

The genus *Aerotegmina* (Orthoptera, Tettigoniidae, Hexacentrinae): chromosomes, morphological relations, phylogeographical patterns and description of a new species

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Abstract The genus *Aerotegmina* Hemp is common on East African mountains. Two species are known and a third, *A. taitensis* n. sp., is described in this paper. *A. kilimandjarica* Hemp is widespread while *A. shengena* Hemp is endemic to the South Pare Mountains and *A. taitensis* n. sp. is known only from the Taita Hills. Morphologically, and from their song, *A. shengena* and *A. taitensis* n. sp. are closely related. In chromosome number *A. kilimandjarica* ($2n=33$) differs clearly from *A. shengena* ($2n=27$). Data presented on other flightless Orthoptera suggest that the South Pare Mountains and the Taita Hills, both belonging to the geologically old mountain chain of the Eastern Arc, show a faunistic similarity not shared by any other mountain range in the area. The mechanisms that led to this phylogeographic pattern in flightless Orthoptera in the Eastern Arc Mountains of northern Tanzania and southern Kenya and the inland volcanoes are discussed. A key to the three *Aerotegmina* species is presented, as well as bioacoustical data of all species compared to the phaneropterine species *Euryastes jagoi*.

Keywords Orthoptera · Hexacentrinae · *Aerotegmina* · *Euryastes* · Taita Hills · Eastern Arc Mountains · East Africa · New species · Bioacoustics · Chromosomes · Morphology · Phylogeography

Introduction

The genus *Aerotegmina* was erected on *A. kilimandjarica* Hemp, 2001, from Mt. Kilimanjaro, Tanzania (Hemp 2001). Another *Aerotegmina* species was described by Hemp (2006) restricted to montane forests of the South Pare Mountains of northern Tanzania. Gorochov (2007) re-established the subfamily Hexacentrinae Karny transferring *Aerotegmina* from Listrocelidinae to this subfamily.

The genus *Aerotegmina* is characterized by highly modified wings and the shape of the pronotum. The tegmina are inflated strongly to form an acoustic chamber, closed by the flap-like alae completing the chamber ventrally. The pronotum is saddle-shaped.

Inflation of the tegmina results in an unusually loud song at a low frequency (Heller et al. 2010). Low-frequency songs have important advantages in acoustic communication, increasing the range between sender and receiver. *Aerotegmina* are flightless insects with low mobility. Thus, the need to be heard by females could have been the evolutionary pressure leading to development in the male sex of this effective communication to attract females.

Hemp (2010) suggested that the origin of the genus *Aerotegmina* lies in the geologically ancient chain of the Eastern Arc Mountains of Tanzania and southern Kenya. Areas obviously generating a high biodiversity in this region were found to be the South Pares and West Usambaras due to the special topography and geographical location of these massive and high mountain chains. The record of another

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Aerotegmina species in the Taita Hills of Kenya sheds more light on the evolution of this taxon and the faunistic relationship of the mountain ranges of the northern branch of the Eastern Arc Mountains.

In this paper we describe a new species of *Aerotegmina* restricted to the Taita Hills of Kenya. We compare song and the acoustic apparatus of the three species, present the chromosomal set of two species and discuss their phylogeographical relationships.

Materials and methods

Collection localities

A. taitensis n. sp. Fig. 1 was collected at night in the two largest remaining pieces of montane forest of the Taita Hills, on Mt. Vuria and the Ngangao forest reserve.

Measurements

Total body length refers to the body length of the insect, disregarding tegmina but not genitalia. Tegminal length is determined as viewed from above.

Song

Recordings of song in the field and in captivity (20 °C) were made with a Pettersson X1000 bat detector using a sampling rate of 100 kHz. The sounds were analysed using the program Amadeus II (Martin Hairer; <http://www.hairersoft.com>). Frequency data were taken from one syllable per specimen (mean in sliding window of 512 points; hamming window). For *A. shenganae* a Sony ECM-121 microphone was also used.

Chromosomes

Seven males of *Aerotegmina kilimandjarica* (CH6825, CH6827, CH6850–54) and one male of *A. shenganae* (CH7268) were used for cytotaxonomic analyses. Chromosome 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. Cover slips were removed by the dry ice procedure and the preparations were air-dried. C-banding was carried out using a slightly modified version of Sumner's (1972) technique. The silver staining method (Ag-NO₃) for localisation of the nucleolus organiser regions (NORs) was performed as previously reported (Warchałowska-Śliwa & Maryńska-Nadachowska 1992). Chromosomes were classified on the basis of the criteria proposed by Levan et al. (1964).

Depositories

MNB: Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin.

Results

Key to *Aerotegmina* species (males)

1 Alae surpassing abdominal apex by about one-third of its length; alae elongate with pointed tips (Figs. 2, 3a and 4a).

A. kilimandjarica Hemp

1' Alae shortened, surpassing abdomen by only a few mm.

