Ecological adaptations of grassland-inhabiting flightless Orthoptera: *Fulvoscirtes* and *Acanthoscirtes*, two new genera of African Karniellina (Orthoptera, Tettigoniidae, Conocephalinae, Conocephalini)

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Abstract. Two new genera, *Fulvoscirtes* **n.gen.** and *Acanthoscirtes* **n.gen.**, are established within the subtribe Karniellina of Conocephalini. *Fulvoscirtes* is based on *Xiphidion kilimandjaricum* Sjöstedt, 1909 and *Acanthoscirtes* on *Phlesirtes kevani* Chopard from northern Kenya. The majority of *Fulvoscirtes* spp. are confined to open grasslands in the submontane zone of mountains. *Fulvoscirtes* contains eight species, seven of which are newly described in this paper. Three species and one subspecies occur on Mt Kilimanjaro. These are *F. kilimandjaricum* (Sjöstedt) constricted to the southern slopes, *F. legumishera* **n.sp.** confined to the northern side and *F. sylvaticus* **n.sp.** occurring on the western side of Kilimanjaro and on the eastern slopes of Mt Meru. *Fulvoscirtes fulvus* **n.sp.** is divided into two subspecies, *F. fulvus fulvus* **n.ssp.** found in the submontane zone of east Kilimanjaro and *F. fulvus parensis* **n.ssp.** in submontane to montane localities of the North and South Pare mountains. *Fulvoscirtes fulvotaitensis* **n.sp.** occurs in the Taita Hills of southern Kenya. *Fulvoscirtes viridis* **n.sp.** is described from savannah habitats between Mts Longido and Meru. *Fulvoscirtes laticercus* **n.sp.** is found in the Kenyan highlands, while the most southerly occurring species, *Fulvoscirtes manyara* **n.sp.**, is found on Mt Hanang and the Mbulu highlands of northwestern Tanzania. *Acanthoscirtes* contains three species, of which *A. albostriatus* **n.sp.** is described newly from savannah habitas of eastern Kilimanjaro. Information is given on the ecology and the acoustic behaviour of some of the species together with keys to the genera of the Karniellina and the species of *Fulvoscirtes* and *Acanthoscirtes*. The genera of Karniellina probably evolved at a time when grasslands spread in East Africa due to an increasing aridification of the climate. The earliest lineage, the genus *Karniella*, is adapted to more forested habitats while the majority of the genera of Karniellina prefer open grasslands. Major splits within Karniellina probably occurred with the emergence of savannah grasslands due to the ongoing fragmentation of forest habitats several millions years ago, but most species within the genera are geologically young, their radiation being boosted by climatic fluctuations of the past 1–2 Ma.

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Introduction

Mountainous East Africa harbours a high biotic diversity and endemism. Especially the Eastern Arc mountains of Tanzania and southern Kenya are well-known hotspots of biodiversity (Burgess *et al.,* 2007). The Eastern Arc mountains have an estimated age of about 30 Ma (Burgess *et al*., 1998) and lie adjacent to geologically young mountain formations aged a few Ma uplifted in connection with the creation of the rift valley system of eastern Africa. These mountain ranges are climatically isolated in the present-day climate, looming to montane and even alpine heights surrounded by hot and dry savanna vegetation which constrains the montane flora and fauna.

Flightless orthopterans, in particular, show arrays of closely related species swarms in mountainous East Africa, each mountain or mountain range harbouring its own species, e.g. the pyrgomorphid genus *Parasphena* with about 25 species in eastern Africa (Hemp *et al*., 2009a), the lentulid genera *Rhainopomma* and *Usambilla* (Hemp *et al*., 2007; Schultz *et al*., 2007), the eumastacoid genus *Chromothericles* (Hemp, 2009b), or species of the recently erected genus *Altihoratosphaga* (Hemp *et al*., 2010a). However, the highest diversity is found within the subtribe Karniellina of Conocephalini with over 30 species distributed over East Africa (Hemp *et al*., 2010b, c). Genera and species of Karniellina described at present (excluding the new genera *Fulvoscirtes* and *Acanthoscirtes*) are listed in Table S1. The study of these small flightless conocephalines might contribute to the understanding of speciation mechanisms and to the reconstruction of the climatical past of East Africa.

We investigated members of the subtribe Karniellina morphologically, bioacoustically, ecologically, molecularly and by comparing their chromosome structure. Our results show that the species formerly united in *Phlesirtes* belong to five well-separated taxa. Hemp *et al*. (2010b) erected the genus *Chortoscirtes* (five species) on species confined to coastal grasslands and savannah habitats. Another well-defined genus, *Melanoscirtes* (four species), is adapted to submontane and montane forest clearings in the area of the northern branch of the Eastern Arc mountains and Mt Kilimanjaro (Hemp *et al*., 2010c). In this paper we erect the genera *Fulvoscirtes* **n.gen.** with *Xiphidion kilimandjaricum* Sjöstedt, as the type species and describe another seven species distributed from hilly to montane elevations along the northern branch of the Eastern Arc mountains of northern Tanzania and southern Kenya, the Kenyan highlands and northwestern Tanzania. The second genus, *Acanthoscirtes* **n.gen.**, is erected on *Phlesirtes kevani* Chopard, containing three species of which one is newly described. We discuss possible mechanisms of speciation observed within the Karniellina.

Material and methods

Depositories

NMB: Museum für Naturkunde, Berlin. NHML: Natural History Museum London, UK. EDNMK: Entomological Department National Museums of Kenya, Nairobi. NHRS Stockholm: Naturhistoriska Riksmuseet, Stockholm, Sweden. All other material remains in the collection of C. Hemp (and K.-G. Heller; animals used for song records).

Molecular analysis

For the analysis of Orthoptera species groups we selected genes for which data already exist and which show sufficient variation between closely related species [mitochondrial genes: 16S rRNA gene 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 (Hemp *et al*., 2010b, c).

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).

The 16S rRNA gene, the cytochrome oxidase subunit I gene (COI) 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 the COI gene (Folmer *et al*., 1994). 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 S2.

Fragments of the 16S rDNA (517 bp), the COI (658 bp), and the H3 cluster (328 bp) of 88 individuals were aligned with the ClustalW software in BioEdit (Hall, 2005). The protein-encoding genes were translated with the invertebrate mitochondrial code to examine conservation of amino acid sequences. There was no length variation among sequences in H3 and COI. The 16S rRNA alignment was manually optimised, considering the rRNA secondary structure of *Drosophila melanogaster* (Gutell *et al*., 1994)

The dataset includes the sequences of 40 individuals of the new genera *Fulvoscirtes* and 4 individuals of *Acanthoscirtes* (SI 2 Table S2), 15 individuals of the genus *Melanoscirtes*, 3 individuals of the genus *Karniella*, 14 individuals of the genus *Chortoscirtes* and 4 individuals of *Phlesirtes*. Additional sequences of six Conocephalini species were used for the phylogenetic reconstruction (see Hemp *et al*., 2010a, b). These were *Conocephalus (Anisoptera) ictus* (Scudder, 1875), *C. (A.) maculatus* (Le Guillou, 1841), *C. (A.) saltator* (Saussure, 1849), *C. (Conocephalus) conocephalus* (Linnaeus, 1767), and *C. longiceps* (Peringuey, 1918). 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 previously placed together with *Phlesirtes* in the Tettigoniinae.

A likelihood ratio test was performed using MrModeltest V2.3 (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 the H3 gene and the HKY + I + G model for the COI gene. Using these assumptions on sequence evolution, a combined Bayesian analysis with MrBayes (V3.1.2; Huelsenbeck & Ronquist, 2001) was performed with two independent analyses consisting of four Markov-chains sampled every 2000 generations for 50 million generations. The combined dataset was partioned by gene, the models were unlinked, and the rate prior was set on variable by using the 'prset ratepr = variable' option in MrBayes. To determine the point at which the Markov chains reached stationarity, the log-likelihood scores were plotted against generation time, and determined visually when the log-likelihood values reached a stable equilibrium. Furthermore, the online version of the ATWY program (Wilgenbush *et al.*, 2004) was used to check for convergence. The first 6250 trees were considered as burnin and discarded and a 50% majority rules consensus tree was calculated in MrBayes.

A maximum parsimony analysis was performed in PAUP* version 4.0b10 (Swofford, 2000). The heuristic search included 10 000 random addition replicates. Bootstrap analyses were performed using 1000 replicates with 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 to visualise the distinctness of the separation of species of the *Fulvoscirtes-Acanthoscirtes* group. A median-joining network based on 16S rRNA, COI and combined data was constructed for the 44 specimens of the genus *Fulvoscirtes* and *Acanthoscirtes* with the Network (V4.5.1.0) program (Bandelt *et al.*, 1999) and overlaid onto a map of Tanzania with the localities where the species have been found to test if phylogeny and distribution patterns are congruent. The median joining networks of the COI and combined data were too complex to display; therefore, we calculated a reduced median network for those two datasets. The settings for the median-joining network calculations were epsilon = 1, criterion = 'connection cost' and an equal weighting of transitions and transversions, for the reduced median networks we set the reduction threshold $r = 2$.

Sound recording and bioacoustical terminology

The calling songs of one *Acanthoscirtes* and seven *Fulvoscirtes* species and subspecies were recorded in the field and/or in the laboratory as follows.

Fulvoscirtes kilimandjaricus 10 males, all Mt Kilimanjaro, in and near Kidia, (CH6806, 08, 19); *F. fulvus fulvus* 11 males East Kilimanjaro; *F. fulvus parensis*, 17 males North Pare Mts. (CH6844-7, CH6854-8), 8 males South Pare Mts.; *F. fulvotaitensis* 6 males, type locality; *F. legumishera* 9 males, northern slopes of Mt Kilimanjaro; *F. sylvaticus* 7 males, all Mt Meru; *F. viridis* 1 male, holotype; *A. albostriatus* 4 males, paratypes (CH7389-92).

All specimens were recorded using a digital bat-detector (Pettersson D1000X) with a sampling rate of 100 or 192 kHz, very few with other sampling rates and other microphones [Genrad GR. 1988 sound-level meter (IET Labs) or Sony ECM-121, connected directly to a laptop computer via an external sound card (M-Audio transit; sampling rate mostly set to 96 kHz)].

The sounds were analysed using the programs Amadeus II (Martin Hairer; www.hairersoft.com) and Canary (Cornell Laboratory of Ornithology). For every specimen the values of syllable and echeme period were based on ten independent measurements.

Terminology. Syllable: sound produced during one cycle of movements (opening and closing of the tegmina resulting in opening and closing hemisyllable); (hemi)syllable duration: time period measured from the first impulse to the last; syllable period: time period from the start of one syllable to the start of the next (reciprocal value: syllable repetition rate); echeme: group of syllables separated from the next by a silent interval; echeme period: time period from the start of one echeme to the start of the next (reciprocal value: echeme repetition rate); 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).

