4 (below). Left to right: dorsal view of *Acrocephalus scirpaceus ammon* paratype SMSD 2014/69, holotype SMSD 2014/64; *A. s. fuscus* syntypes ZMB 260 and 3958, ZMB 2000/40590 (Frank D. Steinheimer)





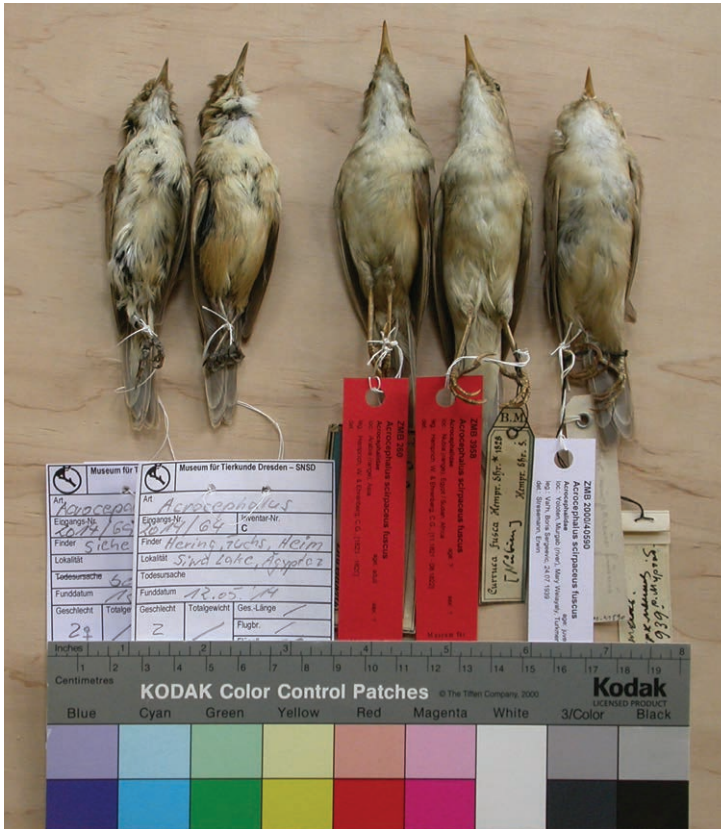


Figure 5 (left). Left to right: ventral view of *Acrocephalus scirpaceus ammon* paratype SMSD 2014/69, holotype SMSD 2014/64; *A. s. fuscus* syntypes ZMB 260 and 3958, ZMB 2000/40590 (Frank D. Steinheimer)



Figure 6 (below). Left to right: dorsal view of *Acrocephalus scirpaceus ammon* paratype SMSD 2014/69, holotype SMSD 2014/64; *A. s. scirpaceus* ZMB 43/1503, 54/81, 1995/42, 76/65 (Frank D. Steinheimer)

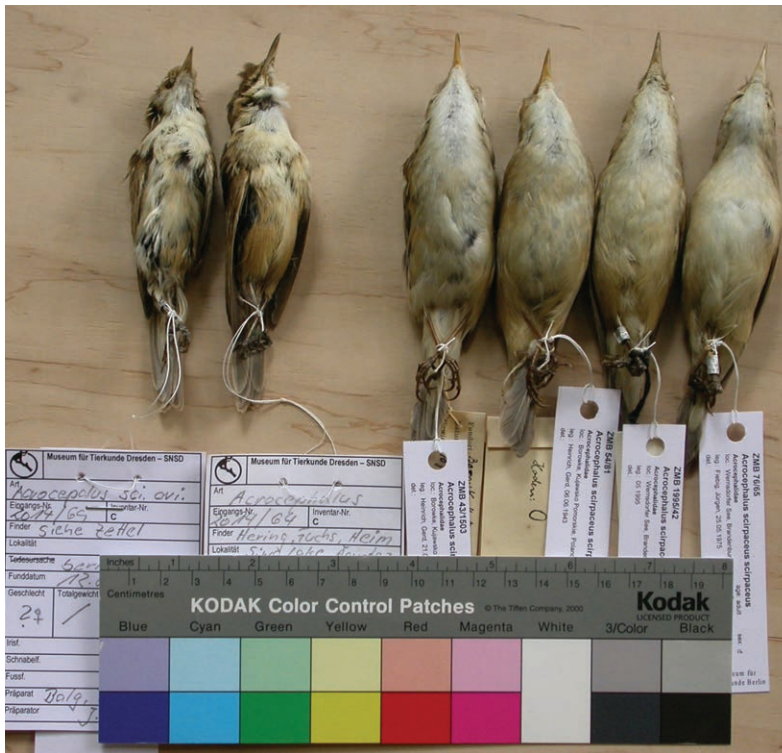


Figure 7. Left to right: ventral view of *Acrocephalus scirpaceus ammon* paratype SMSD 2014/69, holotype SMSD 2014/64; *A. s. scirpaceus* ZMB 43/1503, 54/81, 1995/42, 76/65 (Frank D. Steinheimer)



Figure 8. Left to right: dorsal view of *Acrocephalus scirpaceus ammon* paratype SMSD 2014/69, holotype SMSD 2014/64; *A. baeticatus cinnamomeus* holotype ZMB 48/9; *A. s. avicenniae* SMNS 59305, 59306, 59909–911 (contra label, identified by D. J. Pearson) (Frank D. Steinheimer)