2

2 Alae broadly rounded (Figs. 3c and 4b). *A. taitensis* n. sp.

2' Alae spatulate (Fig. 3b). *A. shenganae* Hemp

Aerotegmina taitensis n. sp. Hemp C. (Figs. 1, 2, 3c, 4b and 5c)

Holotype Male: Kenya, Taita Hills, Mt. Vuria, 1950 m, UTM zone 37 M, 421900 E, 9623400S, canopy of undergrowth tree, November 2010, C. Hemp coll.; depository, MNB.

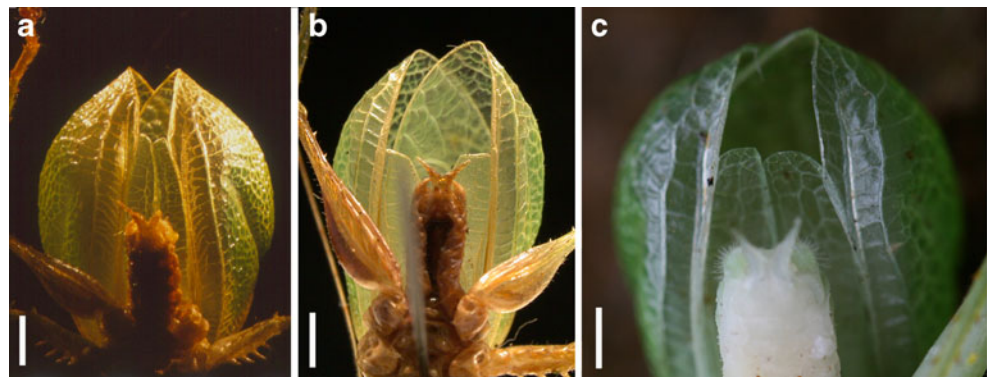


Fig. 1 Habitus of male *Aerotegmina taitensis* n. sp.



Fig. 2 *Aerotegmina taitensis* n. sp.: ventral view of male abdominal apex with subgenital plate and styli

Fig. 3 a–c *Aerotegmina* species, ventral view on tegmina and alae. **a** *A. kilimandjarica*. **b** *A. shengena*. **c** *A. taitensis* n. sp. Bars 3 mm



Paratype 1 male, Ngangao forest reserve, 1900 m, canopy of undergrowth tree, February 2011, collection Hemp.

Description Male. *Color.* Light green. *Head and antennae.* Antenna more than twice as long as length of body, whitish with irregular annulate dark markings (Fig. 1). Cuticle of head smooth. Conical and laterally compressed fastigium of vertex situated before antennal sockets in dorsal aspect. Space between eyes about 2.5 times as wide as diameter of eye. Eyes almost circular, prominent, whitish in living insect, brown in preserved insect. *Thorax.* Green with rugulose callosities. Anterior and posterior margins of pronotum yellow. *Abdomen.* Abdomen milky white (Fig. 2). *Tegmina and alae.* Acoustical chamber imperfectly closed by alae; alae with rounded apices, leaving a gap posteriorly (Figs. 3c and 4b). Tympanum (mirror of right tegmen) oval, about 4.2 mm long and 3.9 mm wide. *Legs.* Fore and mid femora with four stout yellowish spines on the outer sides, and four green smaller stout spines on the inner sides of the fore, and three on the mid femora. Apically with a pair of short spurs. Hind femur with six stout yellow outer and four small inner green spines, distally one spur at each side. Fore and mid tibiae with five pairs of light green predatory spines at each side, apically with a pair of spurs. Hind tibiae with four rows of minute spines. With well developed tarsal arolium.



Fig. 4 a,b Dorsal aspect of male *Aerotegmina* alae. **a** *A. kilimandjarica*. **b** *A. taitensis*

Genitalia. Subgenital plate symmetrical (Fig. 2), of same milky white colour as venter of abdomen, with smooth surface, flattened ventrally, lobes with scattered hairs. Cerci robust with rugose and hairy surface; in the living specimen stretched out from the body.

Measurements Males ($N=2$); Total length of body 13.5 mm; Length of pronotum 3.5–3.6 mm; Length of hind femur 10.8–11 mm; Length of tegmina (as seen from above) 11–14.5 mm.

Female. Not known.

Distribution *A. taitensis* n. sp. was collected in montane forests of Mt. Vuria ranging between 1,950 and 2,200 m and in montane forest of the Ngangao forest reserve at about 1,800 m.