Results

Molecular results

The alignment of the combined dataset (1503 bp) showed 964 constant sites and 515 parsimony informative sites. The phylogenetic trees (Fig. 1) calculated with different tree-constructing methods, single or combined datasets and variation of assumptions on sequence evolution result in almost identical topologies. The phylogenies were well resolved and the main splits were supported by high bootstrap values and posterior probabilities. Figure 1 shows the consensus tree of Bayesian inference based on combined data (16S rRNA, COI, H3). All investigated species of *Fulvoscirtes* proved to be of monophyletic origin. In the subspecies of *F. fulvus*, the population of *F. fulvus parensis* from the North Pare mountains (Q, T and X numbers) seems to be the sister group to *F. fulvus fulvus* of Kilimanjaro, and these two seems to be the sister group to *F. fulvus parensis* from the South Pare mountains. However, the network calculations (Fig. 13A, B; see figs S1 and S2) support a classification into subspecies and show a sister relationship between *F. fulvus parensis* from the North
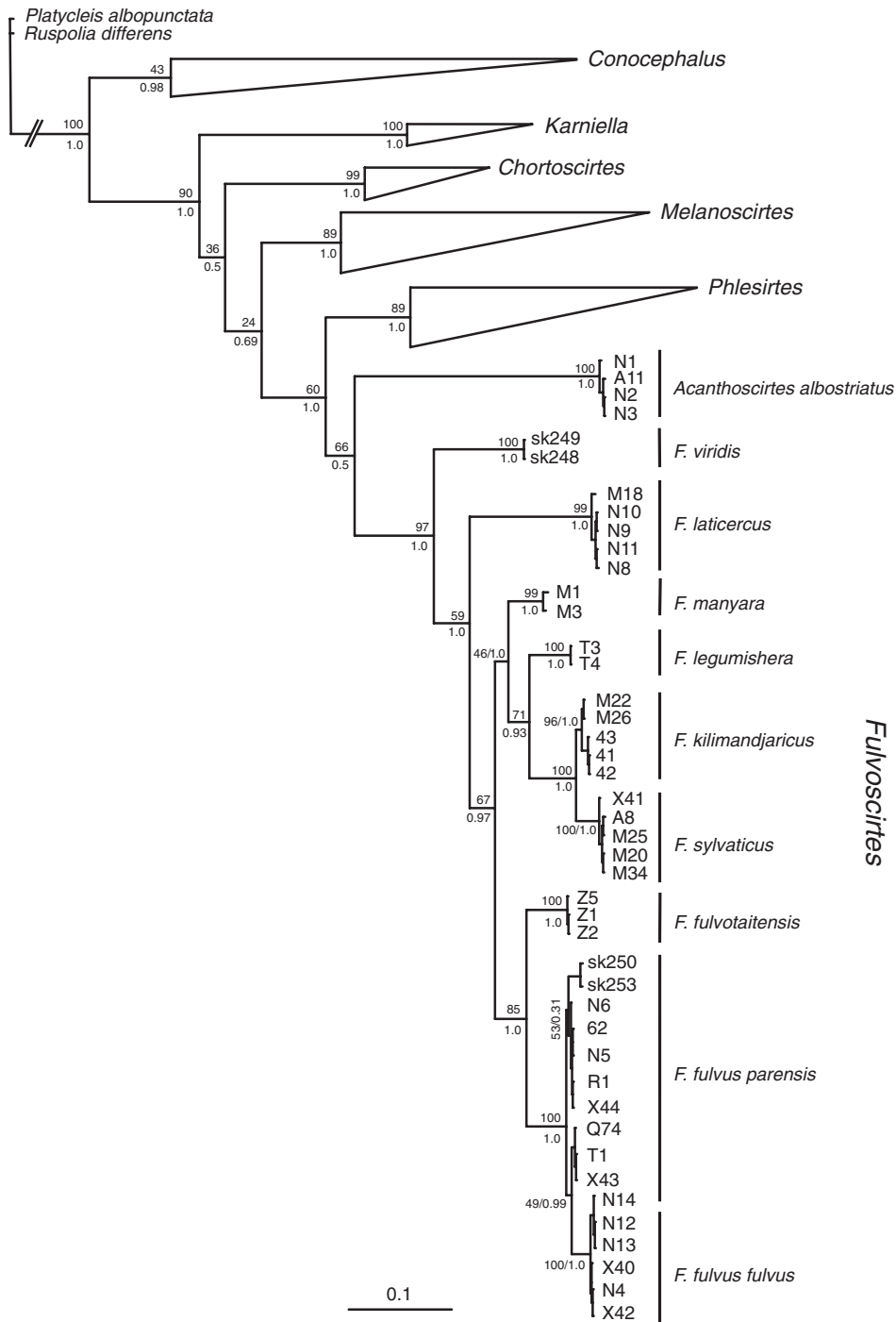
Fig. 1. Molecular phylogeny of the genera *Fulvoscirtes* and *Acanthoscirtes*. Consensus tree of Bayesian inference of combined data (16S rRNA, COI, H3) of 40 *Fulvocirtes* and 4 *Acanthoscirtes* specimens, all investigated Karniellina species, 6 *Conocephalus* species and the outgroup species *Platycleis albopunctata* and *Ruspolia differens* (all in all 88 sequences). Bootstrap values (maximum parsimony) are indicated above branches, posterior probabilities exceeding 0.5 are shown below branches.

Pare mountains and South Pare mountains (Fig. 13; SI 13). *Acanthoscirtes albostriatus* is well separated from all other *Fulvoscirtes* species in the molecular tree topology, supporting the erection of the genus *Acanthoscirtes*.

Acoustics

The male calling song of all examined forms was heard mainly during daytime. It consisted of long continuous

sequences (up to several minutes; maximum of 35 min observed) of either syllables (Figs 10A, 12) or echemes (Figs 10B, 11). In nearly all recordings each syllable consisted of a soft opening and a loud closing hemisyllable. Although no registrations of the stridulatory movements are available, we assume that the closing hemisyllable is the loud one because the echemes always started with a soft and ended with a loud hemisyllable, and because it is the typical pattern in tettigoniids (see Heller, 1988). The amplitude of the opening hemisyllable, however, varied sometimes even between single syllables. Both hemisyllables were composed of series of impulses (Fig. 10).

More than half of the species examined produced calling songs consisting of continuously repeated syllables ('trills'; Fig. 12). The syllable repetition rate varied between 60 and 160 Hz at about 20–30°C, probably mainly an effect of different temperatures during recording. Since the animals prefer to sing sitting in direct sunlight, measurements of the temperature of the surrounding air may often be misleading. On the other hand, it was impossible to register the core body temperature for the syllable repetition rate. In any case, there is no evidence for large differences between species, but we cannot exclude small ones. In all specimens of the subspecies *F. fulvus fulvus* the song was irregularly broken by short gaps (duration 20–70 ms), resulting in continuous sequences of mostly several hundred milliseconds (range 5–1400 ms; see Discussion).

Only in three species of a subclade, the *F. kilimandjaricus* group, the animals produced a continuous song consisting of echemes (Fig. 11). The echemes of *F. legumishera* contained 8–16 syllables and were repeated at a rate of about 5 Hz ($T < 21$°C). The other two species, *F. kilimandjaricus* and *F. sylvaticus*, showed very similar songs with echemes consisting of 4–6 syllables, produced at a rate of about 10 Hz ($T < 20$°C). The syllable repetition rate within the echemes was similar to that in the continuous series of syllables of the other species.

Besides the calling song, in *A. albostriatus* a 'short-song' (isolated group of syllables) was observed (Fig. 10C), quite similar to that described for *Chortoscirtes serengeti* (see Hemp *et al.* 2010b including a discussion about its possible functions). As in this species it was heard at low temperatures without sun, sometimes also immediately before the crescending start of the typical calling song (see fig. 7A in Hemp *et al.*, 2010b).

All eight examined forms of the genus *Fulvoscirtes* showed quite similar broad-band frequency spectra (similar to *Chortoscirtes*; see fig. 6 in Hemp *et al.*, 2010b). The maximum occurred at 25.1 kHz ($\pm$3.1 kHz), with limits 10 dB below and above peak at 19.2 ± 2.2 and 39.5 ± 6.7 kHz (mean $\pm$ SD, $n = 69$ specimens). The single male of *A. albostriatus* which was recorded with the Pettersson D1000X microphone had a distinctly higher maximum (42 kHz) with limits 10 dB below and above peak at 39 and 47 kHz. In the recordings of the other three males of this species it was clearly recognizable that the peak was also higher than in *Fulvoscirtes* species, but the peak could not be determined due to the limited capabilities of the microphone used. The high frequency correlates well with the much smaller size of the tegmina and its resonating structures in this species compared to the others (Fig. 7).

Taxonomy

Fulvoscirtes gen.n. Hemp C.

Type species. Xiphidion kilimandjaricum Sjöstedt, 1909

Male pronotum not or slightly raised, tegmina not strongly inflated. Margin of last abdominal tergite evenly and broadly inwardly curved. Fastigium verticis wider than the width of scapus ranging between 0.7 and 1.1 mm width. Females with long (about length of body or longer), straight or slightly up-curved ovipositor. The ratios of ovipositor length to body length range from 0.97 in *F. kilimandjaricus* Sjöstedt to 1.4 in *F. legumishera* **n.sp.** Fore and mid tibiae with two rows of six spines each. As characteristic for Karniellina femora unarmed and fore coxa with a spine. Meso- and metazona with lobe-like hairy expansions. On legs numerous reddish dots; dots especially dense on fore and mid femora. Species of *Fulvoscirtes* are found in grasslands as well as grassy patches along forest edges and coffee-banana plantations mainly in submontane to montane habitats on various mountains with centre of diversity on Mt Kilimanjaro and adjacent mountain ranges (Table 1). A conspicuous character of many species is the bright orange abdomen of the males (when alive) and the colour pattern of white and dark stripes stretching from head to parts of the pronotum, often continued on the dorsal and lateral sides of the abdomen.

Etymology. Most male *Fulvoscirtes* species have a yellow-orange to bright orange abdomen. The name refers to this orange body colour (latin *fulvor-* = red-yellow, orange).

Acanthoscirtes gen.n. Hemp C.

Type species. Phlesirtes kevani Chopard, 1954.

Acanthoscirtes differs from other genera of Karniellina in the male sex having a pair of acute to blunt spines on the last abdominal tergite and lobster-like forked cerci. Male tegmina smaller than in all other known Karniellina; tegmina pointed at their posterior margins (Fig. 7C). Females with long (as long or longer than body length) and almost straight ovipositor. *Acanthoscirtes* species occur in savannah habitats ranging from northern Kenya over Uganda (undescribed museum material NHM London) to northern Tanzania.

Etymology. The name *Acanthoscirtes* is derived from the latin expression *acanthus* = thorn because of the two thorn-like projections on the posterior margin of the last abdominal tergite.

Diagnosis. The genera *Fulvoscirtes* and *Acanthoscirtes* are typical members of the Karniellina which contains the African

Table 1. Species of *Fulvoscirtes* and *Acanthoscirtes*, their distribution, habitat and altitudinal spans.

Species	Distribution	Habitat	Altitudinal span (m)
F. kilimandjaricus (Sjöstedt, 1909)	Tanzania, South Kilimanjaro	Grasslands and banana-coffee plantations	1100–1900
F. fulvus fulvus **n.sp. n.ssp.**	Tanzania, East Kilimanjaro	Grasslands and banana-coffee plantations	1100–1600
F. fulvus parensis **n.ssp.**	Tanzania, South and North Pare	Grasslands and banana-coffee plantations	1250–1900
F. fulvotaitensis **n.sp.**	Kenya, Taita Hills	Grasslands and banana plantations	1000–1800
F. laticercus **n.sp.**	Kenya, Kenyan highlands, Mt. Sabuk, Mt Machakos	Grasslands and grassy patches along forest edges	? -1800–2150
F. legumishera **n.sp.**	Tanzania, North Kilimanjaro	Grasslands and forest edges	1700–2000
F. manyara **n.sp.**	Tanzania, Mt. Hanang	Grasslands and forest edges	?-1800–1900
F. sylvaticus **n.sp.**	Tanzania, West Kilimanjaro, East Meru	Grasslands and forest edges	1400–2000
F. viridis **n.sp.**	Tanzania, between Mt Longido and Mt Meru	Grassy patches in tree and bush savannah	1300–1400
A. albostriatus **n.sp.**	Tanzania, East Kilimanjaro	Savanna grasslands	1000–1100
A. bilineatus (Chopard, 1954)	Kenya, Chopa Gof crater, Marsabit	Scrub and grass (Chopard & Kevan, 1954)	980
A. kevani (Chopard, 1954)	Kenya, Damassa, Mandera District	Desert grass and thorn bush (Chopard & Kevan, 1954)	400

? indicates that no data are available for the lower ranges of these species.

genera *Naskreckiella*, *Karniella*, *Chortoscirtes*, *Melanoscirtes* and *Phlesirtes*.