Figure 9. Left to right: ventral view of *Acrocephalus scirpaceus ammon* paratype SMSD 2014/69, holotype SMSD 2014/64; *A. baeticatus cinnamomeus* holotype ZMB 48/9; *A. s. avicenniae* SMNS 59305, 59306, 59909–911 (*contra* label, identified by D. J. Pearson) (Frank D. Steinheimer)



Figure 10. Left to right: dorsal view of *Acrocephalus scirpaceus ammon* paratype SMSD 2014/69, holotype SMSD 2014/64; *A. palustris* ZMB 2000/40573, 2000/40575, 54/82, 44/243 (Frank D. Steinheimer)



Figure 11. Left to right: ventral view of *Acrocephalus scirpaceus ammon* paratype SMSD 2014/69, holotype SMSD 2014/64; *A. palustris* ZMB 2000/40573, 2000/40575, 54/82, 44/243 (Frank D. Steinheimer)



Figures 12–13. Comparison of primary projection: left *Acrocephalus s. scirpaceus* and right *A. s. ammon*, Qara, Egypt, 15 May 2014 (Jens Hering)

best seen in length of toes (in two vs. five specimens <8 mm in *ammon*, >8 mm in *cinnamomeus* for hind toe, cf. Table 1) due to differing niches (in *cinnamomeus*, denser vegetation such as reed, bulrushes, sedges and papyrus used for foraging and nest sites, with no special adaptations for tree-dwelling). Measurements cited by Hering *et al.* (2010a) from live birds in Libya indicate a considerably larger bill (measured roughly



from tip to feather bases 10.3–12.0 mm in *ammon* / 15.5–16.0 mm in *baeticatus*) and stronger tarsus (19.4–20.9 mm in *ammon* / 24.5–27.0 mm in *baeticatus*) though measurements of live birds can differ considerably from specimens (*cf.* Deutsche Ornithologen-Gesellschaft 2011) so these data cannot be compared with Table 1. Overall, *cinnamomeus* is morphologically closest to the new taxon.

*A. palustris* (Bechstein, 1798) (Figs. 10–11), which occurs in the region on migration (Schulze-Hagen 1991, Pearson 1997, Dyrzcz 2006), is overall very similar to *A. s. fuscus*, with upperparts uniformly olive-grey without any rufous or cinnamon tinge, margins of wing-coverts and primaries pale buff, not tawny olive or clay as in *ammon*. Underparts warm buff similar to *ammon*, but without any contrast vs. thighs and flanks as in *ammon* (flanks vary between yellow-ochre, clay and pale pinkish buff; thighs rusty clay). The contrast between upperparts and underparts is much less prominent in this plain-coloured species than in *ammon*. *A. palustris* has considerably longer (on average *c.*10 mm difference) and more pointed wings compared to *ammon* (*cf.* tip of primaries in relation to wingtip, Kipp index and emarginations / notches of primaries in Table 1); the toes are *c.*2–3 mm longer, indicating a more distinct usage of vertical structures compared to *ammon*.

**Other plain-coloured species.**—Great Reed Warbler *A. arundinaceus*, with some moving through north-east Africa on migration, Greater *Acrocephalus rufescens* and Lesser Swamp Warblers *A. gracilirostris*, both breeding in Chad and South Sudan, and *A. stentoreus*, which breeds *inter alia* in Egypt are all considerably larger (Pearson 1997, Dyrzcz 2006).

**Live measurements.**—For biometric analysis, 43 individuals trapped in Siwa had wing length (flattened and straightened), and some also had tail, bill, tarsus, length of p3 (numbered ascendently), and mass measured. A conspicuous character of reed warblers from Siwa is their short wings (Figs. 12–14). With a mean length of 56.5 mm (s.d. = 1.2 mm, *n* = 43) they are clearly shorter than the wing length—also measured on live birds—of *A. s. scirpaceus* (mean = 65.4 mm, s.d. = 2.0 mm, *n* = 39; JH unpubl., D. J. Pearson *in litt.* 2016), *A. s. fuscus* (mean = 67.1 mm, s.d. = 1.3 mm, *n* = 21; D. J. Pearson *in litt.*), *A. baeticatus* (Libya) (mean = 61.6 mm, s.d. = 2.6 mm, *n* = 21; Hering *et al.* 2009, 2010a, 2011b; JH unpubl.) and *A. s. avicenniae* (mean = 59.0 mm, s.d. = 1.5 mm, *n* = 16; JH unpubl., D. J. Pearson *in litt.* 2016). Pairwise comparisons of wing lengths of Siwa individuals with those of other taxa were statistically significant (*p*<0.05) in every case (linear models with wing length as dependent variable and the factor subspecies as explanatory variable; *ammon/scirpaceus*:  $F_{1,80} = 612.4$ , *p*<0.001, adjusted  $R^2 = 0.883$ ; *ammon / fuscus*:  $F_{1,75} = 1056.0$ , *p*<0.001, adjusted  $R^2 = 0.933$ ; *ammon / baeticatus*:  $F_{1,62} =$ , *p*<0.001, adjusted  $R^2 = 0.642$ ; *ammon / avicenniae*:  $F_{1,57} = 44.5$ , *p*<0.001, adjusted  $R^2 = 0.428$ ).

