

Bush-crickets with very special ears and songs – review of the East African Phaneropterinae genus *Dioncomena* Brunner von Wattenwyl, 1878, with notes on its biogeography and the description of new species

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Abstract

This study focuses on the genus *Dioncomena* and its acoustics, particularly the unique songs produced by male *Dioncomena* that consist of several distinct elements in a fixed sequence, culminating in a coda that typically elicits a response from a receptive female. We also examine the inflated pronotal lobes, which we term prebullae, that are prominently developed in some *Dioncomena* species but not in others. We discuss the role of prebullae in the context of acoustic communication in *Dioncomena* and other related Phaneropterini genera that have similar lateral pronotal lobes. We found that prebullae size is correlated with habitat distribution, with larger prebullae occurring in isolated species while aggregation-prone species have smaller or less pronounced prebullae. Using micro-computer tomography we show sexual dimorphism in the 3D geometry of the acoustic tracheae, being larger in the male. Interestingly, the tracheae are coupled by a septum, like in field crickets, which suggests potential cross talk.

We define three groups of *Dioncomena* based on altitude preferences, ecology, color patterns, and songs: the *jagoi*-, *tanneri*-, and *ornata*-groups. We describe the songs of several species, including newly identified species such as *D. flavoviridis* **sp. nov.**, *D. magombera* **sp. nov.**, *D. ngurumontana* **sp. nov.**, *D. sanje* **sp. nov.**, *D. tanneri*, *D. versicolor* **sp. nov.**, and *D. zernyi*. We also provide information on the nymphs, development time, and mating behavior of various species reared in the laboratory, shedding light on their phenology and adaptations to their habitats.

Key Words

bioacoustics, biogeography, biology, Eastern Arc Mountains, morphology, phenology, Tanzania

Introduction

Acoustic signals play a vital role in the mating system of almost all bush-crickets (or katydids; Tettigonioidea). The males produce loud calling songs, which are answered by females through either a phonotactic approach or self-produced sounds, depending on the species. In the subfamily Phaneropterinae, females typically respond acoustically, resulting in sophisticated male-female duets (e.g., Heller and Hemp 2020). Unlike the system with stationary singing males waiting for silently approaching

females, in this group, both sexes have to hear, localize, and evaluate sounds. Consequently, the largest ears among Tettigonioidea are found in this group, with auditory bullae “running to the top of the prothorax” (Bailey 1990). Although the exact function of these conspicuous structures is not well understood (for hypotheses, see Mohsin and Schul 2011; Celiker et al. 2022), they undoubtedly enhance hearing capabilities. However, even these inflated auditory tracheae, which nearly completely fill the prothorax, are not the end point in ear evolution. In the genus *Dioncomena*, reviewed here (and in some other

genera; see below), the lateral lobes of the pronotum are inflated, creating an additional space presumably used to improve hearing. Brunner von Wattenwyl (1878) named the genus after these inflated lateral lobes (διογκώνομαι in Greek, latinized to *Dioncomena*, for “inflated”), without having any idea about the function of this structure. Until Ragge’s review of African Phaneropterinae in 1980, only *Letana inflata* (Brunner von Wattenwyl, 1878) was known, in addition to *D. ornata*, to have a similarly shaped pronotum. Some more genera resembling *Dioncomena* in this character were described by Rehn (1914) for *Atlasacris*, Ragge (1980) for some species of *Ivensia*, and later by Massa (2015) and Hemp and Heller (2019), but no hypotheses were made about their function. In the meantime, the understanding of the auditory system of bush-crickets has considerably improved, and it is now well-known that the prothoracic tracheal opening is the main entrance for sound reaching the auditory sensory cells situated in the tibia of the front legs (Bailey 1990; Rössler et al. 2006). For his reviews about the morphology of the ears in tettigoniids, Bailey (1990, 1993) has obviously overlooked the inflations and assumed that all modification of the paranota he found functioned as protection of the tracheal entrance. We will describe the structures in more detail and argue that the modifications, which are often sex-specific in size, have an important auditory function, probably improving the sensitivity of the ears.

Dioncomena is also special concerning sound production. Ragge (1980) discovered that the type species and all six new species he described differed in the structure of their stridulatory files, presenting quite complicated patterns of tooth intervals. The songs themselves remained unknown until the study of Hemp (2021), who provided oscillograms of sections of the very complicated songs of four species. She also presented photographs of living animals and coined the English name “Jewels” for the genus based on the colorful appearance of the species.

The genus *Dioncomena* was established by Brunner von Wattenwyl in 1878, based on the observation of *D. ornata* from Zanzibar, which is a widespread species in Tanzania and Kenya. This genus is characterized by the shape of the tegmina, the open tympana of the fore legs, the dorsally unarmed tibiae of the fore and mid legs, and the inflated lateral lobes of the pronotum. In his review of the African Phaneropterinae with open tympana, Ragge (1980) re-described the genus and added conspicuously hooked spurs of the male mid tibiae as a generic character distinguishing *Dioncomena* from the genera *Meruterrana* Sjöstedt, 1912, and *Pronomapyga* Rehn, 1914, which also have a contrasting variegated colour pattern. Ragge (1980) described six species from eastern Africa, and subsequently, Hemp (2017) described another species, *D. scutellata*, on museum material from coastal Tanzania, and Massa (2021) added *D. takanoi* from Zambia. Hemp and Heller (2019) established the genus *Kefalia*, which is morphologically similar to *Dioncomena*. Like *Dioncomena*, *Kefalia*

species have hooked spurs of the mid tibiae. Males of *Kefalia* species may be confused with *Dioncomena* due to their variegated color pattern and similar body shape. However, female *Kefalia* have strongly reduced scale-like wings, while *Dioncomena* females resemble the males, being fully winged.

In this study, we present data on the bioacoustics of *Dioncomena*, describing their complex structured songs, and highlighting their morphological peculiarities in connection with their acoustics. We also provide data on the biology and phenology of several of these beautifully colored insects, which are found in the last remaining forests in East Africa. Furthermore, we describe six new species and the female of *D. zernyi*.

Methods and materials

Depositories

BMNH British Museum (Natural History), London;
CCH Collection of Claudia Hemp, Bayreuth;
NHMW Naturhistorisches Museum, Vienna.

Sound files of all species studied acoustically are given in the Suppl. materials and will be deposited in OSF (Cigliano et al. 2023).

Rearing and keeping of animals

The specimens were housed either in plastic containers or gauze cages and were provided with a daily diet of *Taraxacum officinale* or *Fragaria* sp. leaves, as well as leaves from other shrubs and trees which were regularly replaced.

Bioacoustics

Specimens studied

For this study sounds from 9 species and 50 specimens (37 ♂♂, 13 ♀♀) were analyzed (about 39 GB sound data corresponding to 84 h recording at 2 × 64 kHz sampling rate), all collected in Tanzania by Claudia Hemp.

- D. flavoviridis* sp. nov.: Nguru Mountains, 2♂♂ + offspring, 4♂♂, 4♀♀, (CH8855-8862), December 2020; 1♂, March 2021.
- D. jagoi* Ragge, 1980: East Usambara Mountains, Amani/Zigi, 1♂ (CH8619), November 2018; 1♂, February 2021.
- D. magombero* sp. nov.: Udzungwa Mountains, 1♂, near Mangula Gate (paratype), 2016; 1♂ 2021.
- D. sanje* sp. nov.: Udzungwa Mountains, 1♂ + offspring – 3♂♂, 2♀♀ (CH8167-70), December 2015; 1♂, 2♀♀ (CH8863-65), December 2020.

- D. ornata* B. v. Wattenwyl, 1878: 1♂, West Usambara Mountains, Lutindi, January 2015; 1♂, East Usambara Mountains, Nilo Forest Reserve, April 2016; 2♂♂, 1♀, East Usambara Mountains, Amani/Zigi, (CH8093-5), November 2015; 1♂, January 2021; 3♂♂, 2♀♀ (CH8951-5), December 2021; 3♂♂, 1♀, Nguru Mountains, February 2021 (CH8150-2); 1♂, Coastal forest: near Kisarawe, Kazimzumbwi Forest Reserve, July 2015; 3♂♂, Zanzibar, near Jozani Nationalpark, June 2017 (CH8450), October 2018 (CH8620), and February 2022.
- D. ngurumontana* sp. nov.: 3♂♂, 1♀, Nguru Mountains above Dibago (CH8986-9), November 2021.
- D. tanneri* Ragge, 1980: 1♂, West Usambara Mountains, Mazumbai Forest Reserve, March 2021.
- D. versicolor* sp. nov.: 1♂, Uluguru Mountains, February 2016.
- D. zernyi* Ragge, 1980: 2♂♂, Udzungwa Mountains (CH8034), July 2015, and February 2016.

We could not obtain acoustic data on the following species: *D. bulla* Ragge, 1980, *D. nitens* Ragge, 1980, *D. scutellata* Hemp, 2017, *D. takanoi* Massa, 2021, and *D. ugandana* sp. nov. From *D. grandis* Ragge, 1980 the tick song (see below) is figured by Naskrecki and Guta (2019).

Recording

The male calling songs were recorded in the laboratory using a digital bat detector (Pettersson D1000X) mostly with a sampling rate of 100 kHz (rarely 192 or 300 kHz), often from field-collected animals, but in some species also from animals reared in the laboratory. The singers were caged in plastic tubes or gauze cages with microphone fixed or handheld at distances between 5 and 60 cm. The female response behavior was studied in the laboratory using virgin females, reared from field-collected nymphs (rarely) or from eggs. Duets were recorded in stereo using a Sony ECM-121 microphone (frequency response relatively flat up to 30 kHz according to own tests) and an Uher M645 audio microphone connected to a personal computer through an external soundcard (Transit USB, “M-Audio”; 64 kHz sampling rate). Here, male and female were placed separately into two plastic tubes (*Drosophila* tube 28.5 × 95 mm, Biosigma, Cona, Italy) mostly standing side by side, with one microphone placed inside or on top of each vial. Both microphones typically picked up male and female sounds, but with different amplitudes. Most recordings were made at temperatures between 20 and 25 °C, only rarely also between 15 and 28 °C.

The stridulatory movements in *D. sanje* sp. nov. were registered using an opto-electronic device (Helvesen and Elsner 1977, modified as in Heller 1988) as well as the equipment described in Montealegre-Z and Mason (2005; output used for Fig. 27). In summary, the equipment used the optical system proposed by Hedwig (2000), and a sampling rate of 100 k-samples/s for both sound and motion traces.

Sound signals were recorded using a wide-bandwidth response 1/8-inch microphone (Brüel and Kjaer, 4138-A-015, with pre-amplifier model 2670, Brüel and Kjaer, Nærum, Denmark), and the Polytec software (PSV 9.2, Waldbronn, Germany) for multi-channel data acquisition.

For the recording of wing vibrations the method of micro-scanning Doppler vibrometry was used, described in previous studies (e.g. Chivers et al. 2017). Specimens were immobilized by exposure to a triethylamine-based mix (FlyNap, Carolina Biological Supply Company, Burlington, NC, USA) for 3–5 min. The specimens were placed on a block of BluTack (Bostik, La Défense, Paris, France) and their legs were gently clamped to the block with small staple clamps. The wings were extended and maintained in position by putting a small drop of a mix of beeswax (Fisher Scientific Loughborough, UK) and Colophonium (Sigma-Aldrich, Dorset, UK) (50:50). The BluTack block was affixed to a brass plate which itself was attached to an articulated aluminium rod allowing the specimen to be maneuvered into the required position.

Vibration-compliant areas of forewings, and associated frequency characteristics, were measured using a micro-scanning laser Doppler vibrometer (Polytec PSV-500; Waldbronn, Germany) fitted with a close-up attachment. The mounted specimens were positioned so that the extended wings were perpendicular to the lens of the laser unit. A loudspeaker was positioned above the laser unit and facing the animal to broadcast the sound stimulus. The acoustic stimulus used was periodic chirps, generated by the Polytec software (PSV 9.2), passed to an amplifier (A-400, Pioneer, Kawasaki, Japan), and sent to the loudspeaker (Ultrasonic Dynamic Speaker Vifa, Avisoft Bioacoustics, Glienicke, Germany). The periodic chirps spanned frequencies between 2 and 100 kHz, and the stimulus was flattened so all frequencies were represented at 60 ± 1.5 dB (SPL re. 20 µPa) at the position of the wings. A Brüel and Kjaer 1/8-inch condenser microphone was placed at the position of the wings to monitor and record the acoustic stimulus at the position of the wings as a reference. The laser system was used in scan mode.

Analysis

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). Data are presented as mean ± standard deviation. For spectral analysis, short song parts (echemes or syllables) were analyzed using the mean of 512 points wide Hanning windows, overlapping by 100 points.

Morphology

The stridulatory files were photographed using a Canon EOS 550 D fixed on a Leica MZ 125 stereomicroscope or a Sony Cyber-shot DSC-P120 on an Olympus SZ Binocular Stereo Zoom Microscope. Programs used for

processing the photos were EOS Utility, Helicon Focus, and Adobe Photoshop.

To get an impression of the three-dimensional geometry, the auditory tracheae of *D. sanje* sp. nov. were scanned using a SkyScan 1172 X-ray μ -CT scanner (Bruker Corporation, Billerica, MA, USA) with a resolution of 12.9 μ m (50 kV source voltage, 200 μ A source current, 200 ms exposure and 0.2° rotation steps). For obtaining a series of orthogonal slices, the μ -CT projection images were reconstructed with NRecon (v. 1.6.9.18, Bruker Corporation, Billerica, MA, USA). The three-dimensional segmentation of the auditory tracheae were performed with the software Amira-Aviso 6.7 (Thermo Fisher Scientific, Waltham, MA, USA) (Celiker et al. 2022).

Acoustical terminology

Tettigonioids produce their songs by opening and closing movements of their tegmina. The sound resulting during one cycle of movements is called a syllable, often separable in opening and closing hemisyllable (Ragge and Reynolds 1998). Syllable duration: time period measured from the beginning of the first impulse to the last; syllable period: time period measured from the beginning of a syllable to the beginning of the next (reciprocal value: syllable repetition rate, SRR). In many species and also in *Dioncomena*, these syllables can be grouped into echemes: first-order assemblage of syllables (duration, period and rate as for syllable). However, the male songs are typically long and complex, contain different elements and cannot be described by syllable and echeme only. The uninterrupted sequence of sounds lasting typically many seconds and which is answered by the female is called main song. Its final part - where typically the female responds - is called coda (a term from music, Italian, meaning tail). Isolated syllables (or short echemes) which are produced in intervals of a few to many seconds are onomatopoeically called ticks (correspondingly ticking song). Each syllable consists of impulses: a simple, undivided, transient train of sound waves (here: the damped sound impulse arising as the effect of one tooth of the stridulatory file).

Results

Aspects of habitat and the ecology

The *Dioncomena* species under investigation can be classified into three groups based on their color pattern, habitat, and ecology. The first group is the *jagoi*-group, characterized by a green and black color pattern with turquoise colors in males (*D. jagoi*, *D. magombera* sp. nov., *D. flavoviridis* sp. nov., *D. sanje* sp. nov., and probably *D. ugandana* sp. nov., Figs 1, 10, 11). Initially, individuals resembling *D. jagoi* were collected from forest areas in Tanzania, but further examination of their morphology

and songs revealed that *D. jagoi* is only found in the East Usambara Mountains and Kimboza Forest Reserve. Similar species collected from the Nguru and Udzungwa Mountains and also Kimboza Forest Reserve were identified as distinct species based on differences in their songs and morphology, particularly in their stridulatory files and color patterns. Therefore, we describe three new species in the *D. jagoi*-group: *D. sanje* sp. nov., *D. magombera* sp. nov., and *D. flavoviridis* sp. nov. These species are common in the Udzungwa Mountains and along the Eastern Arc chain, with *D. flavoviridis* sp. nov. found in lowland wet and submontane forests of the Nguru Mountains. These species are found in low densities scattered in closed forest in Uganda and lowland to submontane forests along the Eastern Arc chain in Tanzania (see map Fig. 36).

The *ornata*-group comprises three species: *D. ornata* found in southern Kenya and northern to central Tanzania, *D. zernyi* inhabiting lowland to submontane forested areas in southern Tanzania, and *D. grandis* distributed in the border region of Mozambique with Zambia. None of the three species were found to occur together (refer to map Fig. 36). Male *D. scutellata*'s color pattern indicates its possible relation to *D. zernyi*, though its live color pattern is unknown as one of the two known specimens has lost its color due to preservation in alcohol (stored in Copenhagen), and the other is preserved in the collection of London. All four species have a three-parted stridulatory file.

D. ornata populations on the mainland exhibit distinct coloration, with black wings and turquoise areas on the head, face, and dorsal abdomen in males. In contrast, the Zanzibar population lacks turquoise coloration, but males have a vivid yellow, yellow-red to red pronotum, similar to females (see Hemp 2021 for images of live specimens). Females of mainland populations of *D. ornata* are less brightly colored, lacking the conspicuous turquoise color typical of males, and their tegmina are often more brown or light black, but not as deep black as males. The body of *D. ornata* is uniformly colored green or yellow-green, without lateral fasciae, as is typical for the *jagoi*-group. A dorsal black or light black fascia is usually present. *D. zernyi* males and females are less conspicuously colored, with brown tegmina and a green body with white and/or yellow fasciae, and both sexes show no differences in coloration (Fig. 16). *D. grandis* has a color pattern very similar to mainland *D. ornata*. Like *D. ornata*, this species produces tick-songs (depicted in Naskrecki and Guta 2019), but its full song is not known. Naskrecki and Guta (2019) state that *D. grandis* is relatively abundant on low herbaceous vegetation along forest edges and thus is classified in the *ornata*-group, occupying a similar habitat. Species of the *ornata*-group are found in forest edges and clearings, often aggregated with several males and females sitting on bushes and tall herb vegetation together (this behavior is known for *D. ornata* and *D. zernyi* only).