In their general appearance the seven genera are very similar. Males of all species of these taxa have shortened tegmina and rudimentary hind wings, while females have scale-like tegmina and lack hind wings; the stridulatory file is always covered by the posterior margin of the pronotum. In addition, all species have densely haired, lobe-like expansions on the meso- and metasterna (or collar shaped projections; see Ünal, 2005). A synapomorphic character of the group is the presence of free plantulae of the hind tarsi (for further characters of the Karniellina, see Hemp *et al.*, 2010b, c).

Fulvoscirtes and *Acanthoscirtes* have fastigia verticis that are broader than the scapi, a character also found in *Phlesirtes, Melanoscirtes, Chortoscirtes* and *Karniella*. In *Naskreckiella* the width of the fastigium verticis is smaller. *Naskreckiella* also differs in the male cerci, which are differentiated into an outer blunt branch and two inner branches of which the more basal one is hook-like (see Ünal, 2005). *Naskreckiella* females have very stout ovipositors in contrast to all other genera of Karniellina which have slender, almost straight to slightly up-curved ovipositors. In *Naskreckiella* and *Karniella* the tegmina are moderately (*Naskreckiella*) to strongly (*Karniella*) inflated while in the other genera of Karniellina *Fulvoscirtes, Acanthoscirtes, Chortoscirtes, Phlesirtes* and *Melanoscirtes* they are never strongly inflated. Similarly the pronotum is raised in the area of the tegmina in *Naskreckiella* and *Karniella* while it is weakly so in *Chortoscirtes*, weakly or not in *Melanoscirtes* and weakly or not raised in *Fulvoscirtes, Acanthoscirtes* and *Phlesirtes*. The shape of the cerci is another diagnostic character facilitating to distinguish the genera of Karniellina. In *Melanoscirtes* the male cerci are differentiated into an outer short and blunt branch, and an inner branch, which is broader at the base becoming slender towards the tip. In *Chortoscirtes* the male cerci are stout and divided into two branches at their ends, both branches being of about the same length and shape. Also the two last abdominal tergites are differently shaped in *Chortoscirtes* – wearing pits and/or ridges on both tergites

while in *Fulvoscirtes* the last two abdominal tergites are more or less undifferentiated and a pair of projections is present in *Acanthoscirtes*.

In *Phlesirtes* and *Melanoscirtes* the inner branches of the male cerci are similar to those of *Fulvoscirtes*, elongated and slender, branching off from the stout outer branch at about midway or further apically. The flattened or spoon-like expanded outer branch of the male cerci is unique for *Fulvoscirtes*, a good diagnostic character for the identification of most members of this genus, except for the species *F. viridis* **n.sp.** where the outer branch is almost round. *Acanthoscirtes* is characterised, beside a pair of spines or blunt processes on the last abdominal tergite, by lobster-like forked male cerci. The females of *Acanthoscirtes* have long to very long, almost straight ovipositors. Compared to other Karniellina, *Acanthoscirtes* species are large in body size, especially the females.

Key to the genera of the subtribe Karniellina of Conocephalini (males)

1. Anterior part of male pronotum raised, tegmina strongly inflated (fig. 2E, F in Hemp *et al.*, 2010b) 2
– anterior part of male pronotum not or slightly raised, tegmina not strongly inflated (Fig. 2A, D, G, I) 3
2. Male cercus with two stout apical branches and an inner dent (fig. 4H in Hemp *et al.*, 2010b). . . . . *Naskreckiella*
– male cercus without inner dent, male cercus divided apically into two short branches (fig. 4F, G in Hemp *et al.*, 2010b) . . .
. . . . *Karniella*
3. Fore and mid tibiae armed with two rows with each six spines 4
– fore and mid tibiae armed with two rows with each five spines, last abdominal tergite with circlic incision and two posterior processes (fig. 1A, E, F in Hemp *et al.*, 2010b) . . . .
. . . . *Phlesirtes*
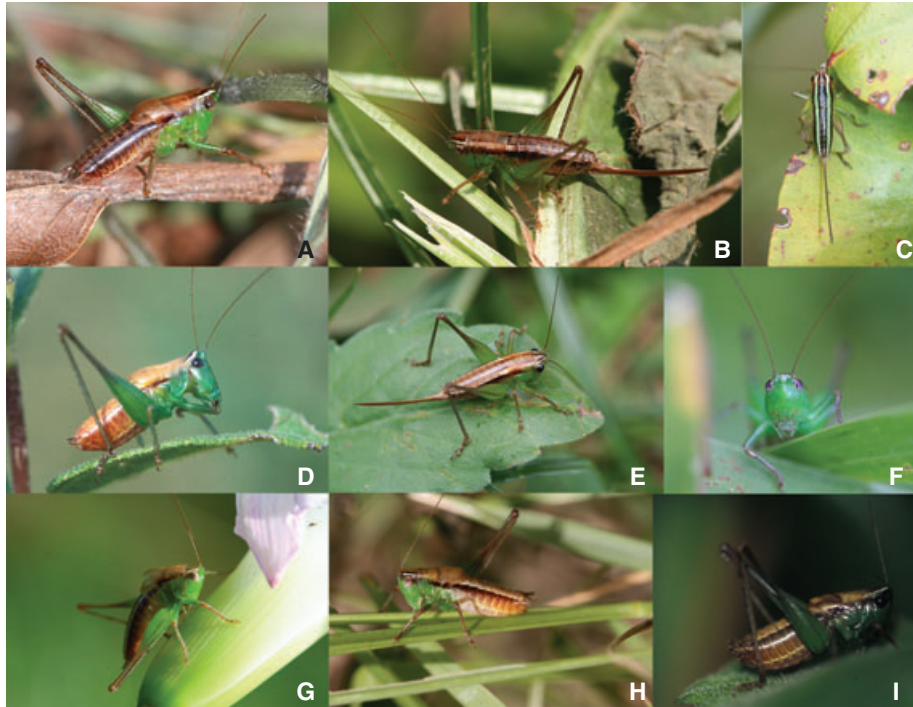
Fig. 2. *Fulvoscirtes* species. (A). Male *F. kilimandjaricus*, Tanzania, southern slopes of Mt Kilimanjaro, plantation belt, 1430 m, Kidia; (B) Female *F. kilimandjaricus*, same locality as male; (C) Female nymph of *F. kilimandjaricus*, same locality as male and female; (D) Male *F. fulvus fulvus* **n.ssp.**, Tanzania, eastern slopes of Mt Kilimanjaro, plantation belt, grassy roadside, 1300 m; (E) Female *F. fulvus parensis* **n.ssp.**, Tanzania, North Pare mountains, swampy grassland, 1300 m; (F) Male *F. fulvus parensis* **n.ssp.**, Tanzania, North Pare mountains, Kiverenge Hill, grassland, 1400 m; (G) Male *F. sylvaticus* **n.sp.**, Tanzania, grassy roadside, West Kilimanjaro, Lerongo, 1400 m; (H) Male *F. legumishera* **n.sp.**, Tanzania, North Kilimanjaro, Kilimanjaro Timbers, forest clearing, 2000 m; (I). Male *F. laticercus* **n.sp.**, Kenya, Mt Sabuk, forest edge, 1950 m.

4. Last abdominal tergite with pair of spines (Fig. 5B, C), branches of male cerci forked like crab pincers (Fig. 5A) . . . .
. . . . *Acanthoscirtes*
– last abdominal tergite without spines 5
5. Outer branch of cercus flattened or spoon-like expanded (Fig. 3A-I, 4A-G) . . . . *Fulvoscirtes*
– outer branch of male cerci of normal shape, not flattened or spoon-like expanded 6
6. Cerci differentiated into two branches, outer blunt and shorter than inner one which is long and slender (fig. 5A–E in Hemp *et al.*, 2010c), male abdomen dark brown or black (fig. 7A, C, D in Hemp *et al.*, 2010c) . . . . *Melanoscirtes*
– male cercus divided apically into two branches of similar length and shape, last tergite with grooves or pit-like structures (fig. 1G, K in Hemp *et al.*, 2010b) . . . . *Chortoscirtes*

Key to the species of *Acanthoscirtes* and *Fulvoscirtes* (males)

1. Last abdominal tergite with pair of spines (Fig. 5B, C, F, G; genus *Acanthoscirtes*) 10
– Last abdominal tergite without spines 2
2. Outer branch of male cerci compressed and broadened, spoon-like (Figs 3, 4) 3

– Outer branch of male cerci short and blunt, only slighly laterally compressed; Tanzania, area between Mts Meru and Longido (Fig. 4I, J) . . . . *F. viridis* **n.sp.**
3. Outer branch of male cerci slender and elongated, much longer than inner branch; inner branch branching off before middle of outer branch; both branches of cerci surpassing subgenital plate as seen from above; Tanzania, montane zone northern side of Mt Kilimanjaro (Fig. 4C, D) . . . .
. . . . *F. legumishera* **n.sp.**
– Spoon-like expanded outer branch of male cerci shorter and more broad 4
4. Apical section of outer branch of male cerci short, as seen from above tip of inner branch surpassing lobe of outer branch; Kenyan highlands (Fig. 4G, H) . . . . *F. laticercus* **n.sp.**
– Apical section of outer cercal branch longer or at about at one level with tip of inner branch 5
5. Posterior margin of last abdominal tergite widely incurved forming knobs or callous ridges at both sides of the posterior margin of the tenth abdominal tergite (Fig. 3A, G); both cercal branches of male cerci longer than subgenital plate . . . .
. . . . 6
– Posterior margin of abdominal tergite widely incurved but without lateral knobs or callous ridges (Fig. 4E, F); Outer cercal branch laterally broadly compressed and comparativley
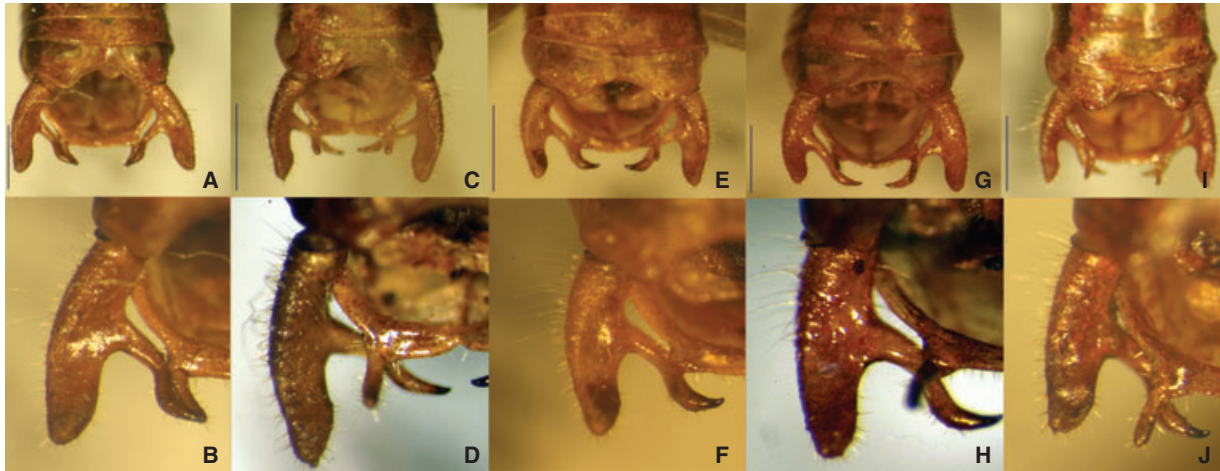
Fig. 3. Abdominal apices and left cercus of male *Fulvoscirtes* species. (A, B) *F. kilimandjaricus* (Sjöstedt); (C, D) *F. sylvaticus* **n.sp.**; (E, F) *F. fulvus fulvus* **n.sp.**, **n.ssp.**; (G, H) *F. fulvus parensis* **n.ssp.** from North Pare locality; (I, J). *F. fulvus parensis* **n.ssp.** from South Pare locality. Scale bar: 1 mm.
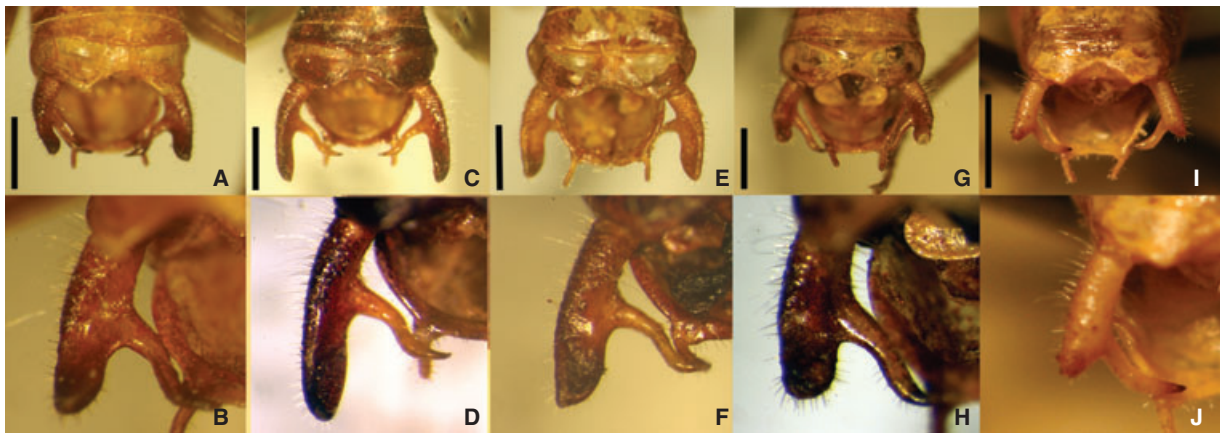