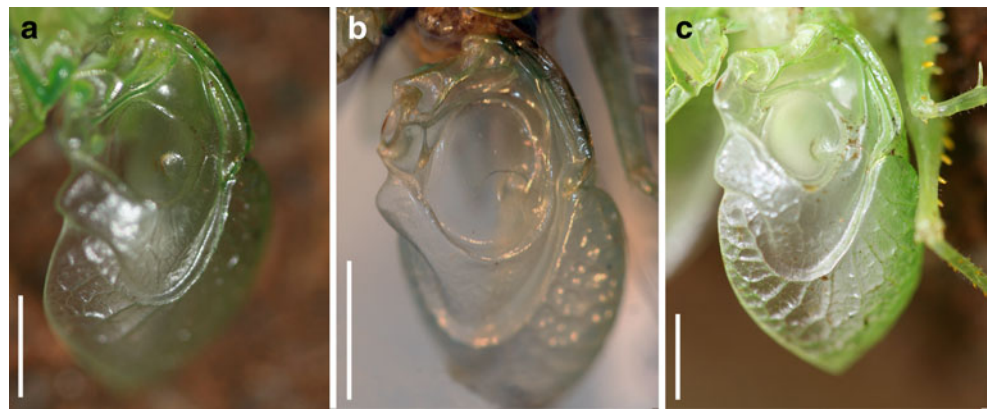
Habitat Closed montane forest with a upper tree canopy of 12–15 m height and 80–90 % coverage on Mt Vuria. The forest is heavily disturbed and probably logged for certain timber species. The Taita forests in which *A. taitensis* n. sp. was recorded belongs to the same forest type as on the South Pare Mountains where *A. shengena* occurs (Hemp 2006). The montane forest of the Ngangao forest reserve is less heavily impacted in its centre thus harbouring still intact afro-montane forest communities.

A. taitensis males were located by their calling songs starting at nightfall. Individuals were collected perched under broad leaves. Most individuals were heard from considerable heights up in the canopy. Only two specimens were encountered at lower heights and were shaken from branches.

Song The calling song of the species was heard in the evening and night hours only. It consisted of long sequences of single syllables produced at a rate of 2–5 Hz (Fig. 6, Table 1). Differences between the recordings are very likely mainly an effect of different temperature. However, the ambient temperature in the field could not be measured close to the animals.

As described for *A. kilimandjarica* (Heller et al. 2010), the spectrum of the song showed two broad bands (Fig. 7), a

Fig. 5 a–c Right tegmen of *Aerotegmina* species, dorsal view. **a** *A. kilimandjarica*. **b** *A. shenganae*. **c** *A. taitensis*



lower and stronger one between 6 and 12 kHz with a slightly varying peak (Table 1) and a higher but weaker one with a broad peak around 25 kHz.

Chromosomes Analysis of the standard karyotype of *A. kilimandjarica* revealed a diploid chromosome number of $2n=33$ for males with the X0/XX sex chromosome mechanism. All chromosomes were acrocentric (FN=33; FN is the number of chromosome arms including the X chromosome), consisting of 1 long and 15 medium or short pairs gradually decreasing in size; the X chromosome was the largest element (Fig. 8a). The C-heterochromatin is characterised by paracentromeric C-bands similar in size. However, in one medium pair and the X chromosome C-bands occupied the region next to the centromere (thick C-bands). Terminal C-bands are present in all autosomes and X (Fig. 8b). Ag-

NO_3 staining revealed the presence of one active NOR in the medium bivalent, probably in the region under the thick C-band (Fig. 8c).

In the male of *A. shenganae* (a single male was studied) the chromosomal number was reduced to $2n=27$ ($26+X$), FN=34; 13 pairs of autosomes could be arranged into two groups, 2 large and 11 medium or small pairs. Two large and one medium pair were submetacentric, whereas the metacentric X chromosomes were similar in length to the large-sized autosomes (Fig. 9a–c). The C-banding of the spermatogonial mitotic metaphase revealed constitutive heterochromatin blocks in the paracentromeric region of all the chromosomal elements. In one large, one medium pair and the X chromosome thick paracentromeric C-bands were observed. Telomeric C-bands were located in the medium and short pairs, in both arms of the large autosomes and the

Fig. 6 Oscillograms of calling songs of *Aerotegmina* species and the phaneropterine *Euryastes jagoi*

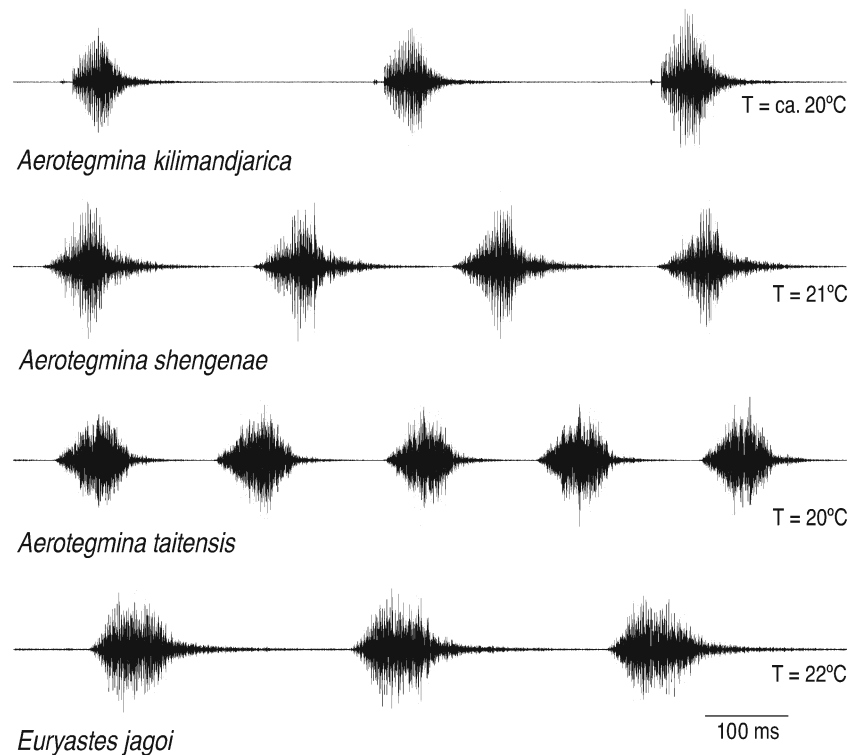


Table 1 Characteristics of the calling song of the three *Aerotegmina* species and *Euryastes jagoi*

