ORIGINAL ARTICLE

# Biogeography, ecology, acoustics and chromosomes of East African *Eurycorypha* Stål species (Orthoptera, Phaneropterinae) with the description of new species

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**Abstract** Although *Eurycorypha* is the most species-rich Phaneropterinae genus in Africa, little is known about the distribution and the ecology of the species. In this study data on distribution, ecology, song and on chromosomes of some East African species are provided. The nymphs of some species are shown, famous for their ant-like appearance and behaviour. The male of *E. punctipennis* Chopard and three species of *Eurycorypha* are newly described. These are *E. resonans* n. sp. and *E. combretoides* n. sp. occurring in different habitats on Mount Kilimanjaro, and *E. conclusa* n. sp from forest habitats along the Tanzanian coast. Bioacoustically, the four recorded species are unusually divers, presenting non-resonant and resonant songs. As four *Eurycorypha* species occur syntopically on geological young Mount Kilimanjaro, the biogeographical pattern and possible speciation mechanisms in the genus *Eurycorypha* are discussed in context of the climatical history of eastern Africa.

**Keywords** Phaneropterinae · Orthoptera · New species · Biogeography · Ecology · Bioacoustics · Chromosomes · Speciation · Tanzania · Mount Kilimanjaro

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## Introduction

The genus *Eurycorypha* is the most species-rich genus of African Phaneropterinae, comprising 36 described species at present, including 3 species from Madagascar and 2 species from the Arabian Peninsula (Ragge 1980). *Eurycorypha* is a morphological uniform genus being easily recognised from its head alone with elongate eyes, a very broad fastigium verticis and frontogenal carinae (Ragge 1980). The genus is in need of taxonomic revision, some of the species probably being synonymously described (Ragge 1980), and there are also many undescribed species, as seen in various collections, for example in the Natural History Museum London, UK, or the entomological collection of Tervuren, Belgium (own observations).

Six species of *Eurycorypha* are described from East African localities. These are *E. diminuta* Chopard and *E. simillima* Chopard only known from around Lake Turkana in Kenya, *E. kevani* Chopard from northern Kenya, *E. punctipennis* Chopard from Mount Elgon in Kenya, *E. meruensis* Sjöstedt and *E. varia* Brunner von Wattenwyl from the volcanoes Mount Meru and Mount Kilimanjaro in northern Tanzania. The latter two species are widespread in East Africa.

Karsch (1889) mentions specimens in the collection of the Naturkunde Museum Berlin labelled as *E. prasinata* Stål from East Africa (Mombasa at the Kenyan coast and the East Usambara mountains in Tanzania) to which Vosseler (1909), in his study about an *Eurycorypha* species from the East Usambara mountains, also refers. Holstein et al. (2005) list *E. prasinata* Stål for the Kakamega forest reserve in western Kenya. They also list two unidentified *Eurycorypha* species for the same area, which were later identified as belonging to the phaneropterinae genera *Vossia* sp. and *Plangia* sp. (J. Holstein, 2012 personal communication).

Except for their description for the majority of *Eurycorypha* species no further distribution data or data on their habitat are known. Vosseler (1909) gives a detailed description of the larvae of an *Eurycorypha* species occurring in the East Usambara mountains of northern Tanzania. The nymphs imitate ants in habitus and in their moving habits in their first three larval stages. He notes that the nymphs are identical to the species *Myrmecophana fallax* Brunner von Wattenwyl described from Sudan and synonymised this taxon with *Eurycorypha*. Vosseler (1909) showed that female *Eurycorypha* species deposit their flat and oval eggs into the tissue between the upper and lower surface tissue of a leaf about 2–3 days after mating. The nymph hatches after about 3 months. The nymphs inhabit branches and leaves of small bushes feeding on flowers and tender leaves. In the Usambara mountains the first instar stages of *Eurycorypha* nymphs live together with *Myrmicaria* and *Camponotus* species.

The aim of this article is to provide data on the ecology and biology of some *Eurycorypha* species, and to describe three new species and the male of *E. punctipennis* Chopard.

## Material and methods

### Identification

The material was checked against the entomological collections of the National Museums of Kenya, Nairobi (EDNMK), the Natural History Museum, London (NHML), the entomological collection of the Musée Royal de l'Afrique Centrale Tervuren, Belgium (MRAC), the Naturkunde Museum, Berlin (MNB), the entomological collection of the Naturhistoriska Riksmuseet, Stockholm, Sweden, and the entomological collection of the Naturkundemuseum of Vienna (NMW).

### Measurements

Total body length, lateral aspect, refers to the midline length of the insect from fastigium verticis to tip of the abdomen, including the subgenital plate. In females, the ovipositor is not included in the measurement of the body length. Measurements of ovipositors are taken laterally from tip to base not regarding the curvature.

### Images

Images were either taken with a Canon 400 D digital camera or a Leica multifocus camera MZ 16A connected to a DFC 500 stereo microscope at the entomological department of the MRAC and a Leica DFC 490 on a Leica microscope MZ 16 of the NMW. The programme AutoMontage Pro was used to process the images.

### Depositories

MNB, NHML and EDNMK. All other material remains in the collection of C. Hemp (except for CH7185-6, 7193, 7378, stored in the collection Heller).

### Field work and ecological analysis

*Eurycorypha* species were recorded at 47 locations on Mount Kilimanjaro and in 1 locality in Kenya (Nairobi, Karen, Ngong Hills; Table 1). Ecological data have been collected since 1996 along 30 transects disposed across wide ranges in elevation; these data include climatic parameters, i.e. rainfall (mainly using funnel gauges, annual means; Hemp A. unpublished), temperature (using Stow-Away Tidbit data loggers with an accuracy of ±0.4 °C at 20 °C; annual means of hourly measurements; Hemp A. unpublished) and vegetation parameters (over 1500 sampling plots = relevés, using the method of Braun-Blanquet 1964). The altitudinal range of the transects extended from 760 m (Rau forest near Moshi) to 5895 m (Kibo peak). For estimates of environmental humidity, mean annual temperatures (MAT) and mean annual precipitation (MAP) were scaled to obtain four humidity categories. In a first step, MAT and MAP were scaled with 1 °C:25 mm to establish a ratio between evaporation as determined by MAT and water input as determined by MAP (Holdridge 1967; Lauer et al. 1996; Walter and Lieth 1967) (Fig. 1). The 1:25 ratio corresponds roughly to the transition from semi-arid to sub-humid conditions in the climate scheme of Holdridge (1967). As an estimate for the transition from sub-humid to humid and from humid to per-humid conditions, a scale of 1 °C MAT:50 mm MAP and 1 °C MAT:100 mm MAP, respectively, was used, following Holdridge's (1967) approach of doubling climatic variables between steps. The resulting four MAT: MAP categories (>1:25; 1:25–1:50; 1:50–1:100; <1:100) correspond to semi-arid, sub-humid, humid and per-humid climate conditions.

### Acoustics

Songs were recorded in the laboratory using a SONY ECM-121 microphone (frequency response relatively flat up to 30 kHz; own tests) connected to a personal computer through an external soundcard (Transit USB, "M-Audio"; 64-kHz sampling rate) and, additionally, a digital bat-detector (Pettersson D1000X) with sampling rates of 100 and 300 kHz (*E. resonans* n. sp. and *E. varia* Brunner von Wattenwyl only). Specimens recorded: *E. punctipennis* CH7512 1–15 February 2012; CH7519 15–31 March 2012; *E. combretoides* n. sp. CH7187 Mount Kilimanjaro, near Lake Chala (3°18'S, 37°41'E), 1 January–28 February

**Table 1** *Eurycorypha* ecology

| Locality | Vegetation | Altitudinal zone | Position | Altitude (m a.s.l.) | Mean annual precipitation (mm) | Minimum temperature (°C) | Mean annual temperature (°C) |
|---|---|---|---|---|---|---|---|
| *Eurycorypha combretoides* n. sp. | | | | | | | |
| Uchira | Tree savanna | Colline | South | 870 | 1020 | 12.8 | 21.6 |
| Mabungu Hill | Tree savanna | Colline | South | 910 | 950 | 12.5 | 21.3 |
| Himo | Maize field with trees | Colline | South | 990 | 964 | 12.2 | 21.0 |
| Chala area | Tree savanna | Colline | East | 1000 | 600 | 11.9 | 20.8 |
| Holili Hill | Tree savanna | Colline | East | 1120 | 865 | 11.3 | 20.2 |
| Kimanga Hill | Tree savanna | Colline | East | 1130 | 710 | 11.0 | 19.9 |
| Mrere | Grassland with trees | Sub-montane | East | 1200 | 1004 | 10.7 | 19.6 |
| Mengwe | Grassland with trees | Sub-montane | East | 1250 | 1082 | 10.4 | 19.3 |
| Holili Hill | Grassland with trees | Sub-montane | East | 1250 | 796 | 10.4 | 19.3 |
| Msangasanga | Grassland with trees | Sub-montane | East | 1290 | 859 | 10.1 | 19.0 |
| Mrere | Grassland with trees | Sub-montane | East | 1300 | 1137 | 10.1 | 19.0 |
| *E. meruensis* Sjöstedt | | | | | | | |
| Kidia | Home garden | Sub-montane | South | 1330 | 1754 | 9.9 | 18.9 |
| Kidia | Home garden | Sub-montane | South | 1430 | 1824 | 9.3 | 18.3 |
| Kidia | Home garden | Sub-montane | South | 1430 | 1882 | 9.3 | 18.3 |
| Kidia | *Agauria-Ocotea* forest edge | Lower montane | South | 1710 | 2268 | 7.7 | 16.7 |
| Siha | *Cassipourea* forest | Lower montane | Southwest | 1850 | 1360 | 6.8 | 15.9 |
| Siha | *Cassipourea* forest | Lower montane | Southwest | 1860 | 1390 | 6.8 | 15.8 |
| *E. punctipennis* Chopard | | | | | | | |
| Msaranga | Riverine forest | Sub-montane | South | 1300 | 1700 | 10.1 | 19.0 |
| Kidia | Home garden | Sub-montane | South | 1330 | 1754 | 9.9 | 18.9 |
| Kidia | Home garden | Sub-montane | South | 1430 | 1824 | 9.3 | 18.3 |
| Kidia | Home garden | Sub-montane | South | 1440 | 1882 | 9.3 | 18.2 |
| *E. resonans* n. sp. | | | | | | | |
| Msaranga | Riverine forest | Sub-montane | South | 1300 | 1700 | 10.1 | 19.0 |
| Kidia | Home garden | Sub-montane | South | 1330 | 1754 | 9.9 | 18.9 |
| Kidia | Home garden | Sub-montane | South | 1430 | 1824 | 9.3 | 18.3 |
| Kidia | Home garden | Sub-montane | South | 1430 | 1882 | 9.3 | 18.2 |
| Nairobi | Garden | Sub-montane | | 1700 | 1600 | 7.6 | 17.5 |
| Kidia | *Agauria-Ocotea* forest edge | Lower montane | South | 1710 | 2268 | 7.7 | 16.7 |
| *E. varia* Brunner von Wattenwyl | | | | | | | |
| Mahoma | Home garden | Sub-montane | South | 1250 | 1502 | 10.4 | 19.3 |
| Mahoma | Home garden | Sub-montane | South | 1260 | 1599 | 10.4 | 19.3 |
| Mahoma | Home garden | Sub-montane | South | 1260 | 1599 | 10.4 | 19.3 |
| Msaranga | Riverine forest | Sub-montane | South | 1300 | 1700 | 10.1 | 19.0 |
| Kidia | Home garden | Sub-montane | South | 1330 | 1754 | 9.9 | 18.9 |
| Mahoma | Home garden | Sub-montane | South | 1330 | 1800 | 9.9 | 18.9 |
| Kidia | Home garden | Sub-montane | South | 1430 | 1824 | 9.3 | 18.3 |
| Kidia | Home garden | Sub-montane | South | 1430 | 1882 | 9.3 | 18.3 |
| Kidia | Home garden | Sub-montane | South | 1430 | 1900 | 9.3 | 18.3 |
| Kidia | *Agauria-Ocotea* forest edge | Lower montane | South | 1710 | 2268 | 7.7 | 16.7 |
| Kidia | *Agauria-Ocotea* forest edge | Lower montane | South | 1720 | 2268 | 7.6 | 16.6 |
| Kidia | *Agauria-Ocotea* forest edge | Lower montane | South | 1720 | 2369 | 7.6 | 16.6 |

**Table 1** (continued)

| Locality | Vegetation | Altitudinal zone | Position | Altitude (m a.s.l.) | Mean annual precipitation (mm) | Minimum temperature (°C) | Mean annual temperature (°C) |
|---|---|---|---|---|---|---|---|
| Uchau | *Agauria-Ocotea* forest edge | Lower montane | South | 1730 | 2300 | 7.5 | 16.6 |
| Kidia | *Agauria-Ocotea* forest edge | Lower montane | South | 1740 | 2362 | 7.5 | 16.5 |
| Kidia | *Agauria-Ocotea* forest edge | Lower montane | South | 1740 | 2369 | 7.5 | 16.5 |
| Siha | *Cassipourea* forest | Lower montane | Southwest | 1770 | 1333 | 7.3 | 16.4 |
| Siha | *Cassipourea* forest | Lower montane | Southwest | 1860 | 1390 | 6.8 | 15.8 |
| Kidia | *Agauria-Ocotea* forest | Lower montane | South | 1900 | 3017 | 6.5 | 15.6 |
| Kidia | *Agauria-Ocotea* forest | Lower montane | South | 1990 | 3124 | 6.0 | 15.1 |
| Kidia | *Ocotea* forest | Middle montane | South | 2200 | 2990 | 4.7 | 13.9 |

2009; *E. resonans* n. sp. CH7378 Mount Kilimanjaro, near Kidia, 1–20 July 2010; CH7513 1–15 February 2012; CH7518 1–8 March 2012, CH7521 15–31 March 2012; *E. varia* Brunner von Wattenwyl CH7186 female, CH7193 male Mount Kilimanjaro, above Kidia (3°17'S, 37°26'E), 1 January–28 February 2009; all collected by C. Hemp in Tanzania, Northern part. Song measurements were obtained using AMADEUS II and AMADEUS Pro (Martin Hairer; http://www.hairersoft.com). Oscillograms of the songs were prepared using TURBOLAB (Bressner Technology, Germany). All recordings were made at temperatures between (15–)17 and 21 °C. The singers were caged in plastic tubes or gaze cages with microphone fixed or hand held at distances between 5 and 60 cm.