Fig. 4. Abdominal apices and left cercus of male *Fulvoscirtes* species. (A, B) *F. fulvotaitensis* **n.sp.**; (C, D) *F. legumishera* **n.sp.**; (E, F) *F. manyara* **n.sp.**; (G, H) *F. laticercus* **n.sp.**; (I, J) *F. viridis* **n.sp.** Scale bar: 1 mm.

stout; width greatest shortly before apex, thus cercus having a round shape; Tanzania, Mt Hanang and Mbulu highlands . . . .*F. manyara* **n.sp.**
6. Posterior margin of last abdominal tergite depressed in area between knobs (Fig. 3G), this depression running to posterior margin of ninth abdominal tergite thus having a triangular shape; abdominal tergites keeled, except for tergite 9, keel of tergite 10 short, sometimes obsolete; Tanzania, North and South Pare mountains . . . . *F. fulvus parensis* **n.ssp.**
– Posterior margin of last abdominal tergite not depressed between knobs, area at level with remaining part of tenth tergite 7
7. Left tegmen evenly rounded; posterior margin of tenth abdominal tergite strongly incurved (Fig. 3A); Tanzania, southern slopes of Mt Kilimanjaro . . . . *F. kilimandjaricus* (Sjöstedt)
– Left tegmen not evenly rounded but acute or with irregular lobes at posterior margin (Fig. 6A) 8

8. Both tegminal lobes with irregular lobes at posterior margin caused by callosities of venation; posterior margin of subgenital plate straight; posterior margin of tenth abdominal tergite strongly incurved (Fig. 4A); Kenya, Taita Hills . . . . *F. fulvotaitensis* **n.sp.**
– Both tegminal lobes pointed; posterior margin of subgenital plate with median indentation and thus curved inwards; posterior margin of tenth abdominal tergite more shallowly and broader incurved 9
9. Both tegminal lobes very acutely pointed (Fig. 6A); ninth abdominal tergite small and not different from tergites 1–8 (Fig. 3C); Tanzania, western side of Mt Kilimanjaro and eastern side of Mt Meru . . . . *F. sylvaticus* **n.sp.**
– Both tegminal lobes not as acutely pointed, more broad; ninth abdominal tergite medially expanded; Tanzania; eastern side of Mt Kilimanjaro . . . . *F. fulvus fulvus* **n.ssp.**
10. spines of last abdominal tergite longer from base to tip than remaining part of tenth tergite (Fig. 5B), spines slender;
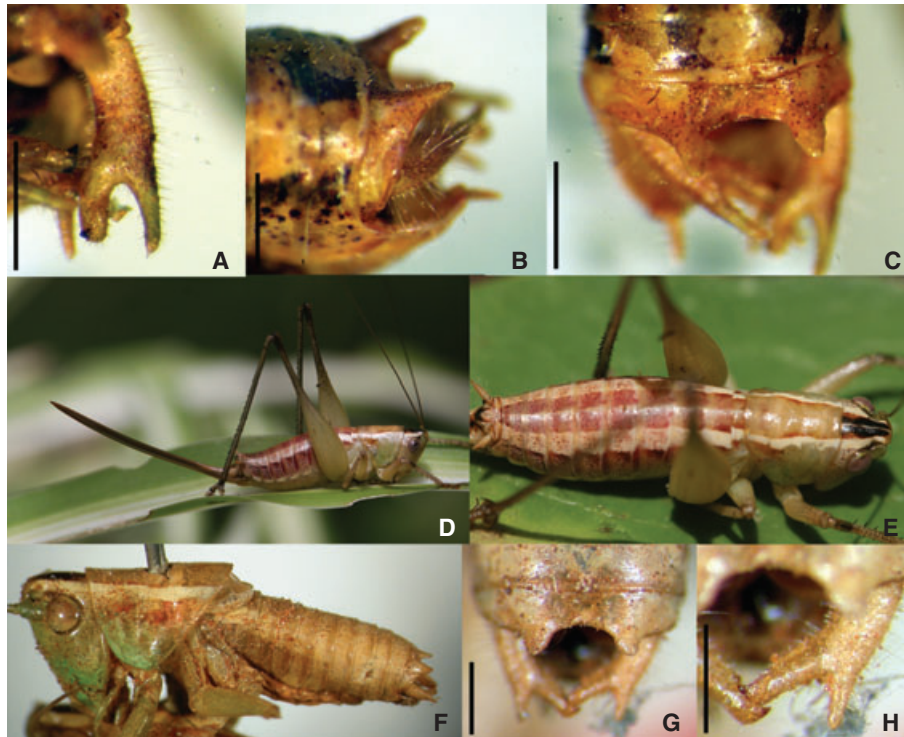
Fig. 5. *Acanthoscirtes kevani* (Chopard) and *A. albostriatus* **n.sp.**; (A–C) Abdominal apex of male *A. albostriatus*; (A) Right cercus; (B) Lateral view of abdominal apex; (C) Dorsal view of abdominal apex; (D, E). Female *A. albostriatus.* (F–H) Male *A. kevani*; (F) Habitus of male paratype (NHML), lateral view; (G) Dorsal view on abdominal apex; (H) Right cercus. Scale bar: 1 mm.
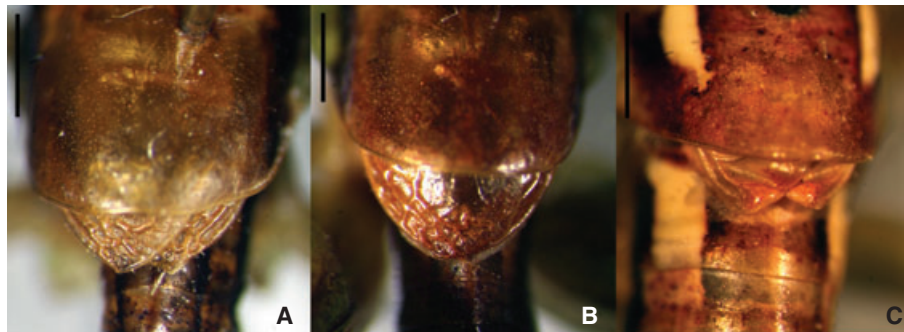

Fig. 6. Detail images of part of male tegmina protruding under pronotum. (A) *F. sylvaticus* **n.sp.**; (B) *F. kilimandjaricus* (Sjöstedt); (C) *A. albostriatus* **n.sp.** Scale bar: 1 mm.

outer branch of male cerci as long as inner branch; Tanzania, eastern side of Mt Kilimanjaro . . . . *A. albostriatus* **n.sp.**
– spines of last abdominal tergit stout, about as long as remaining part of tenth tergite (Fig. 5G); outer branch of male cerci shorter than inner branch; northern Kenya . . . . *A. kevani* (Chopard)

Fulvoscirtes kilimandjaricus (Sjöstedt, 1909) comb.n.

Xiphidion kilimandjaricum Sjöstedt, 1909
Conocephalus (Xiphidion) kilimandjaricus (Sjöstedt, 1909), – Karny 1912: p. 12.

Conocephalus kilimandjaricus (Sjöstedt, 1909), – Karny 1921: p. 27.
(Conocephalus (Anisoptera) kilimandjaricus (Sjöstedt, 1909), – Eades & Otte, 2009: online).
Phlesirtes kilimandjaricus (Sjöstedt, 1909) Hemp *et al.*, 2010b, c.

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

Further material examined. SI 3.

Description. See Sjöstedt (1909).

Song. Continuous sequence of echemes (Fig. 10B, 11); (see Results: Acoustics; see also Hemp, 2010b)

Habitat. Submontane and montane plantations and grass-lands mainly on the southern slopes of Mt Kilimanjaro. It was recorded from 1100 to 1900 m (Table 1).

Coenology. See Hemp & Hemp (2003).

Distribution. Endemic to the submontane and montane zones of Mt Kilimanjaro (Fig. 14).

Diagnosis. Fulvoscirtes kilimandjaricus males have an unmodified ninth abdominal tergite, the posterior margin of the tenth abdominal tergite being strongly curved inwardly. The male cerci are differentiated into a spoon-like expanded outer branch and a slender inwardly curved inner branch (Fig. 3A, B). Females of *F. kilimandjaricus* have a long and slightly upcurved slender ovipositor which has about the length as the body length of the insect. The ratio of ovipositor length to body length in the measured specimens was 0.97 and thus beside 0.98 in *F. laticercus* and 1.0 in *F. fulvotaitensis* the shortest ovipositor lengths in the genus. *Fulvoscirtes kilimandjaricus* inhabits mainly the submontane zone on the southern slopes of Mt Kilimanjaro (Table 1) only occurring syntopically with another member of the Karniellina, *Melanoscirtes kibonotensis* (Sjöstedt), in anthropogenically influenced habitats (e.g. montane plantations).

Measurements. SI 3.

Fulvoscirtes legumishera sp.n. Hemp C.

Material examined. All Tanzania. Holotype, male: Northern slopes of Mt Kilimanjaro, Kilimanjaro Timbers, forest clearing 1930 m, March 2001, UTM Zone 37 M, 301220 E, 9682900 S, NMB; Further material examined: SI 4.

Description. Male. Green, dark and light brown (Fig. 2H). *Head.* Face green; fastigium verticis anteriorly (1.0–1.2 mm) wider than diameter of one eye and more than double as wide than width of scapus; dorsal head with broad brown fascia, bordered by pair of conspicuous white fasciae (Fig. 2H); in most individuals the brown fascia of head in the middle of lighter brown and with median faint white line. Eyes round, light brown, with dark brown spots, bordered by a dark brown line dorsally. *Thorax.* Pronotum dorsally light brown, lateral lobes green; at about half length laterally a dark brown fascia on each side. *Abdomen.* Pattern of light brown and darker brown fasciae in preserved insect, in living insect dull orange, especially ventral sides of abdominal sternites (Fig. 2H). *Tegmina.* Tegmina of same colour as pronotum,

visible part 0.4–0.7 mm. *Legs.* Hind femora green or light brown. Tibiae and tarsi light brown. Hind tibiae with two dorsal rows of dense brown spines, ventrally unarmed. *Genitalia.* Last abdominal tergite evenly curved inwardly. Cerci with outer branch elongate flattenend, inner branch slender, branching off at an angle of about 90° before midlength of outer branch (Fig. 4C, D).