Species	Temperature (°C)	Recording condition	Syllable repetition rate (Hz)	Frequency peak (kHz)	Frequency (kHz) 10 dB below peak	
					Lower edge	Upper edge
<i>A. taitensis</i>	20	Lab	4.9	9.0	6.1	11.7
<i>A. taitensis</i>	14–15	Field	2.7	7.7	6.0	12.1
<i>A. shenganae</i> ^b	19–20	Lab	3.1	8.0	6.3	9.4
<i>A. shenganae</i>	21	Lab	5.0	7.6	6.6	10.0
<i>A. shenganae</i>	24	Lab	6.2	7.7	6.9	10.5
<i>A. shenganae</i> ^a	?	Field	5.1	9.5	6.3	9.4
<i>A. kilimandjarica</i> ^a	14–21	Field + lab	2.7	5.5	4.1	9.8
<i>Euryastes jagoi</i>	22	Field	3.5	8.6	7.7	16.7

^aall data from Heller et al. 2010^ball data based on recording with Sony ECM 121

X chromosome (Fig. 9a–c). In *A. shenganae* a NOR was not seen, due to the absence of a diplotene in the studied cells.

Diagnosis *A. taitensis* is a typical *Aerotegmina* species in its general habitus as well as in its ecological requirements. The genital system of the males is uniform among all known *Aerotegmina* species (Fig. 2) and typical for the subfamily Hexacentrinae with an elongate subgenital plate and long narrow styli (Gorochov 2007). Differences to *A. kilimandjarica* are seen in the size of the acoustical chamber, which is larger in *A. kilimandjarica* and inflated in a more “roundish” manner. *A. taitensis* is very similar to *A. shenganae* in shape and size of its acoustical chamber (smaller and more elongated). The mirror on the right tegmen is oval and similar in dimension in *A. taitensis* n. sp. and *A. shenganae*. However, in *A. kilimandjarica* the mirror is smaller and more oval (Fig. 5a–c). Major differences are seen in the length and shape of the alae between the three species. In *A. kilimandjarica*, the alae are elongated and small with pointed, rounded tips, closing perfectly the ventral side of the acoustical chamber. *A. shenganae* has shortened spatulate alae which surpass the abdomen only slightly. A large gap is left at the ventral

posterior side of the acoustical chamber. *A. taitensis* also has shortened alae. However, the posterior tips of the alae are broadly rounded and surpass the abdomen by several millimetres and are thus longer than in *A. shenganae* but still shorter than in *A. kilimandjarica* (Figs. 3 and 4).

Discussion

Phylogeography

The Eastern Arc Mountains are well-known hotspots of biodiversity and endemism (Burgess et al. 2007). The northern part of these geologically old mountains are arranged as an almost continuous chain of mountain ranges stretching from the Tanzanian coast in the east to the inland to the west. Adjacent of the western range of the Eastern Arc Mountains, the geological young inland volcanoes Mt Kilimanjaro and Mt Meru are situated (Fig. 10) probably serving as stepping-stones for the spread of montane taxa during the climatic fluctuations of the past (Hemp et al. 2013).