Terminology

Syllable: sound produced during one cycle of movements (opening and closing of the tegmina; syllable duration: time period measured from the first impulse to the last; syllable period: time period measured from the first impulse to the first impulse of the next syllable; echeme: first order assemblage of syllables; impulse: a simple, undivided, transient train of sound waves (here: the damped sound impulse arising as the effect of one tooth of the stridulatory file; example see Fig. 2c); pulse: undivided train of sound waves increasing in amplitude at the beginning and containing many similarly sized wave maxima and minima (cricket-like song structure; examples see Fig. 2a, b).

For measurements and pictures of the stridulatory files replicas were made using the cellulose nitrate technique described by Ragge (1969). Length of the file is given as linear distance between ends, tooth spacing is given as the mean of 10 intervals in the middle of the file.

Cytotaxonomic analyses

*Eurycorypha punctipennis* Chopard (one male: CH7512), *E. resonans* n. sp. (four males: CH7518, CH7513, CH7521, CH7378), *E. meruensis* Sjöstedt (two males: CH 7520 and CH7515), *E. combretoides* n. sp. (1 male: CH7187) and *E. varia* Brunner von Wattenwyl (one male: CH7193) were used for cytotaxonomic analyses. Chromosomal preparations were obtained from adult 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 then preparations were air dried. C-banding was carried out according to Sumner (1972). The silver staining methods (AgNO$_3$) for the nucleolar organiser region (NOR) was performed as previously reported (Warchałowska-Śliwa and Maryańska-Nadachowska 1992). Fluorescence in situ hybridisation probing (FISH) was performed using the 1.8-kb fragment 18S rDNA gene of *Isophya longicaudata adamovici* (Orthoptera). The probe was polymerase chain reaction amplified using primers 18 Sai forward (5'-CCT GAG AAA CGG CTA CCA CAT C-3') and 18 Sbi reverse (5'-GAG TCT CGT TCG TTA TCG GA-3') (Whiting et al. 1997) and labeled by nick translation with biotin-11-dUTP (Invitrogen, Tokyo, Japan). The in situ hybridisation technique was applied according to Warchałowska-Śliwa et al. (2009). Probe hybridisation sites were detected with avidin-Alexa 488 (Invitrogen) and mouse anti-digoxigenin antibodies conjugated to Cy3 (Sigma-Aldrich, Tokyo, Japan). Slides were counterstained with 4',6-diamidino-2-phenylindole (Sigma-Aldrich) and then mounted in antifade based on 1-4-diazabicyclo[2.2.2]octane (Sigma-Aldrich). Chromosomes were observed and photographed
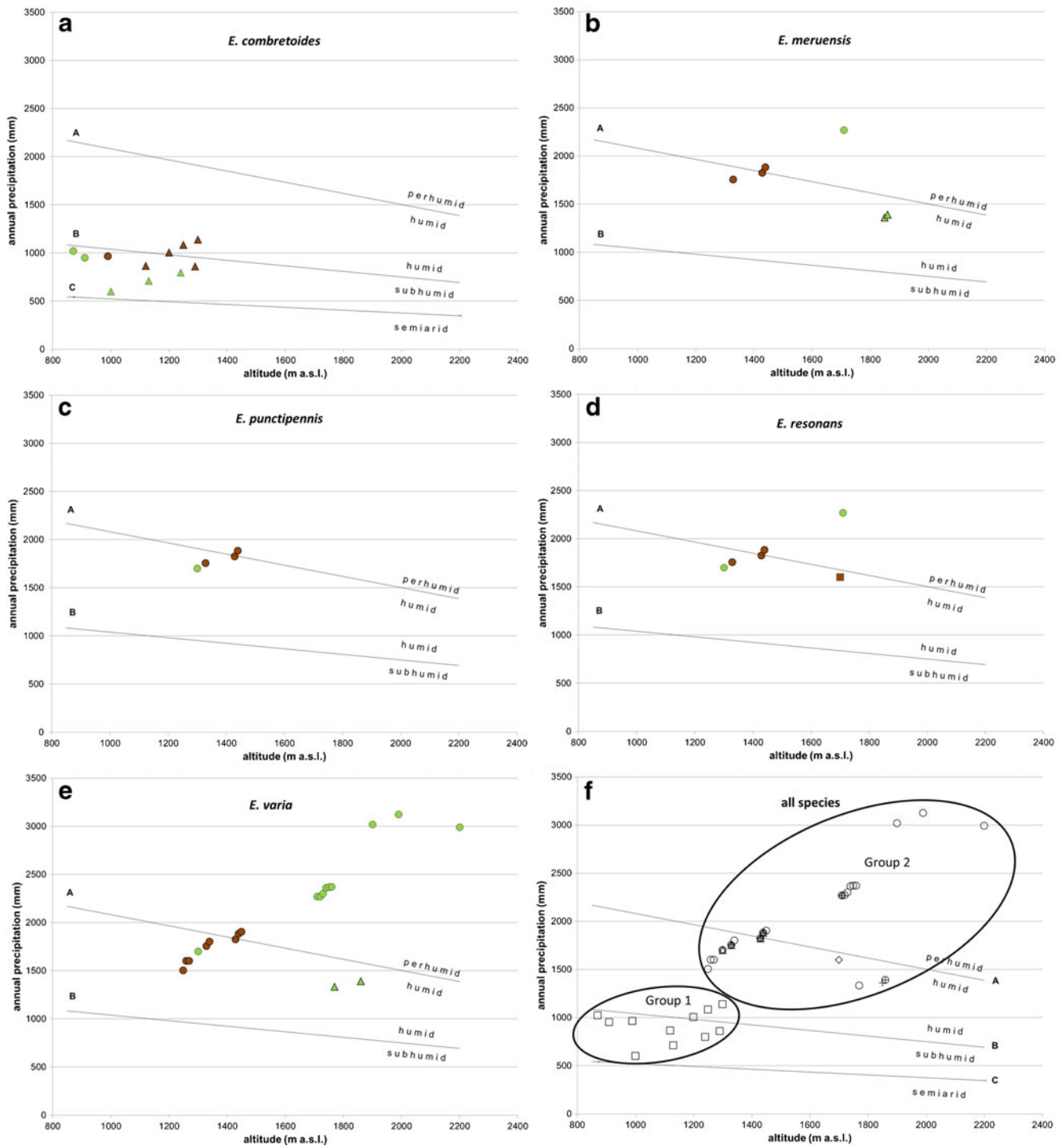
**Fig. 1** Habitat selection and altitudinal distribution of five *Eurycorypha* species on Kilimanjaro in relation to climatic parameters. Line **a**: linear regression of mean annual temperature scaled with 1°C:25 mm precipitation; Line **b**: linear regression of mean annual temperature scaled with 1°C:50 mm precipitation; Line **c**: linear regression of mean annual temperature scaled with 1°C:100 mm precipitation. **Circles**: southern slope. **Triangles**: south-western and (south)eastern slope. **Squares**: Nairobi record of *E. resonans* n. sp. **d**. **Green**: natural habitats (forests, savanna woodlands). **Brown**: anthropogenic habitats (Chagga homegardens, maize fields, grasslands)

with a Nikon Eclipse 400 microscope fitted with a CCD DS-U1 camera using Chroma filter sets (for FISH). The Lucia Image 5.0 software was used and images were processed and arranged with Adobe Photoshop®.

**Fig. 2** Oscillograms presenting details of syllable structure in *Eurycorypha resonans* n. sp. (**a** part of syllable of disyllabic echeme; **b** one complete syllable from the polysyllabic echeme) and *E. varia* Brunner von Wattenwyl (**c** part of syllable)



*Eurycorypha resonans*

*Eurycorypha resonans*

*Eurycorypha varia*

1 ms
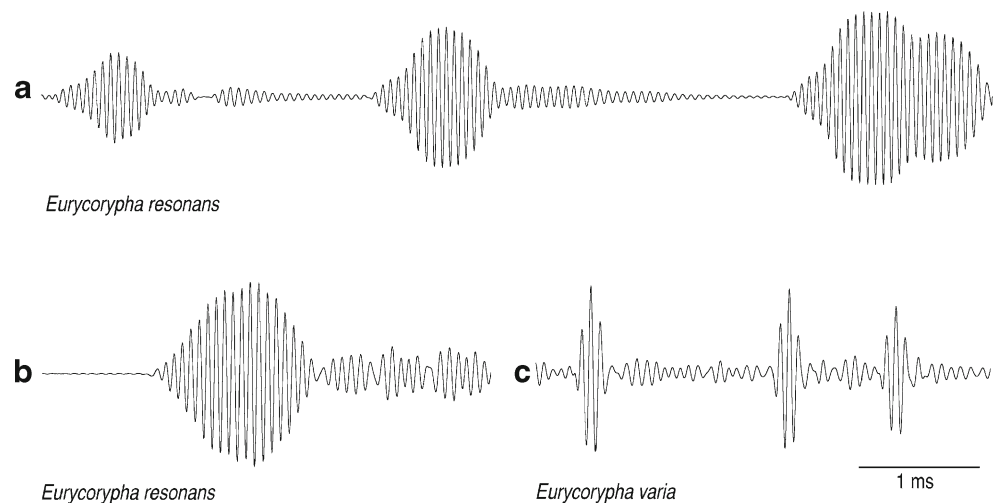
## Results

### Ecology and habitat

*Eurycorypha* species were found on the southwestern, southern and (south)eastern slope of Kilimanjaro. Owing to differences between these parts of Kilimanjaro in respect of climate (the central southern slope is the wettest part of the mountain) and altitudinal vegetation zonation (Hemp 2005a) the altitudinal distribution and—to a lesser degree—habitat selection of *Eurycorypha* species varied. Therefore, these areas were analysed separately.

*Eurycorypha* species were found along an altitudinal span of 1330 m between 870 and 2200 m above sea level (a.s.l.) from the colline savanna foothills of Kilimanjaro over the submontane into the lower montane forest zone. Along this gradient mean annual temperature and mean annual minimum temperature decreased from 21.6 °C to 13.9 °C and from 12.8 to 4.7 °C, respectively (Table 1, Fig. 1), and rainfall increased from 600 mm (i.e., sub-humid conditions) to over 3000 mm (i.e., per-humid conditions).

*Eurycorypha combretoides* n. sp. was found on the colline and sub-montane foothills in sub-humid and humid conditions, on the southern slope between 870 and 990 m, and on the drier eastern slope between 1000 and 1300 m a.s.l.

Climatic preferences of *E. meruensis* Sjöstedt, *E. punctipennis* Chopard and *E. resonans* n. sp. were very similar. All had their main occurrence higher upslope at humid conditions and were partly found even in the per-humid climate. *Eurycorypha meruensis* Sjöstedt occurred on the southern and southwestern slope, were it had 1860 m as its highest record with the same humidity as at the lowest record at 1330 m on the wet central southern slope. In the diagram of *E. resonans* n. sp. an additional record from Nairobi is included, from where we also had the respective climate data. Owing to a similar climate to that of west Kilimanjaro

this record resembles the above described highest records of *E. meruensis* Sjöstedt in respect of altitude and humidity.

*Eurycorypha varia* Brunner von Wattenwyl showed the widest and highest altitudinal span of all *Eurycorypha* species on Kilimanjaro, occurring between 1250 and 2200 m in the humid sub-montane and per-humid lower to middle montane zone with more than 3100 mm rainfall. Again, on the drier western slope, suitable site conditions in the humid zone were located in much higher altitudes compared with the central southern slope (Fig. 1).

The *Eurycorypha* species being canopy dwellers, the habitats were different natural and anthropogenic vegetation types with a sparse to dense tree canopy, ranging from natural savanna woodlands, scattered trees in anthropogenic grasslands and maize fields, and traditional agroforestry systems ("Chagga home gardens"), as well as forests.