Species of the *tanneri*-group, consisting of *D. tanneri*, *D. versicolor* sp. nov., and *D. ngurumontana* sp. nov., are

found in forests of the montane zones along the Eastern Arc Mountains. All three species are highly colorful, with patterns of turquoise, yellow, red to red-brown, and black, especially in males (Figs 12, 15). Like members of the *ornata*-group, individuals of all three species are found along forest edges or on forest clearings, and are often aggregated.

Taxonomy

Dioncomena flavoviridis Hemp, sp. nov.

<https://zoobank.org/C174DC5F-2B7F-4C74-B68F-5344AAD1BF0B>

Figs 1D, E, 2B, 3E, F, 4C, D, 5, 6B, 8A, 19, 20A, B, 21, 22A–C, 23–25, 29, 30, 35A, 36

Type material. *Holotype* male. Tanzania, Nguru Mountains, area between 6°03'40"S, 37°33'13"E 800 m and 6°02'39"S, 37°33'35"E 1500 m, lowland to submontane forest, November 2020. *Paratypes*: 4♂♂, 17♀♀, same data as holotype and February 2017, March 2017, March 2019, March 2020, and November 2022. Depository: CCH.

Description. Male: General habitus and color pattern. Typical for the genus, with a contrasting pattern of green, bluish and black colours. Head & antennae. The fastigium of the vertex is compressed and narrower than the scapus, sulcate above. Thorax & legs. The pronotum has a broad pitch black stripe along the disc, widening at the metazona and completely covering this part (Fig. 1E). The fore coxa is black with a small yellow spine. The fore and mid femora have few very small spinules along ventral ridges, while the hind femur has a double row of widely spaced, irregularly positioned spinules. The fore tibia has a ventral double row of irregularly set small spinules and a pair of short ventral spurs. The mid tibiae have few spines in a double row ventrally, with tiny and only slightly hooked spurs. The hind tibia has four rows of spines irregularly set along its length. Tegmina & wings. The tegmina and wings have a typical shape and coloration for *Dioncomena*. The stridulatory file on the underside of the left tegmen is continuous, about 1.7 mm long, and with around 40 evenly and widely spaced teeth (Fig. 2B). Abdomen. The tenth abdominal tergite is slightly incurved at the posterior margin, with a membranous structure medially (Fig. 3E). The subgenital plate is longer than wide, v-shaped and incurved medially (Fig. 3F).

Female. With a similar habitus, size, and color pattern to males (Fig. 1F), but lack the hooked spines on the mid tibiae. The ovipositor is relatively small and strongly upcurved (Fig. 4C), and the subgenital plate has a broad base with a triangular posterior margin (Fig. 4D).

Nymphs. Nymphs of this species are only a few millimeters long when freshly hatched, with antennae that are 4–5 times longer than the body length. A conical hump is present on the head, a feature typical of all observed L1 stages of *Dioncomena* species (Fig. 5A, B). As they grow, the nymphs become progressively larger and may

stay predominantly green (L2, Fig. 5D) or become more brownish (L3, Fig. 5C), with brown bands appearing along the hind legs from about stage 3.

Measurements, (mm) males (n = 2). Body length 15.2–15.5. Length of pronotum 3.3–3.9. Length of tegmina 24.5–26.5. Length of hind femur 18.0–19.3.

Measurements, (mm) females (n = 6). Body length 15.5–17.0. Length of pronotum 4.2–4.5. Length of tegmina 27.0–27.5. Length of hind femur 19.5–20.1. Ovipositor 4.2–4.5.

Biology. The eggs are black, oval-shaped, and approximately 3–4 mm long and 2 mm wide. They are typically deposited into the midribs of leaves or small twigs (Fig. 6B). In November 2020, females collected from the Nguru Mountains laid numerous eggs that hatched three and a half months later, at the end of February 2021. The first adult emerged at the end of May 2021, three months later. Similar to other species studied, such as *D. sanje* sp. nov. and *D. ornata*, males transfer only small spermatophores to females during mating (Fig. 8A).

Song. See Bioacoustics.

Habitat and distribution. Lowland to submontane forest. Individuals occur single in more or less closed forest. Tanzania, Nguru Mountains.

Etymology. The species is named after the distinctive bright yellowish-green colored lobes of the pronotum which contrast with the black stripe on the dorsal side of the pronotum and the remaining pattern of black, yellowish-green, and bluish-green on the body and tegmina. The name “*flavo-viridi*” is derived from Latin, meaning “yellowish-green”.

Dioncomena magombera Hemp, sp. nov.

<https://zoobank.org/ADA3E824-194A-488C-BF9E-69AF874BA223>

Figs 1G–I, 2C, 3G, H, 4E, F, 7, 19, 21, 22F, G, 26B–D, 30, 36

Type material. *Holotype* male. Tanzania, Udzungwa Mountains, Mangula Gate, lowland wet forest, 7°50'38"S, 36°53'08"E, 340 m, January 2016. Depository: CCH.

Paratypes: all Tanzania; 3♀♀, same data as holotype and March 2016. 1♂, 3♀♀, Magombera Forest Reserve, lowland forest, 7°49'10"S, 36°58'42"E, 280 m, January 2019. 2♀♀, Kihansi Forest Reserve, area between 8°36'35"S, 35°51'08"E, 370 m and 8°35'48"S, 35°50'59"E, 800 m, lowland to submontane forest, January 2016. 1♀, Kanga Hill, Nguru Mountains, 5°59'04"S, 37°45'36"E, 420 m, riverine vegetation, March 2022; 1♂, 4♀♀, Kimboza Forest Reserve, Morogoro Region, 200–300 m a.s.l., 7.03°S, 37.78°E, disturbed lowland forest, March 2022. 1♀, Miombo woodlands, Msaze near Gulwe, Mpwapa District, 6°31'21"S, 36°22'15"E, 1000 m, May 2022. Depository: CCH.

Description. Male. Typical *Dioncomena* in habitus and size, with contrasting green, bluish, and black colors (Fig. 1G, H). Head. Fastigium of vertex compressed, sulcate above. Thorax & legs. Pronotum with slightly

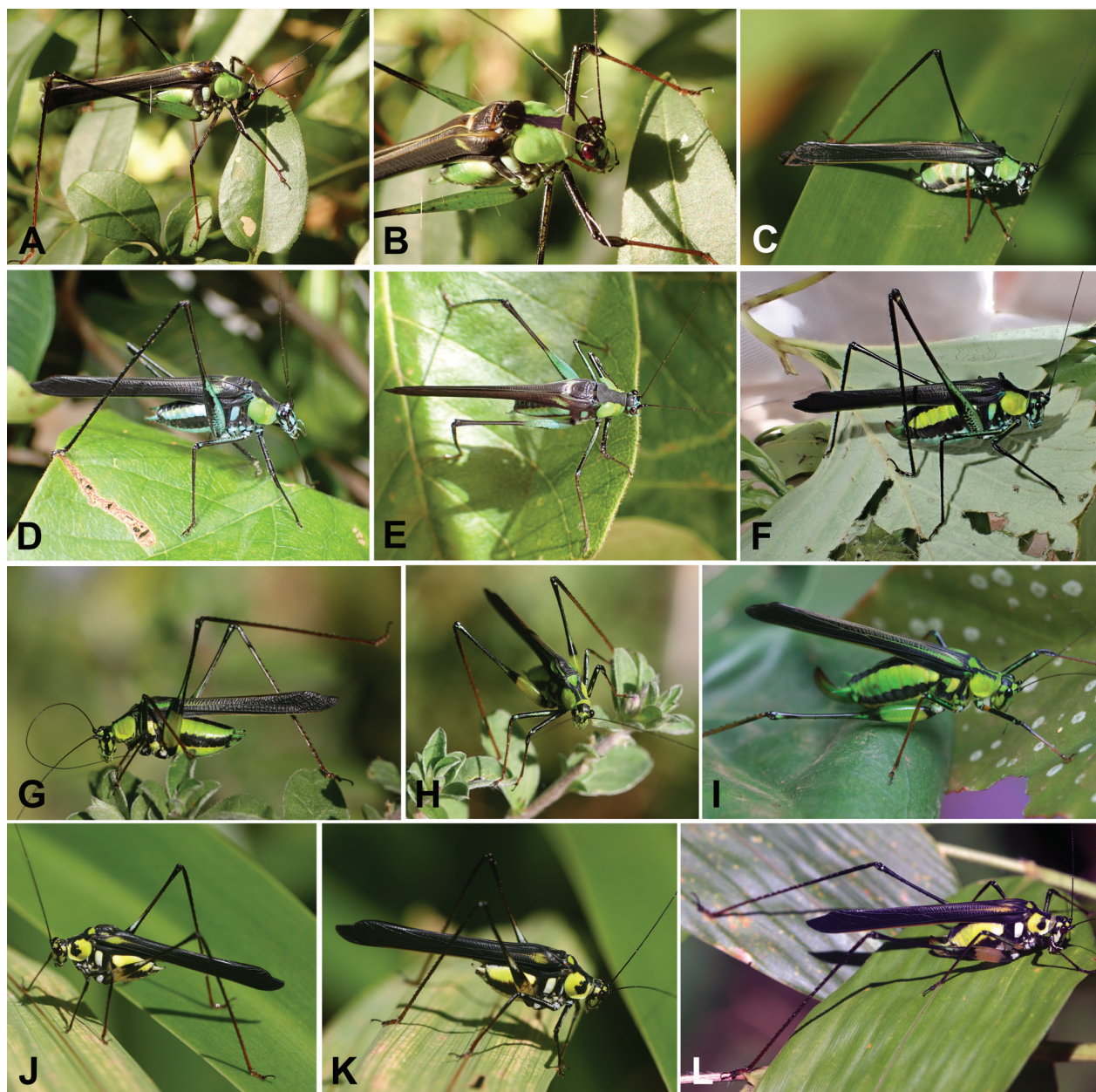


Figure 1. *Dioncomena* species of the *D. jagoi*-group: A–C. Male (A, B) and female (C) of *D. jagoi*, East Usambara Mountains; D, E. Male (D, E) and female (F) of *D. flavoviridis* sp. nov.; G–I. Male (G, H) and female (I) of *D. magombera* sp. nov.; J–L. Male (J, K) and female (L) of *D. sanje* sp. nov.

inflated posterior part of lateral lobes. Broad black stripe with fine median green line on pronotal disc, widening at metazona. Fore coxa brownish or black with broad-based short yellow spine. Fore and mid femora with double row of small ventral spinules, hind femur with widely spaced irregular positioned spines. Fore tibia with ventral double row of irregular set small spinules and a pair of short ventral spurs; dorsal inner side with short spine below tympanum and 1–3 short black spines along length. Mid tibiae with ventral double row of hooked black spinules and spurs, dorsal on mid tibiae at apical part with few hooked black spines. Tegmina & wings. Typical shape and coloration for *Dioncomena*, with continuous stridulatory file on left tegmen (Fig. 2C). Abdomen. Tenth abdominal tergite

incurved at posterior margin with shallow membranous structure medially. Cerci green and stout, with black inwardly hooked tips (Fig. 3G). Subgenital plate longer than wide, v-shaped incurved medially (Fig. 3H).

Female. Similar habitus, size, and coloration as male (Fig. 1I). Ovipositor long and slightly upcurved (Fig. 4E). Subgenital plate narrow and triangular with evenly curved posterior margin (Fig. 4F), without hooked spines on mid tibiae.

Nymphs. Similar to the adults. Fig. 7 shows the last instar of a female *D. magombera* sp. nov.

Measurements, (mm) males (n = 3). Body length 16.8–25.0. Length of pronotum 3.6–4.0. Length of tegmina 22.5–25.1. Length of hind femur 18.2–19.3



Figure 2. Stridulatory files of *Dioncomena* species, tegmen articulation to the right. A–E. *D. jagoi*-group: A. *D. jagoi*; B. *D. flavoviridis* sp. nov.; C. *D. magombera* sp. nov.; D. *D. sanje* sp. nov.; E. *D. grandis* (from Naskrecki and Guta 2019); F. *D. ornata* (Nguru Mts.); G. *D. zernyi*; H. *D. tanneri*; I. *D. versicolor* sp. nov.; J. *D. ngurumontana* sp. nov.

Measurements, (mm) females (n = 6). Body length 14.5–17.8. Length of pronotum 5.4–6.9. Length of tegmina 22.4–27.5. Length of hind femur 18.7–21.7. Ovipositor 5.4–6.9.

Habitat and distribution. Lowland to submontane forest. Mostly found singularly in understory vegetation of closed forest. Distributed in Tanzania's Udzungwa, Uluguru, and Nguru Mountains, as well as Miombo woodlands in the Mpwapwa District.

Etymology. Named after the Magombera Forest Reserve at the Udzungwa Mountains' foothills near Mangula, where the first specimens were collected. Noun in apposition.

Remarks. Ragge (1980) reported two female *Dioncomena jagoi* individuals from Kimboza Forest Reserve at the Uluguru Mountains' foothills. Our team's

specimens collected in March 2022 from the same location belong to the new species *D. magombera*. A female specimen captured at the Nguru Mountains' foothills and another in Miombo woodlands in the Mpwapwa District near Gulwe also belong to this species, indicating *D. magombera* sp. nov. is widespread in lowland forests along the southern branch of the Eastern Arc Ranges. Two female specimens listed by Ragge (1980) from Kimboza Forest Reserve were studied in the Natural History Museum London and found to belong to *D. jagoi*, labelled as paratypes by David Ragge. Further collecting is necessary to determine whether two *Dioncomena* species of the *jagoi*-group exist in Kimboza Forest Reserve, and studies on their song must be undertaken.

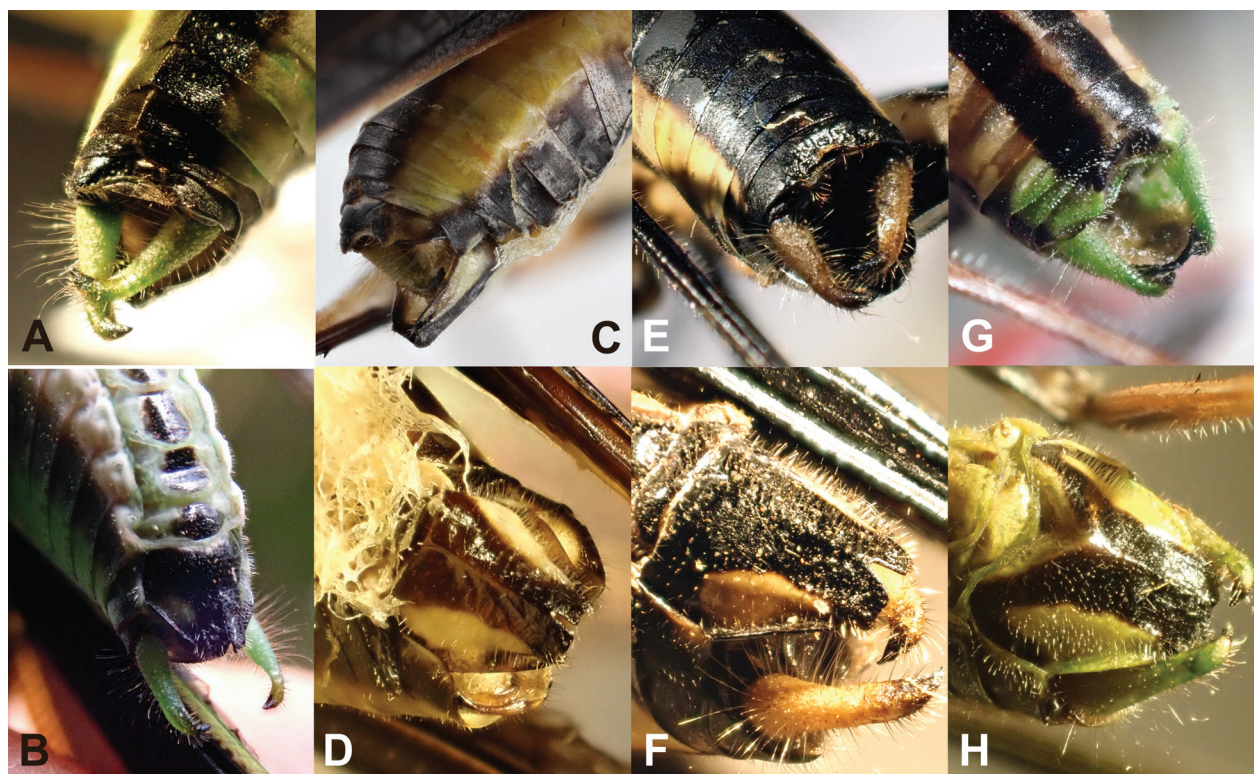


Figure 3. Male apices of the *Dioncomena jagoi*-group. **A, B.** Dorsal (**A**) and ventral (**B**) view of *D. jagoi*; **C, D.** Dorsal (**C**) and ventral (**D**) view of *D. sanje* sp. nov.; **E, F.** Dorsal (**E**) and ventral (**F**) view of *D. flavoviridis* sp. nov.; **G, H.** Dorsal (**G**) and ventral (**H**) view of *D. magombera* sp. nov.