Various authors have regarded the length of the tarsometatarsus (tarsus) as a better parameter of comparative measurement than wing length (Rising & Somers 1989, Freeman & Jackson 1990, Senar & Pascual 1997). However with a mean length of 20.7 mm (s.d. = 0.5 mm, *n* = 34), this character too shows Siwa birds to be the smallest form compared to *A. s. scirpaceus* (mean = 22.4 mm, s.d. = 0.6 mm, *n* = 31) and *A. s. fuscus* (mean = 23.0 mm, s.d. = 0.6 mm, *n* = 6), but not *A. s. avicenniae* (mean = 20.5 mm, s.d. = 0.6 mm, *n* = 8) (Fig. 15). Pairwise comparisons of tarsus lengths of reed warblers from Siwa with those of the other taxa again resulted in statistically significant (*p*<0.05) differences in most cases (linear models with tarsus length as dependent variable and the factor subspecies as the explanatory variable; *ammon / scirpaceus*:  $F_{1,63} = 167.1$ , *p*<0.001, adjusted  $R^2 = 0.722$ ; *ammon / fuscus*:  $F_{1,49} = 116.1$ , *p*<0.001, adjusted  $R^2 = 0.697$ ; *ammon / avicenniae*:  $F_{1,40} = 1.2$ , *p* = 0.289, adjusted  $R^2 = 0.004$ ). In *A. b. cinnamomeus* lengths are similar.

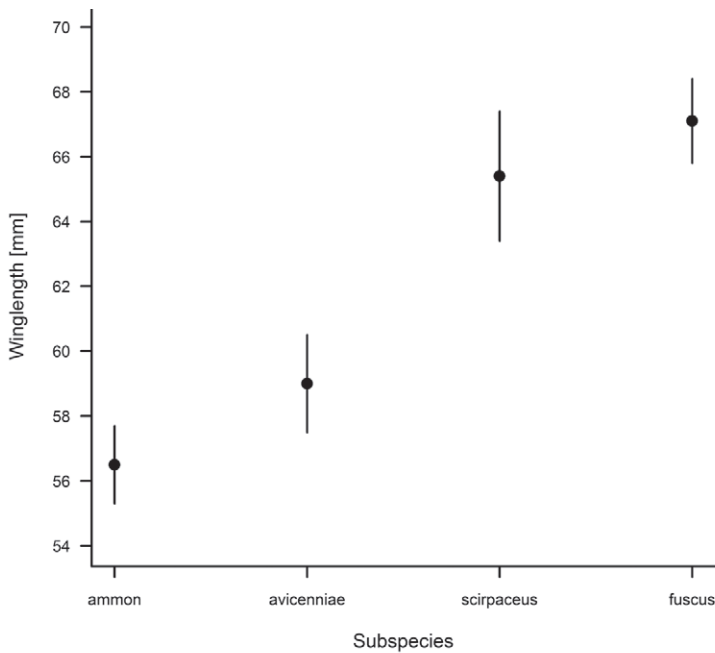


Figure 14. Wing length of Siwa Reed Warbler *Acrocephalus scirpaceus ammon* compared to other reed warbler taxa ( $n$ : *ammon* 43, *avicenniae* 16, *scirpaceus* 39, *fuscus* 21). X-axis: subspecies; y-axis: wing length (in mm).

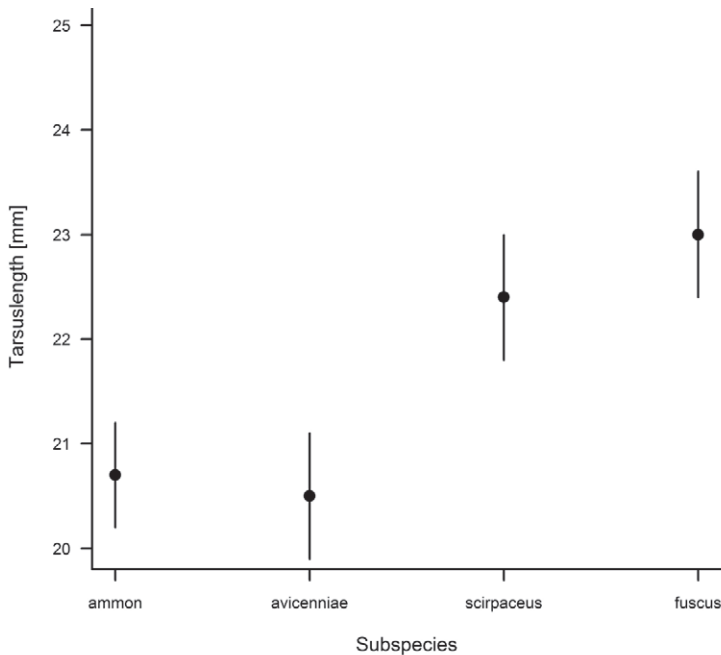


Figure 15. Tarsus length of Siwa Reed Warbler *Acrocephalus scirpaceus ammon* compared to other reed warbler taxa ( $n$ : *ammon* 37, *avicenniae* 8, *scirpaceus* 31, *fuscus* 6). X-axis: subspecies; y-axis: tarsus length (in mm).