The habitats of *E. combretoides* n. sp. comprised natural savanna woodlands and anthropogenic grasslands and maize fields with scattered trees. The remaining species occurred in various wetter types of montane forest, ranging from submontane riverine forests and various lower to middle montane *Cassipourea* and *Ocotea* forests (for the delimination of the altitudinal zones cp. Hemp 2006; for a more detailed description of the forest types, including a vegetation table, cp. Hemp 2005a). On the southern and eastern slope nearly all forests below 1700 m are converted into the coffee–banana fields. These Chagga home gardens with their forest-like structure obviously also offered suitable conditions for *Eurycorypha combretoides* n. sp.

### Bioacoustics

The songs of all four species recorded were relatively similar to each other in spectral composition (Fig. 3). All species used mainly a frequency band between 10 and 20 kHz. However, they differed in bandwidth and position of the maximum. The peak was situated near the lower edge

**Fig. 3** Spectra of calling songs of *Eurycorypha* species
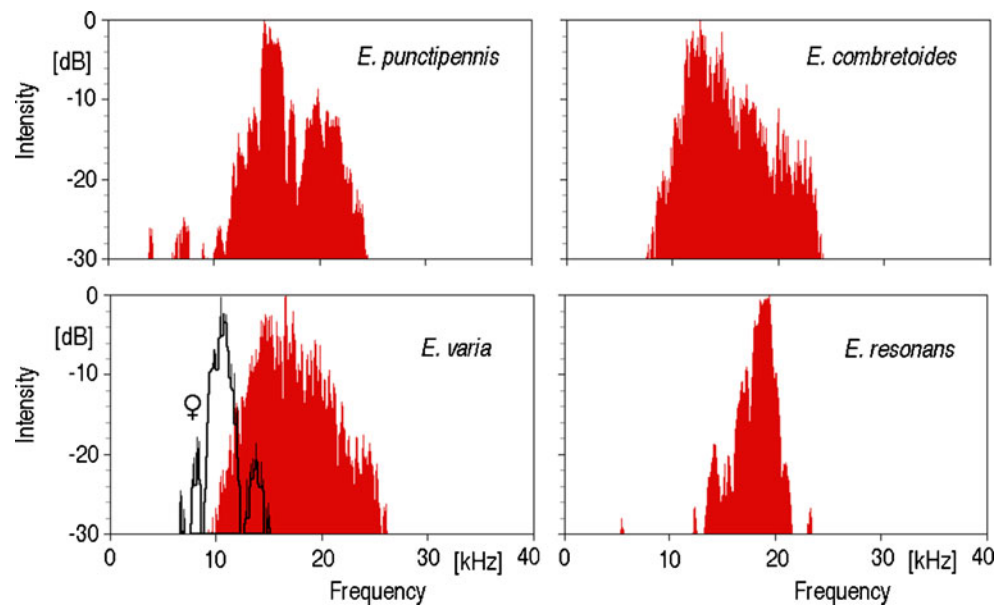


in *E. combretoides* n. sp. (ca. 13 kHz) and near the upper edge in *E. resonans* n. sp. (x=19.5 kHz; n=4). The female of *E. varia* Brunner von Wattenwyl produced a song clearly lower in frequency (10.3 kHz) than that of the male (16.6 kHz). Also, the bandwidth was distinctly smaller in the female (3.0 kHz 10 dB below peak) than in the male (7.7 kHz 10 dB below peak) comparable with that of the male song in *E. resonans* n. sp. (x=2.5 kHz 10 dB below peak; n=4).

Concerning amplitude modulation, however, the songs had nearly nothing in common except that all species had elements in their repertoire that consisted of two parts. These parts, however, differed distinctly in duration between species and were observed in only one of four specimens of *E. resonans* n. sp. Another shared character was that they all produced their songs in quite large intervals, thus having low duty cycles like many other phaneropterid species (see, e.g., Hemp et al. 2010b).

The song of *E. punctipennis* Chopard invariably consisted of echemes containing two parts (Figs. 4 and 5). The first was always softer and shorter (44–51 impulses), the second louder and longer, containing 59–60 impulses (n=3). Similar slight shifts of low amplitude frequency components in both parts support the idea that each of them is produced by one tegminal movement cycle and not during opening and closing. Several (4.5±2.8; n=44) of these disyllabic echemes were repeated at intervals of about 10–16 s. The echeme series were separated by intervals of several minutes up to hours.

The song of *E. combretoides* n. sp. contained two different types of echemes: a louder and a softer one (Fig. 4). In the louder echeme a long syllable was followed first by a distinctly shorter one (Fig. 5) and later by an isolated impulse. Both longer parts consisted of sequences of clearly separated impulses. Between these parts a much weaker

signal was registered occasionally, probably resulting from the opening of the tegmina. The softer echeme was similar in structure, but the first long syllable was replaced by two shorter elements. The isolated impulse was occasionally missing. Louder and softer echemes were produced in pure or mixed order at intervals of a few seconds. These series (typically 3–5 echemes) were separated by intervals of several minutes. However, the louder echemes were rarer and sometimes not heard for many minutes or hours.

The male calling song of *E. varia* was more complex than that of the above-mentioned species. It contained combinations of a soft and a loud part, which are called echemes, because in our opinion they are most likely produced by two stridulatory movements (= two syllables). Several (x=6.7; range 4–13; n=92) of these echemes followed each other in rapid succession, the first ones being shorter and softer than the last ones. At the beginning of such a sequence the louder syllables were regularly followed by some loud and isolated impulses. The position of these isolated impulses was very similar to that of a female response. Females of phaneropterine bush-crickets typically respond acoustically to the male song after a species-specific delay, and the males often produce "imitations" of these signals at the expected time (see, e.g., Heller et al. 2011). In Fig. 4, the registration of a male–female duet is shown (microphone close to the female), the female sounds recognisable by the female specific frequency spectrum (see Fig. 4) and at the end also by the high amplitude. The female responded about 70 ms (69±15 ms; n=10) after the end of the last syllable of a male echeme. In other recordings, however, its answer occurred often before the end of the male echeme, indicating that this character was not the trigger. The male produced often several (rarely up to 18) of these echeme sequences at intervals of about 10 s, these calling bouts separated by many minutes of silence.

*Eurycorypha punctipennis*

*Eurycorypha combretoides*

*Eurycorypha varia*

*Eurycorypha varia*, male-female duet

*Eurycorypha resonans*

1 s
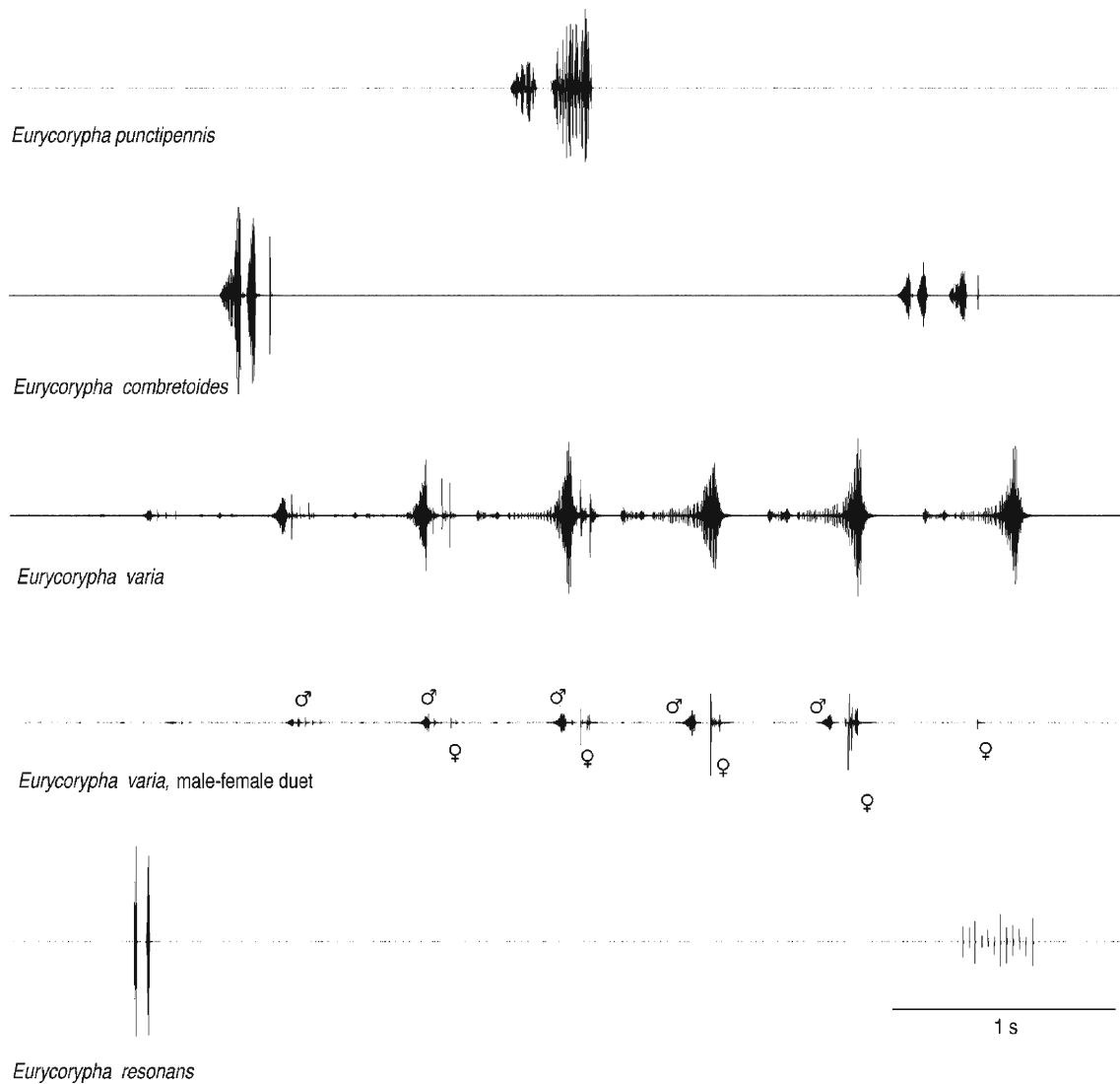
**Fig. 4** Oscillograms of calling songs of *Eurycorypha* species, overview (one echeme in *E. punctipennis* and *E. varia*, sequence of two echemes in *E. combretoides* and *E. resonans*) . In the male–female duet the microphone was positioned at a distance of about 30 cm to the female (in gaze cage) and about 50 cm to the male (in plastic tube)

*Eurycorypha resonans* n. sp. differed very distinctly in song from all the other species. Here, two different types of echemes were registered: an echeme with two syllables and another one with many syllables. The disyllabic echeme was heard sporadically and only from one specimen for unknown reasons. As all specimens were recorded continuously for several hours, or even complete nights, it should not have been a problem of restricted recording periods. This type of echeme was mostly produced at relatively large intervals (1–2 minutes). Both of its syllables were similar in structure, but, contrary to impressions from a large time scale (Figs. 4 and 5), they did not consist of isolated impulses, but of several pulses (Fig. 2a). Polysyllabic echemes were registered from all specimens. They were typically produced in series of quite variable duration, ranging from 15 seconds up to 5 minutes. Intervals between the echemes were mostly about 5–15 seconds. An echeme contained 9–21 syllables, with syllable periods of 26–54 ms. Each syllable consisted of one pulse (Fig. 2b). By visual observation it could be confirmed that these polysyllabic echemes were produced by many fast wing movements.