Female. Colour pattern as in male but more brown, abdomen not as orange in living insect. *Legs.* As in male. *Genitalia.* Ovipositor very long and almost straight, longer as the body length. Last abdominal tergites and lateral morphology of ovipositor as in Fig. 9B, G.

Diagnosis. Fulvoscirtes legumishera is characterised by male cerci in which the outer spoon-like expanded branch is very long and slender. Both branches of the male cerci surpass the subgenital plate considerably when seen from above. The females have a very long ovipositor, usually being considerably longer than the body length (ratio ovipositor/body length: 1.4). The species is restricted to grassy habitats of the montane zone on the northern side of Mt Kilimanjaro.

Song. Continuous sequence of echemes (Fig. 11A; see Results: Acoustics).

Habitat. In the montane zone on forest clearings and grassy road sides at the northern slopes of Mt Kilimanjaro, Tanzania. Recorded between 1760 and 1960 m a.s.l.

Etymology. Named after a side vent, Legumishera, on the northern slopes of Mt Kilimanjaro. Noun in apposition.

Measurements. SI 4.

Fulvoscirtes sylvaticus sp.n. Hemp C.

Material examined. all Tanzania. Holotype, male: West Kilimanjaro, grassy patch within coffee plantation, 1400 m, January 2007, NMB; Further material examined: SI 5.

Description. Male. Brown and dark brown with green (Fig. 2G). *Head.* Face green; fastigium verticis anteriorly (0.85–1 mm) wider than diameter of one eye and more than double as wide than width of scapus; dorsal head with broad light brown fascia, bordered by pair of cream to white fasciae followed laterally by another dark brown fasciae. This pattern is continued over rest of body, except for posterior part of pronotum covering wings; lateral dark brown fascia getting reddish-brown in most individuals (Fig. 2G). Eyes round, light brown, with dark brown spots, bordered by a dark brown line dorsally. *Thorax.* Pronotum dorsally with dark brown fascia continued from head at anterior part, light brown at posterior part covering wings; lower parts of lateral pronotal lobes green.

Fig. 7. Left tegmen of (A) *Melanoscirtes kibonotensis uguenoensis* (CH6841); (B) *F. fulvus parensis* (CH6854); (C) *A. albostriatus* (CH7389). Scale 1 mm.

Tips of tegmina pointed. *Abdomen*. Pattern of light brown and darker brown fasciae continued, lateral sides of abdomen with median light brown fascia, bordered by broader cream to white fascia, and laterally a dark brown to reddish brown fascia. Lower parts of tergites and uppers parts of sternite yellowish (Fig. 2G). *Tegmina*. Tegmina of same colour as pronotum, visible part 0.1–0.9 mm. *Legs*. All femora green, tibiae light brown. Hind tibiae with two dorsal rows of dense brown spines, ventrally unarmed. *Genitalia*. Last abdominal tergite evenly curved inwardly. Cerci with outer branch elongate flattened, inner branch slender, not strongly curved. (Fig. 3C, D).

Female. Colour pattern as in male but more brown, abdomen not as orange in living insect. *Legs*. As in male. *Genitalia*. Ovipositor very long and almost straight, longer as body length. Last abdominal tergites and lateral morphology of ovipositor as in Fig. 9D, I.

Diagnosis. Fulvoscirtes sylvaticus is very similar to *F. kilimandjaricus*. Both species can only be separated by the habitat in which they are found and by small morphological differences of the male abdominal apex and shape of the tegmina. The outer branches of the male cerci are shorter and more stout and the inner branch is more curved in *F. kilimandjaricus* than in *F. sylvaticus*. *Fulvoscirtes sylvaticus* is confined to the western slopes of Mt Kilimanjaro and the eastern side of Mt Meru and occurs in open submontane savanna grasslands, forest clearings and forest edge. *Fulvoscirtes kilimandjaricus* occurs on the southern slopes of Mt Kilimanjaro getting sparse to the western and eastern side. It is found on grassy patches within the plantation belt. The tegmina tips of *F. kilimandjaricus* are rounded while in *F. sylvaticus* they are acute. The females of *F. kilimandjaricus* have a comparatively short ovipositor, being shorter than the body length while the only collected female of *F. sylvaticus* had an ovipositor that was longer than the body length (ratio ovipositor/body length 1.24).

Song. Continuous sequence of echemes (Fig. 11B; see Results: Acoustics).

Habitat. Forest clearings, forest edge and grassland at submontane elevations at the western side of Mt Kilimanjaro and the eastern side of Mt Meru, Tanzania. Recorded from elevations between 1400 and 2000 m (Table 1).

Etymology. Found also in forest habitats; lat.: *silva* = forest.

Measurements. SI 5.

Fulvoscirtes fulvus sp.n. Hemp C.

Fulvoscirtes fulvus fulvus ssp.n. Hemp C.

Material examined. Holotype, male: Tanzania, Mt Kilimanjaro, eastern slopes, grassy roadside within the plantation belt, 1300 m, June 2004, UTM Zone 37 M, 347580 E, 9651060 S, NMB; Further material examined: SI 6.

Description. Male. Green, orange, light and darker brown (Fig. 2D). *Head*. Face green; fastigium verticis anteriorly (0.9–1.1 mm) wider than diameter of one eye but less than double as wide than width of scapus; dorsal head with broad brown fascia which may be lighter brown medially and darker brown at its outer margins; bordered by cream-white fascia (Fig. 2D). Eyes round, dark. *Thorax*. Pronotum dorsally light brown, lower parts of lateral lobes green; at about half length laterally a dark brown fascia on each side. *Abdomen*. Medially broad light to dark brown fascia, lateral side vivid orange in living insects, fading to light brown in preserved individuals. *Tegmina*. Elytra of same colour as pronotum, visible part 0.3–0.8 mm. *Legs*. Femora green. Tibiae and tarsi light brown or greenish. Hind tibiae with two dorsal rows of dense brown spines, ventrally unarmed. *Genitalia*. Last abdominal tergite broadly and evenly curved inwardly, lateral sides on incurvation more callous and this giving the impression of knobs. Cerci with outer branch elongate flattened, inner branch slender, strongly curved (Fig. 3E, F).

Female. Colour pattern as in male but more brown, abdomen not as orange in living insect. *Legs*. As in male. *Genitalia*.
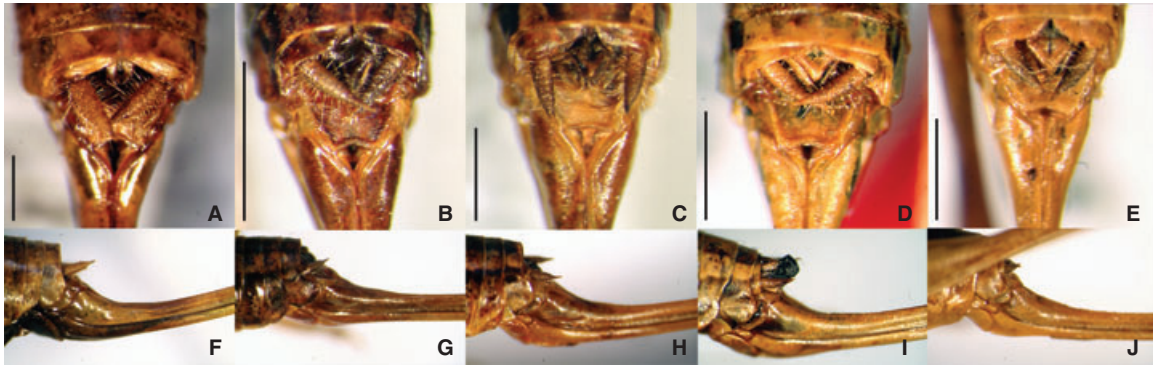
Fig. 8. Abdominal apices of *Fulvoscirtes* and *Acanthoscirtes* females. (A, F) *A. albostriatus* **n.sp.**; (B, G) *F. kilimandjaricus* (Sjöstedt); (C, H) *F. fulvus fulvus* **n.sp.**, **n.ssp.**; (D, I) *F. fulvus parensis* **n.ssp.**; (E, J) *F. fulvotaitensis* **n.sp.** Scale bar: 1 mm.

Ovipositor very long and almost straight, longer than body length. Last abdominal tergites and lateral morphology of ovipositor as in Fig. 8C, H.

Diagnosis. Fulvoscirtes fulvus fulvus is a conspicuous species because of the vivid orange abdomen of the males when alive. The last abdominal tergite is broadly and evenly but shallowly incurved; at both sides of the incurvation knobs are present which are more pronounced as in the subspecies *parensis*. The posterior margin of the subgenital plate is straight in *F. fulvus fulvus* while it is slightly indentated in *F. fulvus parensis*. The outer branch of the male cerci is more slender and not as stout in *F. fulvus fulvus* as in *F. fulvus parensis*. The females of the subspecies *parensis* have a conspicuous longer ovipositor as females in the subspecies *fulvus*. The ratio of ovipositor length to body length is 1.17 in *fulvus fulvus* and 1.24 in *fulvus parensis*.

Song. Continuous sequence of syllables with irregular gaps (Fig. 12 and Results: Acoustics).

Habitat. Fulvoscirtes fulvus fulvus is restricted to the eastern slopes of Mt Kilimanjaro where it inhabits grassy roadsides and ruderal areas, grassy patches within coffee-banana plantations and submontane grasslands. It was recorded from 1150 to 1610 m a.s.l (Table 1).

Etymology. The abdomen of the males is conspicuously bright orange when alive, thus from Lat. *fulvor* = yellow-orange.

Measurements. SI 6.

Fulvoscirtes fulvus parensis **ssp.n. Hemp C.**

Material examined. All Tanzania: Holotype, male: North Pare mountains, swampy grassland, 1300 m, October 2006, UTM Zone 37 M, 353280 E, 9597220 S, NMB. Further material examined: SI 7.