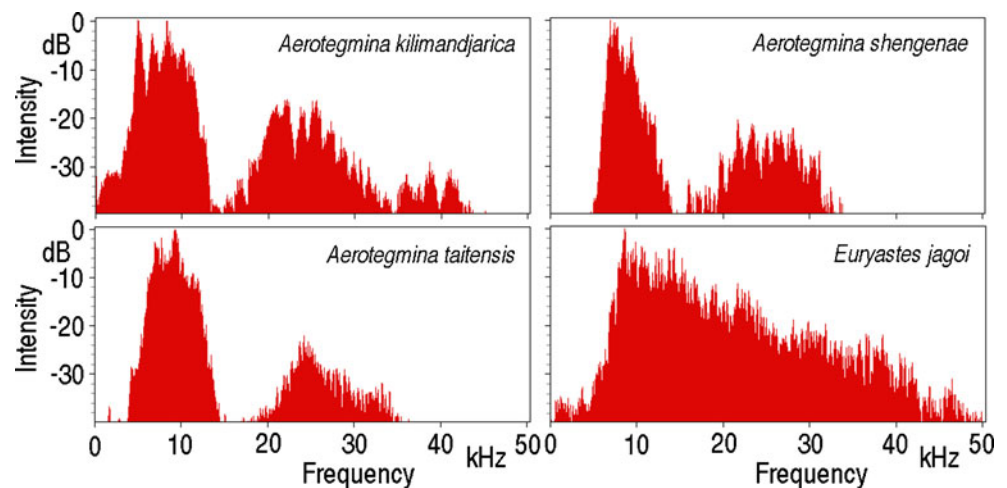
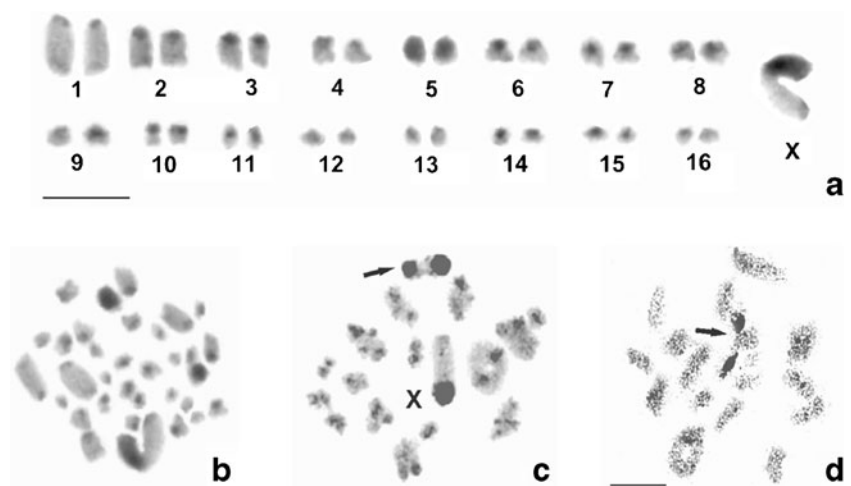
Fig. 7 Spectra of calling songs of *Aerotegmina* species and the phaneropterine *Euryastes jagoi*

Fig. 8 a–d *Aerotegmina kilimandjarica*. **a** Karyotypes, **b** mitotic metaphase and **c** diakinesis; **arrows** thick paracentromeric C-bands on medium pair and X. **d** Silver impregnation of diplotene (**c**) showing the presence of one active nucleolus organiser regions (NOR; **arrow**). **Bar** 10 μ m



The genus *Aerotegmina* is common in montane forests of East African mountains. Two known species, *A. shenganae* and *A. taitensis* n. sp., are restricted in their distribution, recorded only from either the South Pare Mountains or the Taita Hills. *A. kilimandjarica* is more widespread, specimens being collected from various mountains in the area of the Kenyan highlands (Mt Kenya, Mt Sabuk) and northern Tanzania (North Pare, Mt Kilimanjaro, Mt Meru, Manyara escarpment, e.g. Marang forest reserve, Nou forest reserve, Hemp 2010), suggesting an even larger area of distribution in East Africa. From their habitat demands, all species occupy a similar elevational gradient. The lower and upper limit of occurrence could be determined only for *A. kilimandjarica* on Mt Kilimanjaro. Only on this mountain forest cover still stretches from about 1,300 to over 3,000 m due to the protection of the forest belt as forest reserve and, since a few years, as a national park. On most other mountain ranges in East Africa, the former continuous forest cover has been reduced to small patches on few high peaks, e.g. in the Taita Hills, North and South Pare Mountains or Mt Sabuk. Here it was no longer possible to determine the ecological niche of forest bound species such as *Aerotegmina*. On the southern slopes of Mt Kilimanjaro, *A. kilimandjarica* occurs in

forest communities between 1,300 and 2,550 m, being restricted at the lower slopes by humidity becoming too low and by temperature (night frosts) at the upper forest border. Here, night frosts are probably the restricting factor. Assuming that other *Aerotegmina* species also have similar habitat demands, a faunistic exchange of species is not possible under present day climate. An overlap of the distribution areas of *Aerotegmina* species would be possible only at climatic conditions colder and more humid than today, enabling montane forest to spread, connecting *Aerotegmina* populations and species. In light of the global climate getting warmer, *Aerotegmina* is one of the taxa very likely experiencing further habitat restriction or becoming extinct on mountain ranges with few and not very high peaks such as the North Pare Mountains or Mt Kasigau.

As pointed out by Hemp (2006) *A. shenganae* probably is the more basal species compared to *A. kilimandjarica*. Morphological and preliminary molecular data suggest this (Schultz 2004) and the Eastern Arc Mountains are known to harbour various ancient taxa due to their old geological age (e.g. the monotypic genus *Euryastes*). In *A. shenganae*, the acoustical chamber is elongate and smaller than that of

Fig. 9 a–c *Aerotegmina shenganae*. **a** Karyotype, **b** mitotic metaphase and **c** diakinesis/metaphase I; **arrows** banded in two long and one medium pairs. **Bar** 10 μ m