***Dioncomena sanje* Hemp, sp. nov.**

<https://zoobank.org/491B0F5E-501E-4F8B-89AE-184A3CA2CB3E>

Figs 1J–L, 2D, 3C, D, 4G, H, 6A, 8B, 9, 19, 21, 22H, I, 23–25, 27, 30–34, 35B, 36

Type material. *Holotype* male. Tanzania, Mangula, 7°50'38"S, 36°53'08"E, 340 m, lowland wet forest, December 2015. *Paratypes*: 2♂♂, 11♀♀, same data as holotype and March 2015, July 2015, September 2015, January 2016, March 2016, November 2017. Further paratypes: All Tanzania, all Udzungwa Mountains. 7♂♂, 20♀♀, Sanje Trail, lowland wet to submontane forest, August 2019, April 2020, July 2020, October 2020, January and April 2021, May and September 2022. 3♂♂, 1♀, Magombera Forest Reserve, 7°49'12"S, 36°58'42"E, 300 m, lowland forest, January 2019. Depository: CCH.

Description. Male. General Habitus and Color Pattern. The typical *Dioncomena* species can be identified by its contrasting pattern of yellow, white, greenish, and black colors on its general habitus and size (Fig. 1J, K). Head and Antennae. The fastigium of the vertex in the head is compressed and narrower than scapus, sulcate above, and is typical for the genus. Thorax & legs. The pronotum has a posterior part of lateral lobes that are not or only slightly inflated. A black stripe on the pronotum is narrow and widens in metazona, parting between a yellowish triangular field (Fig. 1J, K). The fore coxa is black with a broad-based short yellow spine. The fore

and mid femora have a double row of few small ventral spinules at the apical part, while the hind femur has a double row of few irregularly positioned spines at the apical part. The fore tibia has a ventral double row of irregularly set small spinules and a pair of short ventral spurs. On the dorsal inner side, a short and slender spine is present just below the tympanum, and 1–3 short black spines are along the length. The mid tibiae have a ventral double row of black spinules and three longer black, slender, and clearly hooked spines at the inner ventral apex. Tegmina & wings. Typical shape and coloration for *Dioncomena*. They are black with a yellowish or green field at the base (Fig. 1J, K). The stridulatory file is present on the underside of the left tegmen and is between 1.4–1.6 mm long with around 50 teeth. The teeth are broad and densely set on the inner side, getting continuously narrower towards the apical part of the file, and ending with 8–10 shorter and more widely spaced teeth (Fig. 2D). Abdomen. The tenth abdominal tergite is slightly incurved at the posterior margin with a membranous structure medially (Fig. 3C). The cerci have an apical third that is laterally flattened. The subgenital plate is longer than wide and v-shaped incurved medially (Fig. 3D).

Female. Habitus, size and color pattern are similar to the male (Fig. 1L) but lack hooked spines on the mid tibiae. Ovipositor is short and strongly upcurved (Fig. 4G). Subgenital plate has a broadly-based triangular posterior margin (Fig. 4H).

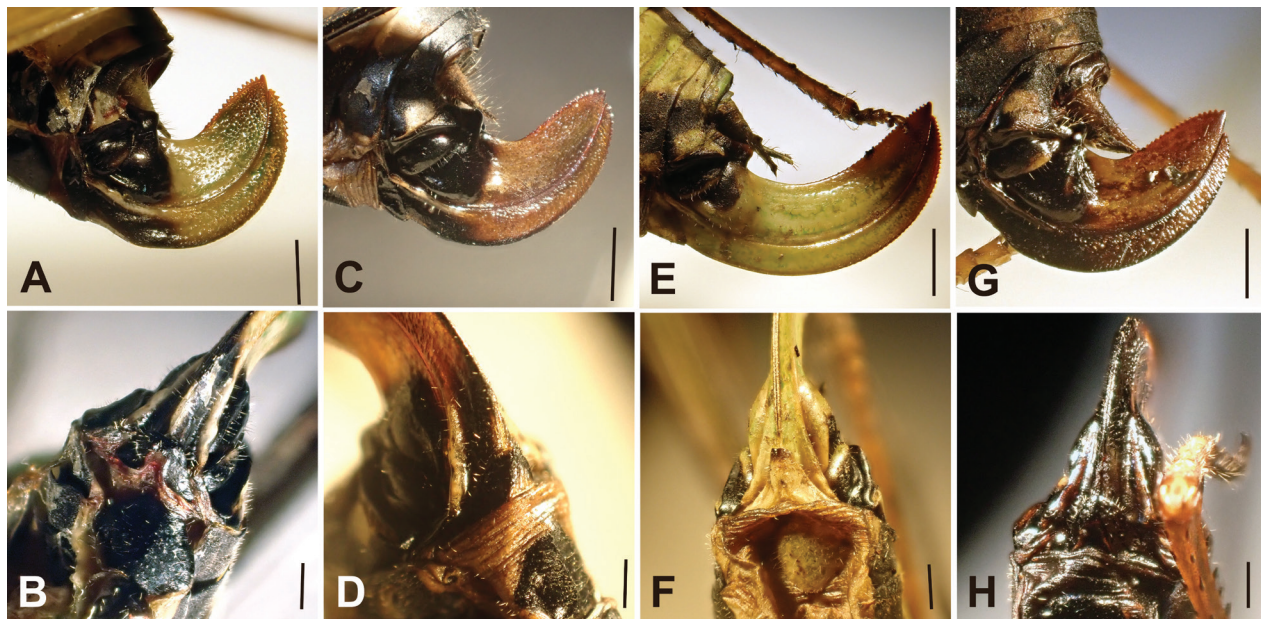


Figure 4. Female *Dioncomena* species. **A, B.** Ovipositor and subgenital plate of *D. jagoi*; **C, D.** Ovipositor and subgenital plate of *D. flavoviridis* sp. nov.; **E, F.** Ovipositor and subgenital plate of *D. magombera* sp. nov.; **G, H.** Ovipositor and subgenital plate of *D. sanje* sp. nov.

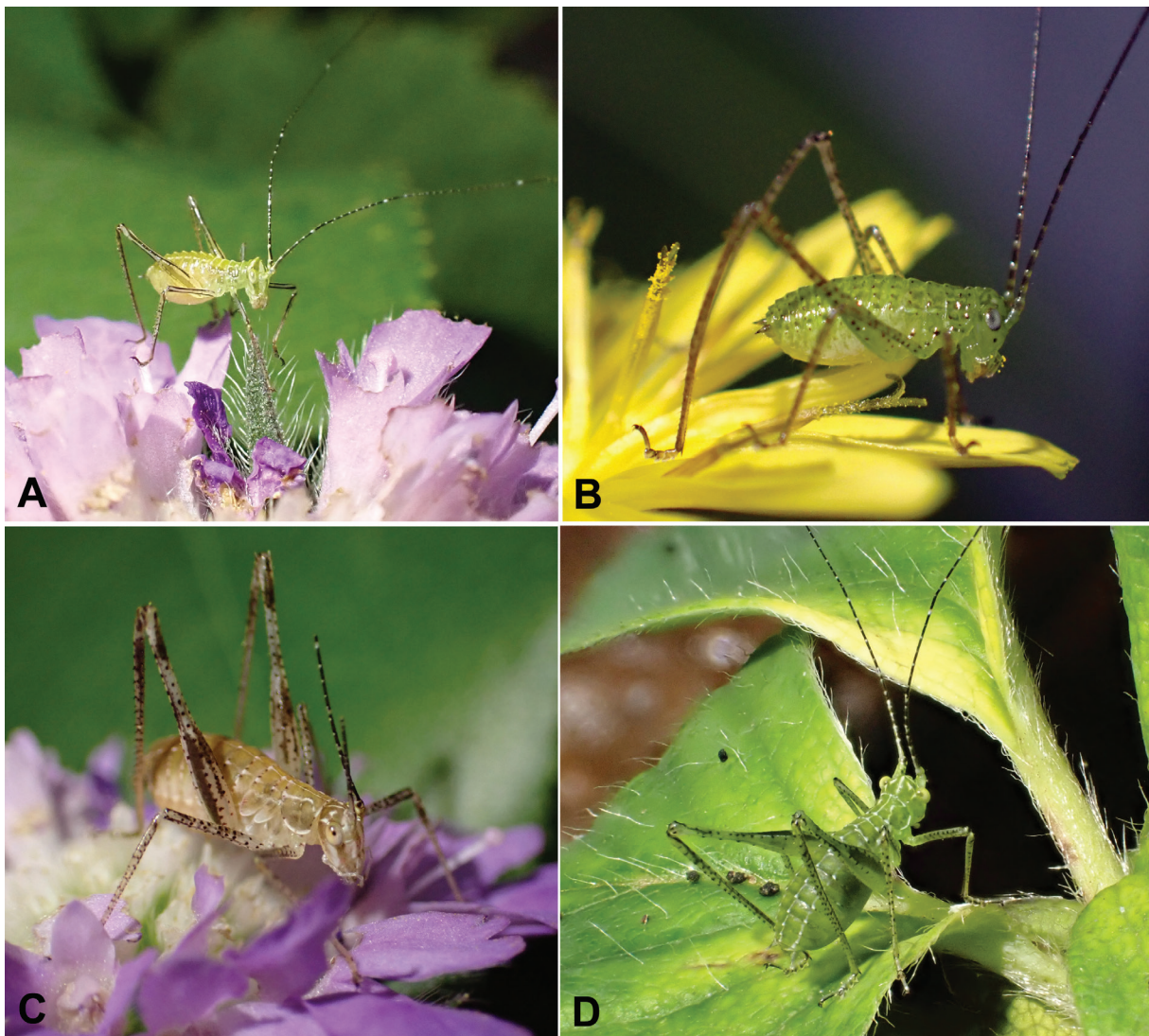


Figure 5. Nymphal stages of *Dioncomena flavoviridis* sp. nov. **A, B.** Freshly hatched nymph; **C.** L3 stage; **D.** L2 stage, about 3 weeks old.

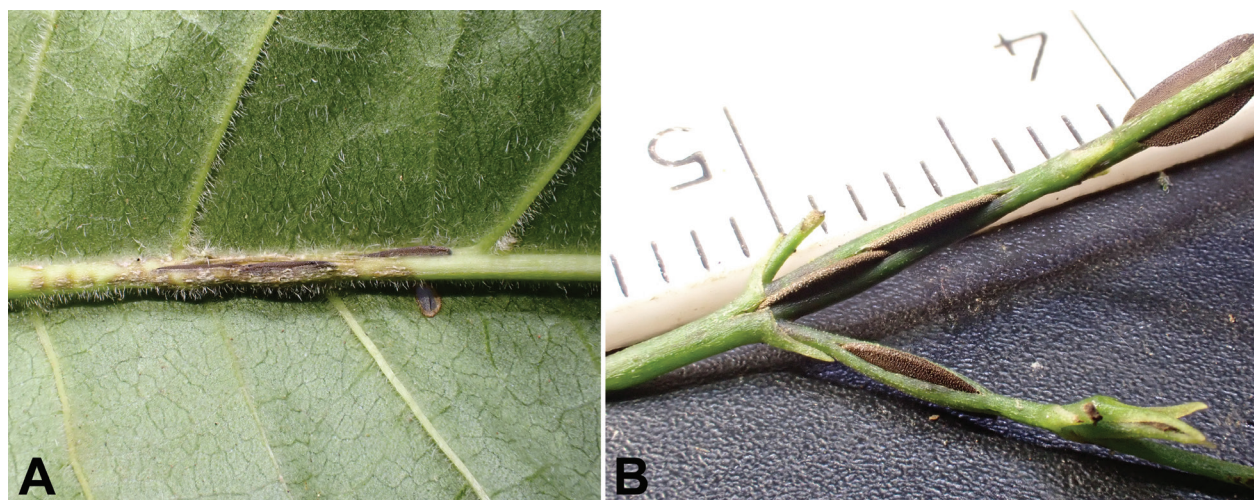


Figure 6. Eggs deposited into the stems of leaves and small branches. **A.** *D. sanje* sp. nov.; **B.** *D. flavoviridis* sp. nov.



Figure 7. Last instar of female *Dioncomena magombera* sp. nov., distinguished by its long ovipositor from *D. sanje* sp. nov. which occurs syntopically.

Nymphs. Freshly hatched nymphs are greenish-yellow with speckles and brown markings along the hind femora (Fig. 9A, B). Nymphs grow in size until stage three without changing their habitus (Fig. 9C, about two weeks old, probably stage 2). From stage 3, wings become visible and grow larger with each stage. Depending on the environment, nymphs may become more greenish or gain more brown colors (Fig. 9D, F). From stage 5 onwards, wings are clearly visible and are slightly inflated a day or so before molting to an adult (Fig. 9E).

Measurements, (mm) males ($n = 3$). Body length 12.8–14.8. Length of pronotum 3.2–3.8. Length of tegmina 23.0–25.6. Length of hind femur 17.11–17.3.

Measurements, (mm) females ($n = 6$). Body length 14.0–16.5. Length of pronotum 3.1–3.3. Length of tegmina 25.0–27.5. Length of hind femur 18.0–20.2. Ovipositor 4.2–4.6.

Biology. The eggs are oval and black and are deposited in the midribs or stems of leaves (Fig. 6A). Eggs laid by a female in October 2020 hatched at the end of February

2021, 4 months later, and developed into adults at the beginning of June 2021. A female collected in April 2021 laid numerous eggs in stems on April 24, which hatched on July 7, 2021. Most individuals were captured in the Udzungwa Mountains during the warm months, from December to March, but single adults were also obtained from July to September, indicating that the species is present year-round. Like the other species studied (*D. flavoviridis* sp. nov. and *D. ornata*), males transfer only very small spermatophores to females during mating (Fig. 8B).

Song. See Bioacoustics.

Habitat and distribution. The species inhabits lowland wet to submontane forests. Individuals were mostly collected as single specimens in the understory vegetation of closed forests. Its distribution is restricted to Tanzania's Udzungwa Mountains.

Etymology. The species is named after the Sanje Trail in the Udzungwa Mountains National Park and is a noun in apposition.

Diagnosis. The four species of *Dioncomena* (*D. jagoi* from the East Usambara Mountains, *D. flavoviridis* sp. nov. from the Nguru Mountains, *D. sanje* sp. nov. from the Udzungwa Mountains, and the widespread *D. magombera* sp. nov.) are morphologically similar, sharing a similar color pattern (Fig. 1). However, there are several distinguishing features. The pronotal lobes in *D. magombera* sp. nov., *D. flavoviridis* sp. nov., and *D. jagoi* are uniformly bright yellow or yellow-green, while both sexes of *D. sanje* sp. nov. have a large central diffuse formed black patch on the pronotal lobes. The 10th abdominal tergite of males is very similar in the four species of the *D. jagoi*-group, being incurved and with a more or less conspicuous membrane between the edges (although it is very shallow in *D. magombera* sp. nov.). The male cerci are mostly green with black incurved tips, but in *D. sanje* sp. nov., the last third or so of the male cerci is laterally flattened, and in *D. magombera* sp. nov., the black tips of the male cerci are hooked inwardly. The pronotal lobes are laterally considerably inflated in *D. flavoviridis* sp. nov. and *D. jagoi*, but less so in *D. sanje* sp. nov. and *D. magombera* sp. nov. In *D. flavoviridis* sp. nov., the hind femur has a ventral



Figure 8. *Dioncomena* females with spermatophores immediately after mating. **A.** *D. flavoviridis* sp. nov.; **B.** *D. sanje* sp. nov.; **C.** *D. ornata*.

black stripe reaching to about the middle or covering more than half of the outer side of the femoral area (Fig. 1D). The outer side of the hind femur is black in *D. jagoi* distally, then turns yellow or green and gets black again basally at the joint with the coxa (Fig. 1A, B), similar to the femoral pattern of *D. magombera* sp. nov. The yellow or green area on the outer side of the hind femur is often more diffuse and smaller in *D. sanje* sp. nov. (Fig. 1J, K). Additionally, *D. ugandana* sp. nov. could belong to the *jagoi*-group because of its general color pattern and the outer genitalic morphology of the male apex. The pronotum is largely deep black with a yellow stripe at the anterior margins of the lateral pronotal lobes (Fig. 10A). In *D. flavoviridis* sp. nov., the black median fascia on the pronotum is solid and broad, a bit narrower along the pro- and mesozona of the pronotum, then extending to cover the whole disc of the metazona (Fig. 1D, E). The central black fascia of *D. jagoi* is much narrower (Fig. 1B). In *D. sanje* sp. nov., the black fascia is also broad and solid but fuses with the black patches of the pronotal lobes on both sides (Fig. 1J, K). In *D. sanje* sp. nov. as well as in *D. magombera* sp. nov., the black fascia parts at the anterior base of the metazona into two stripes leaving a green or yellow-green triangular patch on the disc of the metazona (Fig. 1H, J). While in *D. sanje* sp. nov. the black median stripe of the pronotum is solid, in *D. magombera* sp. nov. a fine central green or yellowish line is present throughout the whole course of the black fascia (Fig. 1H). Characters distinguishing the other species and groups of *Dioncomena* are provided in the key. For song description see Bioacoustics section.

***Dioncomena ugandana* Hemp, sp. nov.**

<https://zoobank.org/57973B18-DC63-4C13-8317-3D1EA0B54ED3>

Figs 10, 11, 36

Type material. *Holotype* male, Uganda, Bwamba Valley, VII 1921, G.D.H. Carpenter, Pres. By Imp. Bur. Ent. Brit. Mus. 1927-77. Depository: BMNH.

Paratypes: 1♀, same data as holotype. 1♀, Bugoma Forest, 21. VI 1933, H. B. Johnston. 1♂, Toro¹, 4000–4500 ft., 25–29. Dec 1911, S.A. Neave, BM 1912-192; 1♀, Mabira forest, 28.6.1913, CC Gowdey, BM 1927-77; 1♀, Mabira forest, Chagwe, 17.-20.7. 1911. Depository: BMNH.