The large difference in the structure of the syllables and also the bandwidth of the song between *E. resonans* n. sp. and the other species is not reflected in all dimensions of the stridulatory file (Fig. 6; Table 3). The length of the file and the number of stridulatory teeth of the relatively small *E. resonans* n. sp. are clearly lower than in the other three recorded species, but the difference in the spacing of the teeth is much less pronounced. Also in structure and dimensions of the mirror and the scraper there are no extraordinary large differences (Fig. 7).
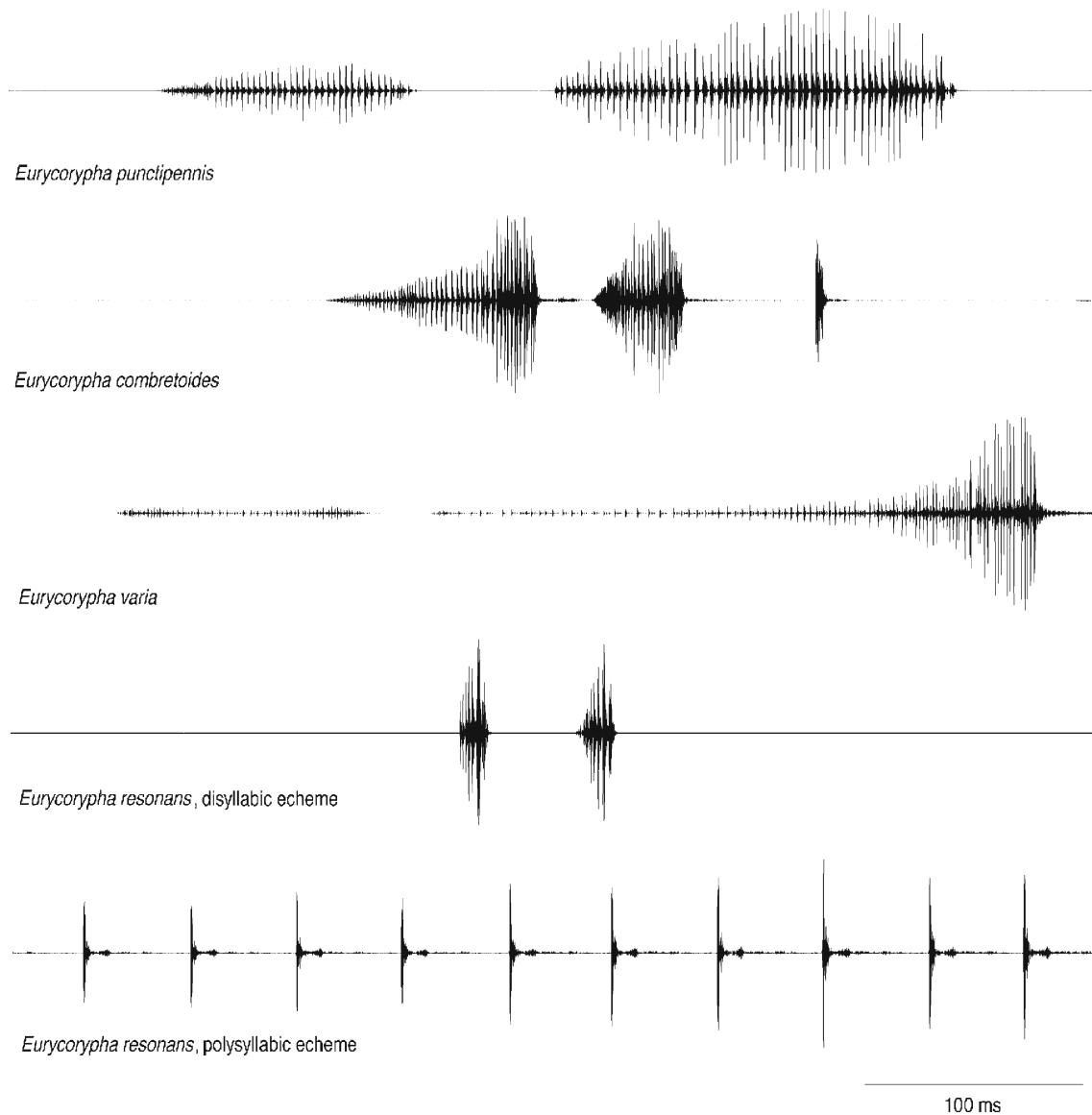
Fig. 5 Oscillograms of calling songs of *Eurycorypha* species, details

Chromosomes

The standard karyotype of *E. punctipennis* Chopard, *E. resonans* n. sp., *E. meruensis* Sjöstedt, *E. combretoides* n. sp., and *E. varia* Brunner von Wattenwyl consisted of 29 chromosomes in the male, with the X0/XX sex chromosome mechanism. Fourteen pairs of acrocentric autosomes could be arranged into 2 size groups: 2 long (L) and 12 medium (M) or short (S) pairs gradually decreasing in size resulting in some problems with precise identification of chromosome pairs. In *E. resonans* n. sp., *E. meruensis* Sjöstedt, *E. combretoides* n. sp. and *E. varia* Brunner von Wattenwyl the acrocentric and in *E. punctipennis* Chopard metacentric sex chromosome (X) was the largest element in the set (Fig. 8a–c). The C-banding revealed some differences in the distribution of constitutive heterochromatin blocks (C-bands)

between the five species analysed. All species had paracentromeric thin C-bands on most of the autosomes, with the exception of one small pair. In this case, the C-band occupied the region next to the centromere (thick C-bands). Additionally, in all species, an interstitial C-band occurred on the $S_8$ or $S_9$ ($S_{8/9}$). Telomeric thick C-bands in *E. resonans* n. sp. were located in two medium-sized chromosomes (Fig. 8b). According to differences in the amount of heterochromatin, two types of X chromosomes were specified. C-bands were thin in *E. combretoides* n. sp. (Fig. 8c) and *E. varia* Brunner von Wattenwyl and thick in the three other investigated species (Fig. 8a, b). Additionally, interstitial C-bands were located near the telomeric region of this chromosome (Fig. 8a–c). $AgNO_3$ staining in all five species analysed revealed the presence of one active NOR in the interstitial region of the $S_{8/9}$ bivalent (Fig. 8d). In these
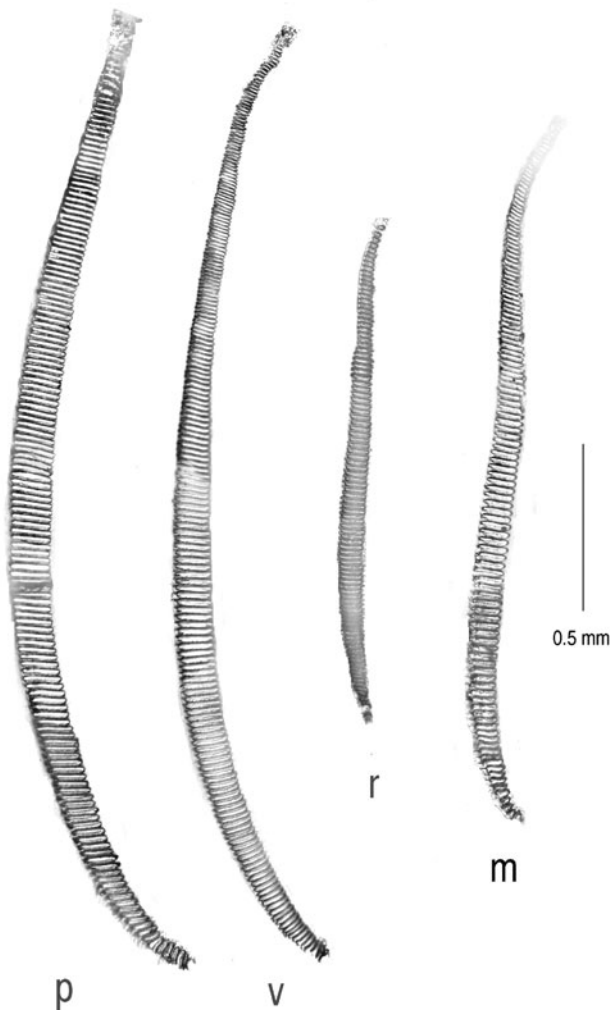
Fig. 6 Stridulatory files of *Eurycorypha* species (photos of replicas). **p**: *E. punctipennis*, **v**: *E. varia*, **r**: *E. resonans*, **m**: *E. meruensis*

species a large cluster of 18S rDNA was observed at the mitotic metaphase or in bivalents from the diakinesis to metaphase I (Fig. 8e), coincident with a single active NOR visualised by Ag–NOR staining.

Taxonomy

*Eurycorypha punctipennis Chopard, 1938*

*Holotype* Female, Kenya, Mont Elgon, Suam Fishing Hut, st.34, 2400 m, NMHN (Paris). New localities: Tanzania, Mt Kilimanjaro and Uganda, Kawanda.

One male, Kidia, plantation belt southern slopes, 1430 m April 2002; depository, MNB; 1 female, Tanzania, Mount Kilimanjaro Mahoma, plantation belt southern slopes, 1330 m, November 2010, depository MNB; 1 male, Tanzania, Mount Kilimanjaro, Msaranga valley, southern slopes, remnant riverine forest, 1300 m, January 2012, depository NHML; 1 female, Tanzania, Mount Kilimanjaro, Msaranga valley, southern slopes, remnant riverine forest, 1300 m, March 2012, depository NHML; 1 male, Tanzania, Mount Kilimanjaro, Kidia, plantation belt southern slopes, 1430 m, March 2002, depository EDNMK; 1 female, Tanzania, Mount Kilimanjaro, Kidia, plantation belt southern slopes, 1430 m, February 2000, depository EDNMK.

Further material: All Tanzania, all Mount Kilimanjaro southern slopes: 3 males, 1 female Msaranga valley, southern slopes, remnant riverine forest, 1300 m, January and February 2012; 3 males, Mahoma, plantation belt, 1330 m, March and April 2012; 2 males, plantation belt 1300–1400 m, January 2005 and December 2011 (collection C. Hemp). One male, Democratic Republic of Congo (DRC), Kibali-Ituri, Kilomines; 3 females, Uganda, Kawanda (collection NHM London, UK).

*Description of the male Colour*: In difference to most other uniformly green *Eurycorypha* species, of yellowish green colour with dark maculae of various size scattered on

Fig. 7 Basal part of tegmina in male *Eurycorypha punctipennis* Chopard, *E. varia* Brunner von Wattenwyl and *E. resonans* n. sp. (scale 5 mm)
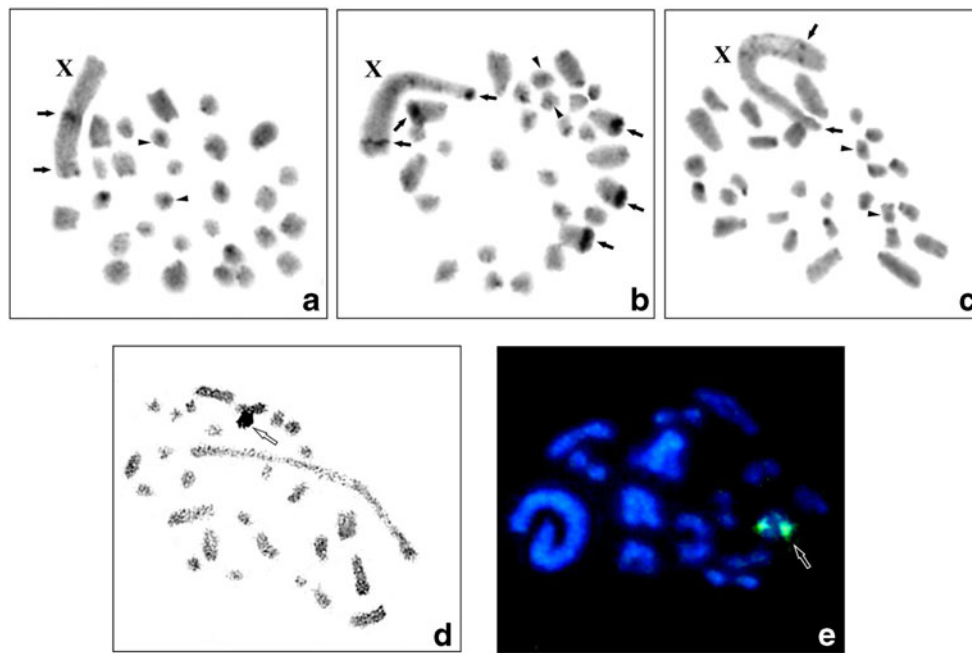
**Fig. 8** C-banded mitotic metaphase **a–c**, silver staining **d** and fluorescence in situ hybridisation with 18S rDNA probes (green) **e** in *Eurycorypha*: *E. punctipennis* Chopard (**a**), *E. resonans* n. sp. (**b, d**), *E. combretoides* n. sp. (**c**) and *E. meruensis* Sjöstedt (**e**). Arrows indicate paracentromeric C-bands on the metacentric (**a**), acrocentric (**b, c**) and interstitial C-bands located near the telomeric region of X chromosome (**a–c**), as well as telomeric C-bands on two medium-sized pairs (**b**). Arrowheads show interstitial C-bands of the $S_{8/9}$ pair. A cluster of 18S rDNA in diakinesis (**e**) coincide with one nucleolar organiser region located on the $S_{8/9}$ pair in the early mitotic metaphase (**d**) (open arrows). X sex chromosome

tegmina. Pronotum and head yellowish green, abdomen of more intensive yellow colour.

*Head and antennae* Antennae yellowish, very thin, almost reaching tips of folded tegmina. Fastigium of vertex broad, almost double as wide as scapus of antenna; fastigium of vertex meeting equally broad fastigium of frons along well-developed horizontal line with deep median sulcus; face with rather obsolete frontogenal carinae; eyes elongate and oval, black and thus very contrasting to yellow head.

*Thorax* Pronotum with well developed lateral carinae with slightly rugose surface; anterior margin of pronotum with median v-shaped indentation; uniformly yellowish, most males with pair of tiny dark dots and each side on disc of prozona.

*Wings* Both pairs of wings fully developed; tegmina elongate, evenly rounded at tips, about 3.5 times longer than broad. Tegmina with veins and veinlets yellow, cells more green; dark maculae usually present, most males with dark area around mirror on left tegmen. Margin of costal area of tegmina more dark, also radius and subcosta, which are contiguous over almost their whole length, marked dark.

Tegmina, thus resembling dropped yellowish brown leaves. Alae shiny with green area near tips which surpass tegmina when folded.

