The *Phlesirtes* complex (Orthoptera, Tettigoniidae, Conocephalinae, Conocephalini) reviewed: integrating morphological, molecular, chromosomal and bioacoustic data

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Abstract. The tettigoniid genus *Phlesirtes* Bolivar and its allies are reviewed. Morphological, ecological and molecular data prompt the erection of the new genus *Chortoscirtes* **gen.n.** with type species *Xiphidion meruense* Sjöstedt. The genera *Phlesirtes*, *Chortoscirtes, Karniella* and *Naskreckiella* are characterized by morphological characters supported by molecular, acoustic, ecological and chromosomal data. Four species, *Chortoscirtes pseudomeruensis* **sp.n.**, *C. masaicus* **sp.n.**, *C. puguensis* **sp.n.** and *C. serengeti* **sp.n.**, are described from localities in northern and coastal Tanzania and one *Karniella, K. crassicerca* **sp.n.**, is described from Uganda. The following **comb n.** are proposed: *Phlesirtes kibonotensis* (Sjöstedt) and *Phlesirtes kilimandjaricus* (Sjöstedt). Subtribal status is proposed for the four investigated African genera. A key to the *Chortoscirtes* species is provided.

Introduction

Montane East Africa has high biotic diversity and endemism (Lovett, 1988; Behangana *et al.,* 2009). The Eastern Arc mountains, geologically ancient formations with an estimated age of 30 Ma (Burgess *et al.,* 1998) and extending throughout Tanzania and southern Kenya, are well investigated for some taxa (Howell, 1993; Emberton *et al.*, 1997; Newmark, 2002; Robertson, 2002; Burgess *et al.*, 2007; Poynton *et al.*, 2007) and are regarded as hotspots of diversity and endemism. However, more intensive recent research on the high mountains of the East African rift valley system, especially the geologically

young volcanoes such as Mts Kilimanjaro and Meru or Mt Hanang (estimated ages of 1–2 Ma, Marek, 2001) also reveals high diversity and endemism (Lambrechts *et al.*, 2002; Hemp, 2006). The geological age of these higher volcanoes may allow calibration for speciation processes. With typical wide savanna plains and the climatically isolated mountains looming to considerable heights, the area can serve as a model system to investigate mechanisms of evolution of tropical species diversity. The flightless Saltatoria are ideal for investigating mechanisms to explain the biogeographical distribution patterns. Many genera show arrays of closely related species isolated on the high mountains. The study of distribution patterns and of the ecology, habitat demands, acoustics and molecular relationships of species groups contributes to an understanding of the climatic and vegetational history of East Africa. Such studies require basic taxonomic work because the fauna remains poorly known.

That allopatric speciation generated the biogeographical patterns found amongst some East African lentulid genera has

been shown for example for *Rhainopomma* species (Hemp *et al.,* 2007; Schultz *et al.,* 2007), a genus presently containing seven species. All are restricted to the montane zones of mountains along the Eastern Arc chain of Tanzania and southern Kenya, and all occupy similar ecological niches (forest edge and clearings) at corresponding altitudes of different mountains. The morphological similarity suggests a recent radiation, probably as a result of past climatic fluctuations. The molecular phylogenetic analysis confirms that related species of *Rhainopomma* occur on neighbouring mountains (e.g. East and West Usambara, South Pare, North Pare) and that species are genetically and geographically separated. Another flightless genus with an array of morphologically closely related species is the pyrgomorphid genus *Parasphena* Bolivar, with 17 so-far known species found on almost every high mountain from southern Tanzania to northern Kenya and eastern Uganda. Species of *Parasphena* are restricted to grasslands of the montane and afroalpine zone. Morphology, ecology and molecular data suggest allopatric speciation as the most plausible explanation for the biogeographical history (Rehn, 1942; Kevan, 1948, 1956; Hemp *et al.*, 2009).

The *Phlesirtes* genus complex is a poorly investigated group of Conocephalinae bush crickets. Because of their small size and nymphal appearance they have been overlooked and poorly sampled since the erection of *Phlesirtes* by Bolivar (1922), for *Xiphidion merumontanum* Sjöstedt from northern Tanzania. New sampling in the past 15 years has revealed over 30 species in the highlands of East Africa.

Sjöstedt (1909) described four *Xiphidion* (Tettigonioidea: Conocephalinae) species (*merumontanum*, *meruense*, *kilimandjaricum*, *kibonotense*) from the Kilimanjaro-Meru area of Tanzania. Although Bolivar (1922) founded the genus *Phlesirtes* on *Xiphidion merumontanum* Sjöstedt, he did not transfer the other three species described by Sjöstedt to his newly erected genus. Karny (1921) stated that *Xiphidion kibonotense* should be placed into the genus *Conocephalus* because of its unarmed prosternum, and noted that the other three species from the Kilimanjaro area should be placed into *Conocephalus* if the prosternum was unarmed. Obviously unaware of Karny's (1921) study, Uvarov (1924) described *Phlesirtes brachiatus*. He transferred *Phlesirtes*, also mentioning the three species *Xiphidion meruense*, *kilimandjaricum* and *kibonotense* as probably closely related, into Decticinae. Chopard & Kevan (1954) added another three species from northern Kenya (Table 1). Ragge (1977) and Rentz (1988) doubted that *Phlesirtes* should be placed under Decticinae, transferring the genus back to the subfamily Conocephalinae. Rehn (1914) erected the genus *Karniella* with the sole species *K. bullata*, quite similar in general morphology to Sjöstedt's three *Phlesirtes* species, but differing strongly in the shape of the pronotum and tegmina. Ünal (2005) described the new Conocephalinae genus *Naskreckiella*, also listing *Phlesirtes* as a genus under Conocephalini. A list of Conocephalini genera is given in Ünal (2005). In the Orthoptera Species File online (Eades & Otte, 2009) the three *Phlesirtes* species *kilimandjaricus*, *kibonotensis* and *meruensis* are erroneously listed under *Conocephalus (Anisoptera)*.

Table 1. Members of the *Phlesirtes* genus complex.

P. bilineatus Chopard, 1954
P. brachiatus Uvarov, 1923
P. kevani Chopard, 1954
P. kibonotensis[a] (Sjöstedt, 1909)
P. kilimandjaricus (Sjöstedt, 1909)
P. latifrons Chopard, 1954
P. meruensis[a] (Sjöstedt, 1909)
P. merumontanus (Sjöstedt, 1909)
K. bullata Rehn, 1914
N. kalamboi Ünal, 2005

[a]According to Bolivar's nomenclature (Bolivar, 1922) the genus name *Phlesirtes* demands a masculine ending of the species name. Therefore the species names ending with -*se* have to have the ending −*is*.

Here we compile knowledge of the hitherto described species of *Phlesirtes*, study their relationships, including the description of a new genus, characterize the genera *Karniella* and *Naskreckiella,* and clarify the taxonomic position of these genera within Conocephalinae.

Methods and materials

Depositories

MNB: Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin. NHML: Natural History Museum London, U.K. EDNMK: Entomological Department National Museums of Kenya, Nairobi. NHRS Stockholm: Naturhistoriska Riksmuseet, Stockholm, Sweden. All other material remains in the collections of C. Hemp and K.-G. Heller.

Molecular analysis

DNA was extracted from the muscles of one hind leg using the QIAamp® DNA mini kit (Qiagen, Germany, following the standard protocol for blood and tissue) and the NucleoSpin® tissue kit (Machery & Nagel, Germany, following the standard protocol for human and animal tissue).

For the analysis of Orthoptera species groups we selected genes for which data already exist and that show sufficient variation between closely related species (mitochondrial genes and especially the barcoding gene cytochrome oxidase subunit I (COI)) and a more conserved gene for deeper nodes in the phylogenetic tree (histone gene H3). Preliminary work confirmed the suitability of the selected genes.

The mitochondrial 16S rRNA gene, the mitochondrial COI gene and nuclear histone H3 gene (H3) were amplified by polymerase chain reaction (PCR) using the primers 16a: 5′-CGC CTG TTT ATC AAA AAC AT-3′ and 16b: 5′-CCG GTC TGA ACT CAG ATC ACG T-3′ for the 16S rDNA (Kocher *et al.*, 1989); H3fwd: 5′-ATG GCT CGT ACC AAG CAG ACG GC-3′ and H3rev: 5′-ATA TCC TTG GGC ATG ATG GTG AC-3′ for the histone H3 gene (Colgan *et al.*, 1998); and LCO1490: 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′

and HCO2198: 5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′ for COI (Folmer *et al*., 1994). Successful PCR products were cleaned with the QIAquick® Gel Extraction Kit (Qiagen, Germany), and sequencing was performed by the Macrogen sequencing service (Korea) and for some sequences by the DNA analytics core facility of the University of Bayreuth. All sequences were deposited in GenBank under the accession numbers given in Table 2.

Fragments of the 16S rDNA (521 bp), the COI (665 bp) and the H3 cluster (339 bp) of 41 individuals (Table 2) were aligned with the CLUSTALW software in BIOEDIT (Hall, 2005). The CLUSTALW alignment was adequate for COI and H3, because there was no length variation among sequences. The 16S rRNA alignment was manually optimized with the help of the secondary structure of *Drosophila melanogaster* (Gutell *et al*., 1994). The two tettigoniid species *Platycleis albopunctata* (Tettigoniidae: Tettigoniinae: Platycleidini) and *Ruspolia differens* (Tettigoniidae: Conocephalinae) were used as outgroup taxa to root the topology. *Ruspolia differens* belongs to the Copiphorini, another subfamily of Conocephalinae. *Platycleis* was placed in the past together with *Phlesirtes* in the Tettigoniinae. Further sequence data used in previous publications were added to the alignment. A likelihood ratio test was performed using MRMODELTEST 2.3 (Nylander, 2004) to find the best-fitting models for the underlying molecular data. The Akaike criterion selected the GTR + G model for the 16S rDNA and the GTR + I + G model for COI and H3. Using these assumptions on sequence evolution, a combined Bayesian analysis with MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001) was performed with four simultaneous Markov chains in 1 000 000 generations. In total, 4000 trees were obtained (samplefreq = 250), and the first 1000 of these were considered as the 'burn-in' and discarded. A simpler maximum parsimony analysis was performed in PAUP* 4.0b10 (Swofford, 2000). The heuristic search included 10 000 random addition replicates. A 50% majority-rule consensus tree of the most parsimonious tree was constructed and exported to the ARB software package (Ludwig *et al.,* 2004), where branch lengths were calculated. Bootstrap analyses were performed with 500 replicates with tree bisection–reconnection (TBR) branch swapping, 100 random addition replicates and the Multrees option in PAUP*.

Because binary trees do not show the reticulations caused either by natural processes (introgression, incomplete lineage sorting) or by artefacts of the analyses (chance similarities, background noise of the data), we used network methods and the variable 16S gene to visualize the distinctness of the separation of species of the *Chortoscirtes* group. A median-joining network based on 14 sequences of the 16S rRNA data was constructed for the five species of the genus *Chortoscirtes* with the NETWORK 4.5.0.2 program (Bandelt *et al.*, 1999) and overlaid onto a map of Tanzania marked with the localities where the species were found to test if phylogeny and distribution patterns are congruent. The H3 and COI data were excluded from network analysis because of the conservatism of H3 and because in the COI data the sequence of *C. puguensis* is missing.

Cytotaxonomic analyses

The number of individuals analysed and the collection localities for *Phlesirtes* and *Chortoscirtes* species studied are listed in Table 3. Chromosomal preparations were obtained from adult male gonads. Testes were excised, incubated in a hypotonic solution (0.9% sodium citrate), and then fixed in ethanol : acetic acid (3:1). The fixed material was squashed in 45% acetic acid. Coverslips were removed by the dry ice procedure and then preparations were air-dried. The fixed material was deposited in the Institute of Systematics and Evolution of Animals PAS (Kraków, Poland).

Sound recording and bioacoustical terminology

The calling songs of three *Phlesirtes* and three *Chortoscirtes* species were recorded in the field and/or in the laboratory. (*Phlesirtes kibonotensis*, four males recorded; *P. kilimandjaricus*, eight males recorded; *P. merumontanus*, three males recorded; more details for *Phlesirtes* in Hemp & Heller, in preparation. *Chortoscirtes meruensis*, field and laboratory, 26.12.2006, 3.01.2007, between Mts Meru and Kilimanjaro, 36°55,47′ E, 02°56,71′S; *C. pseudomeruensis*, field, 30.12.2006, 37°38,11892′E, 03°16,58790′S; *C. serengeti*, laboratory, 5.02–8.03.2007, type locality, specimen CH6888.) All specimens were recorded using a digital bat-detector (Pettersson D1000X) with a sampling rate of 100 kHz; *C. serengeti* was additionally recorded with higher sampling rates and other microphones (Genrad GR 1988 sound level meter (IET Labs) and Sony ECM-121 microphone, both connected directly to a laptop computer via an external sound card (M-Audio transit; sampling rate mostly set to 64 or 96 kHz)). *Karniella crassicerca* was recorded in the field (Congo/Zaire, province Kivu, NP Kahuzi Biega, Poste Patrol, 25.03.1990, specimen CH4968) using a Sony WM-D3 cassette tape recorder (upper frequency limit 15 kHz).

The sounds were analysed using the program AMADEUS II (Martin Hairer; www.hairersoft.com). Each value of syllable periods and durations represents the mean of ten independent measurements.

Terminology

Syllable: sound produced during one cycle of movements (opening and closing of the tegmina; syllable duration: time period measured from the first impulse to the last; syllable period: time period from one syllable beginning to the next (reciprocal value: syllable repetition rate); echeme: first-order assemblage of syllables; impulse: a simple, undivided, transient train of sound waves (here: the highly damped sound impulse arising as the impact of one tooth of the stridulatory file). In the description of the acoustic behaviour of *Chortoscirtes* species the term short-song is used, which is described under *C. serengeti*.

Table 2. Locality data for the specimens sequenced.

Species	Location	Isolate	16SrRNA	COI	H3
Chortoscirtes masaicus **sp.n.**	Between Mt Meru and Mt Longido, savanna grassland (Tanzania)	M28	FM882023	FM882100	FM882060
Chortoscirtes meruensis (Sjöstedt, 1909) comb. n.	Mt Kilimanjaro, western slope, submontane savanna grassland, 1360 m (Tanzania)	R5	FM882022	FM882099	FM882059
Chortoscirtes meruensis (Sjöstedt, 1909) comb. n.	Mt Kilimanjaro, western slope, submontane savanna grassland, 1360 m (Tanzania)	R6	FM882046	FM882114	FM882083
Chortoscirtes meruensis (Sjöstedt, 1909) comb. n.	Mt Kilimanjaro, western slope, submontane savanna grassland, 1360 m (Tanzania)	R8	FM882047	FM882115	FM882084
Chortoscirtes meruensis (Sjöstedt, 1909) comb. n.	Mt Kilimanjaro, western slope, submontane savanna grassland, 1360 m (Tanzania)	R9	FM882048	FM882116	FM882085
Chortoscirtes meruensis (Sjöstedt, 1909) comb. n.	Mt Kilimanjaro, western slope, submontane savanna grassland, 1360 m (Tanzania)	R10	FM882049	FM882117	FM882086
Chortoscirtes pseudomeruensis (Sjöstedt, 1909) **sp.n.**	Mt Kilimanjaro, eastern slope, *Hyparrhenia* grassland (Tanzania)	66	FM882044	FM882112	FM882081
Chortoscirtes pseudomeruensis (Sjöstedt, 1909) **sp.n.**	Mt Kilimanjaro, eastern slope, *Hyparrhenia* grassland (Tanzania)	R7	FM882021	FM882098	FM882058
Chortoscirtes pseudomeruensis (Sjöstedt, 1909) **sp.n.**	Mt Kilimanjaro, eastern slope, *Hyparrhenia* grassland (Tanzania)	Z4	FM882045	FM882113	FM882082
Chortoscirtes pseudomeruensis (Sjöstedt, 1909) **sp.n.**	Mt Kilimanjaro, eastern slope, *Hyparrhenia* grassland (Tanzania)	Z8	FM882043	FM882111	FM882080
Chortoscirtes puguensis **sp.n.**	Pugu Hills, grassland along forest edge (Tanzania)	A12	FM882028	–	FM882065
Chortoscirtes serengeti **sp.n.**	Seronera, Seregenti, savanna grassland (Tanzania)	B1	FM882052	FM882120	FM882089
Chortoscirtes serengeti **sp.n.**	Seronera, Seregenti, savanna grassland (Tanzania)	B2	FM882053	FM882121	FM882090
Chortoscirtes serengeti **sp.n.**	Seronera, Seregenti, savanna grassland (Tanzania)	B3	FM882054	FM882122	FM882091
Karniella bullata Rehn, 1914	Tshivanga, near Bukavu, Kivu Province (Congo)	H2	FM882036	–	–
Karniella bullata Rehn, 1914	Kibale forest, Pine plantation (Uganda)	B7	–	–	FM882092
Karniella bullata Rehn, 1914	Kibale forest, Pine plantation (Uganda)	X4	–	–	FM882073
Karniella bullata Rehn, 1914	Kibale forest, Pine plantation (Uganda)	P11	–	–	FM882094
Karniella bullata Rehn, 1914	Kibale forest, Pine plantation (Uganda)	A17	–	–	FM882093
Karniella crassicerca **sp.n.**	Nyungwe forest reserve, near Cyangugu, 2500 m (Rwanda)	C127	FM882034	–	FM882071
Karniella crassicerca **sp.n.**	Nyungwe forest reserve, near Cyangugu, 2500 m (Rwanda)	C128	FM882035	–	FM882072
Phlesirtes kibonotensis (Sjöstedt, 1909)	Mt Kilimanjaro, southern slope, above Machame, montane grassland, 1790 m (Tanzania)	38	FM882024	FM882101	FM882061
Phlesirtes kibonotensis (Sjöstedt, 1909)	Mt Kilimanjaro, southern slope, above Kidia, montane grassland, 1710 m (Tanzania)	39	FM882050	FM882118	FM882087
Phlesirtes kibonotensis (Sjöstedt, 1909)	Mt Kilimanjaro, southern slope, above Kidia, montane grassland, 1710 m (Tanzania)	40	FM882051	FM882119	FM882088
Phlesirtes kilimandjaricus (Sjöstedt, 1909)	Mt Kilimanjaro, southern slope, above Kidia, montane grassland, 1710 m (Tanzania)	41	FM882020	FM882097	FM882057
Phlesirtes kilimandjaricus (Sjöstedt, 1909)	Mt Kilimanjaro, southern slope, above Kidia, montane grassland, 1710 m (Tanzania)	42	FM882039	FM882107	FM882076
Phlesirtes kilimandjaricus (Sjöstedt, 1909)	Mt Kilimanjaro, southern slope, above Kidia, montane grassland, 1710 m (Tanzania)	43	FM882040	FM882108	FM882077
Phlesirtes kilimandjaricus (Sjöstedt, 1909)	Mt Kilimanjaro, eastern slope, *Hyparrhenia* grassland, 1340 m (Tanzania)	M22	FM882041	FM882109	FM882078
Phlesirtes kilimandjaricus (Sjöstedt, 1909)	Mt Kilimanjaro, eastern slope, Mwika, grassland, 1450 m (Tanzania)	M26	FM882042	FM882110	FM882079
Phlesirtes merumontanus (Sjöstedt, 1909)	Monduli Range, southern slope, Eye clinic, montane grassland, 2000 m (Tanzania)	64	FM882019	FM882096	FM882056
Phlesirtes merumontanus (Sjöstedt, 1909)	Mt Kitumbeine, southern slope, montane grassland, 2100 m (Tanzania)	A13	FM882038	FM882106	FM882075
Phlesirtes merumontanus (Sjöstedt, 1909)	Monduli Range, southern slope, Eye clinic, montane grassland, 2000 m (Tanzania)	A14	FM882018	FM882095	FM882055
Phlesirtes merumontanus (Sjöstedt, 1909)	Mt Meru, eastern slope, near gate of National Park, submontane grassland, 1400 m (Tanzania)	T10	FM882037	FM882105	FM882074
Conocephalus (*Anisoptera*) *ictus* (Scudder, 1875)	Between Valle Nacional and El Mirador, road 175, grassy patches (Mexico)	X51	FM882027	FM882104	FM882064