Description. Male. General Habitus and Color Pattern: Typical *Dioncomena* species in terms of its general habitus and size, with a contrasting pattern of yellow and black colors (Fig. 10A, B). The black fascia of the pronotum is solid and very broad, covering the entire disc of the pronotum and parts of the lateral lobes, leaving only a yellow stripe along the anterior lateral lobes and a small yellow patch at the posterior margin of the pronotum. Around the fastigium verticis, a triangular area is yellow while the remaining head is black, except for a thin line posterior to the fastigium, running to the anterior margin of the pronotum (Fig. 10B), and two broader yellow fasciae parallel on the face. Head & antennae. The fastigium of the vertex is typical for the genus, compressed, narrower than scapus, and sulcate above. Thorax & legs. The pronotum has an inflated posterior part of lateral lobes. The fore coxa is black with a very short, stout black spine. The fore and mid femora are unarmed, while the hind femur has very few small spines at the apical part. The fore tibia has a ventral double row of few irregularly set small spinules and a pair of short ventral spurs. The mid tibiae have a double row of spines near the distal end of the tibia, with four hooked spines on the outer dorsal side. The hind tibiae have a dorsal double row of spines, ventral rows with only a few spines set irregularly at the apical part, and three short spurs on each side. Tegmina & wings. The tegmina and wings have a typical shape and coloration for *Dioncomena*, black with a yellowish or green field at the base. The left tegmen is missing in the holotype, and the stridulatory area is destroyed in the male paratype. Abdomen. The tenth abdominal tergite is incurved at the posterior margin with a membranous structure medially (Fig. 10C). The cerci are yellow, round with strongly inwardly curved black-tipped apices. At the apical third

¹ The label reads Daro or Durro Forest and Toro. Toro is a region in the west of Uganda and could refer to the Toro Semliki Wildlife reserve.

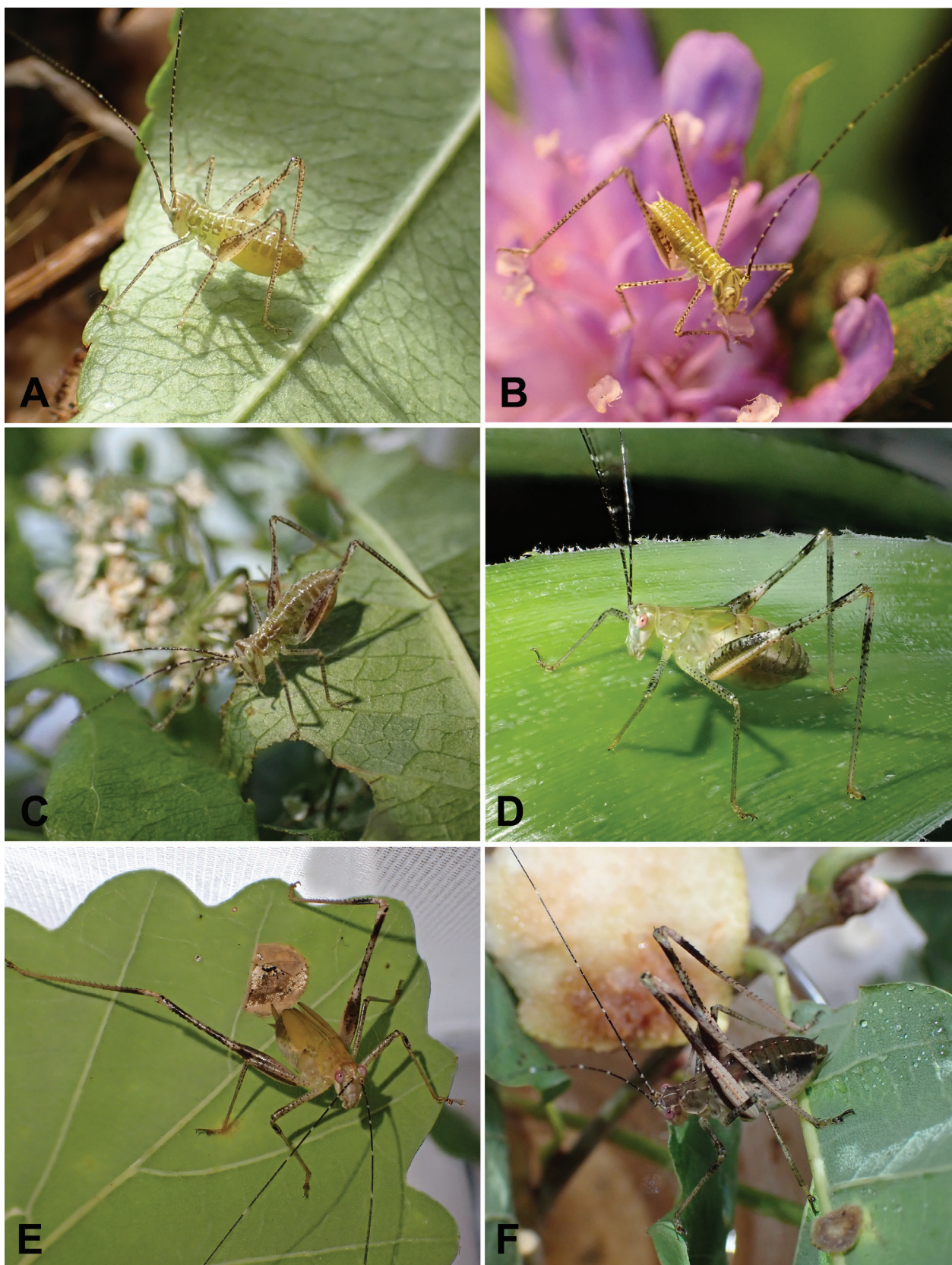


Figure 9. Nymphal stages of *Dioncomena sanje* sp. nov. **A, B.** Freshly hatched nymph; **C.** Nymph about 2 weeks old; **D, F.** L4 stage with wings visible, two different colour forms; **E.** L5 stage, female, shortly before molting to adult.

cerci, on the inner side, there is a small groove (Fig. 10C). The subgenital plate is longer than wide and v-shaped, incurved medially (Fig. 10D).

Female. Habitus, size, and color pattern similar to male with larger yellow spot on the posterior part of the pronotum (Fig. 11A, C). Yellow area at the anterior mar-

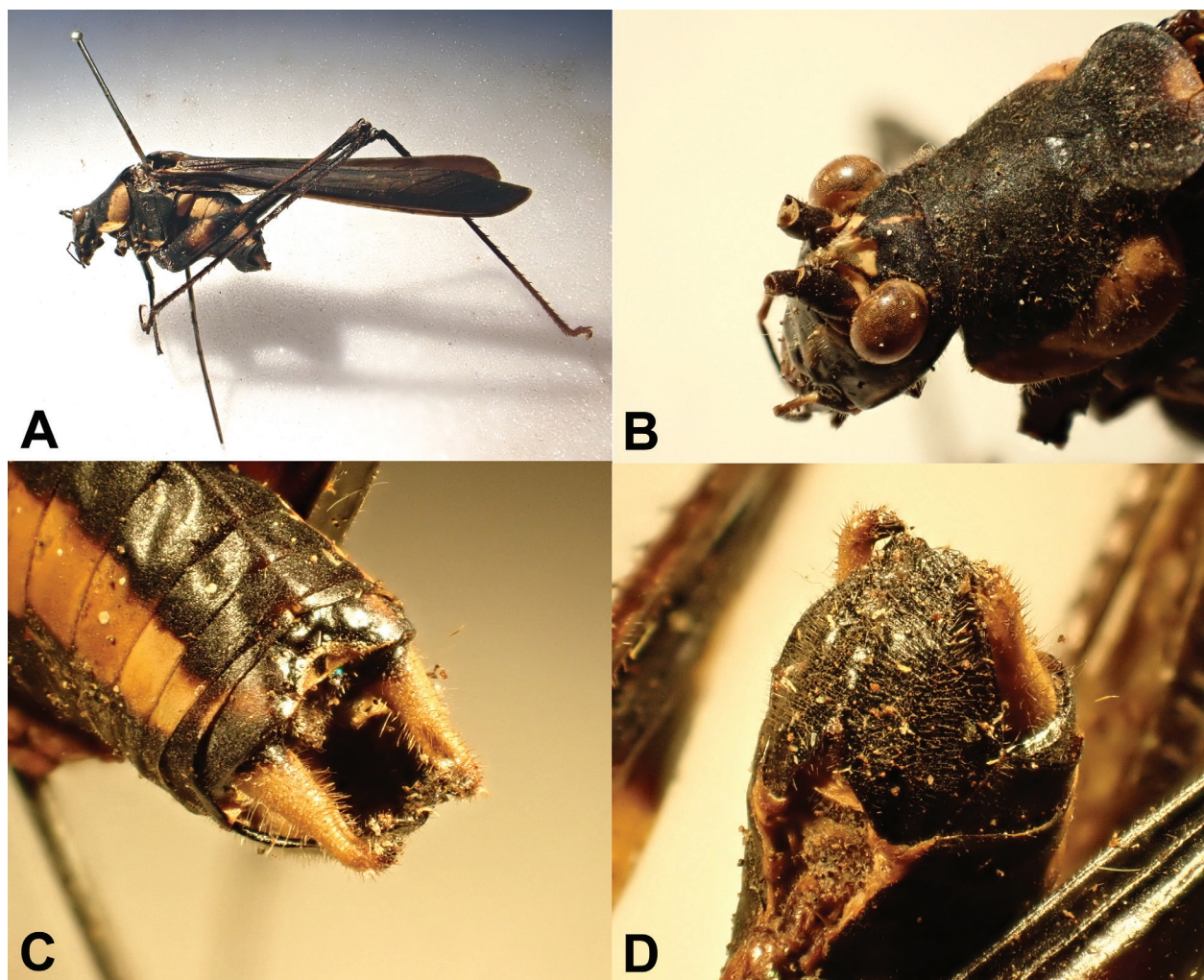


Figure 10. Male holotype of *Dioncomena ugandana* sp. nov. **A.** Habitus; **B.** Head and pronotum; **C.** Dorsal view on apex; **D.** Subgenital plate.

gins of the pronotal lobes is not neatly confined and the margins are uneven and undulating between the yellow and black areas in females (Fig. 11B). Leg spination similar to male but without hooked dorsal spurs on mid tibiae. Ovipositor short and strongly upcurved, basal part black, remaining part yellow (Fig. 11D). Subgenital plate broad-based with triangular posterior margin, median v-shaped incision, and small lateral styli (Fig. 11E).

Measurements, (mm) males ($n = 2$). Body length 15.0–16.0. Length of pronotum 3.2–3.9. Length of tegmina 25.3–26.2. Length of hind femur 17.

Measurements, (mm) females ($n = 4$). Body length 15.5–17.5. Length of pronotum 3.2–3.4. Length of tegmina 26.0–26.5. Length of hind femur 16.8–18.0. Ovipositor 4.8–5.2.

Habitat and distribution. The holotype was found in the Bwamba valley, an area located between Lake Albert in the north and Lake Edward in the south, with the Semuliki National Park in the northwest. This region has an elevation ranging from about 700 to 800 m a.s.l. and is characterized by lowland wet forest.

Song. Unknown.

Etymology. Named after the country Uganda.

***Dioncomena ngurumontana* Hemp, sp. nov.**

<https://zoobank.org/64E8E74D-BE3F-47D0-82B3-EC17943103DF>

Figs 2J, 12, 13E, F, 14, 19, 21, 22P, 23–25, 28E, F, 30, 36

Type material. *Holotype* male. Tanzania, Nguru Mountains, montane forest above Dibago/Maskati, 6°03'05"S, 37°29'09"E, 1950 m, November 2021. Depository: CCH.

Paratypes. 2♂♂, 3♀♀, same locality as holotype. 2♀♀, same locality as holotype but February 2022. Depository: CCH.

Description. Male. General habitus and color pattern. *Dioncomena* species with a very colourful pattern of black tegmina with a blue or greenish field at the basal part, a black and white patterned head, and a pronotum with a central turquoise blue or green line, bordered by irregular black lines and interrupted medially by a black line as well (Fig. 12A, B). Part of the disc and lateral lobes of the pronotum partly yellow, at the lower margin again green or turquoise with an irregular longish black patch. Legs are black except for the hind femora that are of light brown colour at their inflated basal parts. The abdomen is striped green or blue and black. Head and antennae. Fastigium of vertex typical

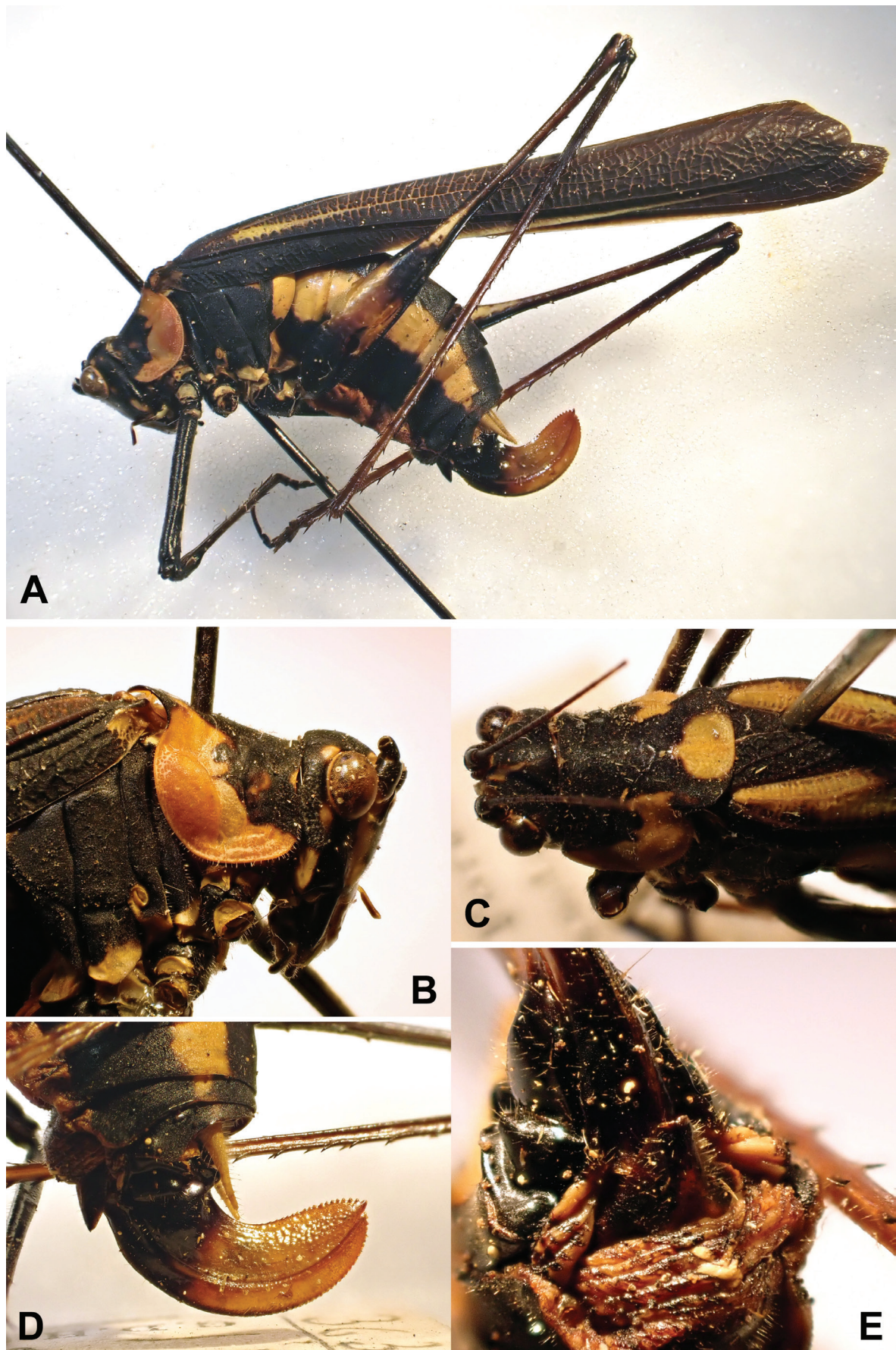


Figure 11. Female *Dioncomena ugandana* sp. nov. **A.** Habitus; **B.** Lateral view on head and pronotum; **C.** Dorsal view on pronotum; **D.** Ovipositor; **E.** Subgenital plate.