## Genetic analysis

On the basis of the 594-base section of the mitochondrial cytochrome-*b* gene sequenced (see Methods for more detail), we identified three haplotypes. The commonest haplotype was represented by six and the second by three individuals. The two haplotypes represent a 0.2% within-population difference. One individual had a mutation that differed from other reed warbler taxa analysed that was most similar to the otherwise commonest haplotype. Uncorrected differences from nominate *scirpaceus* were 1.0–1.3%, from *avicenniae* 1.1–1.5%

and from *fuscus* 0.3–1.2%. We also sequenced the mitochondrial control region II of the same ten birds (*cf.* Bensch & Hasselquist 1999, Hering *et al.* 2009, 2011a). We obtained a section of 543 bases for seven individuals, one of 530 bases for two individuals, and one of 542 bases for one bird. There were only two haplotypes that differed by one mutation alone, which was found in a single individual. This homogeneity is somewhat surprising (*cf.* Päckert *et al.* 2007). The mutation did not correspond to any in the 52 reed warbler sequences analysed.

### Voice

*Song.*—The song (Fig. 16) has a structure typical of reed warblers, consisting of a continuous succession of usually repeated single elements. It is very similar to that of other Eurasian Reed Warbler taxa and African Reed Warbler. However the succession of single elements appears to be slower than in nominate *A. scirpaceus* and thus more like that of *avicenniae* (G. Nikolaus in Leisler *et al.* 1997). A comparative sonogram shows that the full song of both *A. s. avicenniae* and the Siwa birds can be distinguished from that of *A. s. scirpaceus* in central Europe (Hering *et al.* 2011a).

*Warning call.*—The Siwa warblers produced harsh grating sounds (Fig. 17) with a similar structure to those of warning calls described for central European *A. scirpaceus*.

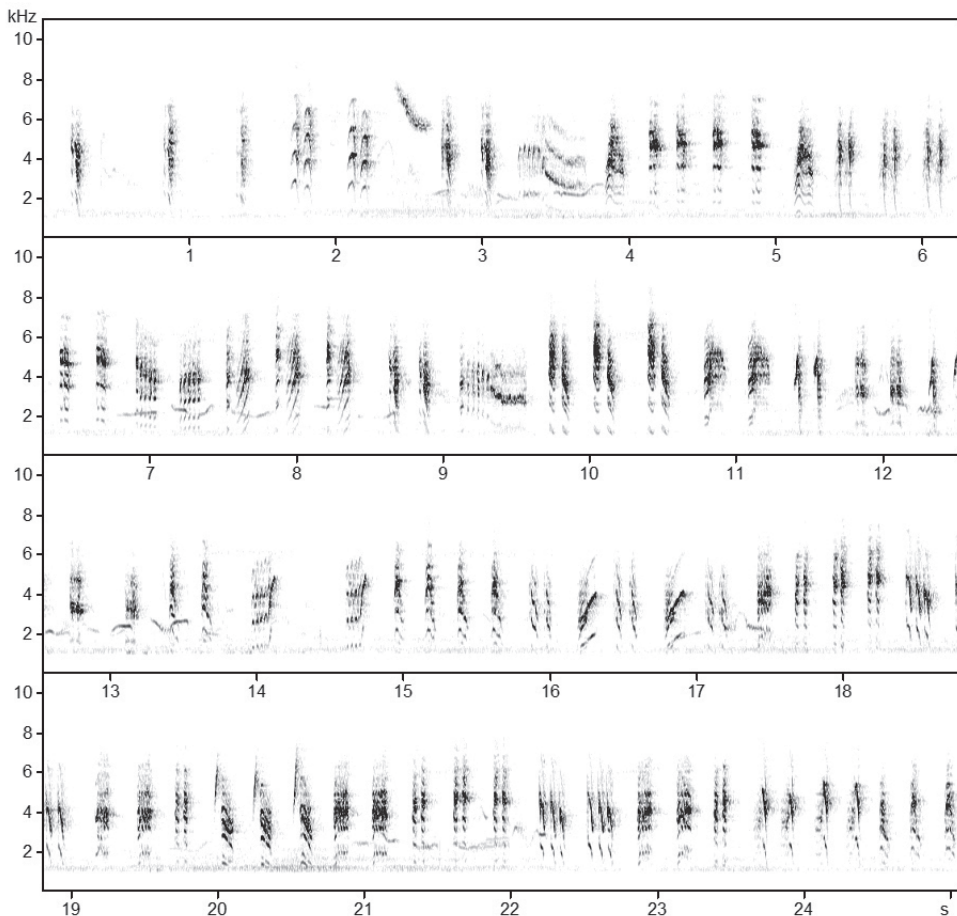


Figure 16. Song of Siwa Reed Warbler *Acrocephalus scirpaceus ammon*, Lake Siwa, Egypt, 12 May 2014 (TSA: *Acrocephalus\_scirpaceus\_DIG0190\_12*). Recording W. Heim, sonogram K.-H. Frommolt.

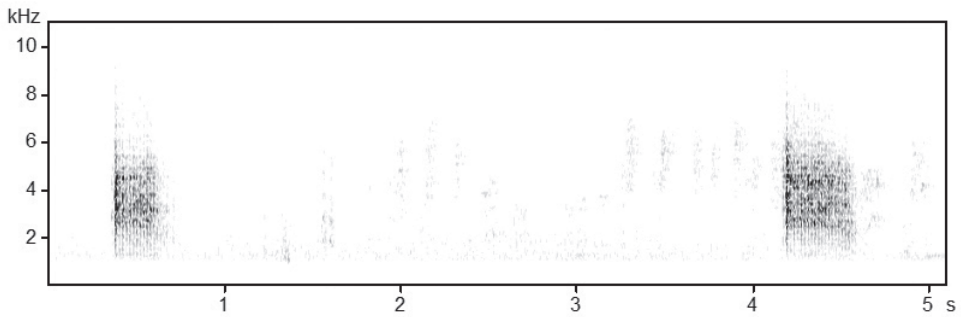


Figure 17. Warning calls of Siwa Reed Warbler *Acrocephalus scirpaceus ammon*, near Siwa Gardens Hotel, Siwa, Egypt, 15 May 2014 (TSA: *Acrocephalus\_scirpaceus\_DIG0190\_22*). Recording W. Heim, sonogram K.-H. Frommolt.