Table 2. Continued.

Species	Location	Isolate	16SrRNA	COI	H3
Conocephalus (*Anisoptera*) *maculatus* (Le Guillou, 1841)	Mt Kilimanjaro, eastern slope, Chala area, savanna grassland, 1020 m (Tanzania)	N64	FM882029	–	FM882066
Conocephalus (*Anisoptera*) *saltator* (Saussure, 1849)	Grassy patches along forest track (Oahu, Hawaii)	N65	FM882033	–	FM882070
Conocephalus (*Conocephalus*) *conocephalus* (Linnaeus, 1767)	Mt Kilimanjaro, southern slopes, Namwi river, grassy patches along river, 1200 m (Tanzania)	N66	FM882026	FM882103	FM882063
Conocephalus longiceps (Peringuey, 1918)	Mt Kilimanjaro, eastern slope, savanna grassland (Tanzania)	M30	FM882030	–	FM882067
Conocephalus longiceps (Peringuey, 1918)	Mt Kilimanjaro, eastern slope, savanna grassland (Tanzania)	M31	FM882031	–	FM882068
Platycleis (*Platycleis*) *albopunctata* (Goeze, 1778)	Frankonia, near Hersbruck, on bolder scree, Houbirg (Germany)	M33	FM882025	FM882102	FM882062
Ruspolia differens (Serville, 1838)	Mt Kilimanjaro, eastern slope, Mwika area, *Hyparrhenia* grassland, 1280 m (Tanzania)	M32	FM882032	–	FM882069

Specimens were sequenced repeatedly to detect intraspecific variation among the sequences. For identification of the specimens in the phylogenetic tree (Fig. 5) the internal isolate numbers are given. The NCBI GenBank accession numbers are listed for each gene. Missing sequences are marked with '-'.

Table 3. Cytotaxonomic analyses of *Phlesirtes* and *Chortoscirtes* species.

Species	N	Collection localities
P. kibonotensis	One male	Tanzania, Mt Kilimanjaro, southern slopes, above Kidia, (3°17′S, 37°26′E), 1700–1800 m, October 2006.
	One male	Tanzania, Mt Kilimanjaro, northern slopes, Kilimanjaro Timbers, 1900 m, July 2007
P. kilimandjaricus	One male	Tanzania, Mt Kilimanjaro, southern slopes, Kidia, 1430 m, July 2007
P. merumontanus	Four males	Tanzania, Mt Meru, eastern slopes, near gate Arusha National Park (3°18′S, 36°52′E), 1450 m, October 2006
	One male	Tanzania, Mt Kilimanjaro, northern slopes, Mosha Farm, 1880 m, July 2007
C. serengeti	One male	Tanzania, Serengeti plains, Seronera area, Pimbi camping site (2°26′S, 34°49′E), February 2007

N, Number of analysed specimens.

Results

Molecular results

Bayesian and maximum parsimony phylogenetic reconstruction (Fig. 5) supports the monophyly of the investigated taxa with a distinct separation of the genus *Conocephalus*, which is represented in this analysis by five species. All main nodes are supported by high posterior probabilities or bootstrap values. Furthermore, we found the same groupings and similar topologies with other phylogenetic methods such as maximum likelihood (not shown) and also when using single or combined datasets. The result is stable and insensitive to the selection of data partitions and optimality criteria. The only difference between maximum parsimony and Bayesian phylogeny is in the positions of the morphologically similar species *C. pseudomeruensis* and *C. meruensis* (Fig. 5).

Within the *Phlesirtes* complex five groups could be detected. A basal branch comprises species assigned in this paper to the new genus *Chortoscirtes* based on *Phlesirtes meruensis*. This new genus contains five species. Sister groups to *Chortoscirtes* are the genus *Karniella* and the remaining *Phlesirtes* species, which also form a monophyletic group. Until now, *Karniella*

was monotypic. In this paper we describe the second species of this genus, *K. crassicerca*. Specimens of *P. kibonotensis*, *P. merumontanus* and *P. kilimandjaricus* each represent a well-separated branch in our analyses, indicating that our material does not contain cryptic species.

The median-joining network plotted on a map of Tanzania (Fig. 13) visualizes evolutionary relationships between the species of the genus *Chortoscirtes*, considering also their distribution. We found a close relationship of *C. meruensis*, *C. pseudomeruensis* and *C. masaicus,* which also have a close geographical distribution. As in other flightless Orthoptera of the area (e.g. Lentulidae, Hemp *et al.,* 2007), the species are distributed along a line connecting populations of the coast with those of the younger volcanoes, and there is also a connection to the Serengeti. The network does not indicate ambiguities that might have resulted from hybridization or lineage sorting.

Chromosomal characters

Analysis of the standard karyotype of *P. merumontanus*, *P. kilimandjaricus*, *P. kibonotensis* and *C. serengeti* revealed

diploid chromosome numbers of 2n = 33 for males, consistent with the X0/XX sex chromosome system. In these four species, the autosomal acrocentric chromosomes varied in size and fell into three size groups: one large (L_1), nine medium (M_2-M_{10}), and six small ($S_{11}-S_{16}$) pairs. The metacentric X chromosome was the largest element in size (Fig. 11A). In two out of five males of *P. merumontanus*, in two males of *P. kibonotensis* and in one male of *C. serengeti* a supernumerary chromosome (B) was detected. The B chromosome was of acrocentric type, similar in size to that of the small pair of chromosomes, mitotically and meiotically unstable. In metaphase I this supernumerary element was seen very often in the periphery of the plate, whereas at anaphase I it was often situated between sister plates, testifying that it is eliminated from the karyotype (Fig. 11B).

Taxonomy

General position of *Chortoscirtes* **gen.n.**, *Phlesirtes* Bolivar, *Karniella* Rehn, and *Naskreckiella* Ünal within Conocephalinae, tribe Conocephalini.

The internal structure of the subfamily Conocephalinae is unclear because putative synapomorphic characters for the diagnosis of the several tribes of Conocephalinae are disputable (Ingrisch, 1998; Naskrecki, 2000). The status of Conocephalini, however, is less disputed. They are characterized by a laterally flattened fastigium of vertex and unarmed fore and mid femora. The pronotum has an auditory swelling.

Members of the Conocephalini are small insects with a shining or subsmooth fastigium verticis that is never longer than the scapus, with a blunt apex. The antennae are inserted close to the dorsal head, and positioned between the eyes. The margins of the antennal sockets are not elevated. The pronotum is mostly without apparent transverse carinulae, dorsally straight, and rarely saddle-shaped.

All studied species of *Conocephalus, Phlesirtes* and *Chortoscirtes* have a chromosome number of 2n = 33, contrasting with that of other tribes, which have lower numbers (Warchałowska-Sliwa, 1998; see Discussion).

The tribe Conocephalini presently has 19 genera (see Otte, 1997; Ünal, 2005), of which seven are found in Africa (excluding Madagascar). These are the world-wide-distributed genus *Conocephalus* (over 150 species), and the African genera *Megalotheca* (4 species), *Thyridorhoptrum* (2 species), *Karniella* (2 species), *Phlesirtes* (7 species), *Chortoscirtes* **gen.n.** (5 species) and *Naskreckiella* (1 species).

Subtribe *Karniellina* subtribe n. Hemp C. & Heller

Four of the above-mentioned African genera, *Naskreckiella, Karniella, Chortoscirtes* and *Phlesirtes*, deviate morphologically from the other Conocephalini genera and are considered as a separate subtribe.

In their general appearance these four genera are very similar. Males of all species of these taxa have shortened tegmina, and rudimentary hind wings, whereas females have scale-like tegmina and lack alae; the stridulatory file is always covered by the posterior margin of the pronotum. In addition, all species share densely haired, lobe-like expansions on the meso- and metasterna (or collar-shaped projections, see Ünal, 2005). A synapomorphic character of the group is free plantulae of the hind tarsi, used by Uvarov (1924) to place *Phlesirtes* into Decticinae.

Of the 18 genera in the tribe Conocephalini as listed by Ünal (2005) and Eades & Otte (2009), *Paulinacris* Chopard, *Enoplocephalacris* Chopard and *Elasmometopus* Chopard have an acute fastigium verticis, thus differing from all other Conocephalini, which have a blunt fastigium. Ingrisch (1998) defines the Conocephalini as having unarmed fore and typically also mesofemora. However, the above-listed members of the three genera have armed femora. At present, they may be at best considered as Conocephalinae incertae sedis. The genus *Philippicentrus* Willemse (1961), listed by Ünal (2005) as a member of Conocephalini (as *Phlippocentrus*), was described as belonging to the Listroscelidinae near to *Hexacentrus*. From figure and description there is no reason to doubt membership of Listroscelidinae or of the recently re-established Hexacentrinae. Obviously Otte (1997) placed the genus in Conocephalini errorneously and Ünal (2005) followed him. The genus *Sphodrophoxus* Hebard listed by Otte (1997) as in Conocephalini was changed to Copiphorini in Naskrecki & Otte (1999) without comment but with a photo of the type.

Conocephalus, Thyridorhoptrum, Oychrelimum, Lipotactomimus and *Fatuhivella* have a pronotum that is divided into a smooth anterior part with lateral lobes that are deeper than long and a posterior part that is slightly upbend, covering only the disc; thus a more or less acute angle is formed at the lateral sides where the pronotal lobes meet the posterior part of the pronotal disc. In the Karniellina the lateral lobes never end abruptly in an acute angle at the anterior part of the pronotum but run smoothly to the anterior margin of the pronotum (the pronotum in lateral aspect thus being triangle-shaped).

In *Conanalus, Euxiphidion, Luzoniella, Nukuhivella* and *Megalotheca* the tegmina are inserted directly at the posterior margin of the pronotum, and thus the stridulatory files are never covered by the posterior part of the pronotum as is typical for Karniellina. Very similar to the Karniellina is the monotypic genus *Odontoxiphidium*. The general habitus of *Odontoxiphidium* resembles especially members of the genus *Phlesirtes*. The fore tibiae have five well-developed evenly spaced spines and the pronotum and the fastigium verticis are similar to in Karniellina. The tegmina are short but not covered by the posterior margin of the pronotum, in contrast to *Phlesirtes* and other Karniellina. Also in contrast to the Karniellina, in which the males have at least rudimentary hind wings, *Odontoxiphidium* lacks hind wings completely (Capinera *et al.*, 2004). *Odontoxiphidium apterum* occurs in southern North America, whereas all genera of Karniellina are restricted to Africa.

The new subtribe Karniellina with the genera *Chortoscirtes, Phlesirtes, Karniella* and *Naskreckiella* can be differentiated from other genera of Conocephalini by the free plantulae of the hind tarsi and the combination of the following characters: a

male pronotum that has more than twice the length of the uncovered part of the tegmina (with the exception of *Karniella*, which has large and inflated tegmina) and the females lacking wings. A reduction of the size of the wings has happened quite often in Conocephalini (even within *Conocephalus*), but not to the same extent as in Karniellina, where probably secondarily the tegmina were enlarged again for sound production. The fore tibiae are armed with five or six well-developed evenly spaced ventral spines. Members of the Karniellina are restricted to Africa south of the Sahara in the areas of East, Central and southeast Africa. The only Conocephalini genus also found in the area, even syntopically with Karniellina members, is *Conocephalus*.

The characters listed above suggest that *Phlesirtes*, *Chortoscirtes*, *Karniella* and *Naskreckiella* should be placed together into the subfamily Conocephalinae, tribe Conocephalini, subtribus *Karniellina*. We suggest that the remaining 11 genera of Conocephalini should be grouped under the subtribe Conocephalina. However, more taxonomic and molecular studies are necessary to define whether the Conocephalina form a phylogenetically related group.

Differentiating characters of Phlesirtes, Chortoscirtes, Karniella and Naskreckiella

Naskreckiella kalamboi Ünal differs from *Phlesirtes* and *Chortoscirtes* in the width of the fastigium verticis. In *Phlesirtes* and *Chortoscirtes* the fastigium verticis is broader than the scapus; in *Naskreckiella* it is smaller. In *Karniella* the fastigium verticis is narrower than in *Phlesirtes* and *Chortoscirtes,* but is still broader than the width of the scapus. Another striking difference is found in the tegmina, which are moderately (*Naskreckiella*) to strongly (*Karniella*) inflated, whereas in *Phlesirtes* and *Chortoscirtes* they are never strongly inflated. Similarly, the pronotum is uplifted in the area of the tegmina in *Naskreckiella* and *Karniella*, whereas it is only weakly so in *Chortoscirtes* and weakly or not raised in *Phlesirtes* (Fig. 2). *Chortoscirtes* differs from *Phlesirtes* in the shape of the male cerci. All species at present united under *Phlesirtes* have male cerci either that are differentiated into an outer blunt and stout branch and an inner slender, sometimes long and twisted branch and a tenth abdominal tergite, which may be excavated (in *P. brachiatus* Fig. 1A, *P. latifrons* Fig. 1E, *P. merumontanus* Fig. 1F) or undifferentiated (*P. kibonotensis* Fig. 1D), or that have a spoon-like expanded outer branch and a slender inner branch (*P. kilimandjaricus* Fig. 1B). *Chortoscirtes* is unique in having a deep pit on the ninth tergite and pits or ridges on the tenth abdominal tergites, characteristics not found in this combination in the other three genera (Fig. 1G–K).

The male cerci of *Karniella* are divided into a blunt outer branch and an inner branch that is longer and more slender (*K. bullata,* Fig. 4G) or of the same length and width as the outer one (*K. crassicerca* **sp.n.** Figs 1L, 4F). *Naskreckiella* has male cerci with an outer blunt cercus and two inner ones of which the more basal is hook-like

(see Ünal, 2005). *Chortoscirtes* always has male cerci that are divided near the apex into an outer and an inner branch, and is thus similar to *Karniella*, especially to *K. crassicerca*. However, the outer branch is more slender than in *Karniella* or *Naskreckiella* (Fig. 4F–H). Females of *Phlesirtes*, *Chortoscirtes* and *Karniella* generally have a slender and slightly up-curved ovipositor, whereas in *Naskreckiella* the ovipositor is very stout, especially in the basal part. Only the typical colour pattern of *Karniella* (Fig. 2E, F) may help to distinguish females from *Phlesirtes* and *Chortoscirtes* females.

An overall cladistic analysis to clarify the position of the new subtribe *Karniellina* within Conocephalini is not feasable at present owing to a lack of data from the other tribes of Conocephalini.