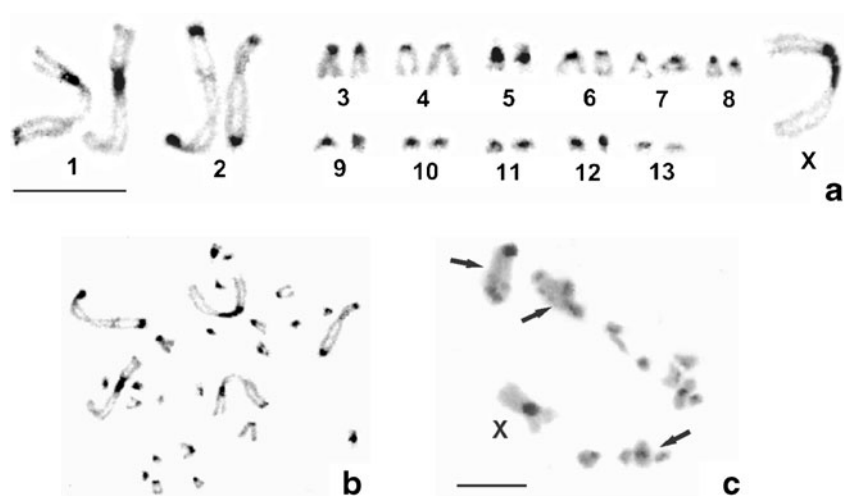
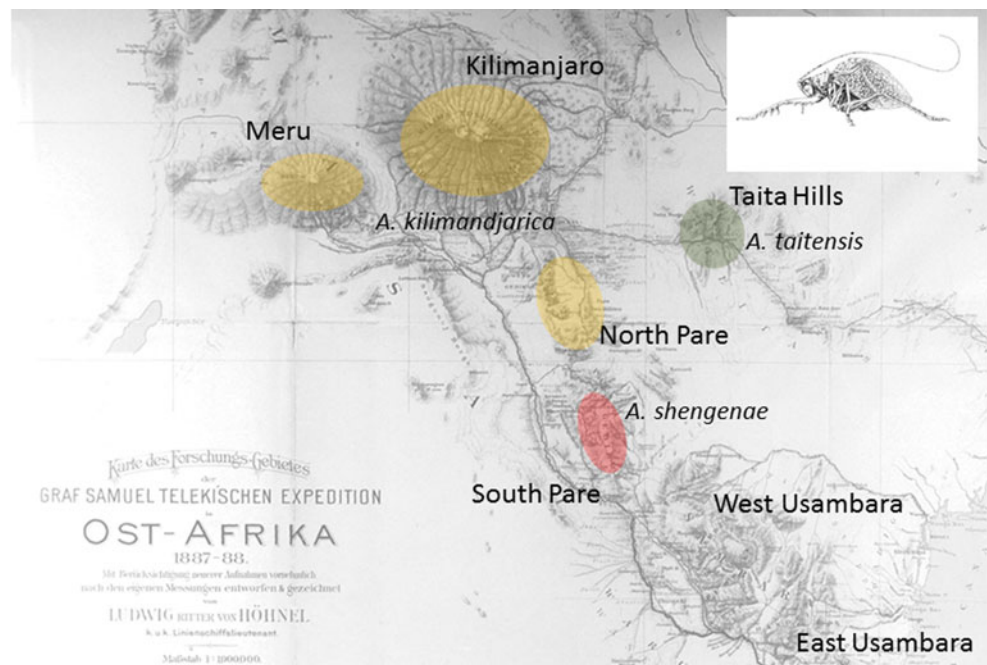


Fig. 10 Map of East Africa in the area of the northern branch of the Eastern Arc Mountains and the inland volcanoes Mt Kilimanjaro and Mt Meru with distribution of *Aerotegmina* species. Map modified from: Karte des Forschungsgebietes der Graf Samuel Telekischen Expedition in Ost-Afrika 1887–88 (Höhnel von 1890). Yellow distribution of *A. kilimandjarica*; red distribution of *A. shenganae*; green distribution of *A. taitensis*



A. kilimandjarica, which has a much more roundish inflated chamber. Furthermore, the chamber is not completely closed ventrally in *A. shenganae* since the alae are shortened and spatulate, leaving a large gap at its posterior end while the alae of *A. kilimandjarica* are longish and pointed, perfectly closing the acoustical chamber ventrally. Thus *A. kilimandjarica* has one of the loudest known songs within Tettigoniidae (Heller et al. 2010) while the song of *A. shenganae* seems not to be as loud. *A. taitensis* has an acoustical chamber similar to that of *A. shenganae*, i.e. more elongate and not perfectly closed ventrally. However, the alae are longer and broadly rounded. The song of *A. taitensis* is very similar to the song of *A. shenganae*—using a higher frequency—and the single syllables are performed at a quicker rate (Table 1). Also the song seems to be not as loud as in *A. kilimandjarica*, obviously the result of the ventral imperfectly closed acoustical chamber, analogous to *A. shenganae* with a similar gap at the ventral posterior end.

Aerotegmina probably evolved in the geologically old mountain chain of the Eastern Arc (Hemp 2010). *Aerotegmina* species are absent in the West and East Usambara Mountains. In the West Usambara Mountains, adjacent to the mountain range of the South Pare, the “acoustic niche” of *Aerotegmina* seems to be occupied by a phaneroptine species, *Euryastes jagoi* Ragge (Figs. 6 and 7; Table 1), differing mainly in the shape of the spectrum. It probably has similar habitat preferences as *Aerotegmina*. It is a flightless dweller in the canopy of montane forest, and its song resembles astonishingly that of *Aerotegmina*. However, *Aerotegmina* is predatory while *Euryastes* feeds on tree and herb leaves. Another *Aerotegmina* species was encountered on Mt Kasigau—a solitary isolated mountain east of the

Taita Hills—and a very distinct species with a balloon-like inflated large acoustical chamber was recorded in the Udzungwa mountains, also part of the Eastern Arc Mountains further south (C.H., unpublished data).