*Legs* Fore coxa with tiny spine; legs yellowish; hind tibiae with dorsal dark markings at base near knee, and ventral dark maculae near apex (Fig. 9a); fore tibiae with open tympanum and, untypical for genus *Eurycorypha*, with dark, stout, short spine at distal end of auditory swelling; also mid-tibiae with two dark marked dorsal spurs. Hind tibiae, as typical for *Eurycorypha* with three slender apical spurs on each side.

*Abdomen* Yellow with dark stigmata; last abdominal tergite flattened, with evenly incurved posterior margin and elevated edges (Fig. 10a, b). Cerci rather stout, decussate with acute and sclerotised tips. Subgenital plate elongate with slightly incurved posterior margin and very short styli (Fig. 10c).

*Female* As described by Chopard (1938). Ovipositor slightly curved upwards, as in Fig. 11a. Subgenital plate as in Fig. 11b. The measurements of female specimens from Mount Kilimanjaro fit the measurements of the holotype as given by Chopard (1938).

**Fig. 9** East African
*Eurycorypha* species. **a**
*Eurycorypha punctipennis*
Chopard, male, Msaranga
valley, southern slopes of
Mount Kilimanjaro. **b**
*Eurycorypha punctipennis*
Chopard, female, same
locality as male. **c** *Eurycorypha
resonans* n. sp., male,
banana–coffee plantation,
village Mahoma, southern
slopes of Mount Kilimanjaro.
**d** *Eurycorypha resonans* n. sp.,
female, same locality as male.
**e** *Eurycorypha combretoides* n.
sp., male, Chala area, savanna,
East Kilimanjaro. **f** Ant-
mimiking male nymph of
*E. combretoides* n. sp. (fourth
instar), collected on a bush
of *Maytenus senegalensis* at
eastern savanna area of Mount
Kilimanjaro and reared to adult
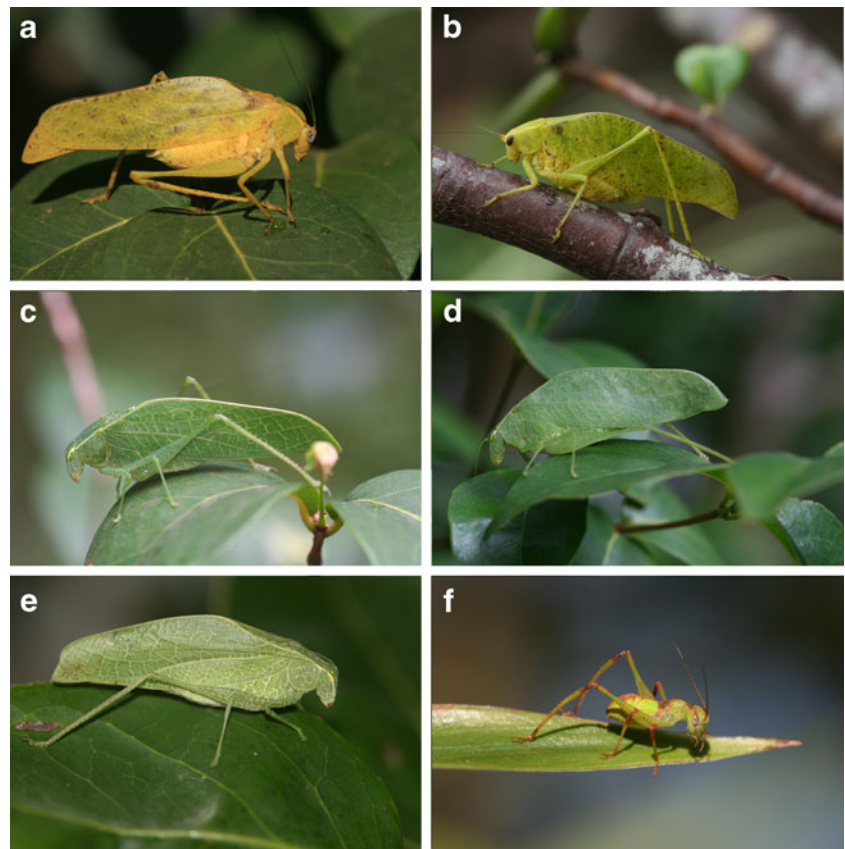


Measurements (mm)

| Males n=6 | | Females n=4 | Chopard 1938 female holotype |
|---|---|---|---|
| Body length | 15.0–18.0 (mean: 16.8) | 17.0–20.0 (mean: 18) | 20 |
| Pronotum | 4.9–5.3 (mean: 5.2) | 4.7–5.4 (mean: 5.1) | 5 |
| Posterior femur length | 15.0–16.5 (mean: 15.4) | 16.5–19.0 (mean: 17.5) | 16 |
| Length of tegmina | 27.0–30.0 (mean: 28.3) | 30.0–32.0 (mean: 30.5) | 31.5 |
| Width of tegmen | 8.0–8.8 (mean: 8.3) | 9.9–11.0 (mean: 10.3) | |
| Length of ovipositor | - | 5.4–6.2 (mean: 5.9) | 6 |

*Habitat and phenology on Mount Kilimanjaro* Canopy
dweller of riverine forest and within coffee–banana planta-
tions at sub-montane elevations. Individuals were mostly
collected during the warm period of the year, between
December and March. Recorded between 1300 and
1500 m on Mount Kilimanjaro (Table 2), the holotype was
collected at 2400 m on Mount Elgon in western Kenya.

*Distribution* East Africa, probably with western boarder
along the Albertine rift.

*Diagnosis* Distinguished from all other *Eurycorypha* species
by its yellowish colour together with brown maculae on
tegmina. Morphologically similar to *E. cuspidata* Krauss,
1901 whose colour is also yellow. Male subgenital plate and
cerci similar. The cerci in *E. cuspidata* are more twisted with a
sclerotised dent at its tip while in *E. punctipennis* the cerci are
curved without a dent although the tip also is sclerotised. Clear
differences are seen in the last abdominal tergite. *Eurycorypha
punctipennis* has sharply marked lateral edges and a medially
depressed zone, while in *E. cuspidata* the lateral sides are
rounded lobes. Medially, an indentation is conspicuous giving
the posterior margin of the last abdominal tergite an undulat-
ing shape (see Eades et al. 2012). *Eurycorypha cuspidata* is
known from southwest Africa (Namibia), while *E. punctipen-
nis* has its centre of occurrence in East Africa.

*Eurycorypha resonans* C. Hemp n. sp.

*Holotype* Male: Tanzania, Mount Kilimanjaro, southern
slopes, plantation belt, Mahoma village, 1300 m February
2009, depository MNB.

  Paratypes, all Tanzania, Mt Kilimanjaro, southern slopes.
One female, remnant riverine forest, Msaranga valley,
1300 m, November 2011, depository MNB; 1 male, same
data as holotype but January 2009, depository NHML; 1
female, lower margin of montane forest above Kidia,

Fig. 10 Detailed images of *Eurycorypha* species. **a–c** *Eurycorypha punctipennis* Chopard. **a**, **b** Male abdominal apex. **c** Male subgenital plate. **d–f** *Eurycorypha resonans* n. sp. **d** Lateral view on male abdominal apex. **e** Dorsal view on male abdominal apex. **f** Male subgenital plate. **g–i** *Eurycorypha combretoides* n. sp. **g** Lateral view on male abdominal apex. **h** Rear view on male abdominal apex. **i** Male subgenital plate. **j–l** *Eurycorypha conclusa* n. sp. **j**, **k** Lateral view on male abdominal apex. **l** Male subgenital plate



1720 m, January 2008, depository NHML; 1 male, 1 female, same data as holotype but March 2012, depository EDNMK.

Further paratype material: all Tanzania, Mount Kilimanjaro, southern slopes: 3 males, 3 females, remnant riverine forest, Msaranga valley, 1300 m, October 2010, November 2010, February 2012; 3 males, 6 females, same data as holotype but June 2004, June 2007, September 2009, August 2010, April 2011, November 2011, January 2012, March 2012; 1 female, Kidia 1430 m, at light, January 2009; 1 female, Kisamu 1300 m, September 2006; 1 female, Kenya, Nairobi, Gigiri, at light, January 2002 (collection C. Hemp).

Fig. 11 Female abdominal apices of *Eurycorypha* species. **a**, **b** *Eurycorypha punctipennis* Chopard, lateral view on ovipositor (**a**), ventral view on subgenital plate (**b**). **c**, **d** *Eurycorypha resonans* n. sp., lateral view on ovipositor (**c**), ventral view on subgenital plate (**d**). **e**, **f** *Eurycorypha conclusa* n. sp, lateral view on ovipositor (**e**), ventral view on subgenital plate (**f**)
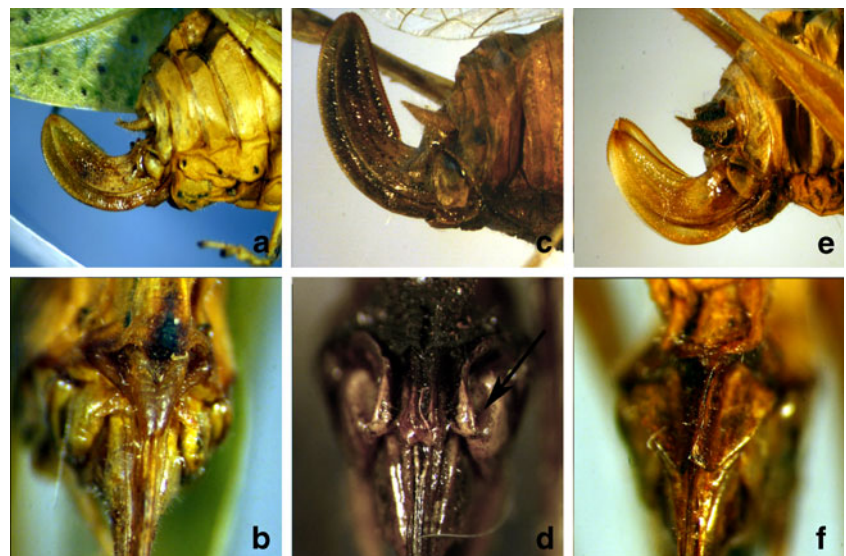
**Table 2** Species of East African *Eurycorypha*, their distribution, habitat and altitudinal spans

| Species | Distribution | Habitat | Altitudinal span (m) |
|---|---|---|---|
| *Eurycorypha conclusa* n. sp. | Tanzania | Tree layer of coastal vegetation between Pangani and Dar es Salaam | 0–30 |
| *E. combretoides* n. sp. | Tanzania, Rwanda | Canopy layer of tree savanna in the colline zone on the eastern slopes on Mount Kilimanjaro | 800–1200 |
| *E. meruensis* Sjöstedt | East Africa | Canopy layer in coffee–banana belt on southern and western slopes of Mount Kilimanjaro | 1300–1850 |
| *E. punctipennis* Chopard | Kenya, Tanzania | Canopy layer in riverine forest and in coffee banana plantations in the submontane zone on Mount Kilimanjaro; in the montane zone on Mount Elgon | 1300–2400 |
| *E. resonans* n. sp. | Kenya, Tanzania | Canopy layer in riverine forest and in coffee–banana plantations in the submontane zone and along the lower border of the montane forest on Mount Kilimanjaro | 1300–1700 |
| *E. varia* Brunner von Wattenwyl | Eastern Africa | Canopy layer in coffee–banana belt to montane forest on southern slopes of Mount Kilimanjaro | 1300–2200 |

Collection NHM London, UK: 1 male, Tanganyika Territory (Tanzania), Morogoro, 1931–2; 1 male, Kenya, Nairobi, April 1921, at light, col. Van Someren; 1 female, Kenya, Nairobi, April 1927, col. Van Someren; 1 female, Kenya, Nairobi, April 1930, col. van Someren, B.M. 1959–468; 1 male, Kenya, Nairobi, June 1931, col. Van Someren, B.M. 1959–468; 1 male, Kenya, Nairobi, January-February 1947, col. F. E. Zeuner, B.M. 1964–194; 1 male, Kenya, Makueni, April 1947, col. van Someren, B.M. 1959–468; 1 female, Kenya, Tsavo West, Kilaguni, 23.11–6.12.1980, col. P. H. Ward, B.M. 1981–467.

*Male description* Colour: As typical for most *Eurycorypha* species, uniformly green.

*Head and antennae* Scapus green, remaining part of antennae dark; very thin and not surpassing folded tegmina.

Fastigium of vertex very broad, about three times as wide as scapus of antenna; fastigium of vertex meeting equally broad fastigium of frons along well-developed horizontal line with median sulcus; face with sharp frontogenal carinae giving face triangular shape; eyes typical for *Eurycorypha*, elongate and oval, brown.

*Thorax* Pronotum with well-developed lateral carinae with slightly rugose surface; anterior margin of pronotum broadly v-shaped, while posterior margin broadly rounded.

*Wings* Both pairs of wings fully developed; tegmina elongate, evenly rounded at tips, about 3.8 times longer as broad. Tegmina with veins and veinlets very light contrasting to darker remaining parts giving tegmina pattern of strongly veined leaf (Fig. 9c). Alae shiny with green area near tips which surpass tegmina when folded.