Taxonomic treatment

Genus *Phlesirtes* Bolivar, 1922

Type species. Xiphidion merumontanum Sjöstedt, 1909.

Phlesirtes bilineatus Chopard, 1954

Material examined. Holotype, female, Kenya, Marsabit District, Chopa Gof Crater; NHML.

Description. See Chopard (1954).

Habitat. Scrub and grass (Chopard, 1954, Table 4).

Distribution. Chopa Gof Crater; the holotype is unique (Fig. 12).

Diagnosis. The largest species known at present (Chopard, 1954). The ovipositor of *P. bilineatus* is as long as its body size. Most other Karniellina have ovipositors that are shorter than the body size, except for females of the *Chortoscirtes* species and *Phlesirtes kilimandjaricus*.

Phlesirtes brachiatus Uvarov, 1924

Material examined. Holotype, male, British East Africa; NHML.

Locality and distribution. Not known.

Description. See Uvarov (1924).

Diagnosis. Phlesirtes brachiatus has a squarely excised tenth abdominal tergite (Fig. 1A). A similar modified tenth abdominal tergite is found in *P. latifrons* (Fig. 1E) and *P. merumontanus* (Fig. 1F). The male cerci of these three species are differentiated into a stout and blunt outer branch and a long slender inner branch. Females of these species have a rather short ovipositor. The habitat of all three species–montane grasslands–is similar, suggesting that these species form a phylogenetic unit.

Phlesirtes latifrons Chopard, 1954

Material examined. Holotype, male, Kenya, Marsabit; NHML.

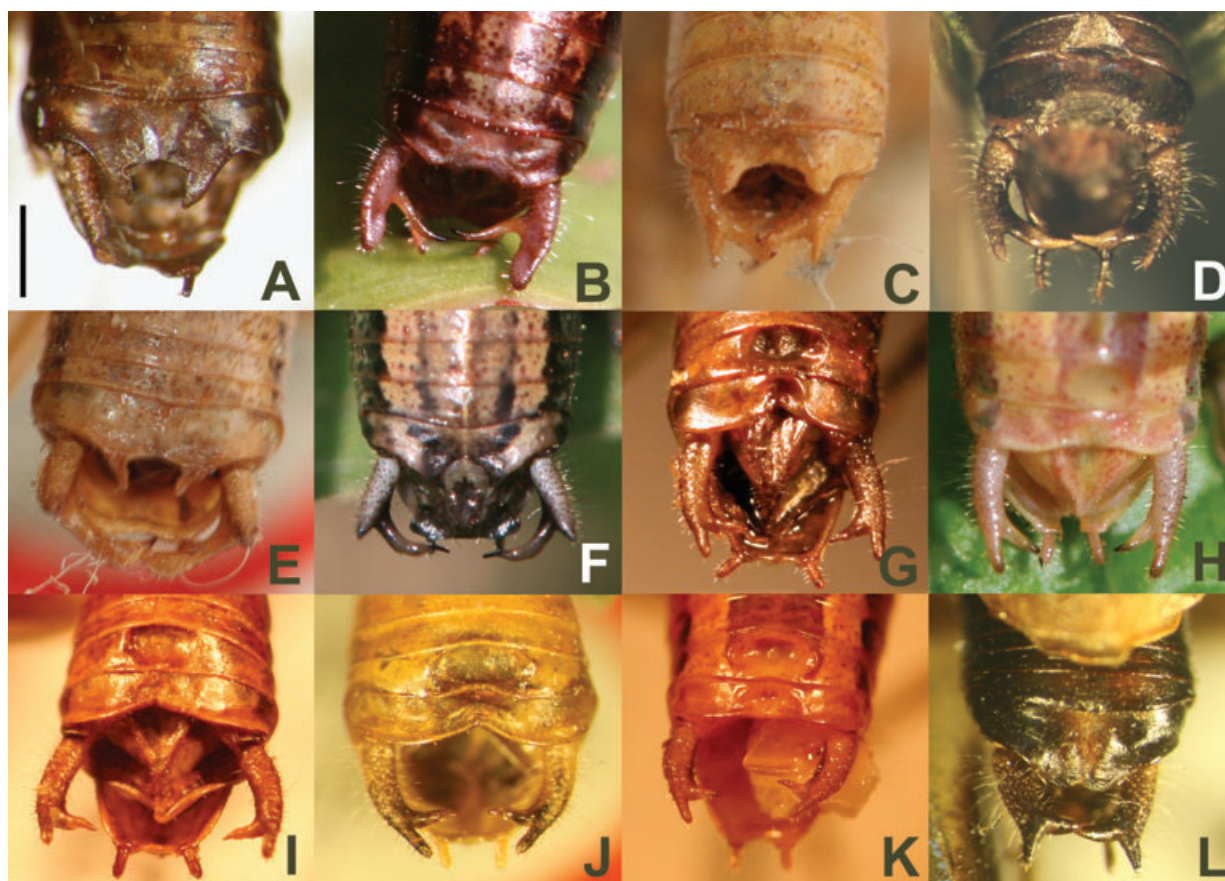Other material: 14 males and females all from the type locality; NHML.

Fig. 1. Dorsal view of male abdominal apices of *Phlesirtes*, *Chortoscirtes* and *Karniella* species: A, *P. brachiatus* (holotype); B, *P. kilimandjaricus* (living male, S Kilimanjaro); C, *P. kevani* (holotype); D, *P. kibonotensis* (N Kilimanjaro); E, *P. latifrons* (holotype); F, *P. merumontanus* (living male, N Kilimanjaro); G, *C. meruensis* (W Kilimanjaro); H, *C. pseudomeruensis* **sp.n.** (living male, E Kilimanjaro); I, *C. masaicus* **sp.n.** (holotype); J, *C. puguensis* **sp.n.** (holotype); K, *C. serengeti* **sp.n.** (holotype); L, *K. crassicerca* **sp.n.** (holotype). Scale bar represents 1 mm.

Description. See Chopard (1954).

Habitat. Upland grassland (Chopard, 1954) (Table 4).

Distribution. Northern Kenya from Mt Marsabit and Moyale (Fig. 12).

Diagnosis. Phlesirtes latifrons forms a morphological and ecological unit with *P. brachiatus* and *P. meruontanus*. See under *P. brachiatus* for further characters.

Phlesirtes merumontanus (Sjöstedt, 1909)

Xiphidion merumontanum Sjöstedt, 1909
Conocephalus (Xiphidion) merumontanus (Sjöstedt, 1909), Karny 1912: 12.
Phlesirtes merumontanus (Sjöstedt, 1909), Bolivar 1922: p. 203.

Material examined. Holotype, male, Tanzania, Mt Meru, montane forest 3000–3500 m; NHRS Stockholm.

Other material: 52 males, 47 females; Tanzania; Mt Meru, eastern slopes, grassy ruderal vegetation, 1400 m; Mt Meru, National Park Headquarters, grassland, 1400 m; Monduli range, open montane grassland, 2000–2180 m; Mt Kitumbeine, open montane grassland 2000 m; Mt Kilimanjaro, northern side, moorland Oloitokitok route, 2600–2700 m; Mt Kilimanjaro, northern slopes, Mosha farm, montane grassland, 1800 m; Mt Kilimanjaro, southwestern slopes, above Siha, forest edge, 1800 m; Mt Kilimanjaro, southern slopes, Nkweseko, montane grassland, 1800 m, collection C. Hemp.

Description. See Sjöstedt (1909).

Song. The calling song of the three recorded males consisted of long, uninterrupted sequences of syllables (Fig. 9) (syllable repetition rate 45 Hz at 17°C, longest uninterrupted recording 5 min). The song could not be heard with the unaided ear, its main components being in the ultrasonic range with a peak frequency at 26 kHz (details of song in Hemp & Heller in preparation).

Habitat. Montane grasslands, forest edge and clearings, afroalpine grasslands (Table 4).
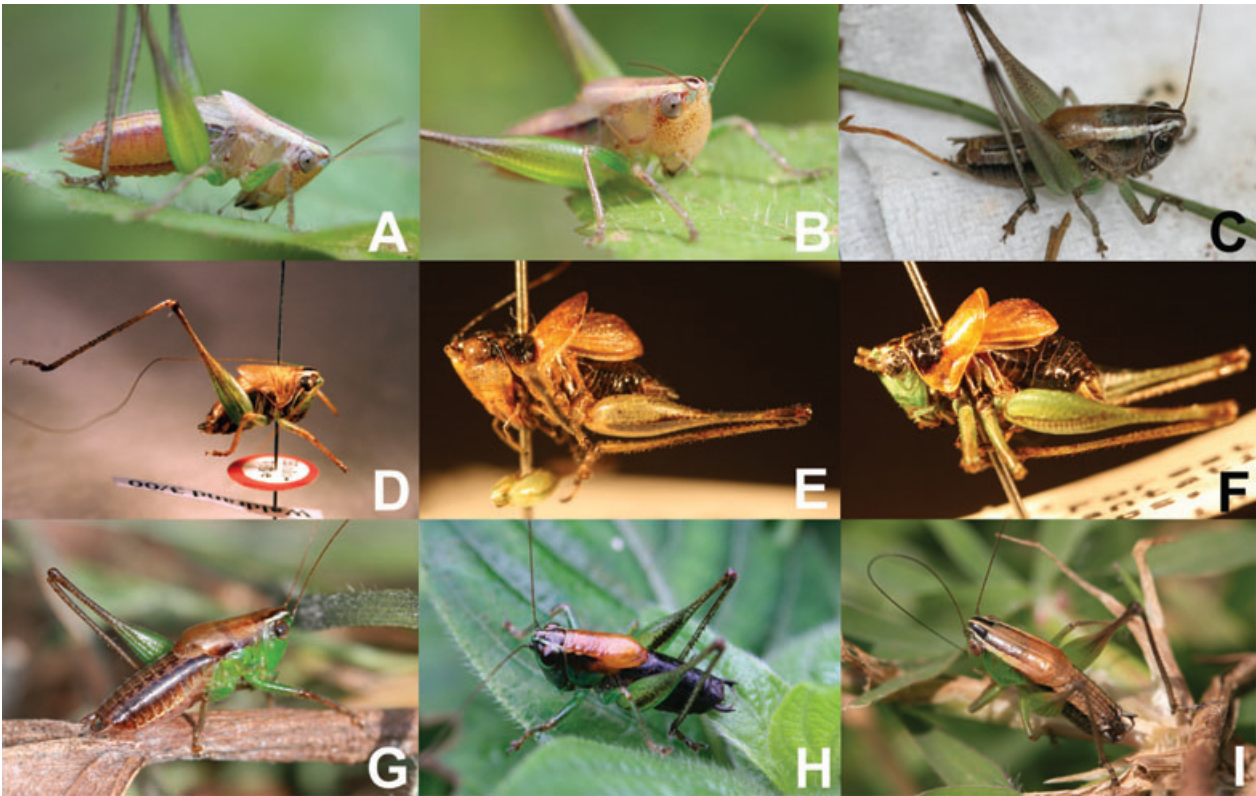
Fig. 2. Habitus of male *Chortoscirtes*, *Karniella* and *Phlesirtes* species. A,B, *C. pseudomeruensis* **sp.n.** (E Kilimanjaro, Chala area, 1150 m); C, *C. masaicus* **sp.n.** (holotype, between Mts Longido and Meru, 1290 m); D, *C. puguensis* **sp.n.** (holotype); E, *K. crassicerca* **sp.n.** (holotype); F, *K. bullata* Rehn (Kibale forest, Uganda); G, *P. kilimandjaricus* (Sjöstedt) (S Kilimanjaro); H, *P. kibonotensis* (Sjöstedt) (S Kilimanjaro, Old Moshi, 1700 m); I, *P. merumontanus* (Sjöstedt) (N Kilimanjaro, Mosha Farm, 1880 m).

Distribution. Northern Tanzania (Fig. 12).

Diagnosis. Phlesirtes merumontanus forms a morphological and ecological unit with *P. brachiatus* and *P. latifrons*. See under *P. brachiatus* for further characters.

Remarks. Uvarov (1924) mentions a male specimen of *P. merumontanus* from Ngabana, British East Africa (coll. Gregory). However, the locality could not be found and the specimen itself is badly damaged at its abdominal apex. Therefore it is not certain whether this specimen belongs to *P. merumontanus*, especially as British East Africa is Kenya and *P. merumontanus* has to date only been recorded on the high mountains of northern Tanzania.

Phlesirtes kevani Chopard, 1954

Material examined. Holotype, male, Kenya, Mandera District, Damassa, 03°09′N., 41°20′E; NHML.

 Other material: one female and one male paratype; NHML.

Description. See Chopard (1954).

Habitat. Desert-grass and thorn bush (Chopard, 1954) (Table 4).

Distribution. Only known from the type locality (Fig. 12).

Diagnosis. The tenth abdominal male tergite of *P. kevani* is exised at its posterior margin with a pair of stout projections and is thus superficially similar to *P. brachiatus*, *P. latifrons* and *P. merumontanus*. However, the male cerci are stout and differentiated into two short branches of similar size and shape. These kinds of cerci are found within *Chortoscirtes*. However, species of this genus have completely different ninth and tenth abdominal tergites. In *Chortoscirtes* the ninth and tenth abdominal tergites have roundish to oval pits or grooves and the posterior margin is never deeply excavated as in *P. kevani*. Furthermore, the habitat of *P. kevani* is unique–desert-grass and thorn bush at low elevations. No other member of the Karniellina is known at present to have a similar habitat and exhibit this combination of male genitalic characters.

Phlesirtes kibonotensis (Sjöstedt, 1909) comb. n.

Xiphidion kibonotense Sjöstedt, 1909
Conocephalus (Xiphidion) kibonotensis (Sjöstedt, 1909), – Karny 1912: 12.
Conocephalus kibonotensis (Sjöstedt, 1909), – Karny (1921: 27).
(Conocephalus (Anisoptera) kibonotensis (Sjöstedt, 1909), – Eades & Otte, 2009: online)

Table 4. Distribution, habitat and altitudinal spans of *Phlesirtes*, *Chortoscirtes*, *Naskreckiella* and *Karniella*, partly compiled from the literature (Uvarov, 1924; Chopard & Kevan, 1954).

Species	Distribution	Habitat	Altitudinal span (m)
P. bilineatus	Kenya, Marsabit, Chopa Gof Crater	Montane (?) grassland	1100[a]
P. brachiatus	East Africa, Ethiopia	Upland grassland (?)	Around 2300[b]
P. kevani	Kenya, Damassa, Mandera District	Desert-grass and thorn-bush	400[a]
P. kibonotensis	Tanzania, Mt Kilimanjaro	Forest paths and clearings, montane forest edge, montane plantations	1400–<u>1800–2200</u>–2400
P. kilimandjaricus	Tanzania, southern slopes of Mt Kilimanjaro	Submontane and montane grasslands, plantations	1100–<u>1400–1800</u>–1900
P. latifrons	Kenya, Mt Marsabit, Moyale	Upland grassland	?–1545[c]
P. merumontanus	Tanzania, Monduli Range, Mt Kitumbeine, Mt Meru, Mt Kilimanjaro	Montane grasslands, forest edge and clearings, afroalpine grasslands	1400–<u>1800–2000</u>–2700
C. masaicus	Tanzania, between Mts Longido and Meru	Savanna grassland	1290
C. meruensis	Tanzania, western side of Mt Kilimanjaro	Colline-submontane savanna grasslands	<u>1100–1300</u>–1400
C. pseudomeruensis	Tanzania, east Kilimanjaro	Colline-submontane savanna grasslands	1000–<u>1100–1300</u>–1400
C. puguensis	Tanzania, Pugu Hills	Coastal grassland	0–220
C. serengeti	Tanzania, Serengeti plains	Submontane savanna grassland	1350–1600
K. bullata	Uganda, Rwanda, Congo	Submontane and montane grassland along forest edge and on forest clearings	1200–3000
K. crassicerca	Uganda, Rwanda, Congo	Submontane and montane grassland along forest edge and on forest clearings	1600–2800
N. kalamboi	Zambia	Submontane forest	1200

[a]Elevation of localities taken from Geonames (http://www.geonames.org/maps/google_6.25_37.567.html).
[b]Elevation estimated from label information of specimens checked in the entomological collection of the Natural History Museum London, U.K.
[c]Highest elevation of Mt Marsabit.
Range of main occurrence underlined.

Material examined. Holotype, male, Tanzania, Mt Kilimanjaro, Kibonoto; NHRS Stockholm.

Other material: 30 males, 23 females; all Mt Kilimanjaro; southern slopes, Kidia, 1430 m, plantation; southern slopes, Mweka gate, 1650 m, forest edge; southern slopes, Rau river, 1780 m, riverine vegetation; southern slopes, above Kidia, 1710 m, montane grassland; southern slopes, above Maua 1900 m; southern slopes, Kidia, plantation, 1590 m; southern slopes, Nkweseko, 1800 m, montane grassland; northern slopes, grassy patches on forest clearing, 2000 m; northern slopes, grassy patches within forest clearing, 2050 m; northern slopes, Oloitokitok route, Kilimanjaro timbers, montane grassland, 2000 m; collection C. Hemp.

Description. See Sjöstedt (1909).

Song. The calling song of the four recorded males consisted of long, uninterrupted sequences of alternating echemes and single sylables (Fig. 9). Each echeme contained 12–17 syllables (syllable repetition rate 20 Hz at 20°C). The song could not be heard with the unaided ear, its main components being in the ultrasonic range with a peak frequency at 26 kHz (details of song Hemp & Heller, in prep.).