Description. As in *F. fulvus fulvus* with slight morphological differences, as given in the key and the diagnosis at *F. fulvus fulvus*. Measurements of the fastigium verticis of males are identical as in subspecies *fulvus fulvus*, ranging from 0.9 to 1.1 mm.
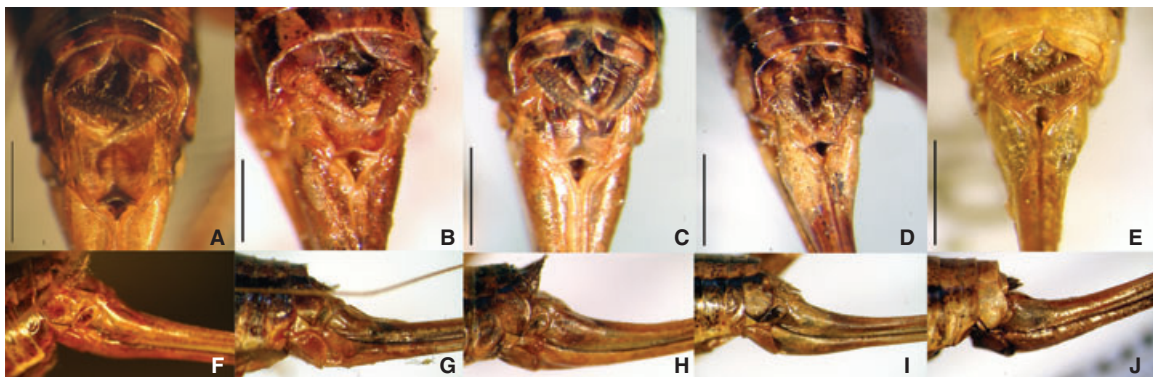

Fig. 9. Abdominal apices of *Fulvoscirtes* females. (A, F). *F. laticercus* **n.sp.**; (B, G) *F. legumishera* **n.sp.**; (C, H) *F. manyara* **n.sp.**; (D, I) *F. sylvaticus* **n.sp.**; (E, J). *F. viridis* **n.sp.** Scale bar: 1 mm.
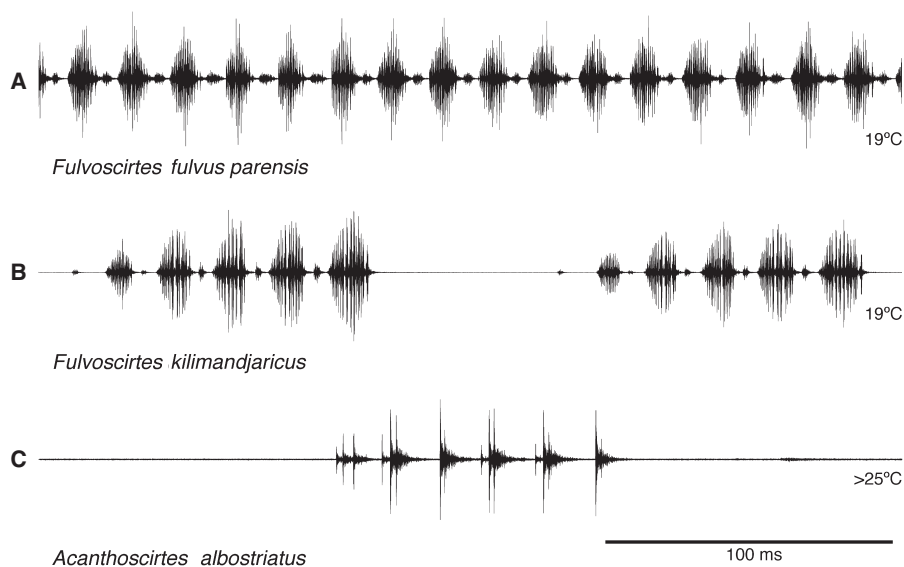
Fig. 10. (A, B) Oscillograms of the two typical amplitude patterns of calling songs in the genus *Fulvoscirtes*; (C) Group of syllables of the 'short song' of *A. albostriatus*.
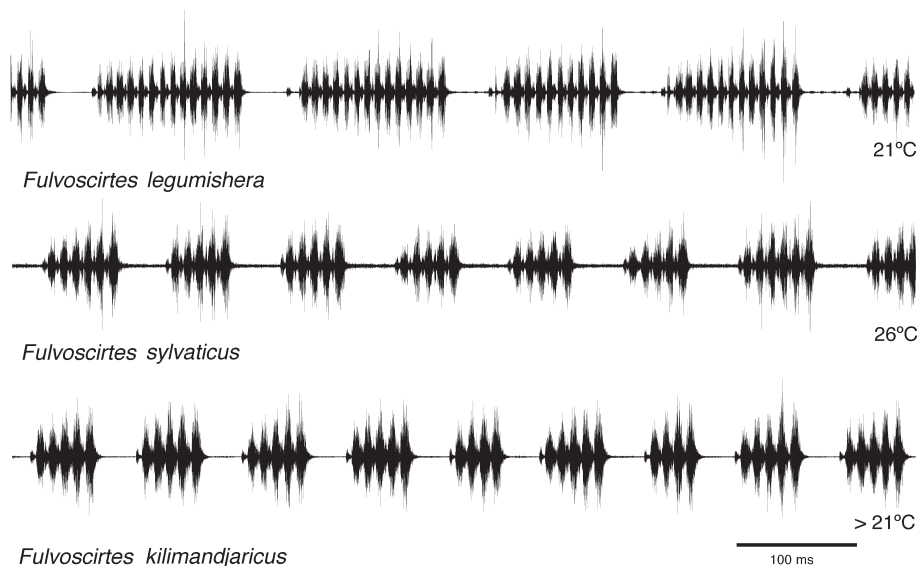

Fig. 11. Oscillograms of calling songs of the species of the *Fulvoscirtes kilimandjaricus* group.

Song. Continuous sequence of syllables (Fig. 10A; Fig. 12; see Results: Acoustics).

Habitat. Recorded from the submontane and montane zones of North and South Pare mountains where this species inhabits grassy roadsides, grassy patches within coffee-banana plantations and open grasslands. In the North Pare mountains it was recorded from 1250 to 1740 m and in the South Pare mountains from 1400 to 1900 m.

Etymology. This subspecies occurs in the mountin ranges of North and South Pare, thus 'parensis'.

Measurements. SI 7.

Fulvoscirtes fulvotaitensis sp.n. Hemp C.

Material examined. All Kenya, all Taita Hills. Holotype, male: Wundanyi, grassland, 1480 m, July 2005, UTM Zone 37 M 0429200 E, 9623310 S, NMB; Further material examined: SI 8.

Description. Male. Green, light and darker brown. *Head.* Face green; fastigium verticis anteriorly (0.8–0.9 mm) wider than diameter of one eye and about double as wide than width
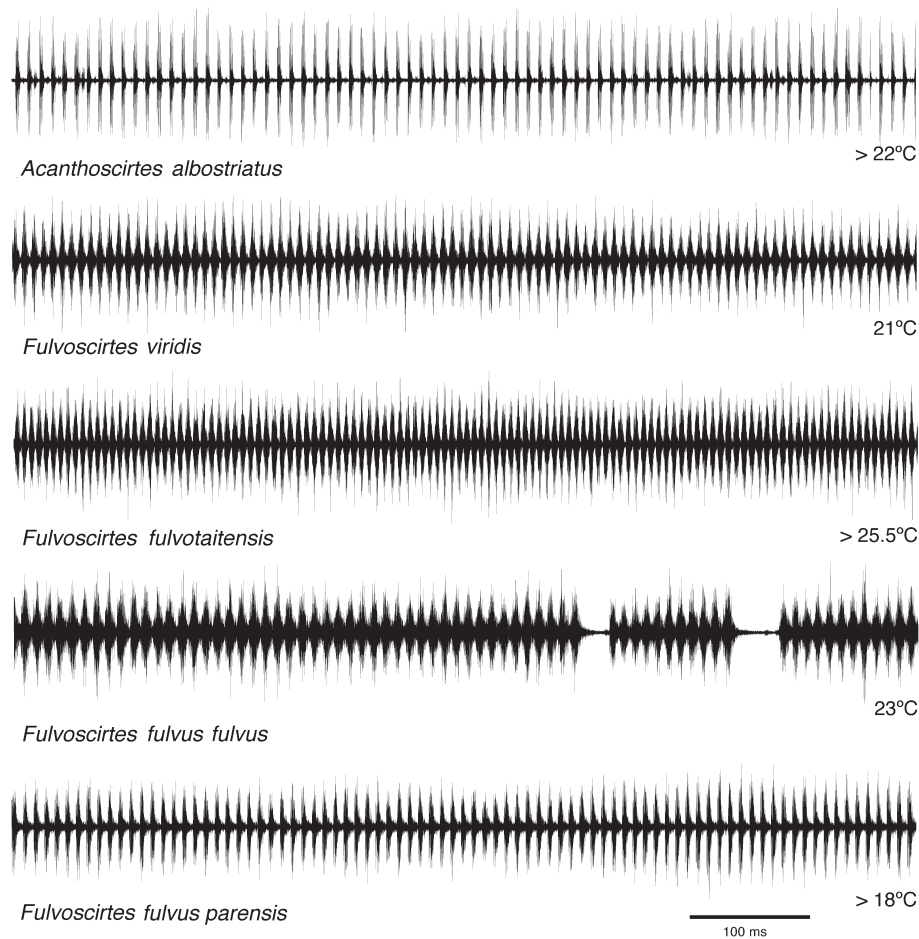
Fig. 12. Oscillograms of calling songs of *Fulvoscirtes* and *Acanthoscirtes* species.

of scapus; dorsal head with typical pattern of median dark brown broad fascia, bordered laterally by white fasciae; Eyes round, dark. *Thorax*. Pronotum dorsally light brown, lower parts of lateral lobes green; from behind eyes till posterior margin of pronotum at both sides of pronotum conspicuous black fascia. *Abdomen*. Orange brown with median fasciae darker brown; lateral margins of tergites bordered yellow. *Tegmina*. Tegmina of same colour as pronotum, visible part 0.1–1.0 mm. *Legs*. Femora green. Tibiae and tarsi light brown or greenish. Hind tibiae with two dorsal rows of dense brown spines, ventrally unarmed. *Genitalia*. Last abdominal tergite strongly curved inward, lateral sides on incurvation with callous knobs. Outer branch of cercus not very pronounced, flattened; in dorsal view inner branch as long or even slightly longer than outer branch (Fig. 4A, B).

Female. Colour pattern as in male but more brown. *Legs*. As in male. *Genitalia*. Ovipositor moderately long, slightly up-curved, as long or little longer as body length. The ratio of ovipositor length to body length in six measured specimens was 1.0. Last abdominal tergites and lateral morphology of ovipositor as in Fig. 8E, J.

Diagnosis. *Fulvoscirtes fulvotaitensis* is characterised by a strong inwardly curved posterior margin of the last abdominal tergite with well-developed knobs at both sides, comparatively short and slender outer branches of the male cerci and rounded tegmina.

Song. Continuous sequence of syllables (Fig. 12; see Results: Acoustics).

Habitat. *Fulvoscirtes fulvotaitensis* is only known from the Taita Hills of Kenya. It occurs in grassy patches in riverine vegetation at lower elevations, along grassy roadsides and ruderal vegetation and submontane to montane grasslands. Recorded at elevations from 1060 to 1715 m.

Etymology. Males also have a vivid orange abdomen when alive and this species is restricted to the Taita Hills, thus from *lat. fulvor* = yellow-orange and from the locality Taita Hills.
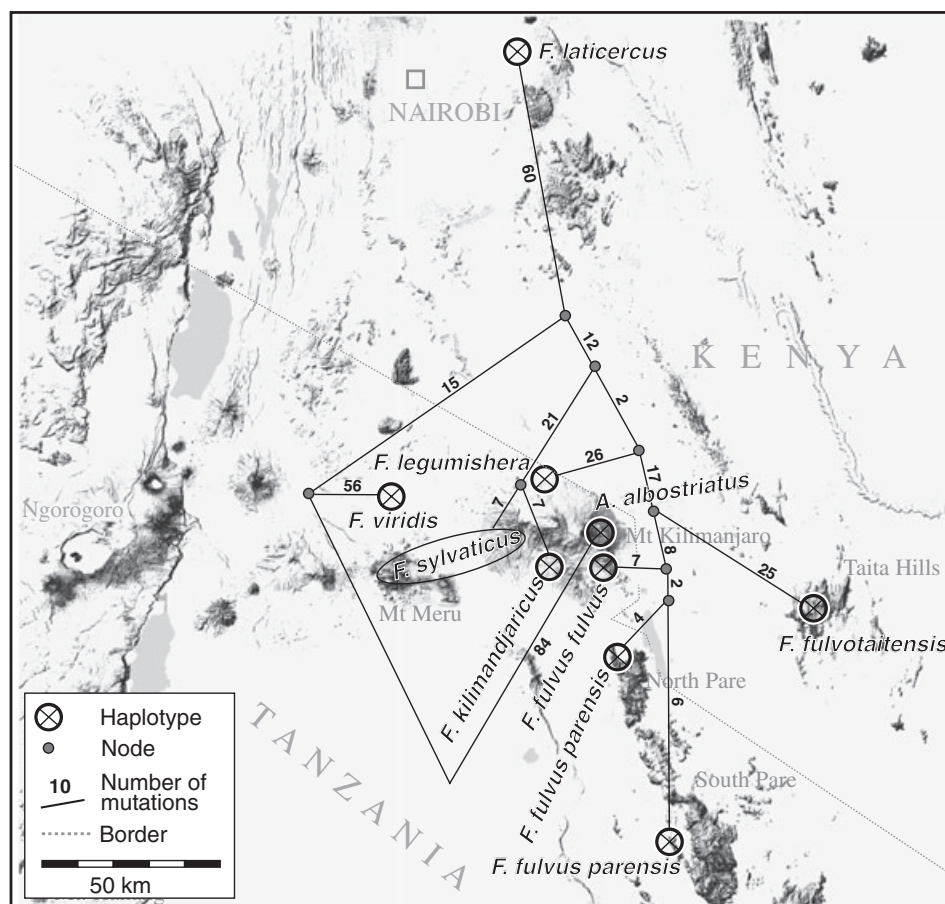
Measurements. SI 8.