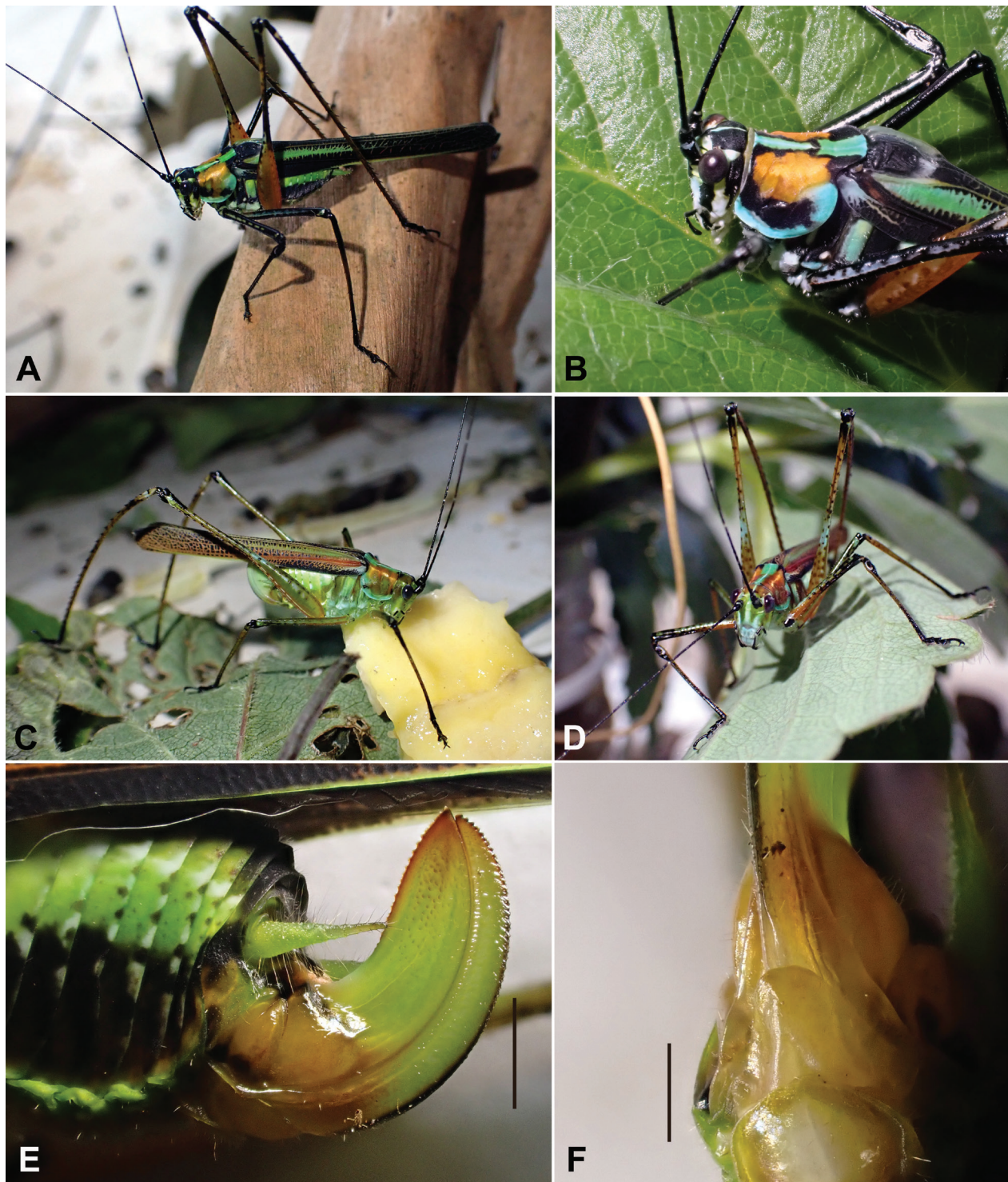


Figure 12. *Dioncomena ngurumontana* sp. nov. **A, B.** Male; **C, D.** Female; **E, F.** Morphological details of female *D. ngurumontana* sp. nov., ovipositor (**E**) and subgenital plate (**F**).

for the genus, compressed, narrower than scapus, sulcate above. Thorax & legs. Pronotum with posterior part of lateral lobes not markedly inflated. Fore coxa without a spine. Fore, and mid femora unarmed, hind femur only at apical slender part ventrally with few very small spines. Fore tibiae ventrally with double row of very few and irregularly set small spinules and a pair of short ventral spurs. Mid tibiae with ventral double

row of very few spinules, spinules at apical part only very slightly hooked; few spinules also apically on dorsal side of mid tibiae. Hind tibiae with dorsal double row of spines getting denser apically and double row of irregular set spines also on dorsal side in apical third of the tibiae. Tegmina & wings. Typical for *Dioncomena*, narrow, tegmina black with an elongated blue or green field at base (Fig. 12A, B). Stridulatory file on the un-

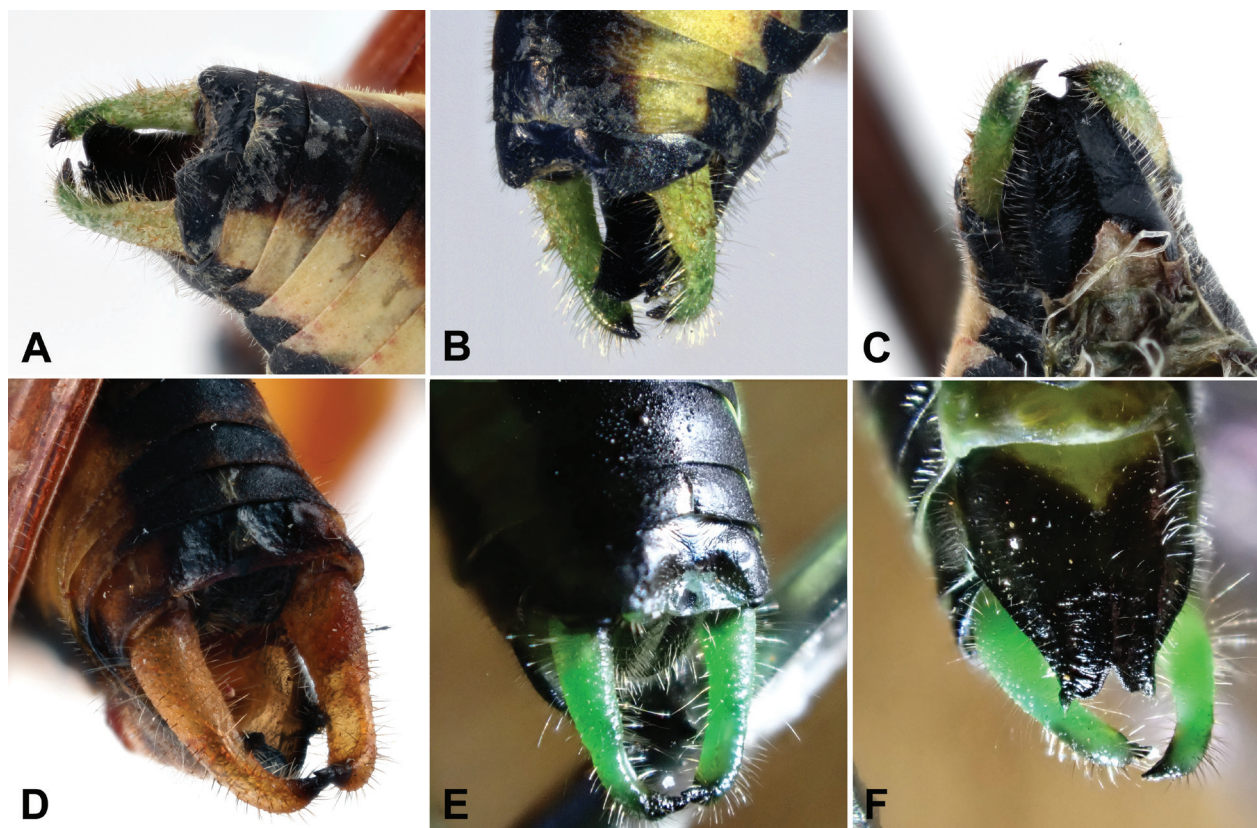


Figure 13. Morphological details of male *Dioncomena* species A–C. *D. versicolor* sp. nov., semilateral view on apex (A, B) and subgenital plate (C) Dorsal view on apex of *D. tanneri* (D), apex (E) and subgenital plate (F) of *D. ngurumontana* sp. nov.



Figure 14. Last instar nymph of *D. ngurumontana* sp. nov.

derside of left tegmen about 1.1 mm long with about 45 teeth ($n = 1$); teeth densely set along length, apically teeth getting smaller and are more widely set (Fig. 2J). Abdomen. Tenth abdominal tergite black, incurved at posterior margin (Fig. 13E, F). Cerci laterally flattened, especially at apex, green with a black tip (Fig. 13E, F). Subgenital plate longer than wide, with v-shaped incision in the middle, beside the incision short slender styli-like processes (Fig. 13F).

Female. With a similar habitus as the male, but with a different color pattern consisting mainly of greenish hues on the head, body, and hind femora (Fig. 12C, D). The pronotal lobes are bordered in bluish to turquoise,

but less prominent than in the male. The pronotal disc and lobes are yellowish to hazel brown, similar to the male. Unlike the male, the tegmina are of greenish to brown color, without the black base and turquoise or green stripe. The ovipositor is green and strongly upcurved (Fig. 12E), while the subgenital plate forms a flap with an evenly rounded posterior margin (Fig. 12F).

Nymphs. The nymphs resemble the adults, but with an inconspicuous greenish coloration with some dark spots on the legs and white dots on the abdomen (Fig. 14).

Measurements, (mm) males ($n = 3$). Body length 12.0–14.7. Length of pronotum 3.2–2.4. Length of tegmina 20.0–21.5. Length of hind femur (one individual with hind femora) 16.

Measurements, (mm) females ($n = 3$). Body length 9.8–15.5. Length of pronotum 2.9–3.3. Length of tegmina 18.5–20.8. Length of hind femur 15.8–16.6. Ovipositor 4.7–5.0.

Phenology. Nymphs were observed in November 2021 on sunny patches along a forest path. Most nymphs were in stages L4 and L5, with only a few smaller nymphs seen. L5 nymphs collected from the forest molted to adults in captivity about one week later. Similar to *D. tanneri*, it is likely that the hatching of *D. ngurumontana* sp. nov. is triggered by rising temperatures from September onwards. This species probably forms only one generation per year as an adaptation to the montane zone.

Song. See Bioacoustics.

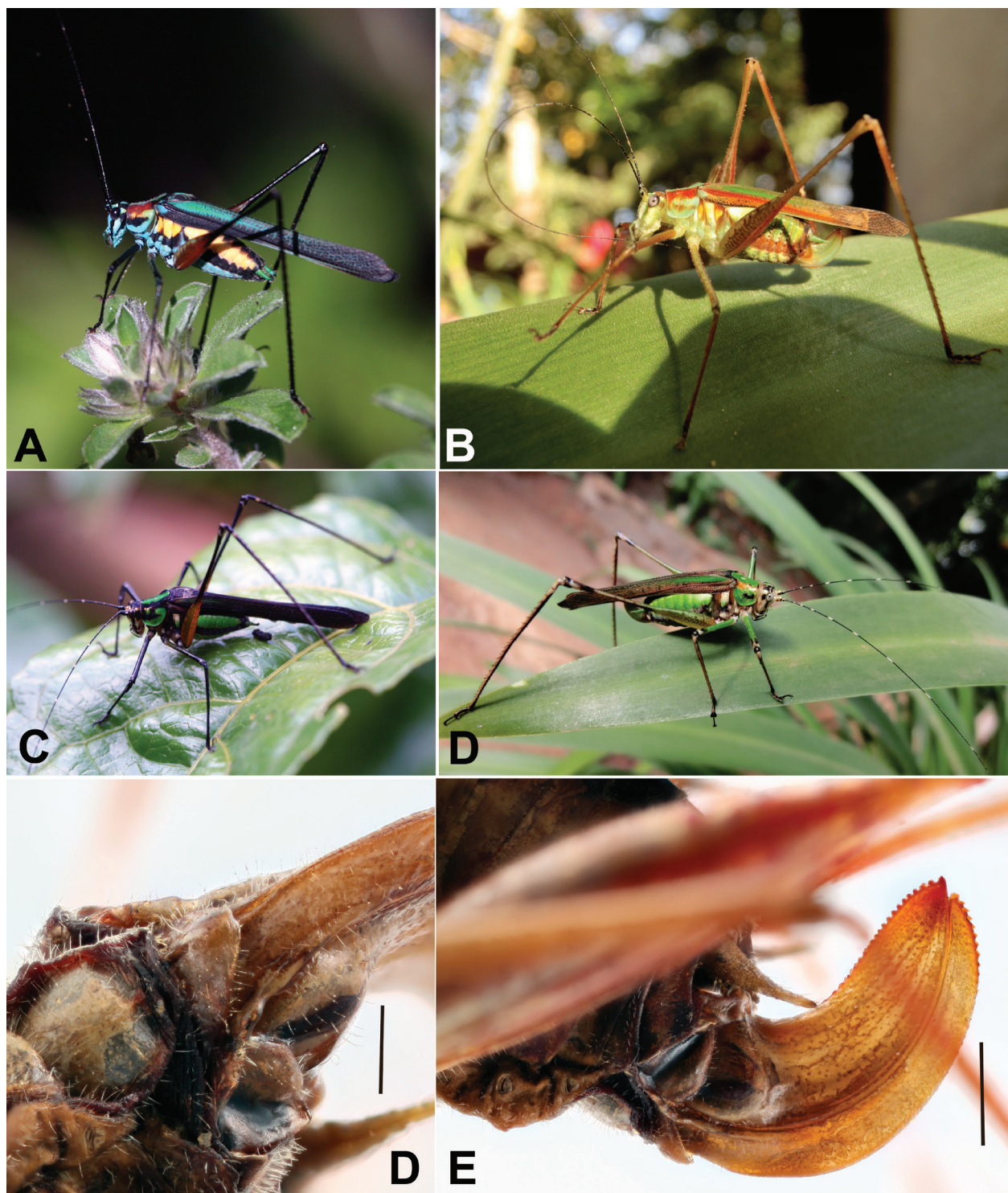


Figure 15. Habitus of male (A) and female (B) *D. versicolor* sp. nov. and male (C) and female (D) *D. tanneri*. Morphological details of female *D. versicolor* sp. nov., subgenital plate (E) and ovipositor (F). Scale bars: 1 mm.

Habitat and distribution. *D. ngurumontana* sp. nov. was found on forest paths and clearings in the montane zone (1850–2000 m). The collected individuals were found clustered together, with adult individuals and nymphs collected sitting nearby on single bushes or herb vegetation. This species is found in the Nguru Mountains of Tanzania.

Etymology. This species is named after the Nguru Mountains and the montane zone in which it occurs.

***Dioncomena versicolor* Hemp, sp. nov.**

<https://zoobank.org/9A696474-1FB6-4318-8412-94A41C74F076>

Figs 2I, 13A–C, 15A, B, D, E, 19, 21, 22O, 26I, J, 30, 36

Type material. *Holotype* male. Tanzania, Uluguru Mountains, montane forest above Morningside, 6°53'46"S, 37°40'14"E, 1600 m, February 2016. *Paratypes*. 2♂♂, 2♀♀, same locality as holotype and February 2017 and March 2020. Depository: CCH.

Description. Male. General habitus and color pattern. Small for *Dioncomena* but with a typical habitus for the genus and a striking color pattern. Head and pronotum blue with black lines or stipes. The pronotum has a green median part bordered by red-brown fasciae, with a longitudinal black stripe in the midline of the pronotal lobes, and the remaining part of the lateral lobes is blue. The abdomen has a yellow broad fascia on the lateral sides, bordered by black fascia, and a median black fascia on the tergites, with a blue venter. The legs are predominantly black, with the hind femora's basal parts in red-brown (Fig. 15A). Head & antennae. The fastigium of the vertex is compressed, narrower than the scapus, and sulcate above, typical for the genus. Thorax & legs. The posterior part of the lateral lobes is not markedly inflated. The fore coxa lacks a spine, only a blunt knob is present. The fore, mid, and hind femora have only a few very tiny spinules ventrally in the apical area. The fore tibia has a ventral double row of irregularly set small spinules and a pair of short ventral spurs. The mid tibiae have a ventral double row of black spinules, with the apical part's spinules only slightly hooked. Tegmina & wings. The tegmina and wings are black with an elongated blue field at the base (Fig. 15A). The stridulatory file on the underside of the left tegmen is about 1 mm or less long, with around 54–55 teeth. The teeth are densely set along the length, with the apically teeth getting smaller and more widely set. The file is slightly downcurved in its apical part (Fig. 2I). Abdomen. The tenth abdominal tergite is black and incurved at the posterior margin (Fig. 13A, B). The cerci are laterally flattened, especially at the apex, green with a black tip (Fig. 13A–C). The subgenital plate is longer than wide, u-shaped incurved medially (Fig. 13C).

Female. The female has a similar habitus to the male but lacks the male's colorful pattern, with mostly brown-red and green colors. The head, pronotum, tegmina, and body lack the blue parts present in males, and the tegmina are brown rather than black (Fig. 15B). The ovipositor is small and upcurved (Fig. 15F), and the subgenital plate is small, triangular, with an evenly curved posterior margin (Fig. 15E).

Measurements, (mm) males ($n = 3$). Body length 10.4–11.5. Length of pronotum 3.1–3.3. Length of tegmina 18.5–19. Length of hind femur 15.5–16.0.

Measurements, (mm) females ($n = 2$). Body length 11.5–13.5. Length of pronotum 2.8–3.0. Length of tegmina 17.7–18.0. Length of hind femur 16.1–16.2. Ovipositor 4.5–4.6.

Phenology. Similar to *D. ngurumontana* sp. nov. and *D. tanneri*, this species likely has only one generation per year, which is an adaptation to the cooler temperatures found in montane elevations. Adult specimens were only collected twice, in February 2016 and March 2020. During all other months when the forest was visited (March, April, June, August, November 2016, February, November 2017, April 2019, October 2020), no adult specimens were observed.

Habitat and distribution. This species can be found in montane forests (1800–2100 m) along open paths and clearings in the Uluguru Mountains of Tanzania.

Song. See Bioacoustics.

Etymology. Named for its distinct and colorful pattern, as reflected in its Latin name, *versicolor*, which means variegated or colorful.

Diagnosis. *D. versicolor* sp. nov. and *D. ngurumontana* sp. nov. are similar in morphology, but can be differentiated by the number of teeth on the male stridulatory files (over 50 in *D. versicolor* sp. nov. and 32 in *D. ngurumontana* sp. nov.) and overall color pattern, which is a stable character in *Dioncomena*. Both species are the sister group to *D. tanneri*, endemic to the Usambara Mountains (Fig. 15C, D). *D. tanneri* has a compact stridulatory file with about 35 teeth, similar to *D. ngurumontana* sp. nov. All three lack a median dark stripe on the pronotum, but have a blue (males of *D. versicolor* sp. nov. and both sexes of *D. ngurumontana* sp. nov.) or green (females of *D. versicolor* sp. nov. and both sexes of *D. tanneri*) colored medial area bordered by brownish fasciae mottled or bordered with white or black areas, while the rest of the pronotum is green, blue, yellow, or hazel (see Figs 12, 15). The tenth abdominal tergite and male cerci are similar in all three species (Fig. 13). See key for differentiation from other species. For song descriptions see Bioacoustics section.