Habitat. Montane plantations, grasslands, forest edge and forest clearings (Table 4).

Distribution. Endemic to the submontane and montane zones of Mt Kilimanjaro (Fig. 12).

Diagnosis. Phlesirtes kibonotensis males have undifferentiated abdominal tergites with membraneous median areas on the ninth and tenth tergites (Fig. 1D). The male cerci are differentiated into a stout outer branch that is densely haired, and an elongated more slender inner branch. Thus the male cerci are similar to those of the species group *P. brachiatus*, *P. latifrons* and *P. merumontanus*. However, the abdominal tergites are differently shaped in this latter group, being deeply excavated at the anterior margin of the tenth abdominal tergite, whereas in *P. kibonotensis* the posterior margin is slightly inwardly curved and membraneous in its centre. *Phlesirtes kibonotensis* females have ovipositors that are clearly shorter than their body length. *Phlesirtes kibonotensis* is found in forest clearings, forest edge, and also within plantations, mainly in the montane zone of Mt Kilimanjaro (see Table 4), whereas the other groups of Karniellina occupy different habitats.

Phlesirtes kilimandjaricus (Sjöstedt, 1909) comb. n.

Xiphidion kilimandjaricum Sjöstedt, 1909
Conocephalus (Xiphidion) kilimandjaricus (Sjöstedt, 1909), Karny (1912: 12).
(*Conocephalus (Anisoptera) kilimandjaricus* (Sjöstedt, 1909), Eades & Otte (2009): online)

Material examined. Holotype, male, Tanzania, Mt Kilimanjaro, Kibonoto; NHRS Stockholm.

Other material: 40 males, 19 females, all Mt Kilimanjaro, western, southern and south-eastern slopes; Mrusunga valley, 1600 m; above Siha, montane grassland, 1850 m; above Kidia, montane grassland, 1700–1800 m; Kidia, on grassy patches within plantations and *Hyparrhenia* grasslands, 1200–1500 m;

Marangu, montane grassland, 1590 m; Mweka, grassy patches in plantation along river, 1130 m; Kifufu estate, on grassy patches in coffee plantation, 1400 m; Mwika area, grassy patches in plantation, 1400–1500 m; Kilema, *Hyparrhenia* grassland, 1440 m; collection C. Hemp.

Description. See Sjöstedt (1909).

Song. The calling song of the eight recorded males consisted of long, uninterrupted sequences of echemes (Fig. 9), each consisting of about five syllables (syllable repetition rate 50 Hz, repetition rate of echemes 5 Hz at 19°C). The song could not be heard with the unaided ear, its main components being in the ultrasonic range with a peak frequency at 26 kHz (details of song Hemp & Heller in prep.).

Habitat. Submontane and montane plantations and grasslands (Table 4).

Distribution. Endemic to the submontane and montane zones of Mt Kilimanjaro (Fig. 12).

Diagnosis. *Phlesirtes kilimandjaricus* males have an unmodified ninth abdominal tergite, the posterior margin of the tenth abdominal tergite being slightly curved inwardly. Unique are the male cerci, which are differentiated into a spoon-like expanded outer branch (Fig. 1B) and a slender inwardly curved inner branch. Cerci of this type are not found in any other member of the Karniellina known at present. Females of *P. kilimandjaricus* have a long and slightly upcurved slender ovipositor that is about as long as the body length of the insect. *Phlesirtes kilimandjaricus* inhabits mainly the submontane zone on the southern slopes of Mt Kilimanjaro (Table 4), only occurring syntopically with *P. kibonotensis* in anthropogenically influenced habitats (e.g. montane plantations).

Chortoscirtes gen.n. Hemp C.

Type species. Xiphidion meruense Sjöstedt, 1909. The genus *Chortoscirtes* is characterized in the male sex by cerci with two almost identical branches and pit-like modifications of the last two abdominal tergites. Fore and mid tibiae bear two rows each of six pairs of spines. The fastigium verticis is more than double the width of the scapus. The metazona of the pronotum may or may not be slightly raised. The females have a comparatively long smooth ovipositor that is moderately upcurved. All species are adapted to colline and submontane savanna grasslands and are tawny-brown coloured insects.

Key to the species of Chortoscirtes

1. Tenth abdominal tergite with well-developed cave-like pit; pit of ninth abdominal tergite almost round; face white or cream (Figs 1G, H; 2B). 2
– Tenth abdominal tergite without pit but with ridges; face brown or green 3

2. Pit on surface of tenth tergite, posterior margin only slightly incurved; male cerci slender, branches of cerci almost parallel, inner branch only slightly curved at apex (Figs 1H, 4B); colline zone of East Kilimanjaro . . . . *C. pseudomeruensis*

– Pit of tenth abdominal tergite located at posterior margin of tenth tergite, margin strongly inwardly curved (Fig. 1G); male cerci more stout (Fig. 4A), submontane grasslands between Mts Meru and Kilimanjaro. . . . .*C. meruensis*

3. Pit of ninth abdominal tergite longish-oval, groove of tenth abdominal tergite shallow; outer branch of cercus straight, inner branch swollen at base and hooked at apex (Figs 1K, 4E); Serengeti plains . . . . *C. serengeti*
– Pit of ninth abdominal tergite round or half-circle-shaped 4

4. Body size and width large for *Chortoscirtes*; face green; large almost half-circle-shaped pit on ninth abdominal tergite (Fig. 1J); outer branch of male cerci slender and straight, inner branch slightly curved (Fig. 4D); coastal area of Tanzania around Dar es Salaam and the Pugu Hills . . . .*C. puguensis*
– Face dark brown, pit of ninth abdominal tergite shallow; ridge of tenth abdominal tergite faint (Fig. 1I); inner branch of male cerci hooked (Fig. 4C); between Mt Meru and Mt Longido . . . . *C. masaicus*

Chortoscirtes meruensis (Sjöstedt, 1909) comb. n.

Xiphidion meruense Sjöstedt, 1909: 138.

Conocephalus (Xiphidion) meruensis (Sjöstedt, 1909), Karny (1912: 12).

(*Conocephalus (Anisoptera) meruense* (Sjöstedt, 1909), Eades & Otte, 2009: online).

Material examined. Syntypes (three males, two females), NHRS Stockholm; one male, MNB.

Other material: five males, four females, all Tanzania, between Mts Meru and Kilimanjaro, coll. C. Hemp; submontane savanna grassland, 1200–1400 m, 36°55,47′E, 02°56,71′S, all December 2006; collection C. Hemp.

Locality. Tanzania, Mt Meru (Meru Niederung, Ngare na nyuki).

Description: see Sjöstedt (1909).

Song. The calling song of several males recorded in the field consisted of long, uninterrupted sequences of pairs of syllables (Fig. 6; syllable repetition rate 71.9–77.5 Hz, repetition rate of syllable pairs 22.7–26 Hz; time of recording 14:00–14:30; six males; T = 26°C; animals possibly in sun). In the laboratory the rhythm of the song was distinctly slower owing to the lower temperature (Fig. 6; syllable repetition rate 46.9 Hz, repetition rate of syllable pairs 14.7 Hz; time of recording 9:30 am; duration of recording 35 s; T = 22°C; animal in shadow). As for *C. serengeti*, the animals produced a short song very similar to that shown in Fig. 7 for *C. serengeti*. Each echeme consisted of a group of 12–15 syllables (syllable repetition rate 74–79 Hz; three males; field recordings) with quite variable intervals, mostly between 0.5 and 3 s. The song could not be heard with the unaided ear, its main components being in the ultrasonic range with a variable peak frequency between 22 and 39 kHz (four males; range 10 dB below peak from 20–27 to 25–48 kHz).

Habitat. Savanna grasslands between 1200 and 1400 m (Table 4).

Coenology. Chortoscirtes meruensis was recorded on six plots in open savanna grasslands between Mt Kilimanjaro and Mt Meru. The first record was in December of the El Niño year 1997/1998 and subsequent ones in the El Niño year 2006/2007 in December 2006 and January 2007. There were 32 species noted on these six plots: *Abisares depressus* Uvarov, 1938; *Acrida bicolor* (Thunberg, 1815); *Acrotylus meruensis* Sjöstedt, 1932; *Allotriusia luteipennis* Ramme, 1929; *Catantops momboensis momboensis* Sjöstedt, 1931; *Conocephalus (Anisoptera) iris* (Serville, 1838); *Coryphosima stenoptera* (Schaum, 1853); *Cyrtacanthacris tatarica tatarica* (Linnaeus, 1758), *Duronia chloronota* (Stål, 1876); *Eyprepocnemis plorans* (Charpentier, 1825); *Gastrimargus verticalis* (Saussure, 1884); *Gymnobothrus temporalis flexuosus* (Schulthess Schindler, 1898); *Horatosphaga heteromorpha* (Karsch, 1889); *Horatosphaga meruensis* (Sjöstedt, 1909); *Lophothericles* sp.; *Metaxymecus gracilipes* (Brancsik, 1895); *Morphacris fasciata* (Thunberg, 1815); *Oedaleus flavus somaliensis* Sjöstedt, 1931; *Ornithacris cyanea* (Stoll, 1813); *Orthochtha dasycnemis dasycnemis* (Gerstaecker, 1869); *Peronura clavigera* Karsch, 1889; *Phaneroptera sparsa* Stål, 1857; *Plagiotriptus hippiscus* (Gerstaecker, 1869); *Pnorisa squalus* (Stål, 1861); *Pycnodictya galinieri galinieri* (Fairmaire & Reiche, 1850); *Pyrgomorphella albini* (Chopard, 1921); *Rhaphotittha subtilis* Karsch, 1896; *Rhaphotittha levis* Karsch, 1896; *Ruspolia* sp. and *Truxalis burtti* Dirsh, 1951. Most of these species are widespread forms within (East) African savanna grasslands. Endemic to the area is *Horatosphaga meruensis* (see Hemp, 2007) and probably *Lophothericles* sp.

Distribution. Tanzania; Mt Meru (Sjöstedt, 1909), Mt Kilimanjaro; endemic to the area between Mts Kilimanjaro and Meru (Fig. 12).

Diagnosis. Both *C. pseudomeruensis* and *C. meruensis* have a white face and two pits on the last abdominal tergites (Fig. 1G, H), whereas *C. masaicus* and *C. puguensis* have differently coloured faces and only one pit on the ninth abdominal tergite. See also the diagnosis of *C. pseudomeruensis* for further differentiating characters (Figs 1G, 3A, E and 4A).

Chortoscirtes pseudomeruensis sp.n. Hemp C.

Material examined. Holotype, male: Tanzania, East Kilimanjaro, *Hyparrhenia* grassland, 1300 m, 37°37,60857′E, 03°19,82256′S, July 2005, coll. Hemp.

Other material: all Tanzania, all East Kilimanjaro, all coll. Hemp; one female, Holili side vent, *Hyparrhenia* grassland, February 2001, MNB; one male, volcanic side vent, *Hyparrhenia* grassland, 1280 m, February 2001, NHML; one female, volcanic side vent, *Hyparrhenia* grassland, 1300 m, July 2005, NHML; one male, grassland, 1160 m, June 2006, EDNMK; one female, volcanic side vent, grassland, 1150 m, February 2001, EDNMK. 31 males, 28 females, 5 nymphs, all Tanzania, Mt Kilimanjaro, coll. Hemp. East Kilimanjaro, savanna grassland, 1170 m, January 2001; East Kilimanjaro, grassland,

1250 m, February 2001; Holili Hill, East Kilimanjaro, grassland, 1250 m, February 2001; Msangasanga Hill, East Kilimanjaro, *Hyparrhenia* grassland, 1280–1380 m, February 2001, July 2005; Chala area, East Kilimanjaro, grassland, 1150 m, February 2001; Mwika area, East Kilimanjaro, *Hyparrhenia* grassland, 1210 m, January 2001; Chala area, volcanic side vent, grassland, 1170–1270 m, July 2005; Chala area, volcanic side vent, grassland, 1160 m, June 2005; collection C. Hemp.

Description. Male. A mix of light brown with darker brown stripes and green (Fig. 2A, B). *Head.* Face white with red-brown spots in living insect, tawny in preserved one. Fastigium verticis broad, about 3× the width of scapus; dorsal at tip of fastigium a pair of blackish fasciae that change colour into dark brown, continuing until mesozona of pronotum; dorsal on head and pronotum broad light brown fasciae, bordered by above-described black and dark brown thin fasciae and then changing into conspicuous white parallel fasciae. This pattern of head and pronotal disk fading on metazona of pronotum. Eyes round-oval, of light colour with a few darker patches; around eyes red-brown spots. *Thorax.* Pattern of head continued on anterior half of pronotum (fascia of cream-white and darker brown colours, see description of head), metazona of pronotum of light cream colour. *Abdomen.* Pattern of head and anterior part of pronotum continued on abdomen: centrally a darker brown broad fascia, bordered by a pair of cream to yellowish fasciae; lateral sides of abdomen again darker brown. *Tegmina.* Elytra of same colour as anterior half of pronotum, visible part about 1 mm. *Legs.* Fore coxa with stout, moderately curved spine. All legs green, light brown at joints, tarsae brown; in preserved insects legs tawny; all femora unarmed. Fore and mid tibiae with six brown spines ventrally on each side. Hind tibiae with two ventral rows of dense spines; tibiae dorsally unarmed. *Genitalia.* Ninth abdominal tergite medially with oval pit; tenth abdominal tergite only slightly inwardly curved, half-open round pit of tenth abdominal tergite shallow (Fig. 1H). Cerci slender with two almost identical slender branches at apex. Cerci brown and hairy (Fig. 4B). Subgenital plate with two short styli (Fig. 1H).

Female. Same colour pattern as male but fainter; ovipositor slender and curved slightly upwards (Fig. 3B). Subgenital plate with central ridge; posterior margin slightly inwardly curved (Fig. 3F).

Song. The calling song of the recorded male consisted of a long, uninterrupted sequence of pairs of syllables (Fig. 6; syllable repetition rate 80 Hz, repetition rate of syllable pairs 29.4 Hz; time of recording 11:44 am; duration of recording 57 s; T = 27.5°C, animal possibly in sun). The song could not be heard with the unaided ear, its main components being in the ultrasonic range with a peak frequency at 21 kHz (range 10 dB below peak 20–29 kHz). Weak sound signals were observed in the record of another species from this site, which may indicate the presence of a short-song also in *C. pseudomeruensis* (see *C. serengeti*).
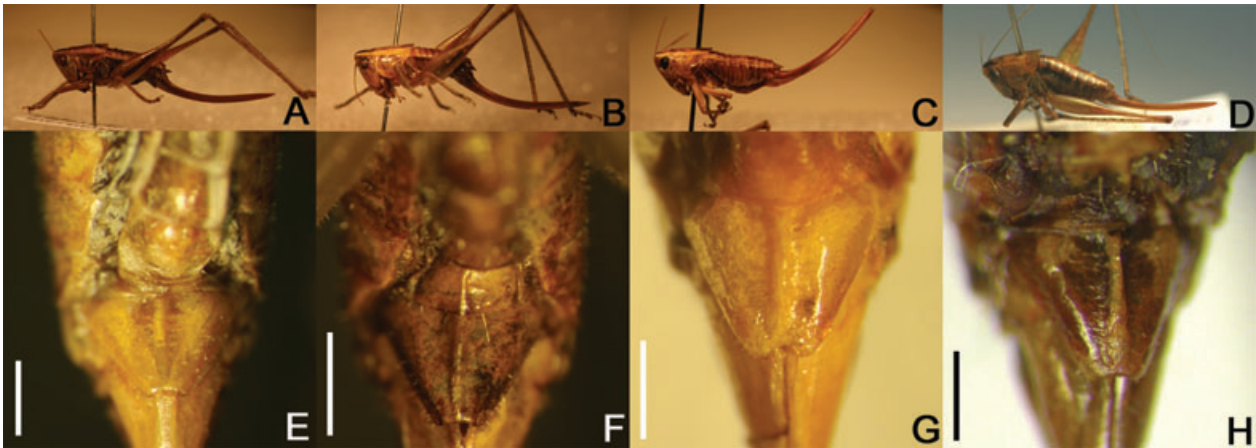
Fig. 3. Habitus and subgenital plates of female *Chortoscirtus* species. A, E, *C. meruensis*; B, F, *C. pseudomeruensis* n. sp.; C, G, *C. serengeti* n. sp. D, H, *C. puguensis*. Scale bar represents 1 mm.
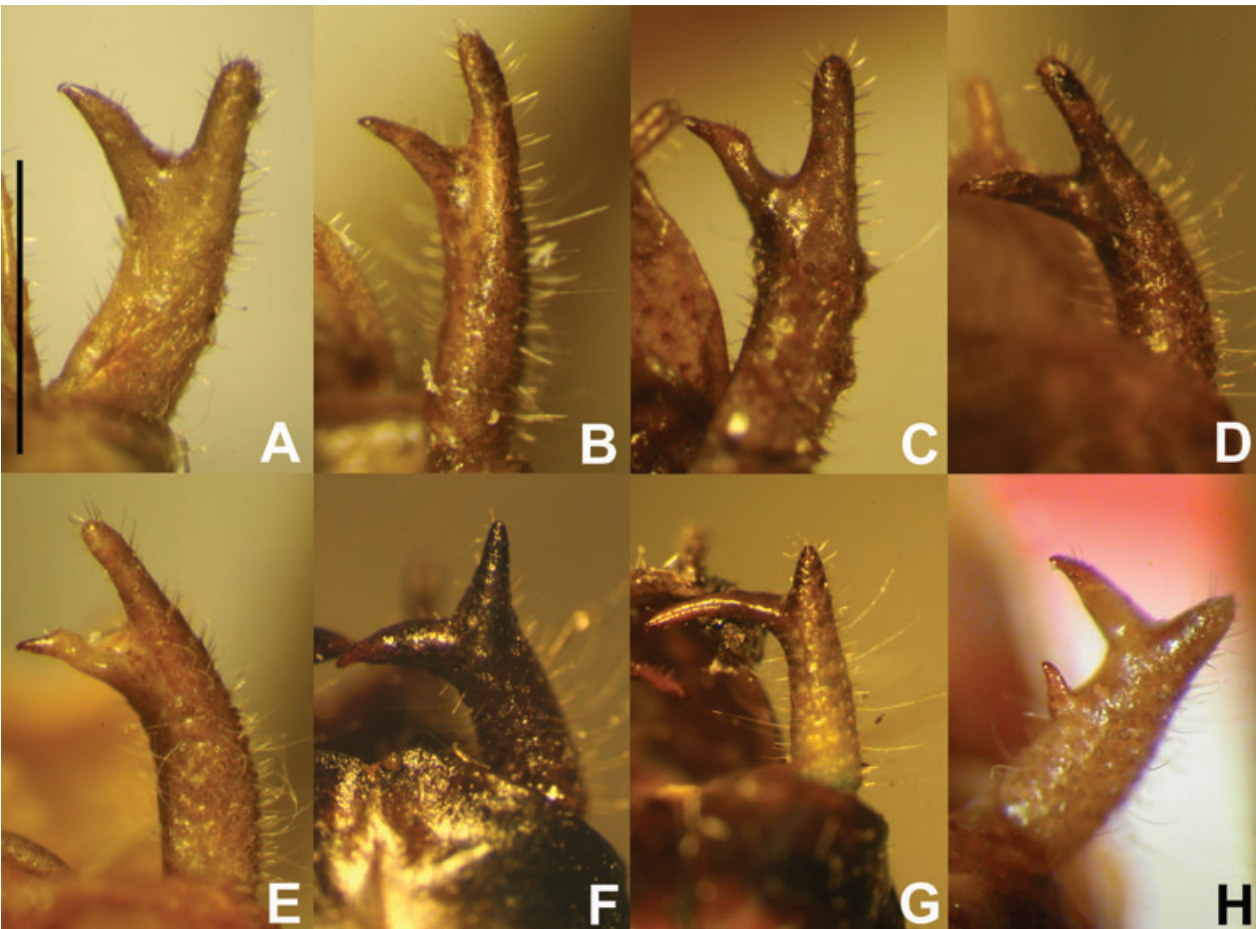