Fig. 13. Reduced median network of haplotypes of *Fulvoscirtes* and *A. albostriatus* based on combined data (16S rRNA, H3, COI) and overlaid onto a relief map of Tanzania and Kenya. The haplotypes are approximately arranged according to their original sampling location. The numbers above connections correspond to the number of mutational steps between each species. For each species, except *F. fulvus fulvus*, only one haplotype with the closest connection to the next species is shown. Haplotype network calculations on the single genes COI and 16S are shown in Figs S1 and S2 in the Supporting Information.

Fulvoscirtes laticercus sp.n. Hemp C.

Material examined. Holotype, male: Kenya, Mt Sabuk, mountain summit, grassy patches within bushland, 2155 m, March 2005, UTM Zone 37 M, 0306050 E, 9879460 S, NMB; Further material examined: SI 9.

Description. Male. Brown and dark brown with green (Fig. 2I). *Head.* Face green; fastigium verticis anteriorly (0.75–1 mm) wider than diameter of one eye and more than double as wide than width of scapus; dorsal head with broad median dark brown fascia, bordered by pair of white fasciae (Fig. 2I); eyes round, dark brown. *Thorax.* Disk of pronotum uniformly light brown. No pattern of brown and cream fasciae present except for upper part of lateral lobes where a broad brown fascia starts which is continuous throughout the pronotum and laterally along the abdomen; lower part of lateral pronotal lobes green. *Abdomen.* Light brown medially, with pair of broad lateral brown fasciae, sternites partly yellowish in living individuals (Fig. 2I). *Tegmina.* Tegmina of same colour as pronotum, visible part 0.4–1.2 mm. *Legs.* Femora green to light brown, tibiae and tarsi light brown. Hind tibiae with two dorsal rows of dense brown spines, ventrally unarmed. *Genitalia.* Last abdominal tergite evenly curved inward with central depression. Cerci with apical part of outer branch very broad and thus rounded; inner branch slender, slightly curved with black tip (Fig. 4G, H).

Female. Colour pattern as in male but pattern of brown fasciae continued on pronotum. *Legs.* As in male. *Genitalia.* Ovipositor long and almost straight, about as long as the body length. The ration of ovipositor length to body length in six measured specimens was 0.98. Last abdominal tergites and lateral morphology of ovipositor as in Fig. 9A, F.

Diagnosis. *Fulvoscirtes laticercus* has male cerci in which the apical parts of the outer branch are broadly rounded; the cercus is comparatively short, not or hardly exceeding the
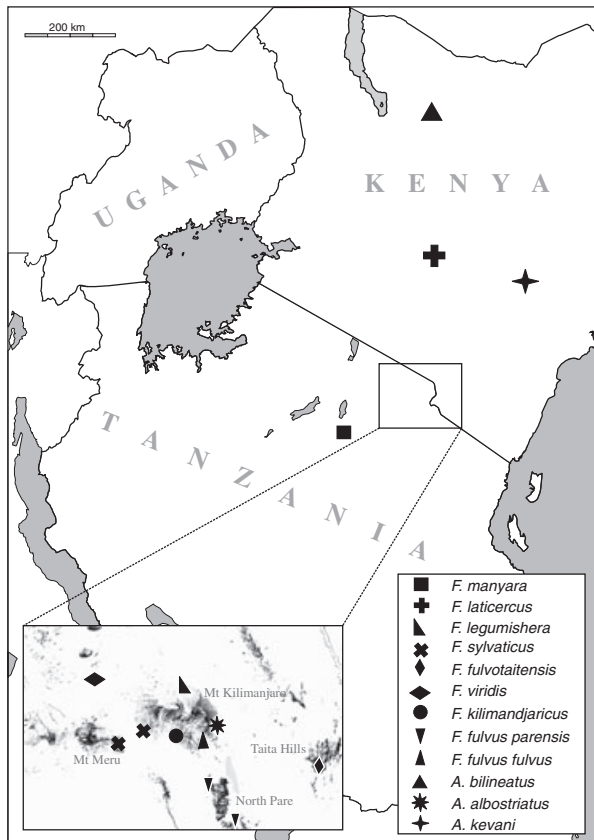
Fig. 14. Distribution of *Fulvoscirtes* and *Acanthoscirtes* in East Africa.

subgenital plate; the inner branch of the cercus is short but slender and little curved.

Habitat. On grassy patches at forest edges, degraded forests and bushland in the Kenyan highlands. It was found along a grassy roadside through a not too densely planted *Eucalyptus* plantation at 2100 m on Mt Machakos and in grassy patches along the lower border of the montane forest on Mt Sabuk to the top of the mountain in grassy patches scattered within degraded bushland at 2155 m.

Song. Unknown.

Etymology. Named after the comparatively broad outer branch of the male cercus; lat.: *lati* = broad.

Measurements. SI 9.

Fulvoscirtes manyara sp.n. Hemp C.

Material examined. All Tanzania. Holotype, male: Mt Hanang, grassland, 1900 m, June 2006, UTM zone 36 M, 0769816 E, 9505197 S, NMB; Further material examined: SI 10.

Description. Male. Brown and dark brown with green. *Head.* Face green; fastigium verticis anteriorly (0.7–0.9 mm) wider than diameter of one eye and more than double as wide than width of scapus; dorsal head with broad median dark brown fascia, bordered by pair of thin cream to white fasciae followed laterally by another dark brown fasciae down to eyes margins. Eyes round, dark brown. *Thorax.* Disk of pronotum uniformly light brown. No pattern of brown and cream fasciae present; lateral lobes of pronotum at anterior part green, at about half of lateral lobes short brown fascia running to posterior margin. *Abdomen.* Dark brown, some individuals with faint lateral darker brown fascia. *Tegmina.* Tegmina of same colour as pronotum, visible part 0.7–1.1 mm. *Legs.* Femora greenish-light brown, tibiae and tarsi light brown. Hind tibiae with two dorsal rows of dense brown spines, ventrally unarmed. *Genitalia.* Last abdominal tergite evenly but strongly curved inward. Cerci with apical part of outer branch elongate flattened, apical part coarsely pitted and more dark; inner branch slender, curved, with black tip (Fig. 4E, F).

Female. Colour pattern as in male. *Legs.* As in male. *Genitalia.* Ovipositor very long and almost straight, longer as body length (ovipositor length/body length: 1.2). Last abdominal tergites and lateral morphology of ovipositor as in Fig. 9C, H.

Diagnosis. Fulvoscirtes manyara is a typical species of submontane to montane elevations. The living individuals are not very brightly orange but with a more brown abdomen. The last abdominal tergite is strongly curved inwards, with no knobs at the outer sides and thus easily distinguished from species with knobs at the posterior margin of the last abdominal tergite as e.g in. *F. fulvus* ssp. or *F. kilimandjaricus* (see key); the outer branch of the male cerci is elongate and not very broadly flattened. The females are comparatively large with very long and straight ovipositors (comparatively short in *F. kilimandjaricus, F. laticercus* and *F. sylvaticus*).

Habitat. Grasslands from submontane to montane elevations on Mt Hanang and the Manyara escarpment in Tanzania. Occurred in a high density on a grassland at 1900 m in May 2006.

Song. Unknown.

Etymology. Occuring on the Manyara escarpment of western Tanzania. Noun in apposition.

Measurements. SI 10.

Fulvoscirtes viridis sp.n. Hemp C.

Material examined. Holotype, male: Tanzania, between Mt Longido and Mt Meru, grassy patches in tree savannah,

1300 m, February 2010, UTM zone 37 M, 0244528 E, 9681998 S, NMB; Further material examined: SI 11.

Description. Male. Green with some brown. *Head.* Face green; fastigium verticis anteriorly (0.7) wider than diameter of one eye but less than double as wide than width of scapus; dorsal head with broad dark brown fascia, medially faint and a thin whitish line. Eyes round, light brown. *Thorax.* Pronotum almost uniformly greenish to light brown, with some darker brown mottles. *Abdomen.* In living insect greenish, tawny in preserved one. *Tegmina.* Tegmina of same colour as pronotum, visible part 1.3 mm. *Legs.* Vivid green in living insect, light green in preserved one, tibiae and tarsi light brown. Hind tibiae with two dorsal rows of dense brown spines, ventrally unarmed. *Genitalia.* Last abdominal tergite strongly curved inward. Cerci with outer branch short, blunt and not flattened, inner branch rather stout and comparatively short and only slightly curved (Fig. 4I, J).

Female. Colour pattern more brown with lateral brown fasciae on abdomen. *Legs.* As in male. *Genitalia.* Ovipositor very long and very straight, longer as body length (ratio ovipositor length/body length: 1.2). Last abdominal tergites and lateral morphology of ovipositor as in Fig. 9E, J.

Diagnosis. The only *Fulvoscirtes* species found in a savannah habitat. Easily distinguished from all other species of the genus by its stout, blunt and almost round outer cercal branch of the males. The living insects, especially the males, are vivid green, markedly the lateral lobes of the pronotum and the legs.

Song. Continuous sequence of syllables (Fig. 12; see Results: Acoustics).

Habitat. Grassy patches in tree and bush savannah between Mts Longido and Meru in Tanzania at an elevation of about 1300 m. Only present during the wet time of the year.

Etymology. Living insects are conspicuously green; lat.: *viridis* = green.

Measurements. SI 11.

Acanthoscirtes kevani (Chopard, 1954) comb.n.

Phlesirtes kevani Chopard, 1954 Chopard & Kevan, 1954

Phlesirtes kevani Chopard, 1954 Hemp *et al.*, 2010b, c.

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 & Kevan (1954).

Habitat. Desert-grass and thorn bush (Chopard & Kevan, 1954).

Distribution. Known only from the type locality in northern Kenya.

Diagnosis. The tenth abdominal male tergite of *A. kevani* wears at its posterior margin a pair of stout projections. The male cerci are stout and differentiated into two short branches of similar size and shape. Similar male 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 nevers wears a pair of projections. The ovipositor of the single known female of *A. kevani* is much longer than the body length (ratio ovipositor length/body length: 1,16).

Diagnosis. Acanthoscirtes kevani differs from *A. albostriatus* males in the shape of the spines of the tenth abdominal tergite. These are shorter and more stout in *A. kevani* (Fig. 5F, G) than in *A. albostriatus* (Fig. 5B, C). The outer branch of the male cerci is shorter than the stout inner branch in *A. kevani* (Fig. 5H), while it is long and slender and of about the same length as the stout inner branch in *A. albostriatus* (Fig. 5A).

The female of *A. kevani* has about the same body size as *A. albostriatus* (15 mm) but both species are smaller than the only known female and the holotype of *A. bilineatus* (19 mm). Both *A. kevani* and *A. bilineatus* have ovipositors that are about body length, while *A. albostriatus* has a considerably longer ovipositor, the ratio of ovipositor length to body length is 1.3.

Acanthoscirtes bilineatus (Chopard, 1954) comb.n.

Phlesirtes bilineatus Chopard, 1954 Chopard & Kevan (1954)

Phlesirtes bilineatus Chopard, 1954 Hemp *et al.*, 2010b, c.

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

Description. See Chopard & Kevan 1954.