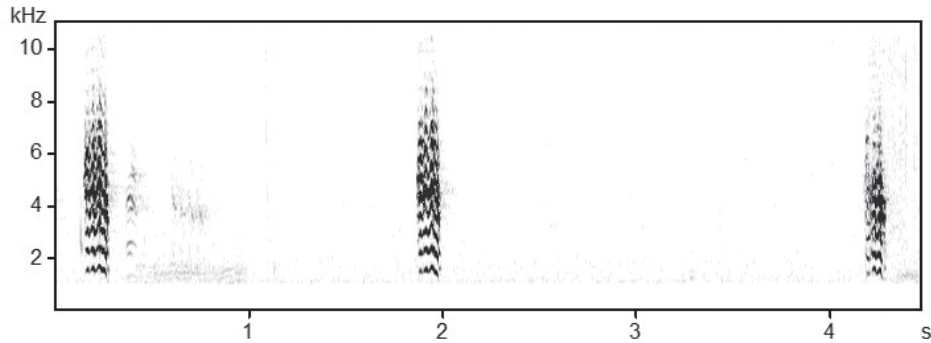


Figure 18. Calls with vibrato of Siwa Reed Warbler *Acrocephalus scirpaceus ammon*, near Lake Siwa, Siwa, Egypt, 15 May 2014 (TSA: *Acrocephalus\_scirpaceus\_DIG0190\_20*). Recording W. Heim, sonogram K.-H. Frommolt.

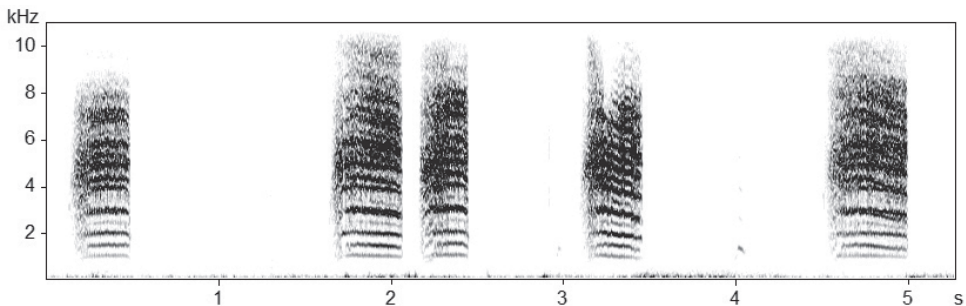


Figure 19. Distress calls while held for ringing by Siwa Reed Warbler *Acrocephalus scirpaceus ammon*, Lake Siwa, Siwa, Egypt, 14 May 2014 (TSA: *Acrocephalus\_scirpaceus\_DIG0190\_23*). Recording W. Heim, sonogram K.-H. Frommolt.

These noisy calls consist of 17–23 elements with a mean duration of 0.37 seconds ( $n = 16$ ; two individuals). The energy of the calls is concentrated over 2–4 kHz.

*Calls.*—In addition to warning calls, a harmonic-rich call with vibrato was noted (Fig. 18). The energy was concentrated in the range 3–6 kHz, and the calls had a mean duration of 0.12 seconds ( $n = 25$ ; one individual).

*Distress call.*—Distress calls (Fig. 19) during ringing of one bird were recorded. The calls, uttered in series, had a mean duration of 0.35 seconds ( $n = 11$ ). The time between calls was 0.16–4.41 seconds. The calls contain a strong ‘noise’ element, with energy concentrated at 4–6 kHz.



## Habitat

*Breeding habitat.*—Among the unique traits of the reed warblers in the Siwa Oasis is their preferred breeding habitat (Figs. 2, 20, 22–25), namely date palm and olive tree gardens (c.250,000 date palms and 50,000 olive trees). In the oasis, the birds nest in stands of trees with closed or half-open canopies, with a remarkably high breeding density in the date palm gardens with olive trees in the understorey (see below). The upper stratum of palm trees, up to 12 m tall, creates a degree of cover of c.75–100%; reed warblers are absent in gardens with an open structure and just single trees. In the cultivated area, the stands of reed, frequently in ponds fed by spring water but often small in area, seem to be unimportant for this *Acrocephalus*. Nevertheless, just like other Eurasian Reed Warbler taxa, the Siwa birds also nest in reedbeds, usually in smaller healthy stands of *Phragmites* at the edges, or in the shallow-water zone of salt lakes or spring-fed marshes. Extensive reedbeds grow for instance in Lake Siwa, and in the eastern part of Qara Oasis. Additionally, where waste water enters, e.g. at the northern edge of Siwa Oasis, stands of southern cattail *Typha domingensis* are occupied. In May 2014 a completely dead stand of reed of c.15 ha in a shallow salt lake harboured breeding reed warblers.