Fig. 4. Male cerci of *Chortoscirtes*, *Karniella* and *Naskreckiella* species. A, *C. meruensis;* B, *C. pseudomeruensis* **sp.n.**; C, *C. masaicus* **sp.n.**; D, *C. puguensis* **sp.n.**; E, *C. serengeti* **sp.n.**; F, *K. crassicerca* **sp.n.**; G, *K. bullata;* H, *N. kalamboi*. Scale bar represents 1 mm.
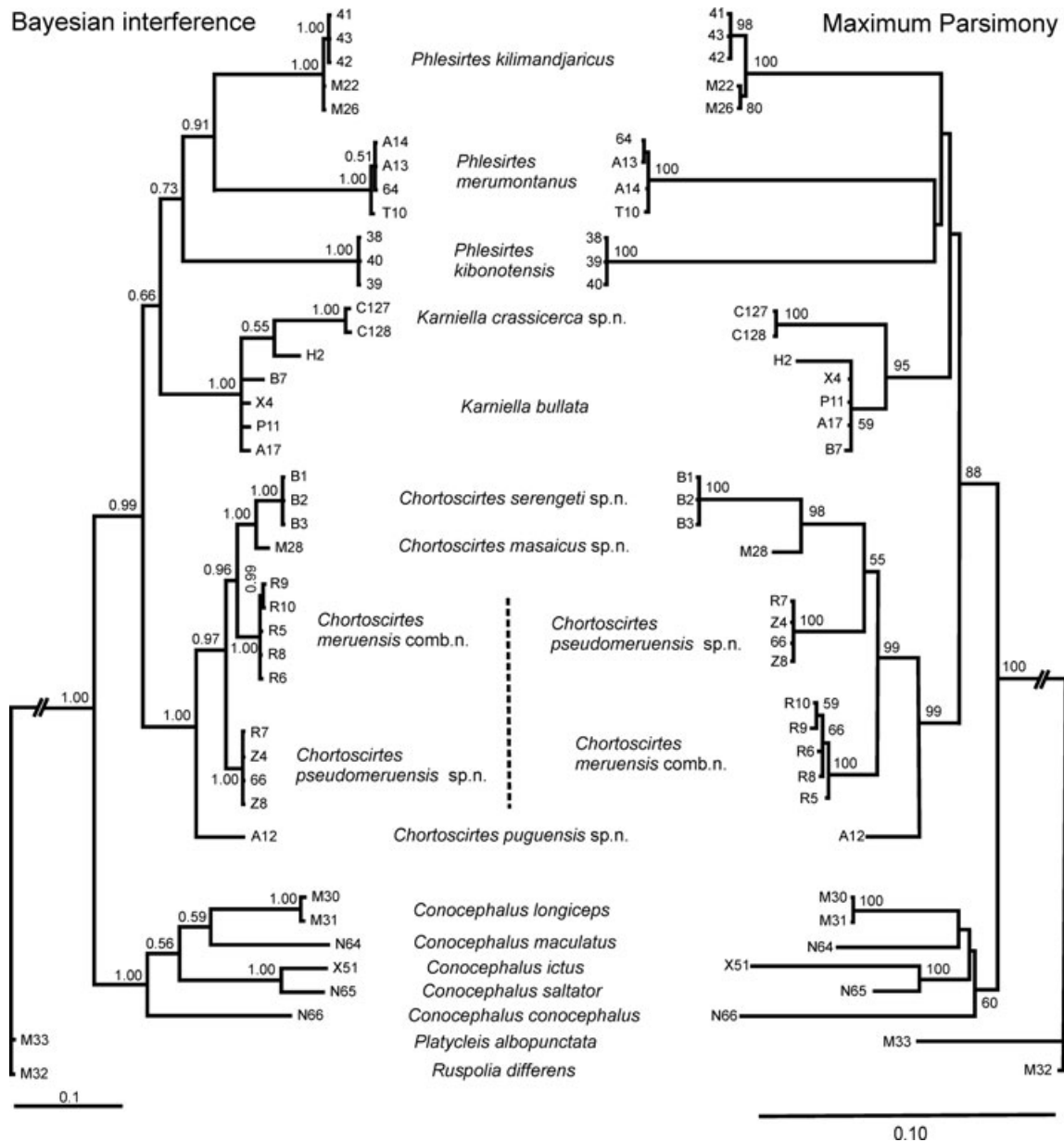
Fig. 5. Trees recovered from Bayesian and maximum parsimony analyses of combined character sets COI, 16S and H3. Posterior probabilities exceeding 0.5 are indicated in the Bayesian consensus tree on the left side, and bootstrap values that exceed 50 are indicated in the majority rule consensus tree of the 897 most parsimonious trees shown on the right (1525 total characters, 1049 constant characters, 436 parsimony-informative characters, consistency index = 0.5852, retention index = 0.8406). *Platycleis albopunctata* and *Ruspolia differens* were used as the outgroup.

Habitat. Savanna and *Hyparrhenia* grasslands from 1000 to 1400 m, with occurrence mainly between 1100 and 1300 m on the eastern slopes of Mt Kilimanjaro (Table 4).

Coenology. Chortoscirtes pseudomeruensis was recorded on 28 permanent plots between 1997 and 2005. Some of these plots were checked more than 40 times, but most plots were revisited 2–6 times and Saltatoria species noted. Species that occurred with very high constancies (recorded in over 80% of the plots in which *C. pseudomeruensis* occurred) were *Pnorisa*

squalus (Stål, 1861), *Epacrocatantops curvicercus* (Miller, 1929), *Orthochtha dasycnemis* (Gerstaecker, 1869) and *Gastrimargus determinatus vitripennis* (Saussure, 1888). These species are widespread, highly mobile forms in the savanna grasslands of eastern and southern Africa. Also present with high constancy (over 60% on all plots) were *Conocephalus (Anisoptera) maculatus* (Le Guillou, 1841), *Metaxymecus gracilipes* (Brancsik, 1895), *Gymnobothrus lineaalba* Bolivar, 1889, and *Brachycrotaphus sjostedti* Uvarov, 1932. Only

Measurements.

	Male (mm) n = 16	Female (mm) n = 11
Body length	9.6−11.9 (mean: 10.3)	9.8−14.8 (mean: 12.6)
Pronotum length	3.9−4.5 (mean: 4.3)	3.9−4.5 (mean: 4.2)
Anterior femur length	2.3−2.6 (mean: 2.5)	2.6−3.1 (mean: 3.0)
Posterior femur length	9.6−12.3 (mean: 10.7)	12.4−13.5 (mean: 13.1)
Tegmina length (visible part)	0.6−1.2 (mean: 1.0)	−
Ovipositor length	−	11.0−13.2 (mean: 11.8)

B. sjostedti is restricted to East Africa, the other species being common in African grasslands. All in all, 97 Saltatoria species were recorded on these 28 plots, more than 50% of them found only one to five times on single plots.

Distribution. Tanzania; endemic to the lower slopes of East Kilimanjaro in the area around Lake Chala (Fig. 12).

Diagnosis. Chortoscirtes pseudomeruensis and *C. meruensis* have a white face (Fig. 2A, B) and two pits on the last abdominal tergites (Fig. 1G, H), whereas *C. masaicus* and *C. puguensis* have differently coloured faces and only one pit on the ninth abdominal tergite. *Chortoscirtes pseudomeruensis* and *C. meruensis* can be distinguished from *C. serengeti* by the shape of the inner branch of the male cerci, which is swollen at the base in *C. serengeti* and the whole branch strongly twisted, whereas the base of this branch is unmodified in *C. pseudomeruensis* and *C. meruensis* and not as twisted over its whole length (Figs 1G, H and K; 4A, B and E).

Morphologically, *C. pseudomeruensis* and *C. meruensis* are closely related. *Chortoscirtes meruensis* has a broader fastigium verticis (almost 4× the width of one scapus) than *C. pseudomeruensis* (about 3× the width of one scapus). Differences are found also in the male genitalia. The posterior margin of the tenth abdominal tergite is more strongly incurved in *C. meruensis* than in *C. pseudomeruensis* and the central pit is of a different form in the two species (Fig. 1G, H). The inner branch of the male cerci is more slender in *C. meruensis* and more curved than in *C. pseudomeruensis*, in which the male cerci have two almost identical branches of the cerci, the inner one being almost straight. The subgenital plate in *C. pseudomeruensis* is strongly excavated (Fig. 1H), whereas the posterior margin of the subgenital plate in *C. meruensis* is only slightly curved inwardly (Fig. 1G).

Chortoscirtes masaicus sp.n. Hemp C.

Material examined. Holotype, male: Tanzania, northern foothills of Mt Meru, savanna grass/bushland, 1290 m, May 2005, 36°42, 12905′E, 02°54, 10895′S; MNB.

Other material: one male, same data as holotype but December 2006.

Description. Male. Light brown mixed with darker brown (Fig. 2C). *Head.* Face dark brown in overall appearance, in magnification pattern of dark brown dots and linules on light brown ground; fastigium verticis broad (1 mm in diameter at broadest point, about 2.5× the width of one scapus); dorsal broad brown fascium, the outer margins of this fascium are dark brown, getting lighter medially; in the centre a white small line is present; area beside this fascium cream-whitish with scattered brown dots more posteriorly. These white-cream fasciae are continued about half way along the pronotum. Eyes round-oval, brown with dark brown patches and/or dots and/or linules; eye encircled by light-coloured band. *Thorax.* Pattern of head continued on anterior half of pronotum (fascia of cream-white and darker brown colours, see description of head), posterior half uniformly lighter brown without striped pattern. *Abdomen.* Pair of lateral cream fascia, medial dark brown fascia. *Tegmina.* Elytra of same colour as anterior half of pronotum, visible part about 1 mm. *Legs.* Fore coxa with stout, moderately curved spine. All legs of light brown colour, except hind femora greenish in living insect (Fig. 2C), all femora unarmed. Fore and mid tibiae with six brown spines ventrally on each side. Hind tibiae with two ventral rows of dense spines; bases of spines of same colour as tibiae, rest dark brown; tibiae dorsally unarmed. *Genitalia.* Ninth abdominal tergite medially with roundish pit; tenth abdominal tergite inwardly curved, with ridges (Fig. 1I). Cerci slightly curved inwardly, inner branch strongly hooked (Fig. 4C). Cerci brown and hairy. Subgenital plate with two short styli (Fig. 1I).

Female. Not known.

Habitat. Savanna grass/bushland (Table 4).

Coenology. Chortoscirtes masaicus was found on a permanent plot that was screened three times in May 2005, May 2006 and December 2006 during periods when this area had had sufficient precipitation, causing a lush vegetation cover. Syntopic with *C. masaicus*, 16 species were recorded during the three checks: *Abisares depressus* Uvarov, 1938; *Acorypha ornatipes* Uvarov, 1950; *Acrida bicolor* (Thunberg, 1815); *Cyrtacanthacris tatarica tatarica* (Linnaeus, 1758); *Eyprepocnemis plorans* (Charpentier, 1825); *Gastrimargus determinatus vitripennis* (Saussure, 1888); *Heteropternis thoracica* (Walker, 1870); *Horatosphaga heteromorpha* (Karsch, 1889); *Humbe tenuicornis* (Schaum, 1853); *Ochrilidia gracilis nyuki* (Sjöstedt, 1909); *Oedaleus flavus somaliensis* Sjöstedt, 1931, *Oedaleus inornatus* Schulthess Schindler, 1898, *Peronura clavigera* Karsch, 1889; *Ruspolia* sp.; *Sphingonotus turkanae* Uvarov, 1938 and *Truxalis burtti* Dirsh, 1951. All these species are widespread forms typical for savanna grasslands in the area.

Measurements.

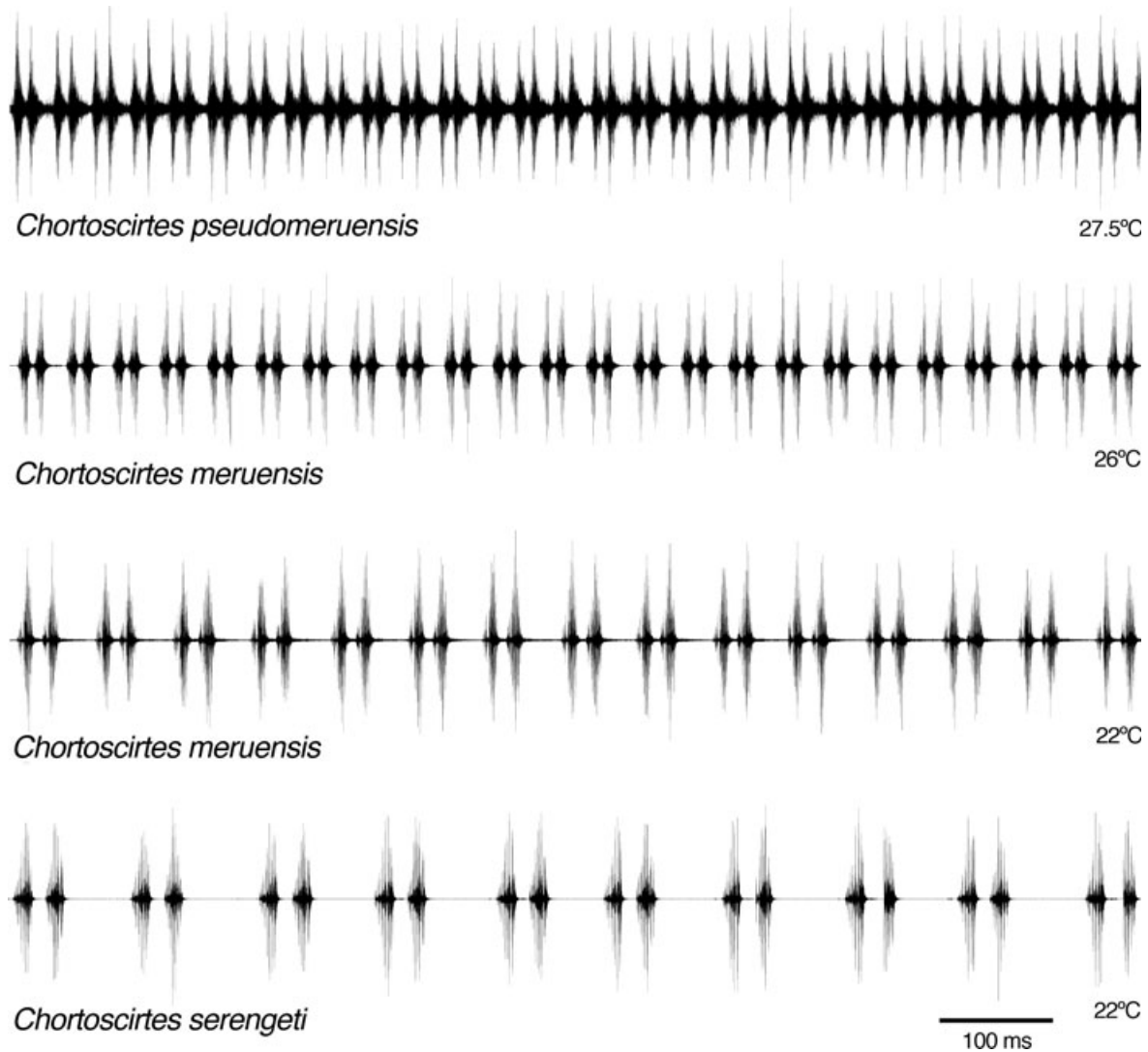|	Msale (mm) n = 2
Body length	9.8−10
Pronotum length	4.6−4.7
Anterior femur length	2.5−2.6
Posterior femur length	11.0
Tegmina length (visible part)	0.9−1.2
Ovipositor length	−

Fig. 6. Oscillograms of calling songs of *Chortoscirtes* species.