D. zernyi Ragge, 1980

Figs 2G, 16, 19, 21, 22M, 26E, F, 30, 36

Note. Ragge (1980) only described the male of *D. zernyi* from a single specimen collected at Lake Malawi (Lake Nyasa, Randberge) and did not describe the female, as the only individual that could have been conspecific with the new species was collected at another locality (near Songea) and differed considerably in size and general color pattern (stored in NHMW). We collected a large series of both males and females of *D. zernyi* in the Udzungwa Mountains, where it is a common species, and describe the female here. Further information on this species is also given in Hemp (2021).

Both male and female *D. zernyi* are colorful, with a pattern of black tegmina, a green body, and legs with some white, yellowish, and blue parts (Fig. 16A–D). Males especially have bluish parts on the pleura, face, and cerci (Fig. 16A). A dark stripe is present dorsally on the pronotum, ending at the margin to the metazona of the pronotum, and not reaching the posterior margin of the pronotum (Fig. 16D). The hind tibiae are uniformly light brown in both sexes.

The male of *D. zernyi* is characterized mainly by its ninth abdominal tergite, which is produced posteriorly, covering most of the tenth abdominal tergite (Fig. 17A). Additionally, the last few tergites are profusely hairy above. The 10th abdominal tergite is raised at its posterior margin and has a deep, circular gap in the middle. The male cerci are rather thick and densely covered with hairs. The stridulatory file is slightly undulating with large and widely set teeth on its inner side, about 10 very densely set teeth in the middle, and smaller and again more widely set teeth at its apical part (Fig. 2G). The file has about 42–45 teeth.

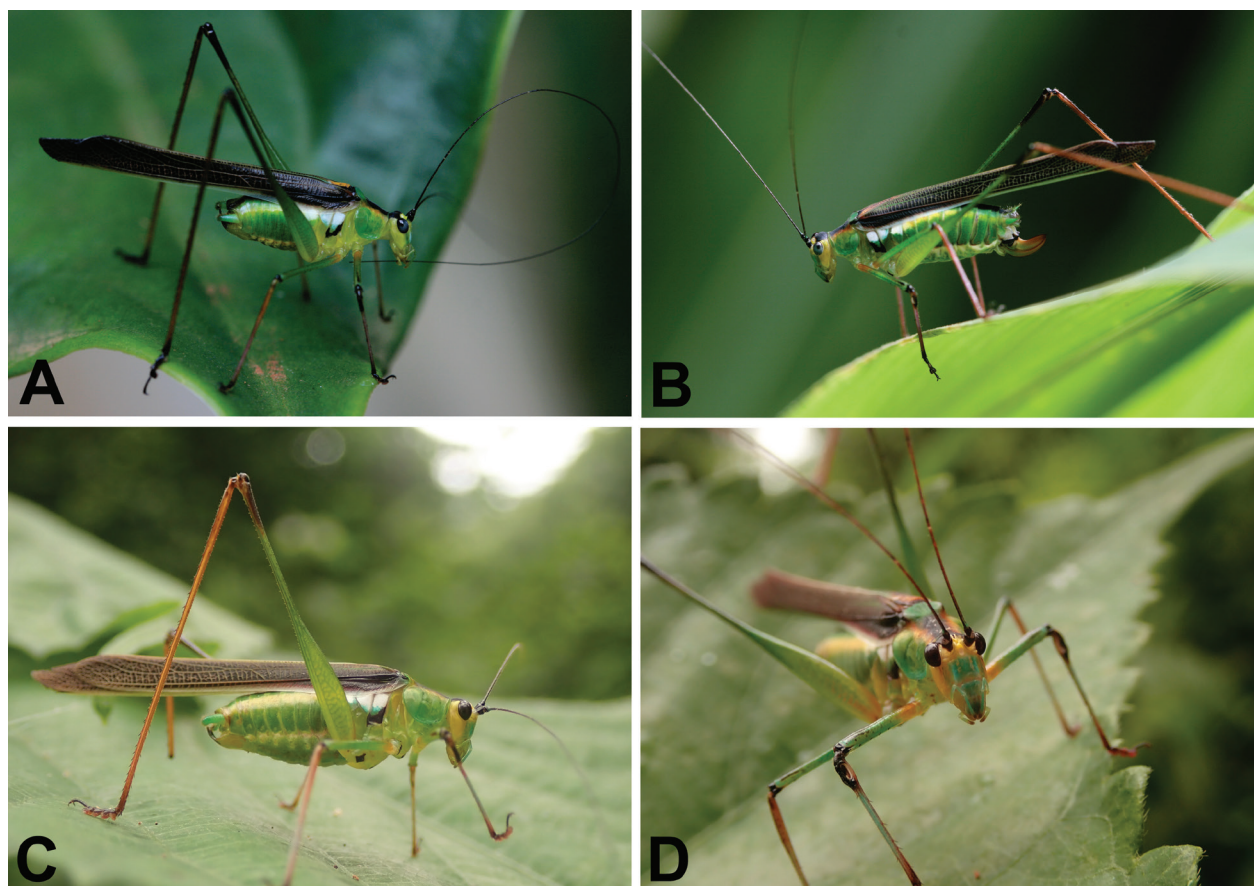


Figure 16. Male (A, C, D) and female (B) *Dioncomena zernyi*.



Figure 17. Morphological details of *D. zernyi*. A. Lateral view on male apex; B. Ovipositor; C. Female subgenital plate.

Material examined. All Tanzania: 13♂♂, 10♀♀, Udzungwa Mountains, Mangula Gate, 7°50'38"S, 36°53'08"E, 340 m, lowland wet forest, 300 m, March 2015, July 2015, September 2015, December 2015, January 2016, February 2016, March 2016, May 2016. 5♂♂, 6♀♀, Udzungwa Mountains, Sanje Trail, 7°46'08"S, 36°54'16"E, 450 m, lowland wet to submontane forest, August 2019, November 2019, April 2020, July 2020, October 2020. 2♀♀, Udzungwa Mountains, Kihansi Forest Reserve, 8°36'35"S, 35°51'08"E, 370 m, January 2016. 2♂♂, 2♀♀, Magombera Forest Reserve, 7°49'10"S, 36°58'42"E, 280 m, lowland forest, 300 m, January 2019. Depository: CCH.

Description of the female. In habitus, size and color pattern similar to the male (Fig. 16B). The ovipositor is typical for the genus, rather small and upcurved, serrated at the valves (Fig. 17B). The subgenital plate is triangular with a v-shaped indentation at its posterior margin (Fig. 17C).

Measurements, (mm) males (n = 6). Body length 14.4–15.5. Length of pronotum 3.1–3.2. Length of tegmina 22–24. Length of hind femur 18.5–19.1.

Measurements, (mm) females (n = 6). Body length 17.2–18. Length of pronotum 2.7–3.2. Length of tegmina 22.5–25. Length of hind femur 19.7–21.0. Ovipositor 4.1–4.4.

Biology. *D. zernyi* individuals were frequently observed in groups on forest paths and clearings. Males, similar to *D. ornata*, often perched openly on branch tips while females were spotted in lower vegetation nearby.

Habitat and distribution. *D. zernyi* inhabits lowland wet to submontane forests and is found in the Udzungwa Mountains of southern Tanzania, which is also the type locality according to Ragge (1980).

Song. See Bioacoustics.

Diagnosis. Male *D. zernyi* can be easily distinguished by the produced 9th abdominal tergite and the dense cover

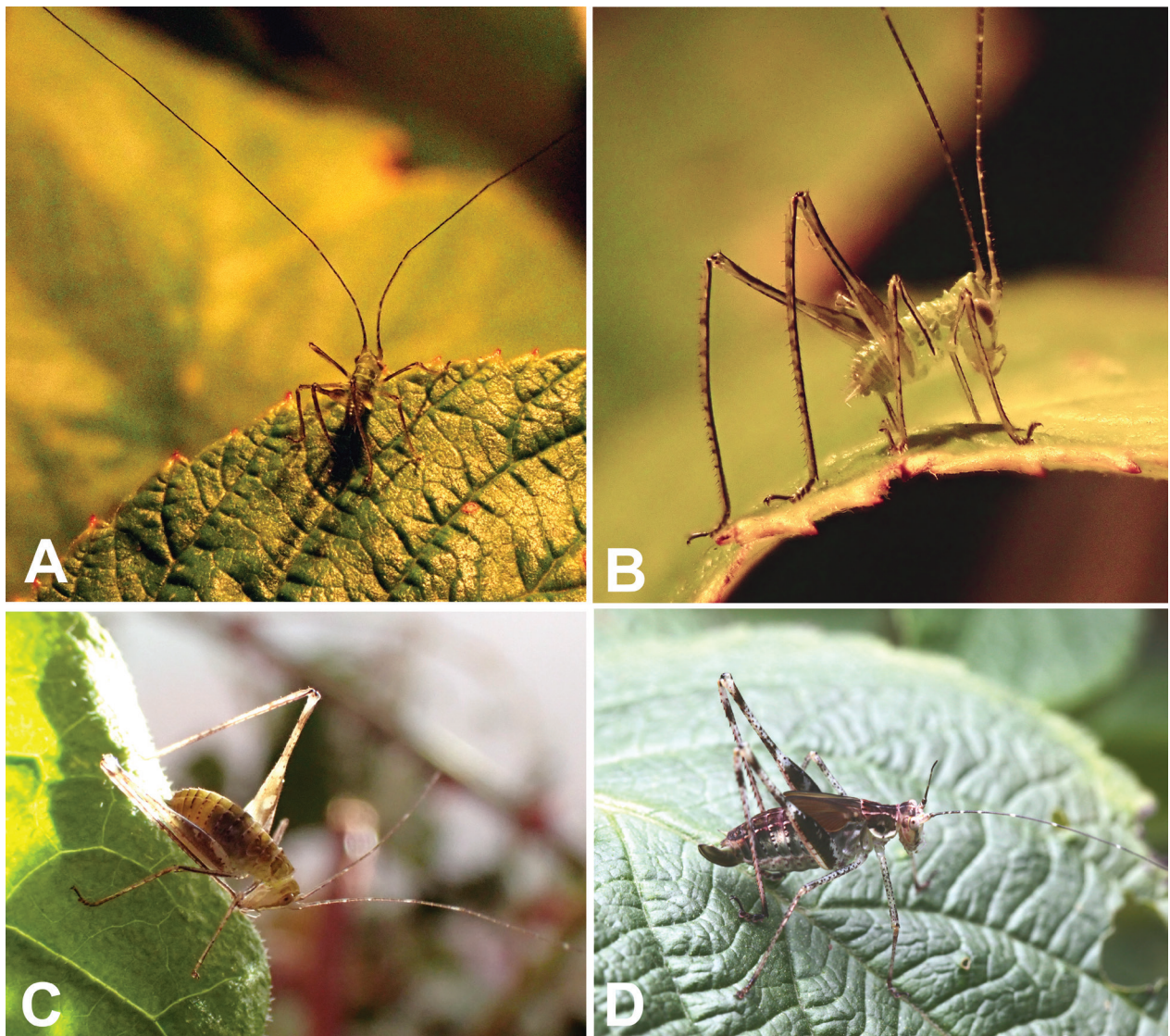


Figure 18. Nymphal stages of *Dioncomena ornata*. **A, B.** Freshly hatched L1, Magoroto Forest Estate, East Usambara Mountains; **C.** L3 stage; **D.** L5 nymph.

of hairs on the last few tergites. Females exhibit a coloration pattern similar to males and have a V-shaped subgenital plate that is indented at its posterior margin (Fig. 17C). Syntopic species belonging to the *D. jagoi*-group, such as *D. magombero* sp. nov. and *D. sanje* sp. nov., have entirely different coloration patterns.

***Dioncomena ornata* Brunner von Wattenwyl, 1878**

Figs 2F, 18, 19, 21, 22J–L, 23, 24, 25, 28A–C, 30, 35C, D, 36

Dioncomena superba Karsch, 1889. Syn.

Biology. Female *Dioncomena ornata*, as well as *D. flavoviridis* sp. nov., *D. tanneri*, and *D. sanje* sp. nov., deposit their eggs into the ribs of leaves or stems of small branches. A female collected from Kazimzumbwi Forest Reserve near the coast of Dar es Salaam deposited eggs in December 2015, with the first nymphs hatching in February 2016 and molting into adults in April 2016.

Another female collected from Magoroto Forest Estate in the East Usambara Mountains laid eight eggs into the midrib of a leaf on August 31, 2019. The first L1 nymph hatched on November 3, 2019, while the last nymph emerged on December 30, 2019, almost two months later. It takes about two to four months for nymphs to develop into adults (Fig. 18).

In the field, individuals of *D. ornata* were often observed in clusters on certain bushes, with males perched at the tops of branches and females gathering further down. In contrast to *D. flavoviridis* sp. nov. and *D. sanje* sp. nov., males of *D. ornata* transfer only small spermatophores to females during mating. However, in the three observed copulations, the process lasted 60 minutes or longer, unlike the other two species.

Phenology. *D. ornata* adults were collected year-round in lowland and coastal forests, while at higher elevations in the submontane zone, such as Amani in the East Usambara Mountains or Lutindi forest in the West Usambara Mountains, only one generation per year was

present, with adult individuals rarely collected between April and October. In the Uluguru Mountains, where *D. ornata* was screened from 2016, the species was only encountered once in March 2020 at elevations between 1700 and 2100 m, indicating that its development is likely triggered by temperature and that only one generation is produced in the montane zone. In Zanzibar, *D. ornata* probably develops only one main generation per year, with adults found from December to April, with highest abundance in February, while only a few individuals were found in October 2018, and the species was not observed during other checks in October (2016, 2017). Eggs from *D. ornata* laid in the laboratory in February 2022 hatched at the end of May 2022, with the first adults molting at the beginning of August 2022. However, laboratory conditions make it difficult to exclude the possibility that high temperatures and constant moisture may have triggered earlier hatching.

Habitat and distribution. *D. ornata* is a species of clearings and forest paths, distributed from coastal to montane forests in Kenya and Tanzania.

Notes on *D. ornata* from Zanzibar and mainland Africa. In 1878, Brunner v. Wattenwyl established the genus *Dioncomena* based on specimens of *D. ornata* collected on Zanzibar. Later, Karsch (1889) described *D. superba* from the East Usambara Mountains, noting that the new species differed from Zanzibar specimens only in its color pattern. Ragge (1980) compared a large series of specimens from mainland Africa and Zanzibar and concluded that the differences between the two populations were only in color pattern, while other features such as stridulatory files, the 10th abdominal tergites in males, and general measurements were similar. Therefore, he synonymized *D. superba* with *D. ornata*.

However, since Ragge only examined dried specimens and did not see alive specimens from Zanzibar and various mainland areas, he may not have been aware of the significant differences in color pattern. Zanzibar populations are distinctly red and black, while mainland specimens never show any red in their color pattern but often have vivid turquoise stripes (see Fig. 35C, D). Generally, the color pattern in *Dioncomena* species, including the widespread *D. ornata* from various mountain ranges and along the coast, is highly

stable, suggesting that subspecies status should be considered for mainland populations of *D. ornata*. Further studies on genetics and chromosomes are needed to clarify the status of the Zanzibar and mainland populations.

***Dioncomena tanneri* Ragge, 1980**

Figs 2H, 13D, 15C, D, 19, 21, 22N, 26G, H, 28D, 30, 36

Notes on biogeography and phenology. *Dioncomena tanneri* is exclusively found in the Usambara Mountains. Despite extensive screening of various forests in the West Usambara Mountains (such as Magamba, Shagayu, Ambangulu, and Lutindi forest remains), *D. tanneri* individuals were only found in Mazumbai Forest Reserve, where they were observed in forest clearings and in tall herb vegetation and low bushes along a sunny road through the forest. The reserve was screened for almost all months of the year, but *D. tanneri* individuals were only captured during the warm period between December and April. A single female that was either conspecific or closely related to *D. tanneri* was discovered in the montane elevations of the Nilo Forest Reserve in the East Usambara Mountains. Further investigation is required to determine whether *D. tanneri* is present at montane elevations in the East Usambara Mountains, or if a closely related species has evolved in these forests.

Biology. Females caught in March 2021 along a road passing through Mazumbai Forest Reserve laid numerous eggs onto thin branches in early April 2021. The first nymphs hatched in mid-September 2021 and became adult at the beginning of December 2021. Development took roughly two and a half months from L1 to the adult. When placed together in captivity, *D. tanneri* fed on each other once individuals became weak or died. This indicates that *Dioncomena* species are partly carnivorous, despite the fact that nymphs were solely reared on herb vegetation such as *Taraxacum officinale*. In the field, individuals were frequently found clustered, with several males and females located in close proximity to one another. However, no individuals were observed in other suitable locations along paths or on clearings.

Habitat and distribution. *Dioncomena tanneri* is typically found along open forest paths and clearings in the montane zone. It is restricted to the Usambara Mountains.