*Legs* Fore coxa with spine; legs green with tibiae of lighter green; fore tibiae with open tympana and without dorsal spines on fore and mid femora. Hind tibiae with three slender apical spurs on each side.

*Abdomen* Light green without any pattern; last abdominal tergite with two well-developed down-curved pair of spines (Fig. 10d, e). Cerci decussate with bifurcate sclerotised tips of which one tip is longer than the other. Subgenital plate elongate with conspicuous median ridge over whole length, with incurved posterior margin and well developed styli (Fig. 10f).

*Female* Larger than male. Ovipositor well developed and curved upwards, as in Fig. 11c. Subgenital plate as in Fig. 11d.

Measurements (mm)

| | males n=6 | females n=6 |
|---|---|---|
| Body length | 19.0–21.0 (mean: 19.7) | 18.0–21.5 (mean: 19.9) |
| Pronotum | 4.4–4.9 (mean: 4.5) | 4.3–4.9 (mean: 4.5) |
| Posterior femur length | 12.5–14.5 (mean: 13.8) | 13.0–15.0 (mean: 14.3) |
| Length of tegmina | 25.0–29.0 (mean: 26.8) | 29.0–32.0 (mean: 30.2) |
| Width of tegmen | 6.0–7.6 (mean: 7.0) | 8.0–9.5 (mean: 8.8) |
| Length of ovipositor | – | 5.9–6.2 (mean: 6.1) |

*Habitat and phenology* Occurs all around the year on Mount Kilimanjaro and also at other localities in East Africa. Canopy dweller in sub-montane elevations on Mount Kilimanjaro.

*Distribution* Kenya, Tanzania.

*Diagnosis* The tenth abdominal tergite with the two downward curved thorns of male *E. resonans* n. sp. are unique among the described species of *Eurycorypha*. Female *E. mutica* Karsch have a similar subgenital plate, but without lateral elevated margins (arrow, Fig. 11d), typical for the subgenital plate of *E. resonans* n. sp.

*Etymology* In contrast to the other studied *Eurycorypha* species and most phaneropterines *E. resonans* n. sp. produces resonant, cricket-like syllables in its calling song (see above).

*Remarks* Further material which is very similar to *E. resonans* n. sp. was studied in the collection of the NHM London, UK. Further studies on their genetics and song patterns have to be undertaken to clarify the status of those taxa: 4 males, Tanzania, Dar es Salaam, light trap, 16 July 1966; The thorns of the last abdominal plate of these specimens (one specimen damaged and without part of abdomen) are shorter than in *E. resonans* n. sp.; the male cerci wear only one sclerotised thorn (two in *E. resonans* n. sp.); the subgenital plate is slightly differently shaped as in *E. resonans* n. sp. and all specimens are considerably smaller in body length than those of *E. resonans* n. sp.

One male, Mozambique, Inhaca Island. The downward curved processes or thorns of the last abdominal tergite of this specimen are shorter and stoutér than in *E. resonans* n. sp.

One male, Nyassaland, Zomba, light trap. The thorns of the last abdominal tergite are stouter and also shorter than in *E. resonans* n. sp.; the area of the tenth tergite is not as broad, but longer as in *E. resonans* n. sp.

One male, South Africa, Krüger NP, 70 miles N of Soukuza, Olifant Camp, at light. The specimen has very short and stout thorns of the last abdominal tergite and the subgenital plate is different from that of *E. resonans* n. sp.

*Eurycorypha combretoides* C. Hemp n. sp.

*Holotype* Male: Tanzania, Mount Kilimanjaro, eastern slopes, 1020 m, tree savanna, UTM zone 37 M, 347390 E, 9629310 S, March 2002, depository, MNB.

*Paratypes* One male, same data as holotype but February 2009; 1 male, eastern slopes, tree/bush savanna, on *Combretum zeyheri*, 1130 m, May 2012 UTM zone 37 M 38' 35.1558" E,19' 49.1838" S; 1 male, south-eastern slopes, near village Uchira, on *Combretum zeyheri*, 870 m, May 2012, UTM zone 37 M 27' 17.5746" E, 22' 29.2728" S.

Further paratype material studied: Collection Tervuren: 1 male, Ruanda, Gabiru, October 1932, col. L. Burgeon.

*Male description Colour*: Uniformly yellowish green.

*Head and antennae* Antennae green; very thin, not surpassing folded tegmina. Fastigium of vertex more than two times as wide as scapus of antenna; fastigium of vertex meeting equally broad fastigium of frons along well-developed horizontal line with median sulcus; face with sharp callous frontogenal carinae giving face triangular shape; eyes of typical shape for *Eurycorypha*, elongate and oval, colour yellowish to light brown.

*Thorax* Pronotum with well-developed lateral carinae with slightly rugose surface; anterior margin of pronotum broadly v-shaped, while posterior margin broadly rounded.

*Wings* Both pairs of wings fully developed; tegmina elongate, evenly rounded at tips, about 3.6 times longer than broad (Fig. 9e). Alae shiny with green area near tips which surpass tegmina when folded.

*Legs* Fore coxa with long and slender spine; legs green; fore tibiae with open tympanum and without dorsal spines on fore and mid femora. Hind tibiae, as typical for *Eurycorypha*, with three slender apical spurs on each side.

*Abdomen* Yellowish green without any pattern; last abdominal tergite elongated and strongly down-curved, shaped like the beak of a parrot (Fig. 10g, h). Cerci stout, slightly laterally flattened and stretched backward with flattened tips curved inwardly (Fig. 10h); tips sclerotised with tri-dentate ridge. Subgenital plate elongate as in Fig. 10i.

*Female* Unknown.

*Nymphal stages* Larval stages 1–3 ant-like (Fig. 12a). The nymphs were seen on bushes of *Maytenus senegalensis* moving between ants imitating their behaviour. The first and second stage is coloured pure black, while from the third stage onward the individuals turn greenish. From larval stage four onwards (Fig. 9f) the nymphs resemble the adult stage, are mostly green but also may still imitate colours of the environment (see Fig. 13c, f, nymphal stages of *E. meruensis* Sjöstedt and *E. varia* Brunner von Wattenwyl).

Measurements (mm)

|  | Males n=4 |
| --- | --- |
| Body length | 17.0–23.0 (mean: 20.5) |
| Pronotum | 4.2–4.6 (mean: 4.4) |
| Posterior femur length | 12.6–15.0 (mean: 13.5) |
| Length of tegmina | 24.0–29.0 (mean: 27.8) |
| Width of tegmen | 6.7–7.5 (mean: 7.1) |
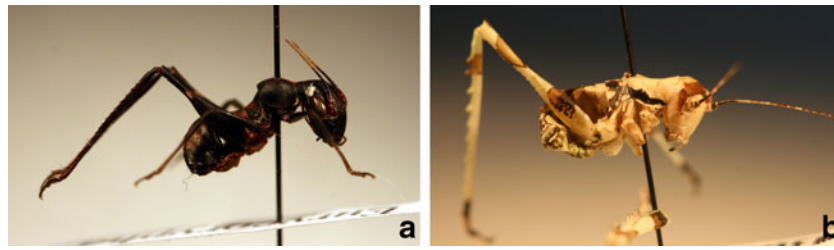
**Fig. 12** Nymphs of *Eurycorypha* species. **a** Ant-like stage of cf. *E. combretoides* n. sp. (third instar), savanna bushland, East Kilimanjaro. **b** Nymph of *E. varia* Brunner von Wattenwyl (probably fourth instar), southern slopes of Kilimanjaro, forest edge above Kidia, 1700 m

*Song* Early afternoon until after nightfall; males on highest branches of savanna trees, often on *Combretum zeyheri* (see Bioacoustics).

*Habitat* Canopy dweller in the colline savanna zone on the southern and eastern slopes of Mount Kilimanjaro.

*Distribution* Rwanda, Tanzania, but probably with a wider geographical distribution in East Africa.

*Diagnosis* *Eurycorypha stenophthalma* Chopard and *E. stylata* Stål also have enlarged tenth tergites. However, the proximal elongated part is up-curved ending in two tips, while it is down-curved and parrot-shaped in *E. combretoides* n. sp. Similar is also the last tergite of *E. meruensis* Sjöstedt, which is elongated and down-curved. However, the tip is bifurcate while it is simple in *E. combretoides* n. sp. The last tergite of *E. velicauda* Karsch is elongated and down-curved, but does not end in an acute tip but is tongue-like shaped.

*Etymology* Most males caught and heard singing in tree savanna habitats were recorded on the tree *Combretum zeyheri*. The underside of the leaves of *C. zeyheri* are very similar to the tegmina pattern of *E. combretoides* n. sp., therefore *combretoides* = like *Combretum*.

*Remarks* In the entomological collection of Tervuren specimens of two undescribed species were studied which are closely related to *E. combretoides* n. sp. Both species possess a similar parrot-shaped tenth abdominal tergite. Specimens of the first undescribed species were labeled Camp de Lukula, collected by Dr Daniel in 1911. An exact localisation of Lukula was not possible, places with this name exist in Tanzania, DRC and Angola. The tenth abdominal tergite is very similar to that of *E. combretoides* n. sp., but the cerci are completely different.

The second undescribed taxon also has a parrot-shaped tenth abdominal tergite. However, the posterior acute part is more flattened compared to *E. combretoides* and the specimens from Lukula. Several specimens of this morphotype were collected in Kibali-Ituri (1 male), West Kivu (2 males) and Equateur, Flandria (3 males) in the DRC, and 3 males are labelled Kongola, possibly a village situated in Namibia.

*Eurycorypha conclusa* C. Hemp n. sp.

*Holotype* Male: Tanzania, Pangani Coast, coastal forest relicts, attracted to light, January 2000, UTM zone 37 04 99 369 E, 93 94 462 S, depository MNB.

*Paratypes* One female, same data as holotype, depository MNB.

Further paratype material studied: 1 male, Dar es Salaam, leg. N. Jago 1971, NHML.

*Male description Colour*: Uniformly green.

**Fig. 13** East African *Eurycorypha* species. **a–c** *Eurycorypha meruensis* Sjöstedt, southern slopes of Mount Kilimanjaro, Tanzania, 1430 m, banana–coffee plantation, male (**a**) and female (**b**), male nymph, fifth instar (**c**). **d–f** *E. varia* Brunner von Wattenwyl, southern slopes of Mount Kilimanjaro, Tanzania, 1710 m, lower border of montane forest, male (**d**), female (**e**), female nymph, fifth instar (**f**)
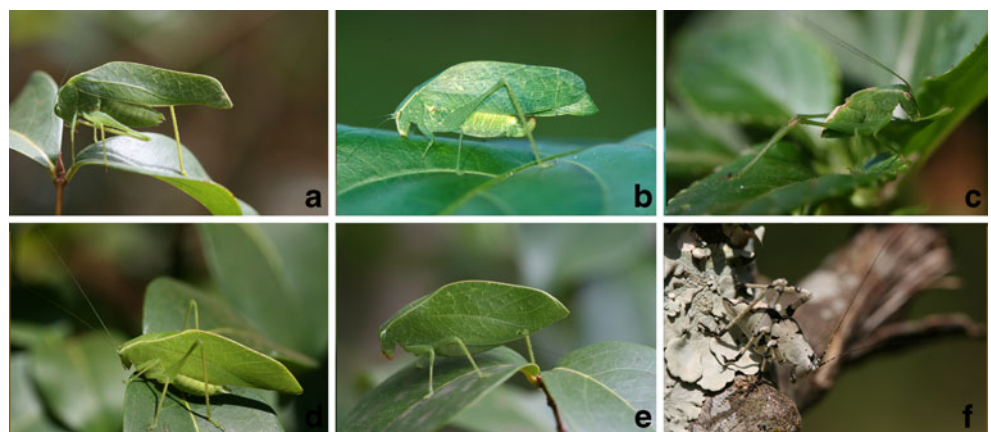
*Head and antennae* Scapus green, remaining part of antennae dark; very thin and reaching tips of folded tegmina. Fastigium of vertex about two times as wide as scapus of antenna; fastigium of vertex meeting equally broad fastigium of frons along well developed horizontal line with median sulcus; face with callous frontogenal carinae; eyes typical for *Eurycorypha*, elongate and oval, brown.

*Thorax* Pronotum with well-developed lateral carinae with slightly rugose surface; anterior margin of pronotum shallowly and evenly curved inwards, posterior margin broadly rounded.

*Wings* Both pairs of wings fully developed; tegmina very broad and broadly rounded at tips, about 2.8 times as long as broad. Alae shiny with green area near tips which surpass tegmina when folded.

*Legs* Fore coxa with spine. Fore tibiae with open tympanum and without dorsal spines on fore and mid femora. Hind tibiae, as typical for *Eurycorypha*, with three slender apical spurs on each side; spinules on hind tibiae with dark tips.

*Abdomen* Green without any pattern; last abdominal tergite with a pair of short and stout processes at posterior margin (Fig. 10j, k). Cerci decussate, of normal shape and length (Fig. 10j). Subgenital plate elongate as in Fig. 10l.

*Female* As male. Ovipositor well developed and curved upwards, as in Fig. 11e. Subgenital plate as in Fig. 11f.