Distribution. Tanzania; between Mt Longido and Mt Meru, lower slopes of Mt Meru; only known from the type locality (Fig. 12).

Diagnosis. Chortoscirtes masaicus is the smallest species of the genus at present and also not as stout as the other four known species. The pattern of white and brown fascia on the head and pronotum is very conspicuous and it is the only species up to now of this genus with a dark brown face. *Chortoscirtes meruensis* and *C. pseudomeruensis* both have white to cream-white faces, *C. puguensis* has a green face, and *C. serengeti* has a light brown face. In contrast to *C. meruensis, C. pseudomeruensis* and *C. serengeti* no pit is present on the last abdominal tergite, but there is a curved ridge. *Chortoscirtes masaicus* may be distinguished from *C. puguensis* by the shape of the pit of the ninth abdominal tergite (see key) in addition to the body size and the different colour of the face.

***Chortoscirtes puguensis* sp.n. Hemp C.**

Material examined. Holotype, male, Tanzania, Pugu Hills, grassy patches along forest edge, 6°53′0″S, 39°05′0″E, March 2000; coll. Hemp, MNB.

Other material: one female, Tanzania, Dar es Salaam, University campus, coll. ND Jago, July 1966, NHML; two males, Tanzania, Dar es Salaam, University campus, coll. N.D. Jago, July 1966, NHML.

Description. Male. Green and brown (Fig. 2D). *Head.* Face green with irregular pattern of brown spots and linules; fastigium verticis broad (about 2.5× width of one scapus), with broad brown fascium, separated laterally and medially by white yellow fascia; more than twice the width of diameter of one eye. Eyes round-oval, with dense patches of brown spots on lighter background; white band encircling eye. *Thorax.* Pronotum light brown, translucent, surface shiny. *Abdomen.*

Slightly darker brown than pronotum and elytra. *Tegmina.* Elytra of same colour as pronotum, visible part 1.2 mm. *Legs.* Fore coxa dorsal with slightly curved spine. Basal two-thirds of all femora green, merging into brown, tibiae and tarsae brown; knee of hind femur dark brown; scattered brown spots on all femora, becoming denser to their posterior ends. All femora unarmed. Fore and mid tibiae with six brown spines ventrally on each side. Hind tibiae with two ventral rows of dense brown spines, dorsally unarmed. *Genitalia.* Ninth abdominal tergite medially with deep pit; tenth abdominal tergite posteriorly bordered with two parallel sclerotized ridges, margin inwardly curved. Cerci curved inwardly, outer branch slender, inner branch slightly hooked (Fig. 4D). Cerci brown and densely hairy. Subgenital plate with two stout styli, slightly shorter than cerci (Fig. 1J).

Female. Same colour pattern as male but fainter; ovipositor slender and curved very slightly upwards (Fig. 3D). Subgenital plate with central ridge; posterior margin slightly curved inwardly (Fig. 3H).

Measurements.

	Male (mm) n = 3	Female (mm) n = 1
Body length	11.9–13.3	14.8
Pronotum length	5.1–6.2	5.0
Anterior femur length	3.0–3.5	3.6
Posterior femur length	12.0–13.5	14.5
Tegmina length (visible part)	1.2–1.5	–
Ovipositor	–	13.4

Habitat. Grasslands and grassy patches along forest edge of coastal forest (Table 4).

Coenology. In March 2000 and October 2006 along the forest edge and in the grassy strip adjacent to the forest patch of the Pugu Hills the following species were recorded: *Pieltainidia mira* Ramme, 1925; *Leptacris monteiroi monteiroi* (Bolivar, 1890); *Paraspathosternum pedestris* (Miller, 1929); *Parepistaurus pugui* Green, 1998; *Oxyaeida brachyptera* Miller, 1929; *Paraprocticus forchhammeri* (Johnsen, 1974); *Catantops momboensis momboensis* Sjöstedt, 1931; *Europacris pompalis* (Karsch, 1896); *Phaeocatantops decoratus* (Gerstacker, 1869); *Tangana* sp.; *Heteropternis thoracica* (Walker, 1870); *Amphicremna flavipennis* I. Bolivar, 1912; *Gymnobothrus flexuosus* (Schulthess, 1898); *Lobopoma mitchelli* Popov & Fishpool, 1992; *Orthochtha dasycnemis alca* I. Bolivar, 1908; *Parodontomelus brachypterus* (Karny, 1915) and *Parodontomelus verticulus* Jago, 1983. Some of the above-listed species are forms typical of coastal savanna grasslands (also see Hemp, 2005a), but the area is also known to harbour many endemics. A number of flightless species have been described from the Pugu Hills, for example *Parepistaurus pugui* and *Parodontomelus verticulus*. *Parodontomelus brachypterus* was also described from this area. *Pieltainidia mira* is known to date only from the East Usambara mountains, suggesting that this species is a dweller of coastal forest in East Africa.

Distribution. Tanzania; coastal Tanzania around Dar es Salaam (University campus, collection NHML) and the Pugu Hills (Fig. 12).

Diagnosis. Chortoscirtes puguensis is the largest known species of the genus *Chortoscirtes*. It is the only species known at present with a green face. On the abdominal tergites there is a large pit on the ninth tergite and a ridge on the last. It can be differentiated from *C. masaicus* by the colour of the face (dark in *C. masaicus*), the larger size and the overall different colour pattern, which is darker in *C. masaicus*.

Chortoscirtes serengeti sp.n. Hemp C.

Material examined. Holotype, male, Tanzania, Serengeti plains, Seronera area, Pimbi camping site 2°26′S, 34°49′E, February 2007, coll. K.-G. Heller, MNB.

Other material: one female, same data as holotype, MNB; seven males, five females, one nymph, same data as holotype (by/coll. C. Hemp and K.-G. Heller).

Description. Male. A mix of light and dark brown and green. *Head.* Face light brown; fastigium verticis broad (1.1 mm in diameter, about 3× the width of one scapus); straw-coloured fascium dorsal on head, bordered by dark brown lateral fasciae; these dark brown fasciae are very broad at the apex of the fastigium, becoming smaller more posteriorly; these are again bordered by fine straw-coloured lines laterally, centrally with thin white line; lateral straw-coloured fasciae continued over pro- and metazona of pronotum. Eyes round-oval, black with some brown patches near the margin; eyes encircled by light band. *Thorax.* On anterior half of pronotum pattern of head is faintly continued, pattern disappearing into uniformly very light brown or almost tawny colour. *Abdomen.* Pattern of parallel brown and lighter brown fasciae. *Tegmina.* Elytra of same colour as anterior half of pronotum, almost white, visible part about 1.2 mm. *Legs.* Fore coxa with comparatively stout, curved spine. Basal parts of femora green, more posteriorly changing into light brown; tibiae and tarsae brown. All over the body and especially on the legs numerous reddish dots. All femora unarmed. Fore and mid tibiae with six brown spines ventrally on each side. Hind tibiae with two ventral rows of dense brown spines, tibiae dorsally unarmed. *Genitalia.* Last two abdominal tergites each with a pit medially (Fig. 1K). Cerci curved inwardly, ending in two branches of which the inner one is swollen at the base and hooked (Fig. 4E). Subgenital plate with two short styli (Fig. 1K).

Female. Same colour pattern as male but fainter; ovipositor of light colour, long and slightly curved (Fig. 3C). Subgenital plate with indentation at posterior margin and a central ridge (Fig. 3G).

Song. The calling song of the recorded male consists of long, uninterrupted sequences of pairs of syllables (Fig. 7; syllable repetition rate 43.7 Hz, repetition rate of syllable pairs 9 Hz; T = 22°C). This type of song is produced for many minutes or even hours (longest recorded sequence 3.5 min). The syllables have durations of 12–15 ms and contain 9–13 impulses, the

Measurements.

	Male (mm) n = 7	Female (mm) n = 4
Body length	9.5–13 (mean: 11.0)	13–15
Pronotum length	4.6–5.1 (mean 4.8)	3.7–5.0
Anterior femur length	2.7–3.2 (mean: 3.0)	3.1–3.7
Posterior femur length	10.0–12.6 (mean: 11.7)	13.0–15.2
Tegmina length (visible part)	1.0–1.8 (mean: 1.5)	–
Ovipositor length	–	12.5–14.7

first syllable of each pair slightly shorter with fewer impulses than the second (Fig. 7C).

This type of continuous buzzing song is also heard in the field (when using a bat detector). However, sometimes a completely different signal can be registered, called a short-song. The first time it was heard was from many animals in the field in an evening after a strong rain. It was then recorded in a captive animal after a disturbance and was followed by the continuous song re-starting. Finally, the same type of song was recorded in the evening and sporadically throughout the whole night after an animal had been placed in the laboratory in Germany. At about 9 am the animal began the continuous song, and the short-song could only be heard before the start of a long sequence (Fig. 7A). Each echeme of the short-song contained 11–13 syllables produced at a homogeneous rate of 39 Hz (T = 20°C). The intervals between the echemes were quite variable (2–8 s), but sometimes two echemes followed each other without any interval. The function of this signal can only be speculated on.

As in the other *Chortoscirtes* species, the calling song is nearly exclusively in the ultrasonic range. In a recording with a 300-kHz sampling rate (animal in a gaze cage, distance to microphone about 0.6 m) the peak frequency was 33 kHz (range 10 dB below peak 21–41 kHz, in other recordings up to 60 kHz) (Fig. 6).

Habitat. Upland savanna grasslands (Table 4).

Distribution. Tanzania; Serengeti plains (Fig. 12).

Diagnosis. Chortoscirtes serengeti is larger than *C. masaicus*, about the size of *C. meruensis* and *C. pseudomeruensis*, and smaller than *C. puguensis*. It is much lighter in colour than any other species of this genus. The overall appearance is straw-coloured with the black eyes being in contrast to the general light colour. *Chortoscirtes serengeti* has two pits on the last two abdominal segments, the one on the ninth tergite being almost rectangular (see key 'pit of ninth abdominal tergite longish-oval'), distinguishing it from *C. meruensis* and *C. pseudomeruensis*, which have a roundish pit on this segment.

Genus *Karniella* Rehn, 1914

Type species. Karniella bullata Rehn, 1914.

Karniella bullata Rehn, 1914

Material examined. Holotype, male, Uganda, western slopes of Ruwenzori (2500 m), coll. Schubotz, Exped. Herzog Adolf Friedrich z. Mecklenburg, 01.02.1908–29.02.1908, MNB.

Other material: two males, two females, Uganda Kibale forest, pine plantation, September 1986, coll. Nummelin, EDMNK. One male, two females, Zaire (Congo), Kivu, Tsivanga im Nationalpark Kahuzi Biega (bei Bukavu) (2°25′S, 28°40′E), 19–26 March 1990, coll. K.-G. Heller & M. Volleth, collection Heller.

Uganda: one male, mile 22 Hoima Rd., August 1935, coll. H. B. Johnston; one male, Hamane, September 1933, coll. H. B. Johnston; one male, Mabira forest, April 1934, coll. H. B. Johnston; one male, one female, W Ruwenzori, Mutanga, 1932, coll. Mus. Congo (Dr. Van Hoof); two males, two females, Kivu, Mulungu, Tshibinda, November 1951, coll. Mus. Congo (P. C. Lefèvre); one male, Musée du Congo, Region des Lacs, coll. Dr Sagona; two males, one female, near Kisoro, Busanza, 11–13 December 1970, coll. W. J. Bailey; one male, Mulange, Chagwe, 25 August 1922, coll. Dummer; one male, Mpanga, 22 July 1969, coll. W. J. Bailey; one male, one female, Kibale forest Res., SE of Ft. Portal, 13 July 1964, coll. N. D. Jago; two males, Mpanga, 22 November 1969, coll. W. J. Bailey; one female, Mpanga forest, 21 October 1965; two females, Uganda, 27 mls W of Ft. Portal, 9 July 1964, N. D. Jago; one female, 12 mls W of Jinja, Mbale forest Res., 18 July 1964, N. D. Jago; two females, nr Kampala, Mpanga forest Res., 3 August 1964, N. D. Jago; one male, 13 mls along Kabale-Kisoro Rd, 6 September 1964, N. D. Jago; two males, one female, Mubende, 6 August 1964, coll. N. D. Jago; six males, three females, Kibale forest Res., SE of Ft. Portal, 12 August 1964, coll. N. D. Jago; one male, one female, 7 mls W of Mubende, 2 July 1957, 1250 m; one male, one female, Buganda, Mabira forest res., Jinja, 33°0′E, 0°25′N, 27 April 1967, coll. N. D. Jago, NHML.

Tanzania: 8 males, 12 females, Tanganyika T., Tshihinda, 21–27 August 1931, coll. J. Oglivie; one female, Tanganyika T., Uvira, 28–29 August 1931, coll. J. Oglivie, NHML.

Democratic Republic of the Congo. One male, one female, Belgian Congo, La Chute forest, Rutshuru August 1949; ten males, ten females, Rutshuru, September 1936, Coll. Mus. Congo (L. Lippens); three males, Kivu, Sake, 1 March 1936, Coll. Mus. Congo (L. Lippens); one female, Congo Belge PNA, 7–15 July 1955, coll. Vanschuybroek; one female, Belgian Congo, Luhoho, Riv. Bunyakiri, 1100 m, 6 September 1957; one female, Masisi, Kishenyo (Kivu), 1935, coll. H. Hermann; one male, Musée du Congo, Kivu, Lulenga, 24 September 1932, coll. L. Burgeon; one male, I.R.S.A. Mus. Congo, Kivu, Loashi, 1350 m, 28–30 September 1949, coll. Dr R. Laurent; one male, Musée du Congo, P. N. A. Ruindi, 18 April 1937, coll. H. J. Brédo; one female, Musée du Congo Belge, Beni, coll. Lt. Borgerhoff; two females, Kivu, Kavumu à Kabunga, km 82 (Mingazi), coll. H. Bomans, NHML.

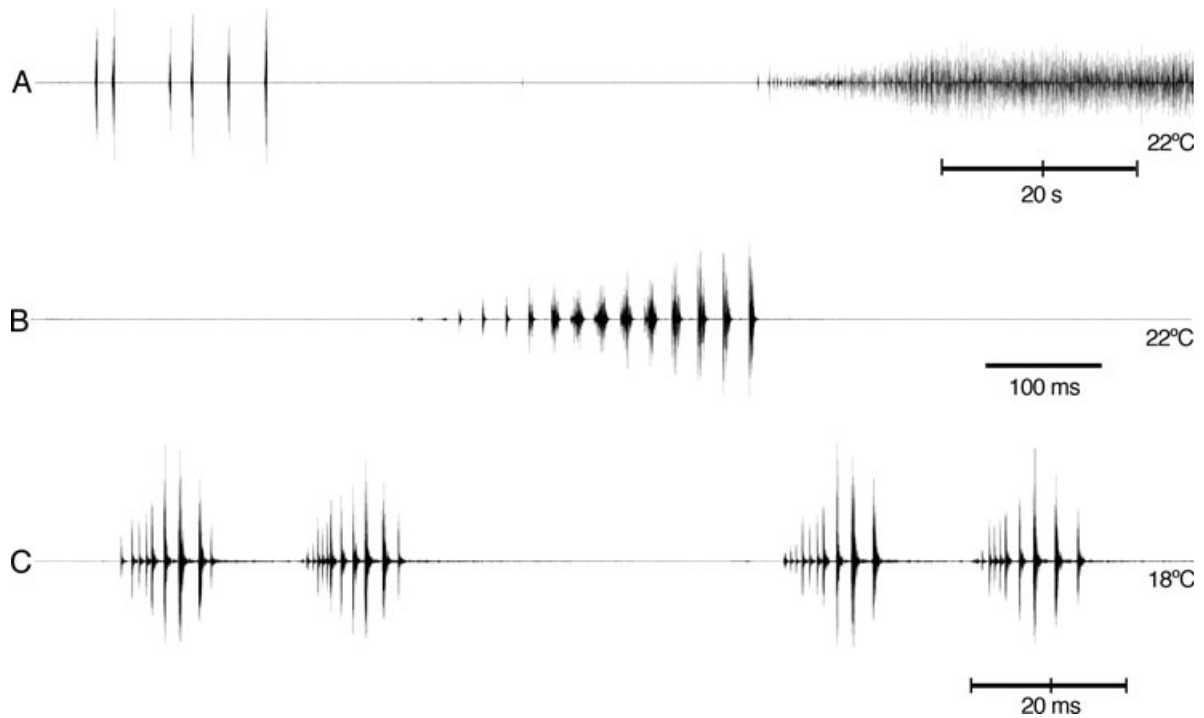Rwanda. One male, Musée du Congo, Ruanda, November 1936, coll. Mde Boutakoff, NHML.