Key to the species of *Dioncomena* (males) (adapted from Ragge (1980) and Hemp (2021))

- 1 10th abdominal tergite flap-like elongated and downcurved. Lowland and coastal forests Tanzania... *D. scutellata* Hemp, 2017
- 10th abdominal tergite not flap-like elongated and downcurved..... 2
- 2 Without a variegated color pattern, predominantly dark on head, pronotum and body. Also, pronotum predominantly of uniform dark color, without fasciae, except for margins of pronotal lobes bordered by light thin fasciae. Zambia *D. takanoi* Massa, 2021
- With a variegated conspicuous color pattern of bright colours on head, pronotum and body contrasting with the black or dark tegmina. Pronotum with a median dark or light stripe and mostly differently colored than the pronotal lobes 3
- 3 Fore wings with a shiny surface. Most of the costal, radial and medial areas translucent with a regular, ladder-like arrangement of crossveins. Zambia *D. nitens* Ragge, 1980
- Fore wings opaque with a matt surface and largely irregular crossveins 4
- 4 10th abdominal tergite with a median dorsal protuberance. Malawi..... *D. bulla* Ragge, 1980
- 10th abdominal tergite without a median dorsal protuberance 5

- 5 9th abdominal tergite markedly produced posteriorly and profusely hairy above. Lowland forests Southern Tanzania *D. zernyi* Ragge, 1980
- 9th abdominal tergite not or produced posteriorly but not hairy above 6
- 6 9th abdominal tergite produced somewhat posteriorly, covering most of the 10th abdominal tergite. Stridulatory file clearly divided into three parts of similar length, one with coarse, one with fine and one with semi-fine teeth (see Fig. 2F). Widespread in lowland forests of the Eastern Arc Mountains, on Zanzibar and coastal forests of Kenya and Tanzania... *D. ornata* B. v. Wattenwyl, 1878
- 9th abdominal tergite unmodified, not covering most of the 10th abdominal tergite. Stridulatory file not clearly divided into three parts of similar length..... 7
- 7 Pronotum without a dark median stripe..... 8
- Pronotum with a dark median stripe..... 10
- 8 Stridulatory file with fewer than 40 teeth 9
- Stridulatory file with more than 40 teeth. Endemic to the Uluguru Mountains..... *D. versicolor* sp. nov.
- 9 Pronotum with an uninterrupted green central stripe bordered lateral black (male) or white to yellowish (females). Endemic to the montane zone of the West Usambara Mountains *D. tanneri* Ragge, 1980
- Central pronotal stripe interrupted by black transverse line (males) or diffuse brownish area (females) at around the middle. Endemic to the montane zone of the Nguru Mountains..... *D. ngurumontana* sp. nov.
- 10 Dark median stripe on the pronotum not extending to the hind margin. Stridulatory file with more than 70 teeth, arranged much more densely towards the centre. Zambia and Mozambique..... *D. grandis* Ragge, 1980
- Dark median stripe on the pronotum extending to the hind margin (near which it becomes wider)..... 11
- 11 Dark median stripe on the pronotum solid, covering the whole of the metanotal disc 12
- Dark median stripe on the pronotum separating into two stripes at metazona, forming green or yellow triangular patch on metazona of pronotum..... 13
- 12 Pronotal median stripe pitch black; thick along length and thus only slightly expanded at posterior part to fully cover the metanotal disc. Stridulatory file with around 40 widely spaced teeth (Fig. 2B). Colline to submontane forests Nguru Mountains..... *D. flavoviridis* sp. nov.
- Pronotal median stripe narrow on pro- and mesozona, then broadly expanded to cover metanotal disc of pronotum. Stridulatory file between 50 and 55 evenly spaced teeth (Fig. 2A). Lowland forests East Usambara and Uluguru Mountains..... *D. jagoi* Ragge, 1980
- 13 Pronotal lobes with median dark patch. Lowland forests Udzungwa Mountains *D. sanje* sp. nov.
- Pronotal lobes without dark patch 14
- 14 Medial dark fascia solid (in some specimens a very thin light line is present medially), very broad covering the whole pronotal disc and parts of the lateral lobes with only a yellow area along the anterior margin of the pronotal lobes being yellow. Uganda *D. ugandana* sp. nov.
- Medial dark fascia narrow, divided into two parallel fasciae with a yellow or green thin line medially, restricted to dorsal part of the pronotal disc with lateral lobes being uniformly green or yellow-green. Lowland to submontane forests along the Eastern Arc Mountains of Tanzania..... *D. magombera* sp. nov.

Bioacoustics

Pattern of male calling songs and female responses

All studied species of *Dioncomena* produced long lasting calling songs, often with durations between one to several minutes (see Fig. 19). These songs differ from the well-known continuous and long lasting tettigoniid songs because they consist of several different elements following each other in a more or less fixed sequence and they end in a coda during or after which a female ready to mate typically responds.

Here at first the songs of the species of the *D. jagoi*-group are described (in alphabetical order: *flavoviridis* sp. nov., *jagoi*, *magombera* sp. nov., *sanje* sp. nov.), then those of *ornata*-group (*ornata*, *zernyi*) and finally those of the *tanneri*-group (*tanneri*, *versicolor* sp. nov., and *ngurumontana* sp. nov.).

D. flavoviridis sp. nov.

The main part of the calling song (Fig. 19; Suppl. material 1) starts with a 25–30 s long series of relatively uniform syllables. At the beginning, the duration of these bi-parted syllables is around 40 ms (SRR 12 Hz), but increases towards the end to 55 ms with a simultaneous reduction of the syllable intervals (SRR 17 Hz). Now the amplitude modulation changes and single long (140 ms) syllables are introduced in a rhythm of about 1 Hz (Fig. 20A). Shortly afterwards short (200–400 ms) silent intervals appear, always before every second long syllable. At the beginning the long syllables are sometimes produced at a lower rate and before each gap (Fig. 21). The (3–5) syllables before the gap have a much higher amplitude (typically > 6 dB) than the song before (Fig. 25). This pattern is produced for another 30 s nearly until the end of the main part. Here often a few soft syllable groups are observed.

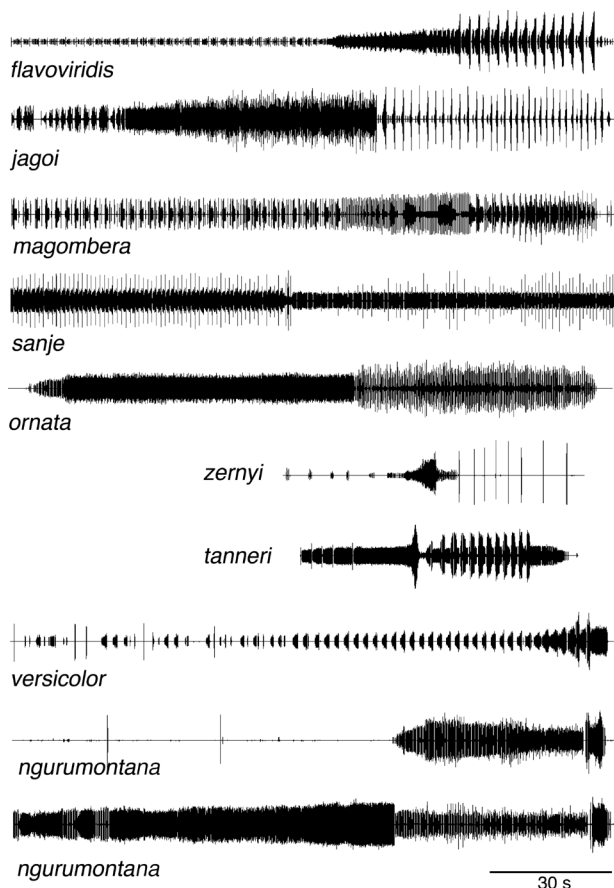


Figure 19. Oscillograms of male calling songs of *Dioncomena* species. Overview (150-s-sections).

As long as the male does not hear a female response it produces this main part at intervals of many minutes. In the mean time long sequences of other song parts can be heard, called here ‘ticking song’ and ‘slow song’. Some time after the end of a main part, typically very short, isolated sound elements can be heard, following each other at intervals of a few seconds – the ticking song (Fig. 22A). These elements consist mainly of an isolated impulse, sometimes accompanied by a second softer and a series of very much softer impulses. After some time they are combined with longer syllables, resulting in the ‘slow song’. Its basic units are echemes repeated at a rate of about 0.5 Hz (Fig. 20B). Each echeme is made up of 10–15 short syllables, the last being an isolated impulse, and is separated from the next by 0.3–0.5 s. The short syllables (25–30 ms; ca. 20 impulses) follow each other with 5 Hz. This ‘slow song’ can change to the next main part. During long lasting tick sequences also isolated impulses combined with an impulse series are observed (Fig. 22B). Two males singing together can alternate (Fig. 22C).

A female ready to mate responds one to many times during the gaps which follow the high-amplitude syllables of the main part of the male song (Figs 23, 24; Suppl. material 2). Its response consists of one to several impulses, often one louder than the others. The delay of the

response is about 200 ms, measured from the end of the last male syllable (Fig. 25).

*D. jagoi*²

The song of *D. jagoi* has some similarities to that of *D. flavoviridis* sp. nov. The main part of the calling song (Fig. 19; Suppl. material 3) starts with a ca. 60 s long series of relatively uniform syllables which show, however, some variability in amplitude modulation and rhythm resulting in an irregular echeme-like pattern. The duration of these bi-parted syllables varies between 50 and 60 ms (SRR 12–17 Hz; Figs 20C, 26A), but does not change with time, while the amplitude increases slowly and continuously. The series ends abruptly (or with a transition phase of some seconds) and 0.5 s long echemes appear, separated by intervals of about 1 s. They consist of 10–12 syllables (SRR ca. 25 Hz) with increasing amplitude (Fig. 26A). At the beginning of this final part (duration 30–60 s) some short echemes are interspersed (or they form the transition part exclusively).

Directly before the main part often a ‘slow song’ is observed (see *D. flavoviridis* sp. nov.). Its basic units are echemes repeated at a rate of about 0.5 Hz (Fig. 20). Each echeme is made up of 10–15 short syllables, the last being an isolated impulse, and is separated from the next by 0.5–0.8 s. The short syllables (40–50 ms) follow each other with 8 Hz. *D. jagoi* produces also ‘ticking songs’ (Fig. 22D) as *D. flavoviridis* sp. nov. However, the ticks are not isolated impulses but nearly always short echemes (duration < 100 ms).

D. magombera sp. nov.

The song of *D. magombera* sp. nov. is even more complicated than that of *D. flavoviridis* sp. nov. and *D. jagoi*. Typically, it consists of a sequence of three large parts (Fig. 19; Suppl. material 14) from which the last two may correspond to the main part in *D. flavoviridis* sp. nov. In the following, they are described using this name. Female sound recordings are not available. This so-called main part starts with a long (30 s), homogeneous series of short echemes (ca. 100 ms; ERR 4 Hz) containing 4–5 syllables each (SRR 30 Hz) (Fig. 26B). Each syllable is made of one large impulse and a series of softer ones its number increasing during the echeme. At the beginning of the second half of the main part these short echemes are interspersed by longer (1.5 s) and more complex combination of syllables (Fig. 26C). Each combination starts with syllables similar to that in the short echemes but then the number of soft impulses becomes larger, the single loud impulse disappears and the rhythm of the now bi-parted syllables becomes faster (50 Hz). With time, this core syllable combination becomes shorter but at the beginning and end other syllables are added (Fig. 26D) until the main part ends with a few short echemes. The first part of the song – before the so-called main part –

2 Only the sound file *Dioncomena jagoi*_C.wav on the DVD (Hemp 2021) belongs to this species.

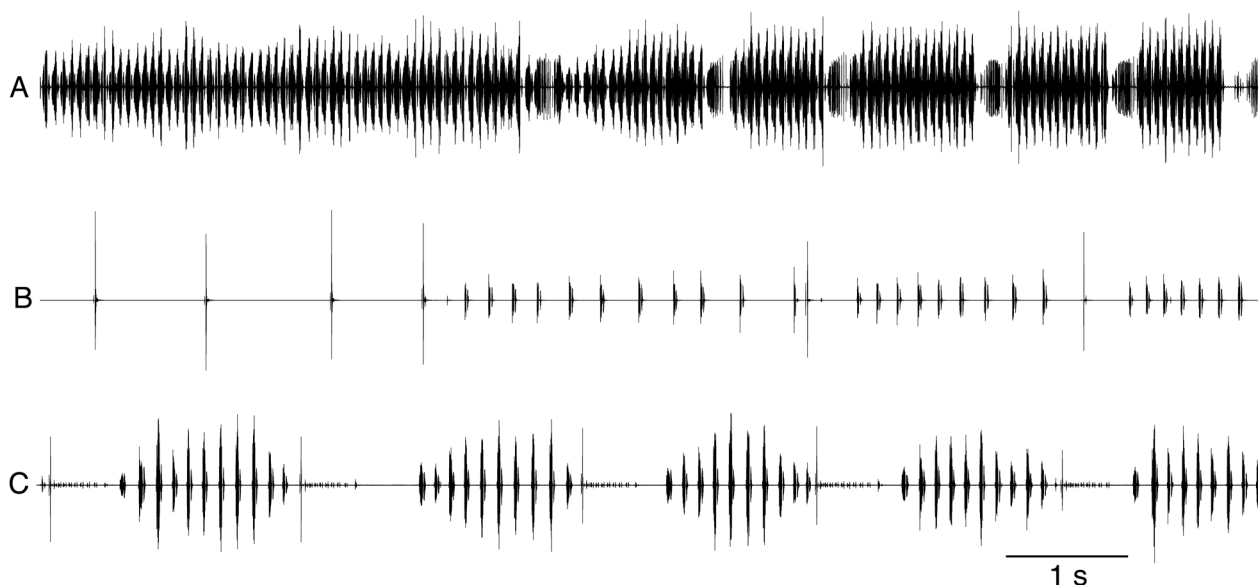


Figure 20. Oscillograms of male calling song of *Dioncomena flavoviridis* sp. nov. (A, B) and *D. jagoi* (C). A. Change of amplitude pattern in first half of the main part; B. Transition from ticking song to 'slow' song; C. 'Slow' song.

contains long syllable combinations quite similar to that immediately after the homogenous echeme series. Sometimes – in contact with other males? – some three-part sequences follow immediately one after another. Occasionally the males produce 'ticking songs' with ticks similar (Fig. 22G) or slightly different (Fig. 22F) as in *D. jagoi*.

D. sanje sp. nov.³

The males of *D. sanje* sp. nov. produce very long uninterrupted sequences. During two hours of recording, for example, an isolated male made two sequences each lasting more than 20 min. These long songs consisted of two parts (section in Fig. 19; Suppl. material 8) each taking several minutes and each consisting of syllable groups followed by one or several impulses. At the beginning one type of combination (ca. 16 syllables with a duration of 30 ms each, SRR 15 Hz) is repeated in a rhythm of 0.7 Hz, but at the end it becomes shorter (1 Hz) while the syllable duration (38 ms) and SRR (19 Hz) slightly increase. Each syllable is separated from the next by a distinct gap of more than 10 ms (and a soft hemisyllable; Fig. 27A). Therefore these sound combinations are called 'gappy'. Each series is followed by a loud, short, tick-like syllable. After a somewhat irregular transition period of ca 10 s another syllable combination is heard, produced a little bit faster (1.25 Hz) (Fig. 21). Here both hemisyllables are similar in amplitude leaving no large gaps in the syllable group (Fig. 27B). This combination is called 'dense'. It is followed by a single syllable of a different type which varies in amplitude between softer and louder than the preceding group (compare Fig. 21 and Fig. 27B) and which ends with a few loud isolated impulses. The syllable is called high frequency (HF) syllable, because the carrier

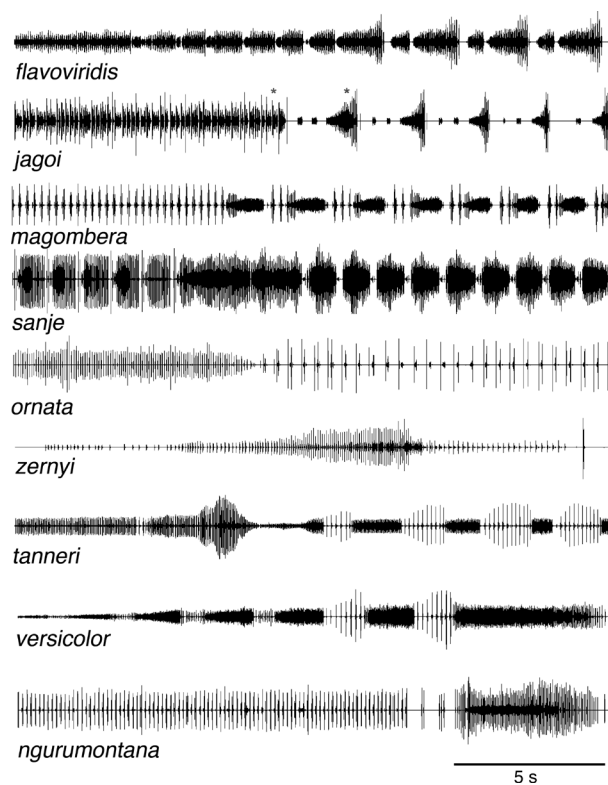


Figure 21. Oscillograms of male calling songs of *Dioncomena* species. Central portion of main part of song; 20-s-sections.

frequencies of the first part are much higher than in all other song parts (Fig. 29; only very weak in Fig. 25 due to the restricted frequency range of this recording; Suppl. material 9). Outside the long uninterrupted sequences the males produce long (1–3 min) series of regularly spaced elements of a ticking song (Fig. 22H). Occasionally also short sequences of gappy sound combinations are observed (Fig. 22I).

³ Sound files *Dioncomena jagoi*_A, B (in text *Dioncomena* sp. nr *jagoi* A, B) on the DVD (Hemp 2021) belong to this species.