Measurements (mm)

|  | males n=1 | female n=1 |
| --- | --- | --- |
| Body length | 16.0 | 18.0 |
| Pronotum | 3.7 | 4.0 |
| Posterior femur length | 12.6 | 13.3 |
| Length of tegmina | 23.5 | 23.0 |
| Width of tegmen | 8.4 | 9.2 |
| Length of ovipositor | – | 6 |

*Song* Unknown.

*Habitat* Canopy dweller of coastal forest.

*Distribution* Collected from coastal Tanzania between Pangani and Dar es Salaam; probably with a wider distribution along coastal habitats of Kenya and Tanzania.

*Diagnosis* Male *E. cereris* (Stål) described from South Africa possess a last abdominal tergite that is similar to that of *E. conclusa* n. sp. However, the posterior margin is undulating in *E. cereris* lacking the conspicuous stout processes. From its habitus with broad tegmina *E. diminuta* Chopard from northern Kenya is similar to *E. conclusa* n. sp. It also has a similar last abdominal tergite and decussate cerci. However, the stout posterior processes of the tenth tergite are lacking. Also, *E. simillima* Chopard from northern Kenya has a last abdominal tergite with very short processes or knobs at its posterior margin. Here, the subgenital plate is much elongated with slender styli, while in *E. conclusa* n. sp. the processes of the posterior margin of the last abdominal tergite are longer and the subgenital plate is rather stout with very short styli.

Female *E. adicra* Karsch described from Cameroon have a very similar ovipositor and subgenital plate as *E. conclusa* n. sp. However, differences are seen in the apices of the ovipositor valves, which are more rounded in *E. adicra* and the subgenital plate, which has a conspicuous median ridge in *E. conclusa* n. sp. while this structure is lacking in *E. adicra*. *Eurycorypha brevipennis* Karsch from Madagascar is similar in habitus (very broad tegmina) and has a similar ovipositor. As in *E. adicra* the ovipositor valves are round in *E. brevipennis* Karsch and acute in *E. conclusa* n. sp. Further, the anterior margin of the pronotal disc is evenly rounded in *E. brevipennis* Karsch, while it is inwardly curved in *E. conclusa* n. sp.

In the entomological collection of Vienna a male of *E. prasinata* Stål was studied. As in *E. conclusa* n. sp. the last abdominal tergite of the male is unmodified, the cerci are of normal shape and also the subgenital plate is of typical structure for *Eurycorypha*. Differences are seen in the posterior border of the last abdominal tergite. *Eurycorypha conclusa* n. sp. has two elongated process-like structures at both edges, while in *E. prasinata* Stål there are two rounded elevations without any processes. *E. conclusa* n. sp. is only known from coastal habitats and the morphology of males and females is similar to the malagassan species *E. brevicollis* and *E. prasinata* Stål.

*Remarks* Karsch (1889) mentions specimens in the collection of the Naturkunde Museum Berlin labelled as *E. prasinata* Stal from East Africa. However, Karsch (1889) also stated that these specimens from South Africa, Mombasa at the Kenyan coast and the East Usambara mountains in northern Tanzania are slightly different from the holotype from Madagascar, being intermediate between *E. cereris* (Stål) from southern Africa and *E. prasinata* Stål with a greater similarity to *E. prasinata* Stål. At this time, only a few *Eurycorypha* species were described from eastern Africa and this could be the reason that similar species belonging to the complex with an unmodified tenth tergite and decussate cerci were identified as *E. prasinata* Stål. Holstein et al. (2005) refer to a specimen stored in the collection of the National Museums of Kenya, Nairobi, which also could have

been labelled *E. prasinata* Stål owing to the similarity to this complex of morphological similar species.

*Etymology* From Latin *conclusus* = rounded, because of the broad, rounded tegmina.

### *Eurycorypha meruensis* Sjöstedt, 1909

The male was described from Mount Meru by Sjöstedt (1909). Chopard (1921) described the female from Mombasa, Kenya.

*Distribution* Common species in East Africa (Chopard and Kevan 1954). Records from Ethiopia, Kenya, Uganda and Tanzania (specimens NHM London, UK).

*Diagnosis Eurycorypha meruensis* Sjöstedt males have an elongated last abdominal tergite that ends into two acute tips and is strongly down-curved (Fig. 14a, b). Elongated down-curved last abdominal tergites are also present in male *E. velicauda* Karsch, 1893, *E. arabica* Uvarov, 1936 and *E. darlingi* Uvarov, 1936. However, the latter three species have very differently shaped last abdominal tergites, which are tongue-like (*E. velicauda*) or with different ridges and laminae and expanded cerci (*E. arabica, E. darlingi*). The females of *E. meruensis* Sjöstedt have a well developed, rather elongated and, for the group, moderately up-curved ovipositor and a flap-like subgenital plate with a broad base (Fig. 14c, d). The combination of a moderately and elongated ovipositor together with a triangular subgenital plate is not known in any other female *Eurycorypha* species.

*Phenology and biology* Adults in November (Sjöstedt 1909); attracted to light (Chopard and Kevan 1954). Adults were collected all around the year, but the species is more frequent on Mount Kilimanjaro during the months of November to February.

*Habitat* Desert grass and thorn bush in northern Kenya (Chopard and Kevan 1954). Coffee–banana plantations of the submontane and montane zone, submontane forests, lower border of the montane forest at Mount Kilimanjaro (Hemp 2005b; Table 2).

*Remarks* In the entomological collection Tervuren, Belgium, several specimens were studied that are similar to *E. meruensis* Sjöstedt. However, they differ in length and stoutness of the elongated tenth abdominal tergite and are thus probably separate species, closely related to *E. meruensis* Sjöstedt. These specimens were collected in the Democratic Republic of the Congo in Albertville and Elisabethville. As in *E. meruensis* Sjöstedt (Fig. 14a) the tenth abdominal tergite is elongated, hood-like-shaped with a bifurcate tip. *Eurycorypha meruensis* Sjöstedt has in difference to these specimens a very slender elongate tenth tergite with very slender bifurcate processes at the tips, while in the DRC specimens the tenth tergite is stouter and the bifurcate processes are also stout.

Another species related to the *E. meruensis* species complex was collected in Tanzania near Moba. The elongate process of the tenth tergite is much shorter than in *E. meruensis* Sjöstedt and the species collected in the DRC, and deeply bifurcate with stout tips.

### *Eurycorypha varia* Brunner v. Wattenwyl, 1891

Described from Kilimanjaro by Brunner v. Wattenwyl (1891) and recorded again by Sjöstedt (1909).

*Distribution* Sudan (Werner in Sjöstedt 1909); East Africa, including Turkana (Chopard 1954); Zimbabwe, Mozambique, Zambia (specimens NHML).

*Diagnosis* Male *E. varia* Brunner von Wattenwl possess an unmodified last abdominal tergite and decussate rather short



**Fig. 14 a–d** *Eurycorypha meruensis* Sjöstedt. **a** Lateral view on male apex. **b** Male subgenital plate. **c** Lateral view on female ovipositor. **d** Female subgenital plate. **e–h** *Eurycorypha varia* Brunner von Wattenwyl. **e** Lateral view on male apex. **f** Male subgenital plate. **g** Lateral view on female ovipositor. **h** Female subgenital plate. Arrow points on characteristic processes lateral of subgenital plate, typical for female *E. varia* Brunner von Wattenwyl

and at their base stout cerci (Fig. 14e). The subgenital plate of the males is elongate with two short styli and parallel ridges leading to the styli (Fig. 14f). Similar last abdominal tergites are found in *E. cereris* (Stål, 1857) from Natal, *E. cuspidata* Krauss, 1909 from southwest Africa and *E. diminuta* Chopard, 1938 from northern Kenya. In *E. cereris* (Stål, 1857) the posterior margin of the last abdominal tergite is more rounded at the lateral edge, while the edges are more acute in *E. varia* Brunner von Wattenwyl. *Eurycorypha cuspidata* Krauss, 1909 has a more undulating posterior margin of the last abdominal tergite and, medially, a v-shaped indentation. The cerci are more slender and undulating at their tips. *E. diminuta* Chopard, 1938 has a last abdominal tergite with a more deeply medially incised posterior margin than found in *E. varia* Brunner von Wattenwyl. All four species also resemble each other in the general morphology of the habitus and have adjacent distribution centers, and may well be closely related to each other.

*Ecology and biology* Adults in January (Sjöstedt 1909). Males attracted to light (Chopard and Kevan 1954). Adults found from September to April; many nymphs in December; feeding on *Agauria salicifolia* at the lower border of the montane forest at the southern slopes; in captivity feeding on *Morus* sp. and *Rubus* sp.

A male and a female of *E. varia* Brunner von Wattenwyl mated twice in captivity at an interval of 2 weeks (held separately in the meantime). The body mass of the male before mating was 464–466 mg, that of the female 778–796 mg. During mating, the male transferred a spermatophore of 12.9–14.2 % of his body mass to the female, including a relatively large ampulla of 7.7 % of his body mass (both matings).

*Habitat* Thorn bush country (Chopard and Kevan 1954); plantation belt southwest Kilimanjaro (Sjöstedt 1909); Hemp 2005b; sub-montane and montane coffee–banana plantations, sub-montane and montane forest on Mount Kilimanjaro (Table 2).

*Remarks* Further material was studied in the NHM London, UK, that varies slightly in the male genitalia, but is labelled *E. varia* Brunner von Wattenwl: 1 male, Prot St. Johns (South Africa); 1 male, South Africa; 2 males, Natal (South Africa); 1 male, Grand Comore (Comoro islands); 1 male, Bwamba, Uganda.

## Discussion

Biogeography and ecology

The genus *Eurycorypha* is constricted to Africa south of the Sahara, Madagascar and the Arabian Peninsula. However, the highest diversity of this genus is found in eastern, central and southern Africa. Although the most species-rich genus of African Phaneropterinae, for the majority of species only the holotypes and occasionally a few paratypes are known, and so far there is no study illuminating the biogeography and ecology of species of this genus.

From the picture presented from specimens held in various collections most *Eurycorypha* species seem to have restricted areas of occurrence, although all species are fully alate and highly mobile. This study, focusing on some East African species, shows that at least those species investigated more closely all have a larger distribution area being recorded from several East African countries. Thus, *E. punctipennis* Chopard, the single female type known from montane elevations on Mount Elgon in Kenya, is a common species in submontane elevations on Mount Kilimanjaro. It was always collected from higher trees and could not be attracted to light by light trapping. Thus, the living habit and the indifference of this species to light very likely is the reason that it was so rarely collected in East Africa. Screening of entomological collections during the past few years showed that more specimens have been collected from various localities in East Africa, showing a wider geographical distribution of this beautiful and easy recognisable *Eurycorypha* species.

Analogous *E. resonans* n. sp. is common in sub-montane elevations on the southern slopes of Mount Kilimanjaro in Tanzania and was also collected in a forested area near Nairobi, Kenya. Further material of this species was detected in the Natural History Museum of London, UK, and also from Nairobi and from central Tanzania, labelled Morogoro, situated at the foothills of the Uluguru mountains. As *E. punctipennis* Chopard, *E resonans* n. sp. is a canopy dweller and not attracted to light, on Mount Kilimanjaro it occurs syntopically with *E. punctipennis* Chopard in sub-montane riverine forest communities and coffee-banana plantations with a dense tree cover, but was also collected from the lower border of the montane rain forest. Thus, both species seem to have a broad ecological niche, preferring forest habitats from sub-montane to montane elevations (see below and Fig. 1). The same habitat preferences and a similar biogeographical pattern were found for another two *Eurycorypha* species, *E. meruensis* Sjöstedt and *E. varia* Brunner von Wattenwyl. *Eurycorypha meruensis* Sjöstedt was described from Mount Meru in Tanzania, a volcano situated adjacent to Mount Kilimanjaro, but is also recorded from Kenya, Uganda and Ethiopia. *Eurycorypha varia* Brunner von Wattenwyl was described from Mount Kilimanjaro, but material in various entomological collections suggests that this species also occurs in the Sudan, Kenya, Zimbabwe, Mozambique and Zambia. All four species occur syntopically on Mount Kilimanjaro in sub-montane to montane forests and plantations with a dense tree cover. As Mount Kilimanjaro is a geologically

young mountain with an estimated age of 1–2 Ma years (e.g., Nonnotte et al. 2008) it may be concluded that the *Eurycorypha* species easily colonise new habitats. The simultaneous occurrence of four *Eurycorypha* species with a similar habitus and ecological niche (Fig. 1) suggests that the ancestors of these species evolved in other areas of East Africa at a time with a different climatic regime, probably restricting the species to certain habitats and areas then isolated from each other. A changing climate enabled forest species to spread, and to find habitat on other mountains and forested areas in East Africa and to occur nowadays syntopically. The uplift of high volcanoes serving as stepping stones could have facilitated the spread over such a large area as seen in *E. punctipennis* Chopard, *E. resonans* n. sp., *E. meruensis* Sjöstedt and *E. varia* Brunner von Wattenwyl.