Until now, stands of bushes or trees as the main breeding habitat of Eurasian or African Reed Warblers was unknown. Besides *Phragmites* and *Typha*, *A. s. scirpaceus* and *A. s. fuscus* breed very rarely in other vertically structured vegetation, occasionally in planted beds of osier *Salix viminalis* or thickets of dense willow *Salix* shoots (e.g. Schulze-Hagen 1991). G. Nikolaus (pers. comm.) found a nest constructed by the Middle Eastern *fuscus* population in a tamarisk *Tamarix* sp. in Riyadh, Saudi Arabia. However, such habitats were regarded as insignificant (e.g. Schulze-Hagen 1991, Cramp 1992). It is now known that *A. s. avicenniae* breeds exclusively in mangroves, building nests low down, mainly in *Avicenna marina* (Ash *et al.* 1989, Kennerley & Pearson 2010, Porter & Stanton 2011, Hering *et al.* 2012, 2013, 2015). All taxa of African Reed Warbler inhabit wetlands with vegetation consisting predominantly of reed, bulrush (cattail) and sedge, except subspecies *A. b. suahelicus*, which also nests in mangrove. In addition, African Reed Warblers occupy papyrus swamps, floodplains, densely vegetated riverbanks and drainage ditches, fields of sugarcane, irrigation channels and, away from water, wetland copses (Pearson 1997, Dyrce 2006).

*Winter habitat.*—The first indications of overwintering *A. s. ammon* were noted in December 2009 / January 2010 and December 2010 in the surroundings of Al Jaghub oasis. Short-winged *Acrocephalus* were observed in reeds on the banks of two salt lakes. Winter records were also obtained at Siwa, e.g. in December 2012 in the northern part where waste water is disposed of. In contrast, the reed warblers were not seen in the oasis gardens, where they occur in large numbers during the breeding season. It is possible that food availability plays a decisive role. Our winter observations indicate that the birds probably can be considered sedentary.

## Density

The extent of potential breeding habitat in the oasis gardens at Siwa is considerable. The area of highest concentration is certainly the core of the oasis, where the oldest and densest date palm and olive tree gardens are sited. In April 2011, in an area of just 0.75 ha at Shali, six active nests and two additional territories were counted, corresponding to 107 territories / 10 ha, which if extrapolated across suitable habitat in the centre of Siwa Oasis alone would equate to 13,205 territories within 1,238 ha. It would be interesting to compare this with the breeding density of the closely related 'Mangrove Reed Warbler', but data are lacking (Ash *et al.* 1989, Kennerley & Pearson 2010). There is also an absence of breeding density data for



Figures 20–21. Left, *Acrocephalus scirpaceus ammon* in the oasis garden; right, *A. s. ammon* on *Phragmites*, Siwa, Egypt, 1 May 2011 and 14 May 2014, respectively (Jens Hering)

Figures 22–23. Nests of Siwa Reed Warbler *Acrocephalus scirpaceus ammon* in old olive trees, Siwa, Egypt, 30 April 2011 and 2 May 2011, respectively (Jens Hering)

Figures 24–25. Nest sites of Siwa Reed Warbler *Acrocephalus scirpaceus ammon* in date palms, Siwa, Egypt, 30 April 2011 and 16 May 2014, respectively (Jens Hering)

other tree-dwelling reed warblers, except Cape Verde Warbler *A. brevipennis*, where a mean breeding density of 0.65 territories / 10 ha in a study area of c.2,000 ha was estimated (Hering & Fuchs 2009). Reed-breeding populations of *A. scirpaceus* reach up to 532 territories / 10 ha, albeit such densities have never been confirmed for large-scale habitats (Schulze-Hagen 1991), where on average there are up to 50–60 territories / 10 ha (Dorsch & Dorsch 1985).

### Breeding biology

*Nest site.*—Unique within the Eurasian / African Reed Warbler superspecies is the frequency with which nests are sited in trees, palms and shrubs in oasis gardens. The first nest was found in an olive tree on 29 April 2011, in Siwa near Cleopatra's Spring. Further nests were found in April / May 2011 and again during our studies in May 2014. Data were collected for 16 nests in olive trees, 11 in date palms and one in a pomegranate *Punica granatum* bush (Figs. 22–25). A close relationship with irrigation channels, which in gardens are mostly in shade, chiefly free of vegetation, and sometimes lined with concrete, is plausible. Near one c.150-m long channel we found four nests, in some places just 20 m apart, but nests are also sited far from channels. What is remarkable is that nests are also sited near buildings and houses; one was just 5 m from a hotel. Tree nests are woven onto a twig with supporting side twigs, in a fork on a branch, or suspended between thin twigs. They are mostly sited above dry land in relatively open sites (in the shade of foliage) but also hidden in the canopy. Tree nests are sited 1.8–5.0 m above ground. Those in palm trees are generally fixed to the side of a leaf stalk, woven into the branching leaflets, and 2.5–6.0 m above ground, but it is probable that nests in palms are built at much greater heights.

*Nest.*—Compared to nests in reeds, those in trees are constructed of different materials, mostly bast fibres and dry grasses. The cups appear carefully constructed and are of varied shapes. Also used are spider webs, cocoons, animal hair, coloured string and occasionally thin plastic foil or paper. The foundation and outer wall are of coarser material, often with cocoons and gossamer woven in. The cup is of fine fibres. Measurements show no real difference to nests in reeds: outer diameter 6.1–8.0 cm, inner diameter 3.2–4.5 cm, depth of cup 3.0–4.5 cm, nest height 5.0–7.5 cm ( $n = 14$ ). Nests found in old reeds, though most were in young reeds ( $n = 8$ ) were no different in site, construction and material from those of other Eurasian and African Reed Warbler taxa. Six eggs had mean dimensions of  $18.1 \times 13.5$  mm (range  $17.3\text{--}19.1 \times 13.4\text{--}14.3$  mm). These are within the range of Eurasian Reed Warbler eggs, nor can any differences be observed in shape or colour (e.g. Schönwetter 1975, 1976, Schulze-Hagen 1991, Cramp 1992).