Fig. 7. Oscillograms of the song of *Chortoscirtes serengeti*. A, transition from short-song to calling song; B, short-song, detail; C, calling song, detail (see Fig. 6 for a longer portion of the song).
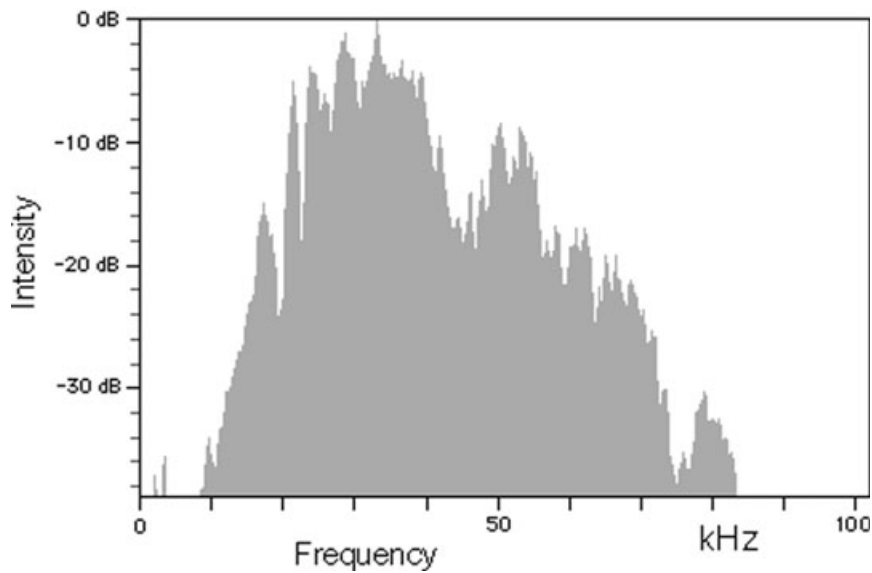

Fig. 8. Frequency spectrum of male calling song of *Chortoscirtes serengeti*.

Kenya. One female, British East Africa, Ngare Narok, Masai Reserve, 3 December 1913, about 6000 ft, coll. A. O. Lukman, NHML.

Burundi. One female, Urundi, Muyeha (Riv Kishubi), 1700 m, 18 July 1952, coll. Dr R. Laurent; two males, two females, Urundi, Bururi, 1800–2000 m, 5–12 March 1953, coll. Mus. Congo (P. Basilewsky), NHML.

For additional figures see: http://www.biologie.uni-ulm.de/systax/cgi-bin/query_all/details.pl?sid=T&lang=e&extid name=osfspeciescode&extid=2503 and http://osf2x.orthoptera.org/Common/basic/Taxa.aspx.

Habitat. Grassy patches in the vicinity of forest or in forest clearings (Table 4).
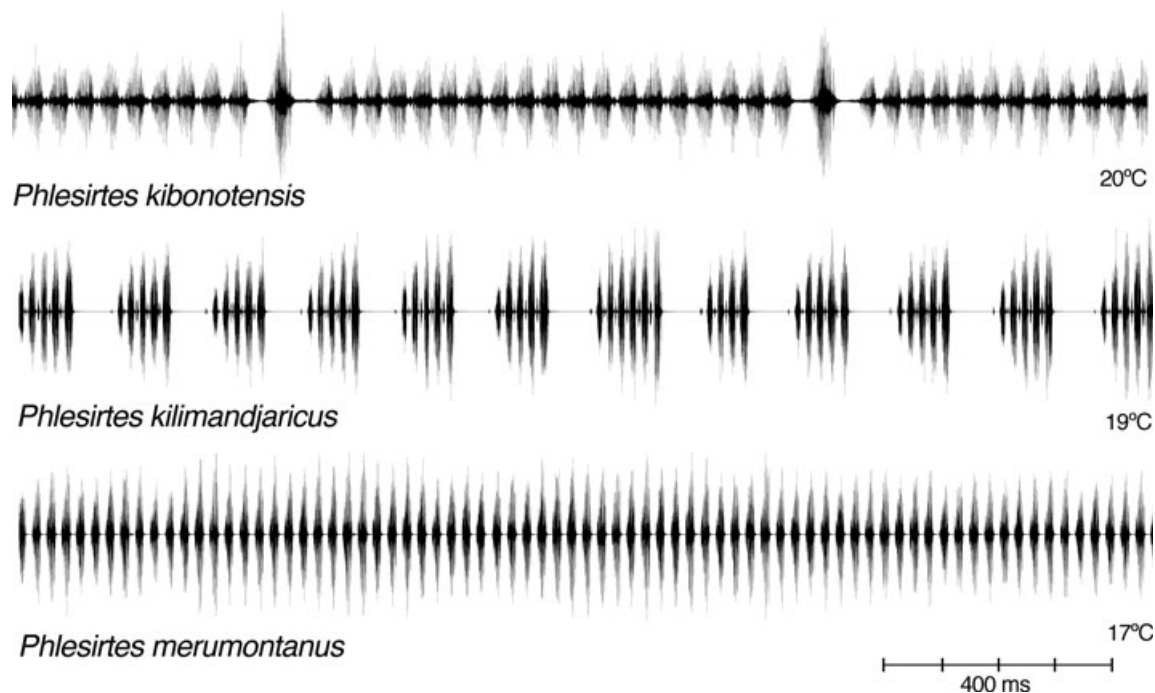
Fig. 9. Oscillograms of calling songs of *Phlesirtes* species.

Distribution. Uganda, Rwanda, Burundi, Democratic Republic of the Congo, western Tanzania, western Kenya (Fig. 12).

Karniella crassicerca sp.n. Hemp C.

Material examined. Holotype, male, Uganda, impenetrable (Bwindi) forest; along path from Ruhiza to swamp, September 1986, coll. Ritchie & Nummelin, EDNMK. Other material: two males, Rwanda, Nyungwe Forest Reserve near Cyangugu (2°30′S, 29°18′E), 2500 m a.s.l., March 1990, coll. K.-G. Heller & M. Volleth; one male, MNB; one male collection Hemp; one male, Congo (Zaire), Kivu, Poste Patrol im Nationalpark Kahuzi Biega (2°22′S, 28°35′E), March 1990, coll. K.-G. Heller & M. Volleth, CH4968; collection Heller; two males, Urundi: Bururi 1800–2000 m, 5/12-III-1953, Coll. Mus. Congo (P. Basilewsky), NHML; one male, Kivu: Kavumu à Kabunga km 82 Mingazi, IV-1951, Coll. Mus. Congo (H. Bomans), NHML; one male, Nyongwe, 2000 m, Forest Rugege VIII-49, I.R.S.A.C. Mus. Congo (Dr R. Laurent), NHML.

Description. Male. A mix of black, brown and green. *Head.* Face brown (in other specimens green); fastigium verticis as broad as scapus (0.5 mm in diameter); dorsum of head black (Fig. 2E). Eyes large, round, brown with black spots. Antennae thin and very long (about 5 cm length). *Thorax.* Disk of pro- and mesonotum and centrally on lateral lobes black; on dorsum of head and anterior part of pronotum lateral brown fascia are indicated but these are not continuous over the whole length; margins of lateral lobes of pronotum light brown, of same colour as uplifted part of pronotum and tegmina (in other specimen margin of pronotal lobes green at anterior part and light brown at posterior part). Tegmina strongly inflated, forming an acoustical chamber, partly covered by uplifted part of pronotum, protruding part about 3 mm. *Abdomen.* Shiny black, tergite of ninth and tenth abdominal segment dark brown. *Legs.* Green with numerous brown-red dots; fore coxa with spine. Femora unarmed, fore and mid tibiae each with two rows each with six spines ventrally; hind tibiae with two rows of 10–12 brown stout spines. *Genitalia.* Disk of tenth abdominal tergite depressed, anterior margin with central indentation (Fig. 1L). Cerci differentiated into two stout branches, the inner one with acute tip, but the two branches of almost same length (Figs 1L, 4F). Subgenital plate with two short styli, anterior margin incurved.

Female. Not known.

Measurements.

	Males (mm) n = 7 (dried)	One male in alcohol
Body length	9.0–11.5 (mean: 10.4)	16
Pronotum length	4.0–4.7 (mean: 4.5)	5.6
Anterior femur length	3.1–3.6 (mean: 3,5)	4.0
Posterior femur length	9.5–10.6 (mean: 10.1)	11.5
Tegmina length (visible part)	1.8–2.9 (mean: 2.4)	2.7

Air-dried specimens and the single male in alcohol are listed separately because the latter male was conspicuously larger than the other three males. The large male in alcohol originated from the National Park Kahuzi Biega (see above). A similarly

large variation in size was described for *K. bullata* by Rehn (1914), even for specimens from one locality.

Song. The calling song of the recorded male is composed of alternating groups of long and short syllables (Fig. 10; repetition rate of short syllables 23.4 Hz, of long syllables 8.3 Hz; duration of recording 65 s; time of recording 14: 30; T = 21°C; animal possibly in sun). Typically, 10.3 long syllables (duration of syllable 66.9 ms) were followed by a series of eight short syllables (duration 22.5 ms).

Habitat. Grassy patches in the vicinity of forest or in forest clearings (Table 4).

Distribution. Uganda, Rwanda, Congo; distributed along the western branch of the rift valley between Lake Kivu and Lake Edward (Fig. 12).

Diagnosis. Karniella crassicerca shows all the generic characters given by Rehn (1914): a saddle-shaped pronotum in the male and lateral pronotal lobes that are blunt; the tegmina are shorter than the pronotum and strongly inflated; alae are much reduced scales; the prosternum is unarmed and the meso- and metasternum have angular lobes. *Karniella crassicerca* shares habitus and colour pattern with *K. bullata*. Differences are found in the male genitalia: in *K. bullata* the tenth abdominal tergite is not as elongated and is much more broadly incurved than in *K. crassicerca*. The inner branch of the male cerci is acute and elongated and longer than the outer stout branch in *K. bullata* (Fig. 4G), whereas they are of almost the same shape and length in *K. crassicerca* (Fig. 4F). The fastigium verticis in *K. bullata* is slightly smaller than the width of the scapus, in *K. crassicerca* it is of the same width. *Karniella bullata* has same number of fore and midtibial spines, but these are shorter and stouter than in *K. crassicerca*.

Genus *Naskreckiella* Ünal, 2005

Type species. Naskreckiella kalamboi Ünal, 2005

Naskreckiella kalamboi Ünal, 2005

Material examined. Holotype, male, Zambia, northern province, Kalambo Falls, 10 mls from Abercorn, Sizi forest, NHML.
  Other material: one female paratype (NHML).

Description. See Ünal (2005).

Habitat. (Table 4).

Distribution. Known only from the type locality (Fig. 12).

Diagnosis. Naskreckiella kalamboi exhibits a similar habitus to species of the genus *Karniella*. Its pronotum is uplifted in the male sex to cover part of the inflated tegmina. However, whereas in *Karniella* about two-thirds of the tegmina are visible, in *N. kalamboi* males most of the tegmina are covered by the posterior part of the pronotum. Unique within *Karniellina* are the male cerci. There is one main branch which has an inner small dent and an apical one which is larger. Thus both projections originate from one major branch (Fig. 4H).

Discussion

In this paper we have discussed aspects of the taxonomy, distribution and phylogeny of members of the *Phlesirtes* genus complex. Morphology, habitat and molecular data suggest a new genus status of *Phlesirtes meruensis* and for further four species newly described in this paper. However, the songs and chromosomal data show that all members of the *Phlesirtes* genus group investigated here are uniform, suggesting a subtribe position as Karniellina within Conocephalini.

Phylogeny of the Phlesirtes genus complex

The molecular approach, morphology and ecology (habitat demands and acoustics) support the erection of the new genus *Chortoscirtes* for *Phlesirtes meruensis*. In the phylogram (Fig. 5), *Chortoscirtes* species are the sister group to a larger clade consisting of the species of *Phlesirtes* and *Karniella*. Although the sister group relationship of *Karniella* and *Phlesirtes* is not highly supported in the Bayesian analysis, we found *Karniella* always clustering between the genus *Chortoscirtes* and the remaining *Phlesirtes* using combined or single datasets and other phylogenetic methods such as maximum parsimony and maximum likelihood. A comparison of the phylogeny with the distribution of these clades suggests that different lineages have different histories: younger speciations occurred in *Phlesirtes* in montane habitats, whereas in *Chortoscirtes* we see more recent speciations in savanna regions.

We did not succeed in sequencing the COI gene for any specimen of the genus *Karniella*, and the 16S rRNA sequence is missing for most sequences (B7, X4, P11 and A17; see Table 2 and Fig. 5). This explains the differences in the combined tree (Fig. 5) between the *K. bullata* isolate H2 and the above-mentioned specimens of *K. bullata*, and may also explain the low support value.

The three *Phlesirtes* species investigated here each represent a well-defined group of which most species are still undescribed. *Phlesirtes kibonotensis* (Fig. 2H) is one member of a group of species distributed within the Eastern Arc mountains of northern Tanzania and southern Kenya and Mt Kilimanjaro. Species belonging to this group are adapted to montane forest clearings and exhibit a uniform morphology. Males have an abdominal unmodified tenth tergite and cerci that are differentiated into a blunt outer branch and a long and slender inner branch (Fig. 1D). *Phlesirtes merumontanus* (Fig. 2I) belongs to an array of species distributed over wide areas of mountainous East Africa in the montane and afro-alpine zones of mountains. *Phlesirtes brachiatus* and *P. latifrons* also belong into this group, and probably also *P. bilineatus* (see distribution Fig. 12). Because differences between females of the genus complex are small, further studies must show whether *P. bilineatus*, of which only the female is known, belongs in this group of montane and afroalpine dwellers. However, the distribution (Fig. 12) and habitat of *P. bilineatus* suggest that this species belongs to this group, which is characterized morphologically by a male tenth abdominal tergite that

Fig. 10. Oscillograms of the calling song of *Karniella crassicerca* at different time-scales (A, B).
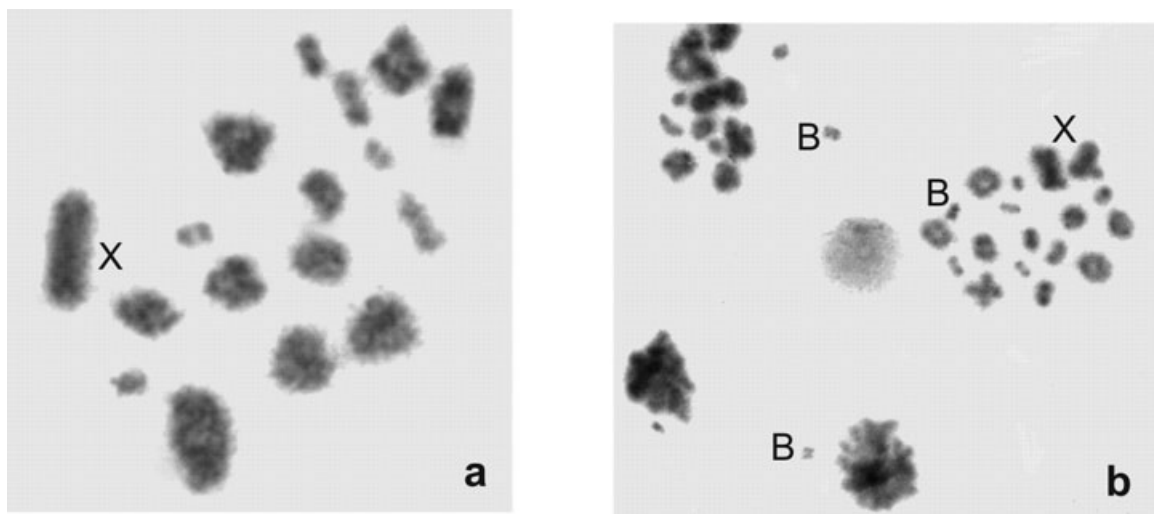

Fig. 11. *Phlesirtes merumontanus* meiotic cells. (a) $n\male = 16 + X$, the metacentric X chromosome (X); (b) diakinesis and anaphase showing the B chromosome (B).

is broadly excavated (Fig. 1A, E, F) and cerci differentiated into a blunt outer and slender, often twisted inner branch. Another group of the *Phlesirtes* genus complex is represented by *P. kilimandjaricus* (Fig. 1G). Members of this branch are distributed over the submontane zones of East Africa with their centre around northern Tanzania and southern Kenya. Males are characterized by a more or less unmodified tenth abdominal tergite and cerci with a spoon-like expanded outer branch and a short slender inner branch (Fig. 1B). Most members of this group are conspicuous in submontane grasslands because of their brightly orange-coloured abdomen. The position of *P. kevani* is unclear at present as there is no molecular information available for this species. However, the morphology of the male tenth abdominal tergite (Fig. 1C) suggests a placement as an independent branch within the *Phlesirtes* genus

group. Moreover, its habitat, 'desert-grass and thorn-bush' (see Table 4), indicates that this species occupies a different ecological niche from that of all other groups treated here. All the above-listed groups of *Phlesirtes* will be handled in subsequent papers. Altogether, over 30 new species of the *Phlesirtes* genus complex were collected over East Africa.