A clearly different niche is occupied by *E. combretoides* n. sp. on Mount Kilimanjaro. *Eurycorypha combretoides* n. sp. was only found on the eastern foothills of Mount Kilimanjaro in savanna habitats and occasionally in sub-montane banana plantations. It seems to prefer the tree *Combretum zehyeri* (Combretaceae), the large-fruited bush-willow, on Mount Kilimanjaro as the singing males were noted and collected mainly from this tree species. *Combretum zeyheri* is a common tree in a variety of habitats and is distributed from South Africa through Zimbabwe, Mozambique, Botswana and Namibia to tropical Africa (Schmidt et al. 2002). Whether *E. combretoides* is adapted to *C. zeyheri* as the tegmina pattern resembles, astonishingly, the vein and colour pattern of the underside of the leaves of *C. zeyheri* has to be further investigated. In captivity most *Eurycorypha* species feed readily on leaves of other trees common in the sub-montane zone of Mount Kilimanjaro, such as *Margaritaria discoidea* (Phyllanthaceae), but also on introduced trees, for example *Morus* sp. However, *E. meruensis* Sjöstedt and *E. combretoides* n. sp. could not be caged more than a few days before they died, while *E. resonans* n. sp., *E. punctipennis* Chopard and *E. varia* Brunner von Wattenwyl could be kept alive for several weeks. A caged nymph of *E. combretoides* n. sp. could be reared from about nymphal stage 4 (Fig. 9f) to adult, feeding only on *Combretum* species and *Maytenus senegalensis* from savanna habitats although other tree plants were also offered for food.

The ecological distribution of the five investigated *Eurycorypha* species showed two groups that are clearly separated by their demands (Fig. 1f). *Eurycorypha combretoides* n. sp. occurred in savanna and savanna-like habitats on the foothills with an open tree canopy in sub-humid–humid conditions. It had a narrow niche living mainly on *Combretum* trees. The remaining four species had a syntopic distribution, all occurring in denser forest and forest-like habitats in humid–per-humid climate. Our diagrams show that in respect of site humidity all species follow Walter and Walter´s (1953) rule of the stenotopy of an area (in German referred to "Relative

Standortskonstanz"). At a given humidity regime they occurred at lower altitudes and/or in more open habitats with lesser micoclimatic moisture (e.g., home garden instead of forest) on the southern slopes. The same observation was made for *Lunidia viridis* Hemp (Hemp et al. 2010a). As records of canopy species are lacking from many areas it is still possible to assess the potential altitudinal distribution of species by applying the rule of the stenotopy of an area. Based on our climatic transect data we can, for example, predict that *E. varia* Brunner von Wattenwyl will probably not occur on the northern slopes (where we actually did not find it) and that *E. combretoides* n. sp. has its potential lowermost occurrence at 700 m at the central southern slope of Kilimanjaro.

From ant to leaf mimicry

The nymphal stages of *Eurycorypha* are completely different in the first three larval stages imitating perfectly ants in habitus (ant-shaped head with buckled antennae, long legs and elongated slender abdomen) and behaviour (fidgety running along branches). Nymphs from larval stage three onwards (fourth instar see Fig. 9f; fifth instar see Fig. 13c, f) resemble more and more the adults also abandoning the behaviour of ants now relying on camouflage. One of the early descriptions of *Eurycorypha* species was the nymphal stage of *E. fallax* (Brunner von Wattenwyl, 1884) from Sudan, then described as *Myrmecophana fallax*. Vosseler (1909) realised that these ant-like phaneropterines belong to the genus *Eurycorypha*. Living among ants requires special chemical adaptions to be accepted to live among ants. Probably *Eurycorypha* imitates ants to obtain protection for the tender nymphal stages. As a pure plant feeder is not very likely that *Eurycorypha* species are parasites in the nests of ants, but only use the similarity in habitus, colour and behaviour to escape the notice of predators. To date, no studies have been undertaken to illuminate this biologically fascinating system of the adaption of orthopterans to cope with life among ants. Also, in this respect, the genus *Eurycorypha* would be highly interesting to illuminate the chemical, behavioural and molecular adaption of a genus to perform such profound changes in its life cycle from ant to leaf mimicry.

Radiation of *Eurycorypha* species groups

That the diversification of *Eurycorypha* is still in progress is seen in a number of morphological similar species that were seen in various entomological collections. Thus, another four species morphologically similar to *E. resonans* n. sp. were studied. All the species of the *E. resonans* species group have in common that the last abdominal tergite has two thorn-like processes. The longest and most slender processes are found in *E. resonans* n. sp. in eastern Africa, while these structures get stouter and shorter in the further south-occurring species.

Species with an elongated tenth tergite form another complex of morphologically closely related species. The tenth tergite is elongated tapering to the end and is strongly down-curved. The tip ends either blunt, acute, laterally compressed or bifurcate. Described species of this type are *E. meruensis* Sjöstedt (with a bifurcate tip) and *E. combretoides* n. sp. with an acute tip. At least six additional species occur in central and eastern Africa belonging to the *E. meruensis/combretoides* species complex. The relationship of these species is not understood as there are almost no data available. Further studies on the distribution, as well as ecological and molecular analyses of *Eurycorypha*, would shed light on these processes, which could contribute to the understanding of the drivers of large-scale speciation of taxa in Africa.

Bioacoustics

The songs of the four recorded *Eurycorypha* species differ clearly in amplitude modulation, so that no problems with species recognition are to be expected, even if they all occurred syntopically. In carrier frequency, however, the species are relatively similar except of the quite narrow-banded song of *E. resonans* n. sp.

The structure of the song of *E. resonans* n. sp. is the most unexpected result of the present study. Resonant songs are known from several tettigoniid subfamilies (see Montealegre-Z 2008), but are obviously quite rare among phaneropterines. In his study of resonant singers, Montealegre-Z (2008) did not list any species of this group. Only in Heller et al. (1997) a phaneropterine with relatively narrow-banded song, *Arnobia ocellata* (Ingrisch, 1994), is described (as *Stictophaula ocellata*), and from the spectra figured in Braun (2002) it can be assumed that at least another two species (*Ceraia* sp. 2, *Hyperphrona* sp. 1) have probably resonant songs. The syllables in the song of some species of the genus *Barbitistes* Charpentier, 1825 and of the related species *Ancistrura nigrovittata* (Brunner von Wattenwyl, 1878) consist also of resonant pulses (see Figs. 12 and 14 in Heller 1988). In species of this flightless group it has been demonstrated by behavioural (Dobler et al. 1994) and neurophysiological experiments (Stumpner 1997, 2002) that the correct carrier frequency of the song is essential for song recognition. As frequency is relatively similar in all studied *Eurycorypha*, this character may not be important for interspecific song differentiation, but possibly for intraspecific competition.

In *Ancistrura nigrovittata* the frequency of the relatively broad-banded female response song is also important for the male phonotactic response (Dobler et al. 1994). This could easily apply also to the female song of *E. varia* Brunner von Wattenwyl, which is much narrower than that of the long-winged phaneropterines studied by Heller et al. (1997).

If the delay of the female response with 70 ms to the end of the preceding echeme was the correct interval, it would be relatively short, especially when compared with other long-winged phaneropterines (see Bailey and Hammond 2003). According to these authors the delay time (duet interval) is correlated with the male call length. In this respect, each echeme has to be considered separately as the female is able to respond several times to a complete male song (echeme series). However, the situation may be more complicated because the female was never observed to answer to the first echeme of a series, but seems first to hear and then to respond after a positive evaluation using an unknown part of echeme as trigger.

While there are many data on songs and hearing in bush-crickets from other species are available, much less is known about species-specific differences in muscle physiology and mechanics. As can be calculated from the data presented in Table 3, and Figs. 3 and 4, a male of *E. varia* Brunner von Wattenwyl moves the scraper with a speed of about 23 mm/s (impulses separated by about 1 ms, tooth spacing 23 μm) along the file. In *E. resonans* n. sp., however, the scraper obviously runs with 360 mm/s (sound wave maxima separated by about 0.05 ms, tooth spacing 18 μm). This velocity is at the upper edge of the speeds given by Montealegre-Z et al. (2006) for the "normal" production of resonant ultrasonic songs. Species using high ultrasonic frequencies with higher scraper speeds must—according to their hypothesis (Montealegre-Z et al. 2006)—switch to the production of "short spaced tonal pulses". However, there is no indication of such syllable structure within polysyllabic echemes (one pulse per syllable; see Fig. 2b). It may occur, however, in the syllables of the rare disyllabic echemes. Both tegmina of *E. resonans* n. sp. are obviously narrower than that of the other two species (Fig. 7) what may make fast movements easier, but this is probably not the only difference between the species. Unfortunately, there is no information about the song of *E. meruensis* Sjöstedt which is intermediate between *E. resonans* n. sp. and the other species in file dimensions (Table 3).

At present, there are no concrete hypotheses about the physiological and morphological changes necessary to come

**Table 3** Dimensions of male stridulatory file and pronotum

| Species | Number of teeth | Length of file (mm) | Tooth spacing (μm) | Length of male pronotum |
|---|---|---|---|---|
| *Eurycorypha punctipennis* | 150 | 3.0 | 22 | 5.2 |
| *E. combretoides* n. sp. | ca. 150 | 3.0 | - | 4.4 |
| *E. varia* | 190 | 3.0 | 23 | 4.7 ($\bar{x}$; n=6) |
| *E. meruensis* | 115 | 2.3 | 24 | 3.9 ($\bar{x}$; n=5) |
| *E. resonans* n. sp. | 95 | 1.5 | 18 | 4.5 |

from a non-resonant to resonant song or reverse. In the genus *Panacanthus* (Conocephalinae), similarly as in *Eurycorypha* resonant and non-resonant songs have been observed (Montealegre-Z and Morris 2004). Surprisingly, however, the morphological differences are in the opposite direction: the resonant singing species has the longest file with the most, and most densely packed teeth, just the opposite to what is found here.

Another open question concerns the selective pressure responsible for the change of the song type. Montealegre-Z and Morris (2004) discuss the advantages of non-resonant songs, assuming that this song type is the advanced type in *Panacanthus*. Also in Pseudophyllinae, where resonant songs are quite common (e.g., Heller 1995; Montealegre-Z 2008), a few species with broad-band songs exist (Heller 1995), which may represent a derived state. In *Eurycorypha* and phaneropterines in general, however, the opposite transition is much more likely considering the vast majority of species with non-resonant songs (see Hemp et al. 2009, 2010a, b for East African species) and the isolated appearance of pure-tone singers in different continents. Probably, song-type changes happened many times in both directions, but the reasons are largely unknown.

Chromosomes

Our results corroborate previous studies (for a review see Warchałowska-Śliwa 1998), which revealed that Phaneropterinae species show an advanced karyotype evolution. The diversity of diploid numbers in the subfamily probably results from the modal karyotype present in most tettigoniids, 2n=31 in the male with acrocentric chromosomes and the X0/XX sex determination mechanism. Cytotaxonomic analyses of species of the African genera *Altihoratosphaga*, *Horatosphaga*, *Monticolaria* and *Lunidia* show this typical karyotype of acrocentric chromosomes that is probably basic to most Phaneropterinae (Hemp et al. 2010a, b). This ancestral chromosome number is reduced to 2n=29 in 5 *Eurycorypha* species as a result, probably of 1 tandem fusion between 2 pairs of small-sized autosomes. Variation in the number of acrocentric chromosomes among this genus involved only the sex chromosomes. Pericentric inversions modifying the position of the centromere changed the morphology of the ancestral acrocentric to the metacentric X chromosome in *E. punctipennis* Chopard. A biarmed X chromosome (subacro-/submeta-/metacentric) has also been reported in some phanopterid species. Both tandem fusion and pericentric inversion constitute the common mode of karyotype evolution within Phaneropterinae (e.g., for a review see Warchałowska-Śliwa 1998; Warchałowska-Śliwa et al. 2011). The application of different staining techniques, classical (C-banding and NOR Ag-staining) and molecular (FISH, rDNA) methods generally enables a better characterisation of tettigoniid karyotypes and the identification of genus/species-specific patterns (Grzywacz et al. 2011; Warchałowska-Śliwa et al. 2011). The chromosomes of *Eurycorypha* revealed discrete differences between species within this genus and other representatives of African Phaneropterinae genera in the amount of heterochromatin and C-banding patterns of interstitial and telomeric C-bands, which vary among genera and even between species of a genus (see Hemp et al. 2010a, b). Mapping the location of rRNA-coding genes of chromosomes using FISH and silver staining (AgNO₃) permit evaluation of the activity of rDNA clusters and were useful in comparing the karyotypes in some Palaearctic bushcrickets belonging to the genera *Isophya* and *Odontura* (Grzywacz et al. 2011; Warchałowska-Śliwa et al. 2011). In all five *Eurycorypha* species, the 18S rDNA loci revealed by FISH were coincident with a single active NOR visualised by Ag-NOR staining located in interstitial region on the short autosome. Cytogenetic analysis of the African genus *Lunidia* also revealed one NOR with rDNA–FISH signal, but it was located in the telomeric region of the large autosome (Hemp et al. 2010a). In conclusion, the cytogenetic study presented herein constitutes the next step towards a better understanding of chromosomal organisation and the evolution of African Phaneropterinae species and genera.

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