*Breeding period.*—Based on clutches and nestlings, the main laying period of the reed warblers in Siwa is probably late April / early May, with several mid-May observations of fledged or newly fledged young; only two nests still with eggs were found this late, while a female with quivering wings begging food from a male might indicate a second brood.

### Behaviour

*Activity.*—Synchronous singing by males was heard in April–May, mostly at dawn and dusk, but sometimes in the extreme heat of midday and afternoon. For example, on 13 May 2015 several birds sang at 14.00–15.00 h, perched in the open, in windless conditions and 36°C, in the dead reeds at a salt lake in the west of the oasis. Interesting behaviour in very high temperatures of 42°C in the shade was also noted during midday at a nest of a freshly hatched brood. During changeovers between brooding the young, the adults were observed panting almost continually with heat stress (illustration in Hering *et al.* 2011a). An adult visited the nest twice with soaked belly feathers (presumably to cool the nestlings).



*Foraging.*—Reed warblers breeding in cultivation searched for food exclusively in oasis gardens, in the canopy of trees and palms where they gleaned invertebrate prey from leaves and twigs. There are definite parallels between their foraging behaviour and that of reed warblers on Pacific islands (e.g. Leisler & Schulze-Hagen 2011). Several times, reed warblers were observed searching for food in palm bast, moving down to c.1 m above ground.

*Antagonistic behaviour.*—Isolated observations were made of aggression between *Acrocephalus* and Eastern Olivaceous Warblers *Iduna pallida*, which are also common breeders in the oasis gardens. As a rule, reed warblers dominated, chasing other warblers out of their territory.

## Discussion

Studies during recent years in Libya and Egypt have revealed that the biogeographical relationships of reed warblers in North Africa are complex (Hering *et al.* 2009, 2010a,b, 2011a,b, Winkler *et al.* 2013, in prep.). Based on current knowledge, we can postulate the existence of two separate phylogeographic units, each comprising sedentary and migratory forms. In central North Africa, and west as far as Iberia, breeders of the African *baeticatus* complex (treated as a species by Kennerley & Pearson 2010) occur. Siwa Reed Warbler occurs in eastern North Africa, geographically and ecologically isolated in desert depressions. Further east, in the Nile Valley, Eurasian Reed Warblers of the race *fuscus* have recently been discovered to breed, as has the race *avicenniae* in mangroves of the Red Sea, including the first breeding in the Western Palearctic.

Divergence data are much too low to yield reliable molecular dating. However, very speculatively applying the often used 2% rule (Lovette 2004, Päckert *et al.* 2007) would suggest that the oasis warblers diverged from a possible *fuscus* relative rather recently, between 600,000 and 250,000 thousand years BP. This period would certainly suffice for evolving the morphological and physiological adaptations necessary to survive the extreme conditions in the isolated Siwa Oasis. The short wings of Siwa Reed Warbler probably reflect selection pressures also at work on oceanic islands (Leisler & Winkler 2015). Birds that attempt to disperse longer distances could end up in unsuitable habitats.

Wing length not only varies with the bird's structure but is also dependent on, for example, migratory behaviour. Intra- as well as interspecific comparisons have demonstrated that populations that migrate further have on average longer wings (Fiedler 2005, Förschler & Bairlein 2011). Consequently, in Eurasian / African Reed Warbler complex, taxa with the longest wings are the two breeding furthest north (*scirpaceus*, *fuscus*), while African taxa are shorter winged reflecting their different migratory behaviour.

Siwa Reed Warbler breeds in reedbeds and also, like island *Acrocephalus* species, in mainly dry habitat among shrubs and trees. This is remarkable, as until recently it was thought that the Eurasian / African Reed Warbler superspecies was stenotopic (restricted to a single narrow niche) in its choice of nesting sites. Accordingly, we must assume that *scirpaceus* is capable of a higher level of ecological plasticity in nesting sites than previously thought, from vertical structural elements in reedbeds to horizontal branches in the gardens of Siwa. Extensive date palm and olive tree gardens, with their multi-strata structure, effective shading, and rich prey availability, provide eminently suitable breeding habitat. Birds utilise all strata from low shrubs to canopy of date palms and olive trees.

Reed warblers can be evolutionarily successful in exploiting arboreal habitats because of pre-adaptations, such as a non-specialised foraging technique, excellent climbing abilities and the special way they attach their nests (see Leisler & Schulze-Hagen 2015). In addition, establishing a new niche in utilising trees for nest sites due to simultaneous absence of tree-dwelling competitors (though Eastern Olivaceous Warbler *Iduna pallida*



breeds sympatrically) has enabled high breeding densities. Adaptation of reed warblers to an ‘island habitat’ is an example of niche expansion. In this way, new foraging techniques could have developed (or be in the process of developing) in the crowns of palms and fruit trees.