Part of the northern branch of the Eastern Arc Mountains—East Usambara, West Usambara, South Pare, and North Pare, are arranged as an almost continuous chain from the east coast of Tanzania stretching westward into the hinterland and gaps between the ranges are small (Fig. 10). Further, these mountain ranges are “connected” by the Pangani river system draining the Mt Kilimanjaro area along the northern side of the Eastern Arc chain to the Indian Ocean. The Taita Hills are an exception to this arrangement, being situated further north, about 100 km apart from the North Pare Mountains with no river drainage from the Taitas directly to the South Pare Mountains.

Nevertheless, the Taita Hills and the South Pare share a number of closely morphologically and molecularly related species of various flightless Orthoptera genera. Example of the close faunistic relationship of these geographically and ecologically separated mountain ranges are the sister species *Peronura hildebrandtiana* Karsch and *P. uguenoensis* Hemp (Phaneropterinae, Hemp 2011), *Rhainopomma montanum* Kevan and *R. magnificum* Jago (Lentulidae; Hemp et al. 2007; Schultz et al. 2007), *Parepistaurus vansomeri* Kevan and *P. robertsoni* Green (Acrididae, Coptacridinae, Hemp & Kehl 2010), which are morphologically and molecularly sister pairs. Conocephalinae from the subtribe Karniellina of Conocephalini in the genus *Fulvoscirtes* Hemp also show this pattern. *F. fulvotaitensis* Hemp occurs in the Taitas and *F. fulvus parensis* Hemp in the South and North Pare Mountains (Hemp et al. 2012).

The same pattern is observed in the two *Aerotegmina* species. However, molecular data are lacking for *Aerotegmina taitensis* n. sp. Preliminary molecular analyses showed, that *A. shenganae* is separated clearly from *A. kilimandjarica* while differences are very small between *A. kilimandjarica* populations from various mountains (Schultz 2004), suggesting a very recent dispersal of the latter species in East Africa.

That major climatic fluctuations are the driver behind speciation events in the area of East Africa was also shown on *Hyperolius* frogs. Lawson (2010) showed that, in two lineages, diversification happened around 2–2.2 Ma years ago. During this time period, flightless grasshoppers of the genus *Parepistaurus* (Orthoptera) also diversified from coastal elements spreading along the Eastern Arc mountains (Hemp & Kehl 2010). This period was proposed by Trauth et al. (2005) as being a humid and warm period in East Africa.

Furthermore, Hemp & Kehl (2010) showed for the flightless coptacridine genus *Parepistaurus* with an array of closely related species on East African mountains, that radiation within the northern branch of the Eastern Arc Mountains is younger than the geological young volcano Mt Kilimanjaro with an estimated age of 1.5–2 Ma (Nonnotte et al. 2008). It was shown that the sister pair of the two *Parepistaurus* species endemic to Mt Kilimanjaro and the North Pare Mountains developed after Mt Kilimanjaro built up, a time when also the sister pair *P. vansomeri* (Taita Hills) and *P. robertsoni* (South Pare) evolved.

As discussed above, major climatic changes affecting large areas of Africa must have been the cause of enlarging forest communities to such a degree that an exchange of montane taxa could have been possible as observed between the Taitas and the South Pares. Not understood is why the direct adjacent mountain ranges to the South Pares such as the West Usambaras in the East and the North Pares in the West did not exchange as many montane elements during such humid phases, especially since the Pangani river system must have facilitated a quick expansion of forest along its course, as was shown for the lentulid taxon *Usambilla* (Hemp & Hemp 2008) or *Parepistaurus* (Hemp & Kehl 2010). A possible explanation is that species found migration routes via the Pangani river to the Mt Kilimanjaro area and then found corridors to the Taitas connecting Mt Kilimanjaro with this mountain range. Drought or eruption events of Mt Kilimanjaro affected the directly adjacent and not very massive North Pare Mountains, leading to a loss of the montane forest belt and with it its dependent flora and fauna. When the sister pair *Aerotegmina taitensis* n. sp. and *A. shenganae* split up cannot be determined. That *Aerotegmina* seems to be an old taxon may be suggested from the fact that this genus is present also in the southern part of the Eastern Arc chain and that morphologically related taxa such as *Nephiliphila* Hugel

(Hugel 2010) exist on remote islands in the Indian Ocean. Additional molecular studies will be necessary to illuminate the answers to these questions.