Habitat. Scrub and grass (Chopard & Kevan, 1954).

Distribution. Chopa Gof Crater; the holotype is unique.

Diagnosis. With 19 mm body length and 18 mm ovipositor length the largest *Acanthoscirtes* and Karniellina species known at present. In Karniellina the species of the genera *Phlesirtes* and *Melanoscirtes* have ovipositors that are shorter than the body size. In *Chortoscirtes* and *Fulvoscirtes* females also have ovipositors that are as long as body length or longer. Although no male is known of this species, the body size of the female holotype of *A. bilineatus* and the size and shape of the ovipositor as well as the habitat (dry conditions in northern Kenya) in which the holotype was collected indicates that this species belongs to *Acanthoscirtes*. However, more material, especially males, is needed to confirm the status of this species within the Karniellina.

Acanthoscirtes albostriatus sp.n. Hemp C.

Material examined. All Tanzania, all East Kilimanjaro. Holotype, male: tree-bush savanna, 1020 m, July 2004, UTM Zone 37 M, 347390 E, 9629310 S, NMB; Further material examined: SI 12.

Description. Male. Light and darker brown with some green parts. *Head.* Face green to yellowish green; fastigium verticis anteriorly (0.8–1.1) wider than diameter and about double as wide than width of scapus; dorsal head with brown to black broad fascia with a median very thin white line on dorsum of head; broad brown fascia bordered laterally by pair of conspicuous white fasciae; Eyes round, whitish-tawny. *Thorax.* Colour pattern of head continued on dorsum of pronotum, median brown fascia may be dark brown or of more obsolete colour. *Abdomen.* Striped pattern continued on abdomen, but general colour more whitish to light brown, many males with orange tinge. *Tegmina.* Tegmina pointed and callous, visible part 0.3–0.7 mm (Figs 6C, 7C). *Legs.* Green to greenish-tawny; tibiae and tarsi light brown. Hind tibiae with two dorsal rows of dense brown spines, ventrally only a few short and stout spines. *Genitalia.* Last abdominal tergite with two stout thorn-like appendages at posterior margin (Fig. 5B, C). Cerci with slender outer branch which is only slightly longer than the more stout and inwardly curved inner branch, giving the appearance of a lobster claw (Fig. 5A).

Female. (Fig. 5D, E). Colour pattern more brown with lateral brown fasciae on abdomen; *Legs.* As in male. *Genitalia.* Ovipositor very long and very straight, longer as body length (Fig. 5D). Ratio of ovipositor length to body length 1.33. Last abdominal tergites and lateral morphology of ovipositor as in Fig. 8A, F.

Diagnosis. The thorn-like pair of projections on the posterior margin of the last abdominal tergite are more slender and longer than the more stout projections of *A. kevani*. The females with an average size of 15.1 mm about the size of *A. kevani* (15 mm) but are considerably smaller than the female of *A. bilineatus* (19 mm). However, *A. albostriatus* has an ovipositor that is longer than the body length while both in

A. bilineatus and *A. kevani* the ovipositor is about body length. The colour pattern, especially in males, is conspicuous because of the contrasting white and dark stripes along head, pronotum and part of the abdomen.

Song. Continuous sequence of syllables (Figs 12; 10C 'short song'; see Results: Acoustics).

Habitat. Grasslands in tree- and bush-savannah at the eastern slopes of Mt Kilimanjaro. Recorded between 1000 and 1100 m (Table 1).

Etymology. The striped pattern dorsal on head, pronotum and abdomen is conspicuous, thus from lat. *alba* = white and lat. *stria* = stripe.

Measurements. SI 12.

Discussion

Biogeography and ecology

The genera *Fulvoscirtes* and *Acanthoscirtes* are sister taxa and these form the sister group to *Phlesirtes*. All three genera are well separated genetically, morphologically and ecologically. While *Karniella* is a genus which is distributed further west in the area of the Albertine rift valley, inhabiting forest edges and clearings, *Chortoscirtes* has adapted to open savannah grasslands in eastern Africa (Hemp *et al.*, 2010b). *Melanoscirtes* species are found in submontane to montane forest clearings and also occur in moist open grassland habitats such as swamps (Hemp *et al.*, 2010c). *Phlesirtes* species are also adapted to open grasslands. However, all *Phlesirtes* species – most of them yet undescribed (Hemp *et al.*, in preparation) – are found in montane to subalpine elevations. *Fulvoscirtes*, however, has found its niche in grassland of submontane elevations in eastern Africa, while species of *Acanthoscirtes* are found in savannah habitats. A few individuals of a yet undescribed species of *Acanthoscirtes* are held in the collection of the Natural History Museum of London, UK. These are labelled Budanga, a village in western Uganda.

As Voje *et al.* (2009) showed for East African Phaneropterinae species inhabiting the savannah evolved from forest dwellers probably at a time when the African climate got drier and more variable during the late Miocene and early Pliocene (see also deMenocal, 1995). The same process can be inferred for the Karniellina. The most ancient lineage *Karniella* is a forest-dependent taxon, whereas all other known genera prefer open grasslands. An exception is *Melanoscirtes* adapted to forest clearings and edges in the area of the northern branch of the Eastern Arc mountains with one subspecies found on Mt Kilimanjaro. However, *Melanoscirtes* is always associated with grass and never found in purely herbaceous vegetation. Major splits within Karniellina happened approximately simultaneously, and it seems that this

radiation might have been favoured by the spread of savannah grasslands in the Miocene. Many niches opened when forest cover retracted, boosting speciation especially around high mountains or mountain ranges. However, that the high species diversity found within the single genera of Karniellina is geologically young can be deduced from the fact that geologically young volcanoes (Nonnotte *et al.*, 2008) such as Mt Kilimanjaro, Mt Meru, the Ngorongoro crater highlands and Mt Hanang, also harbour a high diversity of Karniellina.

The sister taxa to species of the genus *Acanthoscirtes* are the species of the genus *Fulvoscirtes*. Both groups differ in the morphology of the male genitalia and are also ecologically separated. *Fulvoscirtes viridis* in an exception to all other species in its genus in occurring in submontane elevations between the mountains Longido and Meru. The predominant vegetation there may be regarded as tree-savannah with more or less open grassy patches. Molecularly and morphologically *F. viridis* is well separated from other *Fulvoscirtes* species which show a very uniform morphology and all occupy submontane to montane habitats on high mountains or mountain ranges. All of these latter species are closely related and differences in their genetics and morphology are small, suggesting recent radiation events. Species of adjacent mountains or mountain ranges are sister taxa while species found on more distant mountains are morphologically and molecularly more different. Thus, *F. laticercus*, occurring in the Kenyan highlands, forms the sister group to all species found further south, where they inhabit the mountain ranges of the northern branch of the Eastern Arc mountains and the inland volcanoes of the rift valley.

A remarkably high diversity of *Fulvoscirtes* species is found on Mt Kilimanjaro. The molecular and morphological pattern seen in some of the species suggests that the massive volcano offered a variety of niches for *Fulvoscirtes* at submontane elevations, the preferred habitat of *Fulvoscirtes*. Further studies are needed to investigate whether adaptive radiation led to the pattern we see today in the species complex of *F. sylvaticus*, *F. kilimandjaricus* and *F. legumishera,* which form a monophyletic clade (Fig. 1). All three species occupy analogous habitats but on different sides of the mountain. *Fulvoscirtes sylvaticus* is found only on the western side of Mt Kilimanjaro and the eastern side of Mt Meru, *F. kilimandjaricus* is a common species at submontane elevations along the southern slopes and *F. legumishera* was only recorded on the northern slopes of the mountain. The latter species occurs in the montane zone in the much drier conditions of the northern side of Mt Kilimanjaro. Grasslands with sufficient precipitation, and thus the favoured microclimate of *Fulvoscirtes*, are found several hundred metres higher on the northern than on the southern slopes, which receive much more precipitation (Hemp, 2006; see fig. 12, precipitation map of Mt Kilimanjaro).

An obviously very recent radiation is represented by the species complex of *F. fulvus*. This species occurs on the eastern slopes of Mt Kilimanjaro, in the submontane zone of the North Pare mountains and the adjacent South Pare mountains. In the South Pares *F. fulvus parensis* was found in submontane and also in montane grasslands due to anthropogenic opening of areas which were formerly forested. This shift is also seen in the North Pares, where *F. fulvus parensis* was recorded up to 1750 m at Mt Kindoroko, the lower border of the montane forest. On Mt Kilimanjaro *F. fulvus fulvus* is also found in an analogous situation in montane plantations up to the lower forest belt between 1700 and 1800 m. However, highest densities of *F. fulvus* ssp. are seen in submontane, often humid grasslands, while the population density of this species is low at higher elvations; also specimens are conspicuously smaller in body size in the montane zone than in submontane elevations. Molecularly the subspecies of *F. fulvus* are very closely related and morphologically only small differences are seen. Because *F. fulvus fulvus* is endemic to Mt Kilimanjaro, the split of the subspecies is likely to have been very recent as Mt Kilimanjaro is geologically young (1–2 Ma; Nonnotte *et al.*, 2008). As in various flightless orthopteran genera, species of the South Pares and the Taita Hills are sister taxa, a fact seen also in *F. fulvus* and *F. fulvotaitensis*. Because Mt Kilimanjaro harbours a subspecies of *F. fulvus* it can be supposed that ancestors spread from the South Pares via the North Pares to the eastern slopes of Mt Kilimanjaro, where this taxon established. The North Pare mountains consist of only a few peaks looming to montane elevations while the South Pare mountains are a massive mountain range with Mt Shengena reaching 2400 m. Beside taxa obviously having originated from rather young radiations such as *Fulvoscirtes* or *Peronura* (Hemp, 2011), the South Pare mountains also harbour archaeoendemics due to the geological old age of the Eastern Arc mountains (estimated 30 Ma).

Acoustics

In contrast to the related genera *Chortoscirtes* and *Melanoscirtes*, where all species of the genus show the same or at least a very similar pattern, in *Fulvoscirtes* one subgroup produces a distinctly different song type. The calling song of the three species of the *F. kilimandjaricus* group consists of groups of syllables (echemes), separated from the next by a distinct interval. This evolutionary step from a continuous sequence of syllables to a sequence of echemes – in cricket terminology from trill to chirp – seems to be a common change in the diversification of songs (e.g. Otte, 1992). In *Fulvoscirtes* it has probably happened once in the ancestral species occupying Mt Kilimanjaro and Mt Meru. It is tempting to speculate that this has occurred under the pressure of species recognition in the whole assembly of Karniellina species, but without knowledge of the songs and distribution of the species of the genus *Phlesirtes* it is too early to go into details. In any case, the difference in the amplitude pattern between the two song types is certainly large enough to allow a sympatric occurrence (see the song differences in sympatric *Tettigonia* species; Schul, 1998).

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2012.00622.x

Table S1. Genera and species of Karniellina and their distribution (compiled data from Hemp *et al.*, 2010 a, b).

Table S2. Accession numbers of investigated *Fulvoscirtes* and *Acanthoscirtes* individuals.

SI 3–12. Information about additional examined *Fulvoscirtes* and Acanthoscirtes specimens and measurements.

Fig S1. Reduced median network of the COI haplotypes of *Fulvoscirtes* and *A. albostriatus* overlaid onto a relief map of Tanzania and Kenya. The haplotypes are approximately arranged according to their original sampling location. The numbers above connections correspond to the number of mutational steps between each species. For each species, except *F. fulvus fulvus*, only one haplotype with the closest connection to the next species is shown.

Fig S2. Median-joining network of the 16S rRNA haplotypes of *Fulvoscirtes* and *A. albostriatus* overlaid onto a relief map of Tanzania and Kenya. The haplotypes are approximately arranged according to their original sampling location. The numbers above connections correspond to the number of mutational steps between each species. For each species, except *F. fulvus fulvus*, only one haplotype with the closest connection to the next species is shown.

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