What is striking is that a clear spatial separation exists between Siwa Reed Warbler and *A. stentoreus*. A dedicated search for the latter in the oases inhabited by *ammon* failed to find it. Given that *stentoreus* is strikingly large with a conspicuously loud song and calls (Cramp 1992, Kennerley & Pearson 2010), its occurrence can be excluded. Our field experiments in the oases of Bahariya and Dakhla, where Clamorous Reed Warbler is dominant, revealed that *stentoreus* almost always reacts immediately to playback of Eurasian Reed Warbler song by quickly approaching. While the more robust (compared to *ammon*) Eurasian Reed Warbler race *fuscus* nests in the Nile Delta and Valley alongside *stentoreus*, very recent studies reveal that the smaller *Acrocephalus* is clearly subordinate (JH unpubl.). This situation is doubtless comparable to the interspecific territoriality between Great and Eurasian Reed Warblers in Europe, with the larger bird dominating the smaller species and sometimes destroying its nests (e.g. Schulze-Hagen 1991).

It is remarkable that the reed warbler was not discussed in earlier publications on the avifauna of Siwa Oasis. In the few cases where an *Acrocephalus* was mentioned, no attention was paid to it subsequently (Al Hussaini 1937, Almond 1937, Moreau 1941, Goodman & Ames 1983, Goodman *et al.* 1986, Goodman & Meininger 1989). For example, it is probable that J. Omer-Cooper observed the species during the Armstrong College Zoological Expedition of June 1935. A species list contains the following remark: ‘? *Acrocephalus* sp. “A reed-warbler with fledged young” at Sitra t 5 vi (OC)’ (Moreau 1941). This record was ignored subsequently, and another record on 9 May 1985 in the centre of the oasis near Aghurmi of a singing Eurasian Reed Warbler also failed to arouse suspicions (Goodman & Ames 1983, Goodman *et al.* 1986, Goodman & Meininger 1989). Apart from these observations, there is a complete lack of reference to the (undoubtedly common) Eurasian Reed Warbler in eastern Libyan Desert oases during spring or autumn migration (Goodman & Ames 1983, Goodman *et al.* 1986, Goodman & Meininger 1989). That the species does make migration stopovers in the region—probably frequently—is evidenced by our sight records and mist-netted individuals (nominat form  $n = 10$ ) during April / May 2011 and May 2014. However, it must be noted that, apart from current research on the Libyan avifauna (e.g. Hering *et al.* 2009, 2010a,b, 2011a,b, 2012, 2013, Isenmann *et al.* 2016), there is a huge deficit in our knowledge of the Eurasian / African Reed Warbler superspecies elsewhere in North Africa and the Middle East (see Isenmann & Moali 2000, Isenmann *et al.* 2005, Jennings 2010).

The ‘island’ population of Siwa Reed Warbler presents excellent opportunities for investigations in the fields of evolutionary biology and genetics. Such a well-defined area is very well suited to become an open-air laboratory (see Eising *et al.* 2001). Exciting questions concerning ecology and breeding biology remain unanswered. For example, it is unclear if there is strict segregation between the reed-dwelling birds and those breeding in oasis gardens, whether there is interchange especially in the area of overlap between gardens and reed, and during which period the oasis gardens are occupied and how food-rich the reed stands are in the non-breeding season.

No threats to Siwa Reed Warbler are currently known. A change in the agricultural utilisation of Siwa Oasis and its traditional garden cultures, especially the growing of olive trees and date palms, seems unlikely. However, large fires such as that in February 2012, which destroyed >1,700 ha of agricultural land may cause considerable losses. Melioration as well as the burning and mowing of reed probably have little effect on the population.

Direct human predation (hunting, bird catching) was not recorded during our research. Potential natural predators such as Common Kestrel *Falco tinnunculus*, Black Rat *Rattus rattus*, feral cats *Felis silvestris catus* and Diadem Snake *Spalerosophis diadema* have been noted near nests, but probably have little effect on overall breeding success. The greatest natural threat to Siwa Reed Warbler would be if the dominant *A. stentoreus* should colonise the desert depressions. To what extent designation of the entire Siwa Oasis as a 'protected area' in 2002 (see Baha el Din & Sinibaldi 2002, Mikhail 2011) has had a positive impact on its fauna and flora cannot be judged due to lack of data.

Applying the Biological Species Concept of Mayr (1942), the less pronounced molecular differences indicate a very short period of divergence, while the overall very similar morphology and song types suggest that Siwa Reed Warbler is not a separate species, despite being ecologically and geographically isolated from other breeding populations of *A. scirpaceus* / *baeticatus*. Nevertheless, the occurrence of a second haplotype argues for two colonisation events separated by c.250,000 years, with the two subgroups subsequently merging. We consider that another quarter of million years of presumed isolation have not produced sufficient genetic and behavioural disparity that a new colonisation event by *A. scirpaceus* / *baeticatus* would leave two genetically isolated sympatric populations. The new taxon therefore qualifies for treatment at subspecies level. Moreover, the Eurasian / African Reed Warbler superspecies is still not understood in detail, e.g. the divergence between North African populations of *baeticatus* and those grouped under *scirpaceus* requires further study. So far, a well-established phylogeny based on extended DNA profiles for African races is lacking, while newly discovered reed warbler populations in Libya and Morocco might suggest that there is just a single species in North Africa (D. J. Pearson *in litt.* 2016), but an investigation of those birds in the central Sahara and Cyrenaica, where sympatry of *scirpaceus* and *baeticatus* has been reported, is needed. Given this, we have included the new taxon in the older established name *scirpaceus* (Hermann, 1804) rather than in *baeticatus* (Vieillot, 1817).

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