Cytotaxonomy

Cytotaxonomic studies of the Conocephalinae are scarce. Karyological information is available only for some species belonging to Conocephalini, Cophiporini and Agraeciini.

The chromosome number in this subfamily ranged in the male from $2n = 33$ to 21, and only a X0/XX sex mechanism has been described to date. In this group the highest and
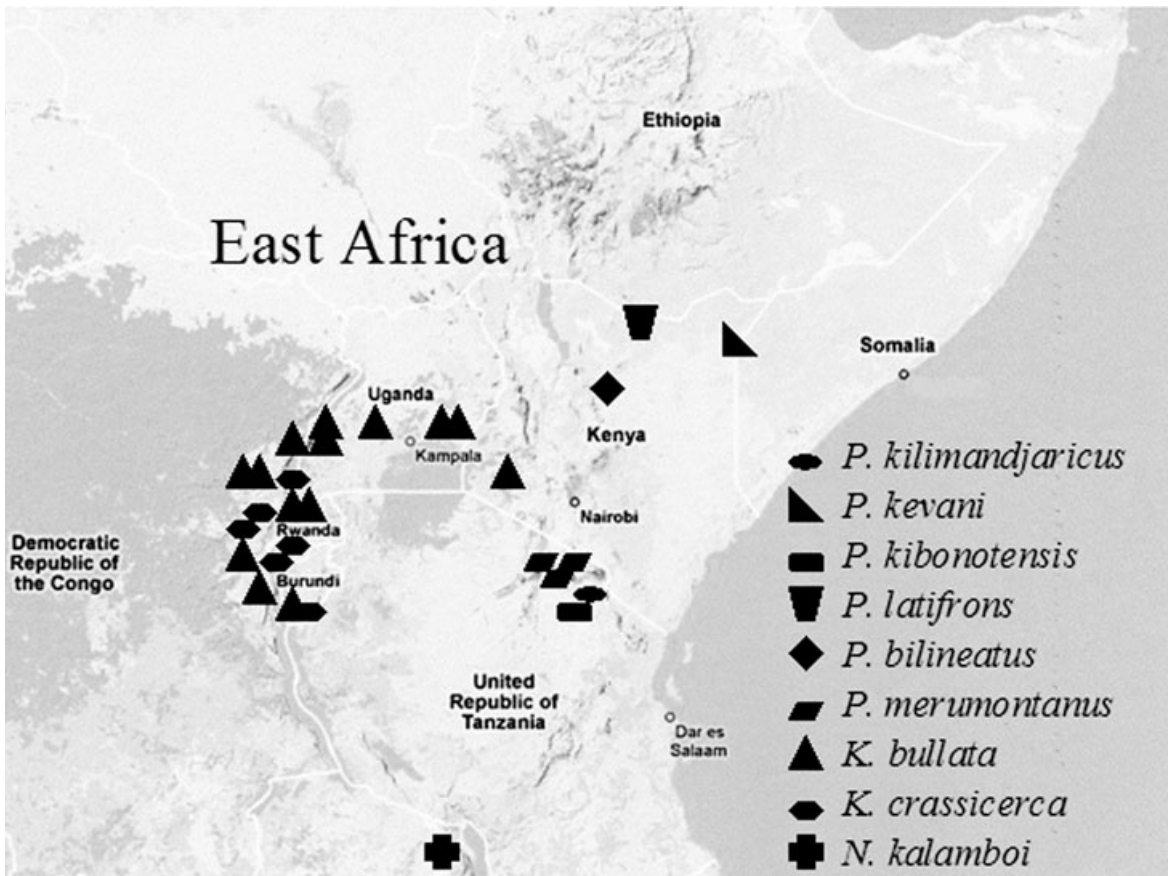
Fig. 12. Distribution of *Phlesirtes* and *Karniella* species in East Africa (source of map: google maps). For more detailed information on the localities see Table 4.

most common complement contains $2n = 33$ chromosomes in the male, in both Old and New World species (Hewitt, 1979; Ueshima & Rentz, 1990; Warchałowska-Sliwa, 1998; Gorochov & Warchałowska-Sliwa, 1999; Warchałowska-Sliwa & Gorochov, 2000). It should be noted that in the tribe Conocephalini (from the Palearctic area and America) eight species belonging to the genus *Conocephalus* possess a karyotype with $2n = 33$ chromosomes in the male (Warchałowska-Sliwa, 1998). White (1973) and Warchałowska-Sliwa (1998) suggested that this is a basic/ancestral number of chromosomes in this group. Cytotaxonomic analysis of *Phlesirtes* and *Chortoscirtes* individuals show that *P. merumontanus*, *P. kilimandjaricus*, *P. kibonotensis* and *C. serengeti* possess a diploid number and a type of sex determination system similar to those reported with higher chromosome numbers occurring in Conocephalinae. The available literature suggests that within this subfamily species with a metacentric X chromosome are dominant (Warchałowska-Sliwa, 1998; Warchałowska-Sliwa & Gorochov, 2000). A similar situation is found in four species of the genus *Phlesirtes* and one species of *Chortoscirtes* investigated here. The chromosome number of $2n = 33$ is probably an apomorphic character evolved at the base of the Conocephalini.

The B chromosomes, also referred to as supernumerary chromosomes, are extra elements to the standard complement that occur in many organisms. B chromosomes are very frequent in Orthoptera, especially in grasshoppers, but so far the presence of these elements of the karyotype of Conocephalinae has been reported only in *Conocephalus gladiatus* (Redtenbacher, 1891) from Korea (Kim *et al.*, 1987). The small B chromosome in individuals of *P. merumontanus, P. kibonotensis* and *C. serengeti* was mitotically and meiotically unstable. An explanation for the origin of this chromosome in this species is unfeasible at the moment and requires further cytogenetic studies, including of other species from this group.

Phylogeography of Chortoscirtes

Species of the *Phlesirtes* genus complex are distributed widely over eastern Africa (Figs 12, 13). Most species have a nymph-like appearance and were thus possibly overlooked by collectors, although the group is extremely rich in species and each mountain or mountainous area harbours one or more species. Molecular, morphological and ecological analyses showed that this group contains several well-defined genera.
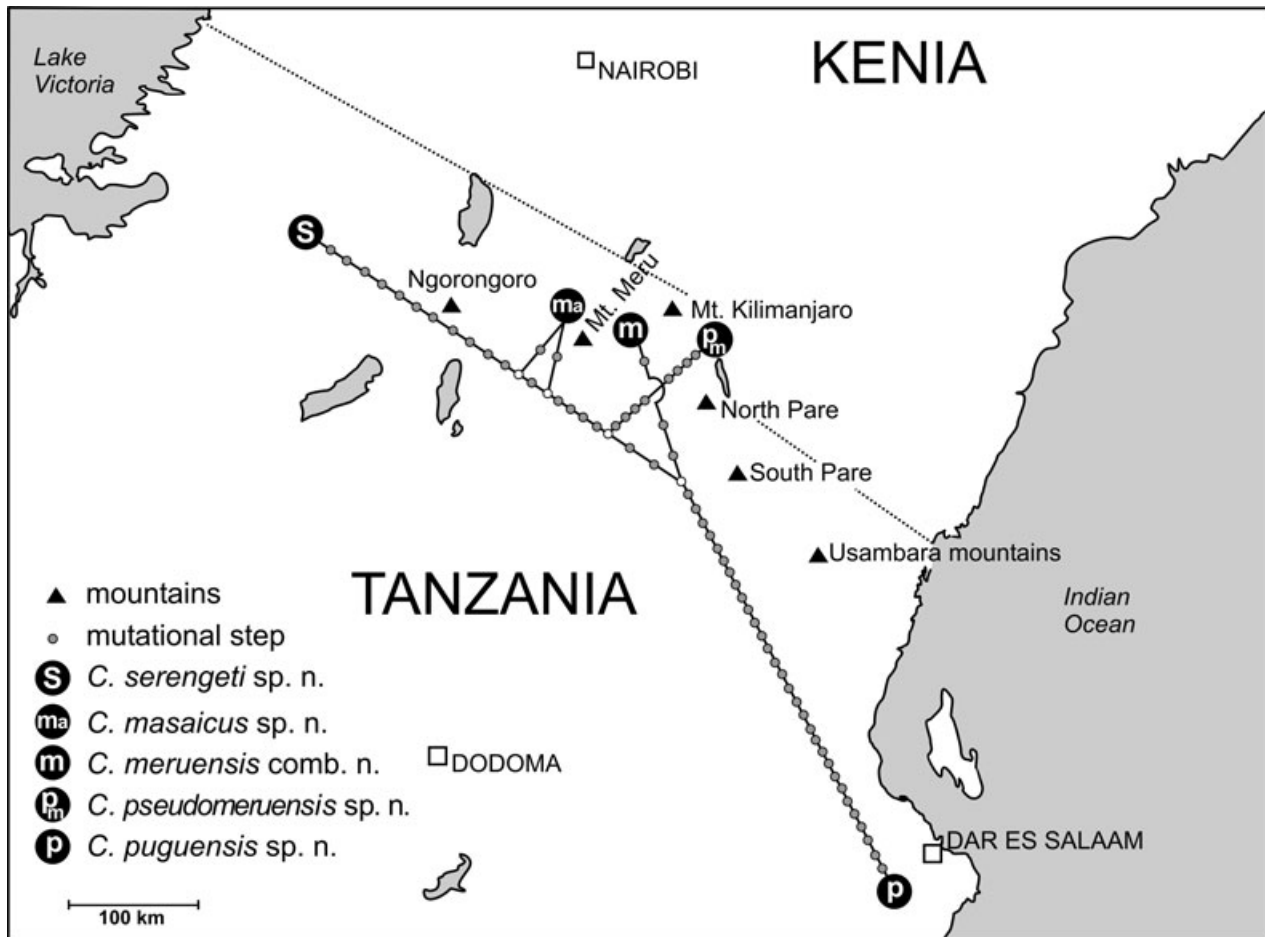
Fig. 13. Median-joining network of *Chortoscirtes* **gen.n.** based on 16S rRNA data, overlaid onto a map of Tanzania. The haplotypes are arranged according to original sampling locations. The number of grey circles corresponds to the number of mutational steps between each species.

Here we address from a morphological, molecular and ecological view the genus *Chortoscirtes*, which constitutes the first lineage branching off in the Karniellina tree. *Chortoscirtes* species are inhabitants of savanna grassland and except for the species *C. puguensis*, which occurs in grasslands in the vicinity of coastal forest, are all found at submontane to montane elevations around foothills of mountains or on savanna highlands (*C. serengeti*) (see Fig. 12). Species of adjacent areas are genetically and morphologically the most closely related, suggesting that the ancestors were once more widespread but were ecologically separated at some point owing to a changing climate. This is reflected in the allopatric speciation pattern found for this genus (Fig. 13). A similar pattern of allopatric speciation is found within the lentulid genera *Usambilla* and *Rhainopomma*, for which species occurring in adjacent areas are also the most closely related (Hemp *et al.*, 2007; Schultz *et al.*, 2007; Hemp & Hemp, 2008). Thus *C. puguensis*, a coastal species, stands most basally in the phylogram (Fig. 5) and is also geographically distant from the rest of the known species of this genus. The remaining four species are closely related to each other and

geographically are located close together. Fig. 13 illustrates a median-joining network based on the 16S rRNA for the five *Chortoscirtes* species. It shows a close relationship between *C. meruensis*, *C. pseudomeruensis* and *C. masaicus*. Morphologically, *C. meruensis* and *C. pseudomeruensis* are sister taxa, and *C. masaicus* is close to *C. serengeti*. This relationship is not clearly visible in the network but is supported in the Bayesian phylogenetic tree.

Thus, summarizing the data from morphology, the Bayesian tree and the median-joining network, as well as considering the geographical pattern, the species *C. pseudomeruensis* endemic to the colline and submontane zone of East Kilimanjaro shares a common ancestor with the lineage of the *C. meruensis* group. *Chortoscirtes meruensis* occurs only in the savanna grasslands of the submontane zone between the two volcanoes Mt Meru and Kilimanjaro. The sister group of *C. meruensis* comprises the two species *C. masaicus*, living in savanna grasslands between Mt Meru and Mt Longido, and *C. serengeti*, a grassland dweller of the Serengeti plains, also at submontane elevations. The species of *Chortoscirtes* described herein

probably represent only a fraction of the species diversity, and others may be found if the area is surveyed more intensively.

Phenology

Chortoscirtes species usually only emerge in the rainy season, from April to June. Exceptions are found in El Niño years, when rains prevail from October to June, producing lush and green savanna grasslands. In areas that are usually very dry, for example the area of the northern foothills of Mt Meru and the area between eastern Meru and western Kilimanjaro, which are the habitats of *C. masaicus* and *C. meruensis*, these species do not attain high population densities. Thus *C. meruensis*, described by Sjöstedt (1909) from the grasslands between Meru and Kilimanjaro, was found only twice between 1996 and 2008. In El Niño years the October short rains merge into the long rains usually starting in April, and the savanna plains are exuberant with vegetation, whereas in 'normal' years these areas are dry and with sparse vegetation from January to March. A similar observation was made for the phaneropterid species *Horatosphaga meruensis*, which is endemic to the same area (Hemp, 2007). It was found twice from 1996 to 2008 during the El Niño years of 1997/1998 and 2006/2007. These findings indicate that *Chortoscirtes* species are adapted to a habitat where the hatching of the nymphs is triggered by sufficient precipitation. Other species of the *Phlesirtes* genus group, for example *P. merumontanus* occurring in the montane zones of Mts Meru and Kilimanjaro, *P. kilimandjaricus* of the submontane zone of Kilimanjaro (also see Hemp, 2005b), and *P. kibonotensis* (for coenology and habitat demands of this species see Hemp & Hemp, 2003), are found over a longer period of the year, usually building up individual-rich populations. In a square metre sometimes more than 30 individuals of *P. merumontanus* were counted, whereas, for example, single *C. meruensis* individuals (for example in the El Niño year of 2006/2007) were found at greater distances on a homogenous grassland, with a maximum of a single specimen every 5–10 m (registering male songs with the aid of a bat detector).

Acoustics

Continuous songs as observed in the species examined here are typical for grassland species and are also found in other genera of Conocephalinae (for a review see Korsunovskaya, 2008). Compared with species with a larger body size (most *Neoconocephalus* and *Ruspolia* species), the songs of the small *Phlesirtes* and *Chortoscirtes* have higher frequencies, mainly in the ultrasonic range, and thus are not or are only weakly audible to humans.

The stereotypic temporal pattern, which is important for species and mate recognition, showed a different pattern of variation in *Phlesirtes* and *Chortoscirtes*. In *Phlesirtes*, the three analysed species differed distinctly in amplitude modulation, comparable to the variation found between sympatric species (e.g. genus *Platycleis;* Samways, 1976). In

Chortoscirtes, however, the songs of all three species were quite similar, as is typical for allopatric forms (Heller, 2006). A continuous sequence of pairs of syllables as observed in *Chortoscirtes* is a common song pattern in tettigoniids (e.g. *Tettigonia viridissima* Schul, 1998; genus *Neoconocephalus* Walker, 1975; for further examples see e.g. Heller, 1988; Korsunovskaya, 2008). In the three species, the repetition rates of syllables and of syllable pairs were in the same range. An exact comparison between the species is complicated by the fact that the specimens were recorded at different temperatures. However, even the ratio between the rates, which should be relatively independent of temperature, was very similar, at least between *C. meruensis* and *C. pseudomeruensis*. The specimen of *C. serengeti* differed slightly, but for safe conclusions about species-specific differences more data will be necessary. All three species probably also share the use of a short-song (see *C. serengeti*). The function of this unusual song type among tettigoniids remains obscure. It can be interpreted as a test for the presence of acoustically hunting predators, whose approach may be difficult to detect during the continuous calling song, or as indicating the animal's presence to rivals without the use of expensive calling songs at times when females are unlikely to approach.

The regular alternation between two groups of different syllables found in *Karniella crassicerca* represents a song type observed very rarely among tettigoniids, although songs with different syllable types are not uncommon among Conocephalinae (e.g. Heller, 1988; Elliott & Hershberger, 2007; Korsunovskaya, 2008; Walker, 2008). To our knowledge there are only two species with similarly structured songs. The most similar song seems to be that of the tettigoniine *Acrodectes philopagus* (Rentz & Birchim, 1968; Walker, 2008). However, nothing is known about the function of the song parts in this species. More information is available about the song of *Metrioptera sphagnorum*, in which not only the temporal structure of the syllables is different between the two groups, but also the spectral composition (Morris, 1970). Owing to the limited frequency range of our recording we have no information on whether this is also true for *Karniella crassicerca*. However, since both syllable types were picked up by the recorder, the difference may at least be not as large as in *M. sphagnorum*. In this species one part of the song alone attracted some females (the other part alone had no effect), but for full attractiveness both parts were necessary (Morris *et al*., 1975).

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