Cytotaxonomy

Cytotaxonomic studies of the Hexacentrinae (sensu Gorochov 2007) are scarce. Karyological information is available only for some species belonging to the genus *Hexacentrus* and *Euhexacentrus*. Here chromosome numbers ranged from $2n=33$ to $2n=12$ in males with a X0/XX and neo-XY sex mechanism (Aswathanarayana 1998; see review Warchałowska-Śliwa 1998). The modal chromosome number in most tettigoniids is $2n=31$ in the male and 32 in the female, with acrocentric chromosomes and a X0/XX sex mechanism, whereas complements containing $2n=33$ chromosomes are rarely present (e.g. White 1973; Warchałowska-Śliwa 1998). The pattern of the chromosome evolution in the two species of the genus *Aerotegmina* is interesting and differs from the ancestral karyotype in terms of chromosome number and morphology. *A. kilimandjarica* has a chromosome number of $2n=33$ in the male, similar to the species described as *Hexacentrus japonicus hareyamai* Furukawa (Hareyama 1937) and *H. inflatissimus* Gorochov & Warchałowska-Śliwa (Gorochov & Warchałowska-Śliwa 1999) from Vietnam ($2n=34$ in the female). Other studied species of this genus (*H. japonica japonica* Karny, *H. unicolor* Serville, *H. mundus* (Walker), *H. mundurra* Rentz) are characterised by a karyotype consisting of $2n=31$ in the male (Asana et al. 1938; Ueshima 2001). No interpretation of why we find a chromosome number of 33 in Hexacentrinae is possible with the available data set.

In *A. shenganae* the chromosome set is reduced to $2n=27$ (FN=34). Such a karyotype is probably the result of three Robertsonian fusions between the autosomes (leading to the formation of biarmed chromosomes) and pericentric inversion (centric shift) in the X chromosome. This chromosome set is thus probably an apomorphic character for *A. shenganae* as the chromosome number for *Hexacentrus* species range between $2n=33$ and $2n=31$ and *Aerotegmina* evolved from *Hexacentrus* ancestors as proposed by Hemp (2010).

Orthoptera species with high chromosome numbers tend to show a reduction in their chromosome numbers by means of centric fusion, tandem fusion and/or pericentric inversion, e.g. in the grasshopper genus *Dichroplus*, characterized by an extreme karyotypic diversification in the male ranging from $2n=23$ to 8 (e.g. Colombo et al. 2005). Such rearrangements appear to have played an important role in chromosome evolution at inter-specific levels, e.g. in the Australian tettigoniid genera *Ixalodectes*, *Nanodectes*, and *Lanciana* (Ueshima & Rentz 1990, 1991) or the Palearctic genus *Montana* (Warchałowska-Śliwa et al. 1994). These species are most frequently restricted to specific habitats and/or are isolated

geographically. Similar to the aforementioned examples, we cannot exclude habitat restriction as a possible mechanism for the fusion and pericentric inversion in the chromosome set of *A. shenganae*. Chromosomal variation between *Aerotegmina* species may be due to the ecological fragmentation of populations in the past and their allopatric and peripatric speciation. Similar events have been suggested to have affected the speciation of African mole-rats (Rodentia) of the genera *Cryptomys* and *Fukomys*—endemic to sub-Saharan regions (Van Daele et al. 2004) or *Arvicanthis* (Castiglia et al. 2006), which are characterized by extreme chromosomal variation. However, future karyotype analyses with different chromosomal markers should be carried out on larger sample sets, and more species of *Aerotegmina* and other related genera should be studied to gain a more comprehensive view of the chromosome evolution in Hexacentrinae.

Conclusions

The findings on the chromosomal set seems to stand in contradiction to the findings of our preliminary molecular study and from its morphology (see above), showing that *A. shenganae* is more basal than *A. kilimandjarica* (Schultz 2004). A possible explanation could be that the reduction of the chromosomal set in *A. shenganae* occurred after the split from *A. kilimandjarica*, perhaps due to shrinking habitat in the South Pare Mountains and the Taita Hills during the past 1–2 million years in the course of the general aridification of Africa. The fusion is assumed to have happened during this time scale since *A. kilimandjarica* shows a wide geographical distribution of nowadays isolated populations, occurring mostly on geologically young mountains, thrown up during the past 1–2 million years along the rift valley (Nonnotte et al. 2008). Unfortunately it was not possible to analyse the chromosomes of the new species *A. taitensis*. However, it might be possible that both taxa, *A. shenganae* and *A. taitensis* n. sp., share a similar chromosomal set due to their similar morphology and the similar state of isolation of the geologically old ranges of the Eastern Arc Mountains as discussed above. However, since it is proposed here that the fusion of the chromosomes is a more recent process due to a shrinking habitat, it is also possible that the tandem fusions happened only in *A. shenganae* and that *A. taitensis* n. sp. could show other morphological differences in its genome.

A study of the chromosomes of all available *Aerotegmina* species and populations of *A. kilimandjarica* together with a molecular analysis will be necessary to further illuminate the past history of this genus, possibly adding fundamentally to the understanding of vegetation corridors enabling taxa to spread and the effects of habitat restriction on the genome

of montane species. The genus *Aerotegmina* serves as an ideal model group with which to study consequences of ongoing global warming in reducing montane forest cover, not only in eastern Africa, thereby isolating and threatening montane flora and fauna.

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