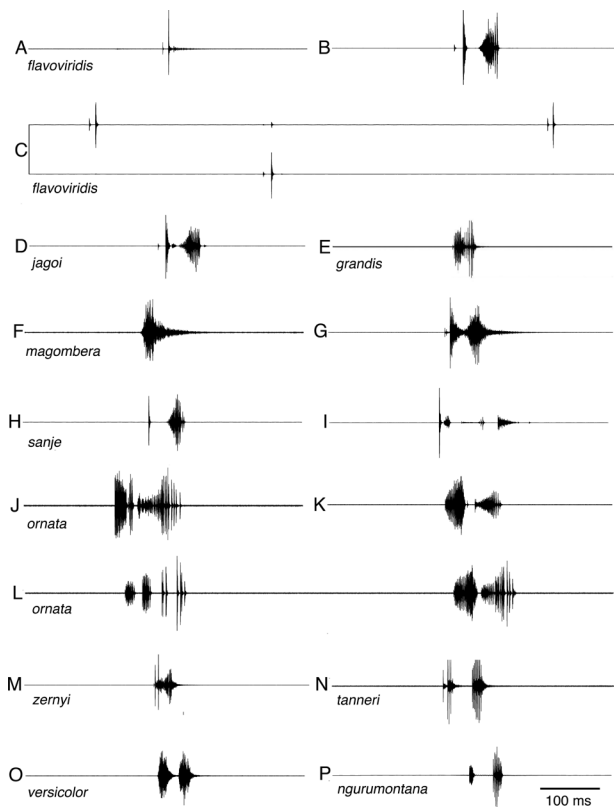


Figure 22. Oscillograms of male tick songs of *Dioncomena* species. A–C. *D. flavoviridis*; A, B. ticks; C. alternating males; D. *D. jagoi*; E. *D. grandis* (from Naskrecki and Guta 2019); F, G. *D. magombera* sp. nov.; H, I. *D. sanje* sp. nov.; J–L. *D. ornata*; M. *D. zernyi*; N. *D. tanneri*; O. *D. versicolor* sp. nov.; P. *D. ngurumontana* sp. nov.

The females respond preferentially and regularly to the dense sound combinations (Figs 23, 24; Suppl. material 10). Their sounds follow about 50–70 ms after the end of the male impulse group (Fig. 25). If the male switches ‚back’ to the gappy pattern, the females stop responding. However, they react acoustically sometimes also to the gappy combinations.

D. ornata

The main part of the song of *D. ornata* contains two long parts (Fig. 19; Suppl. material 6). It begins with a long homogeneous series of hemisyllables (SRR 14–25 Hz (–30 Hz at 26 °C), duration 15–150 s; Fig. 28A). Only one male was found to produce bi-parted syllables (Fig. 28B). The directly following part consists of a characteristic short combination of a few sound elements (Fig. 28C) which is repeated for many seconds (repetition rate 2.3–2.6 Hz; durations up to 110 s observed). How these sound elements are produced is unclear and not all elements are found in every recording. Possibly each group results from one stridulatory movement cycle (syllable) using all parts of the complicated file (Fig. 2). Sometimes a series of syllables resembling that from the first half of the main part are found isolated without the second half of the main part. Between the main parts often single ticks or occasionally even long series of ticks can be heard, rarely

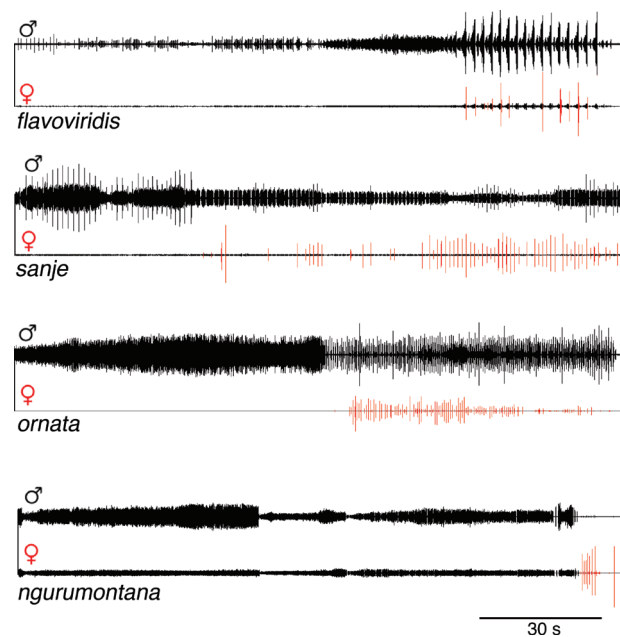


Figure 23. Oscillograms of male-female-duets in *Dioncomena* species. Overview (150-s-sections).

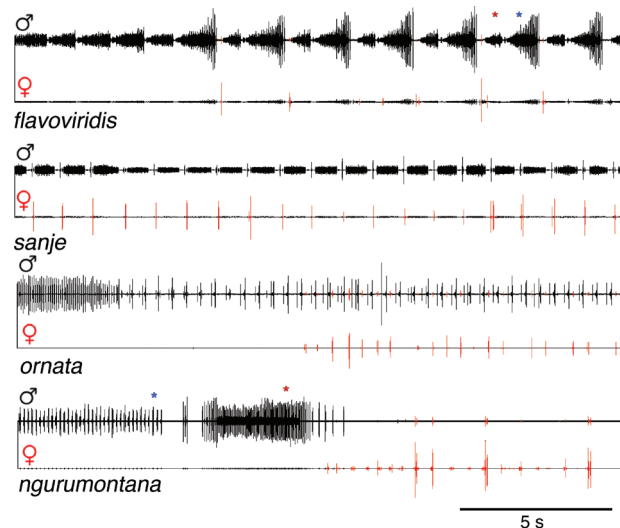


Figure 24. Oscillograms of male-female-duets in *Dioncomena* species. Detail (20-s-sections).

immediately before a main part. These short sounds often consist of pairs of syllables (Fig. 22K), but more complicated combinations are also observed (Fig. 22J, L).

The females respond only during the second half of the main song (Figs 23, 24; Suppl. material 7). Typically, the responses are registered 50–150 ms after the end of the longest part of the short combination (Fig. 25).

D. zernyi

From *D. zernyi* only few recordings are available. According to the data, the main part of the song (uninterrupted part) is relatively short (Figs 19, 21; Suppl. material 13). It starts with a series of hemisyllables with an irregular but slowly increasing SRR (e.g., 2 Hz to 15 Hz in 10 s). During the next few seconds the syllables be-

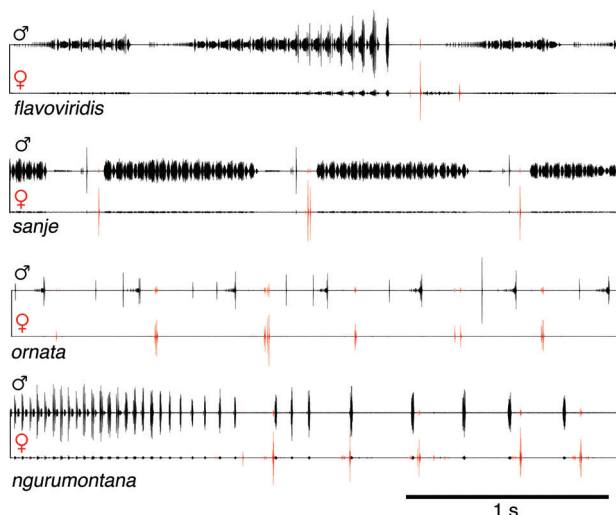


Figure 25. Oscillograms of male-female-duets in *Dioncomena* species. Detail (3-s-sections).

come bi-parted until the pattern changes into a sequence of short isolated syllables (or echemes?) (SRR 5 Hz; Fig. 26E). This part lasts about 5 s. Then the singing continues with a kind of ticking song with elements separated by intervals of about 3–6 s (Fig. 22). This ticking song is sometimes heard for hours without the main part. Before the main part often the male produces short echeme sequences (Fig. 26F).

D. tanneri

Also from *D. tanneri* only few recordings are available. In structure, the song has some similarities to that of *D. versicolor* sp. nov. In the longest recording of the main part, the song starts with several combinations consisting of two different types of syllables (Figs 19, 21; Suppl. material 11). A series of about 30 syllables (SRR 14 Hz) each with ca. 12 impulses is followed by a single short syllable (1–2 impulses). After a few of these combinations one distinctly longer one of the same type is heard. Then a long series of syllables (18 s) is observed, which is relatively homogeneously in rhythm but shows changes in amplitude (Fig. 28F). After its end a short (2 s) series of bi-parted syllables (SRR 25 Hz) is produced followed by some short isolated syllables (or echemes?) (SRR 6 Hz) (Fig. 26G). These combination of two different types of echemes is repeated several times with varying durations. At the end the isolated syllables become longer (Fig. 26H) and are followed at first by one or two impulses which finally disappear.

D. ngurumontana sp. nov.

An isolated male of *D. ngurumontana* sp. nov. produced the main part of its song typically at intervals of many minutes. It often lasted about one minute and consisted of two parts (Fig. 19; Suppl. material 4). The song started with a long (ca. 50 s), homogeneous series of syllables (SRR 7 Hz) which was – after some irregular echemes – followed by a much shorter final part (Fig. 21). This

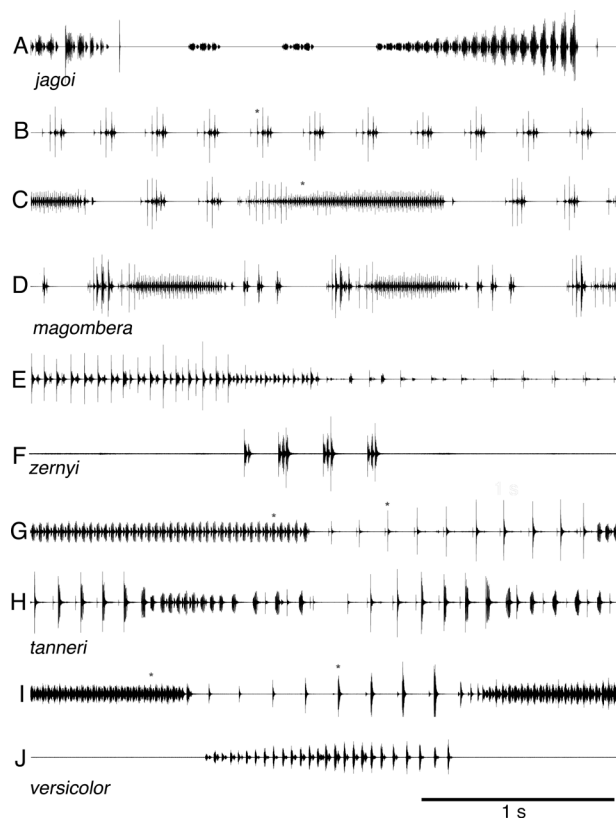


Figure 26. Oscillograms of male calling songs of *Dioncomena* species. Detail (3-s-sections). A. *D. jagoi*; B–D. *D. magombera* sp. nov.; E, F. *D. zernyi*; G, H. *D. tanneri*; I, J. *D. versicolor* sp. nov.

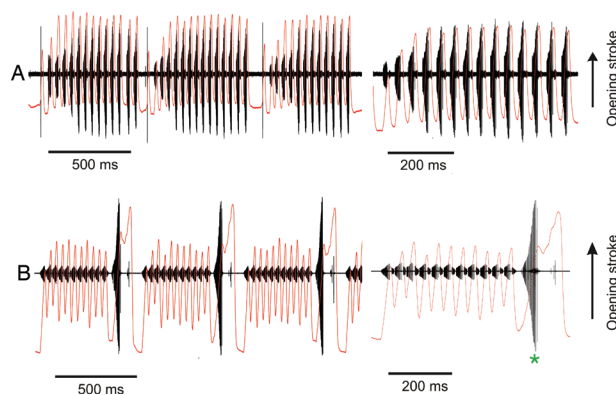


Figure 27. Oscillograms of stridulatory movement and song [synchronous registration of left tegmen movement (red; upward deflection represents opening, downward closing) and sound (black)] in *D. sanje* sp. nov. A. Gappy sound combination; B. Dense sound combination with HF-syllable (*).

,coda' began with a series of bi-parted syllables (SRR 28 Hz) and closed with a short (≤ 1 s) sequence of hemi-syllables slightly decreasing in amplitude and SRR (25 to 10 Hz; Fig. 28E). In between the main parts single tick elements were observed. If a male is or has been in acoustical contact with a female it often produced much longer (up to 5.5 min documented) songs. While the coda remained similar in structure, the first part became much longer and the SRR changed often. Fast series with 15–20 Hz alternated with 6 Hz parts (Fig. 28F), both lasting several to many seconds (5–60 s).

A female ready to mate responds with a series of impulse-like syllables after the male coda (Fig. 23; Suppl. material 5). Sometimes the responses overlap with the latest syllables of the male but there was no short-time relation to any male song parts as in the other *Dioncomena* species (Figs 24, 25). The response series sometimes lasted nearly one second.

D. versicolor sp. nov.

Also from *D. versicolor* sp. nov. only few recordings are available. According to the data, the main part of the song (uninterrupted part) is relatively short (Figs 19, 21; Suppl. material 12). Before this part, the song consists of 1–2 s long series of bi-parted syllables (SRR 20–28 Hz) crescendoing slightly in amplitude (Fig. 26J). These echemes are produced continuously and with silent intervals (ERR ca. 0.4 Hz) for about a minute. Then the male starts to fill the intervals with a series of isolated syllables (at first syllable period 65 ms). During the last two ‘intervals’, these syllables (or echemes?) become longer, louder and more widely spaced (SRR 7 Hz; (Fig. 26I) 1), until after a very long (ca. 4 s) echeme the song ends. Outside this main part the male produces also a ‘ticking song’. It can be heard for quite a long time and consists often of two syllables (Fig. 22O).

B Stridulatory organs

The areas containing the stridulatory organs differ clearly in structure between the left and the right tegmen. The part of the left tegmen which carries the stridulatory file at its lower side is non-translucent and shows the typical species-specific coloration like the other parts of the tegmen. In the corresponding part of the right tegmen in all species one large translucent mirror cell is found

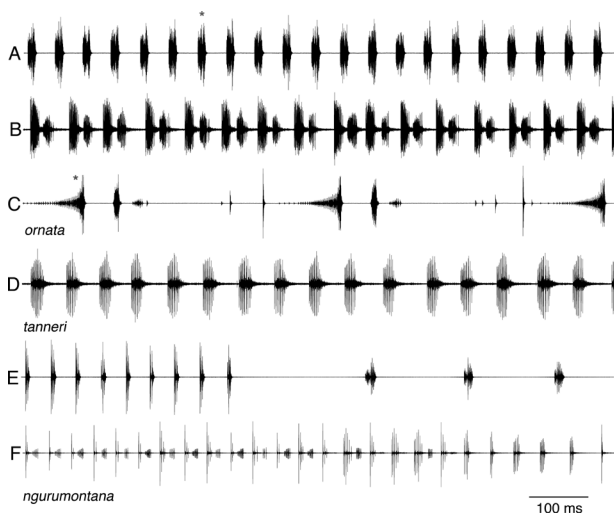


Figure 28. Oscillograms of male calling songs of *Dioncomena* species. Detail (1-s-sections). A–C. *D. ornata*: A. Section of first part; B. Section of first part in atypical male; C. Section of second part; D. *D. tanneri*; E, F. *D. ngurumontana* sp. nov.: E. Change from fast to slow rhythm; F. ‘coda’.

(Fig. 29A). Its frontal edge (right edge in resting animal) is distinctly elevated above the mirror plane.

The stridulatory files in *Dioncomena* species differ widely in tooth number, length and structure (Fig. 2, Table 1). The lowest tooth numbers are found in *D. ngurumontana* sp. nov. and *D. nitens*, followed by a broad range with many species similar in number and two species (*D. ornata* and *D. grandis*) with high numbers. Five species (*flavoviridis* sp. nov., *jagoi*, *sanje* sp. nov., *grandis*, *scutellata*) have longer files than the others. The variation in complexity does not seem to be correlated with any other file characteristic. Several species (*grandis*, *scutellata*, *ornata*, *zernyi*; see Fig. 2) have very unusual tri-parted files with three regions differing in file density, but even in these four species length and tooth number of the different parts vary distinctly.

The stridulatory organs of females are typical for Phaneropteridae (see e.g. Heller et al. 1997); several to many short rows of teeth on cross veins in the upper side of the right tegmen are present, while the scraper is formed by the amplified inner edge of the left tegmen.

C Spectral characteristics of the male songs

As to be expected for songs consisting of damped impulses (non-resonant song), in most species studied the spectra are relatively broad-banded with the carrier frequencies showing the highest amplitudes situated between 20 and 30 kHz (Fig. 30). Checking sonograms for spectral differences, often in some components (hemisyllables etc.) the higher frequencies (partly harmonics) are stronger than in others parts of the song (for examples see Fig. 28; details see legend). Only in *D. sanje* sp. nov. one special type of hemisyllable was registered with the main part having its maximum at 60 kHz (Fig. 30; green), called HF-syllable (high frequency). The syllables before and the following impulses are much lower in frequency (Fig. 31). When studied by laser Doppler vibrometry, the single mirror cell shows a narrow peak around 40 kHz (Fig. 32; n = 2 specimens: 33 kHz, 46 kHz), demonstrating a distinct mismatch of natural frequency of the mirror and the peak frequencies of the either of the call types. The left wing is completely damped and probably not involved in sound radiation.

D Stridulatory movements

After the observation that in *D. sanje* sp. nov. one syllable type has a different spectral composition from the others, we began to analyze the stridulatory movements in this species (Fig. 27). Interestingly, in the gappy as well as in the dense sound combination the most intense song parts are produced during opening movements of the tegmina. In the gappy combination the opening hemisyllables are much louder than the closing ones, and also the tick-like syllable of this combination is produced during an opening movement (Fig. 27A). In the dense combination the differences in amplitude between opening and closing

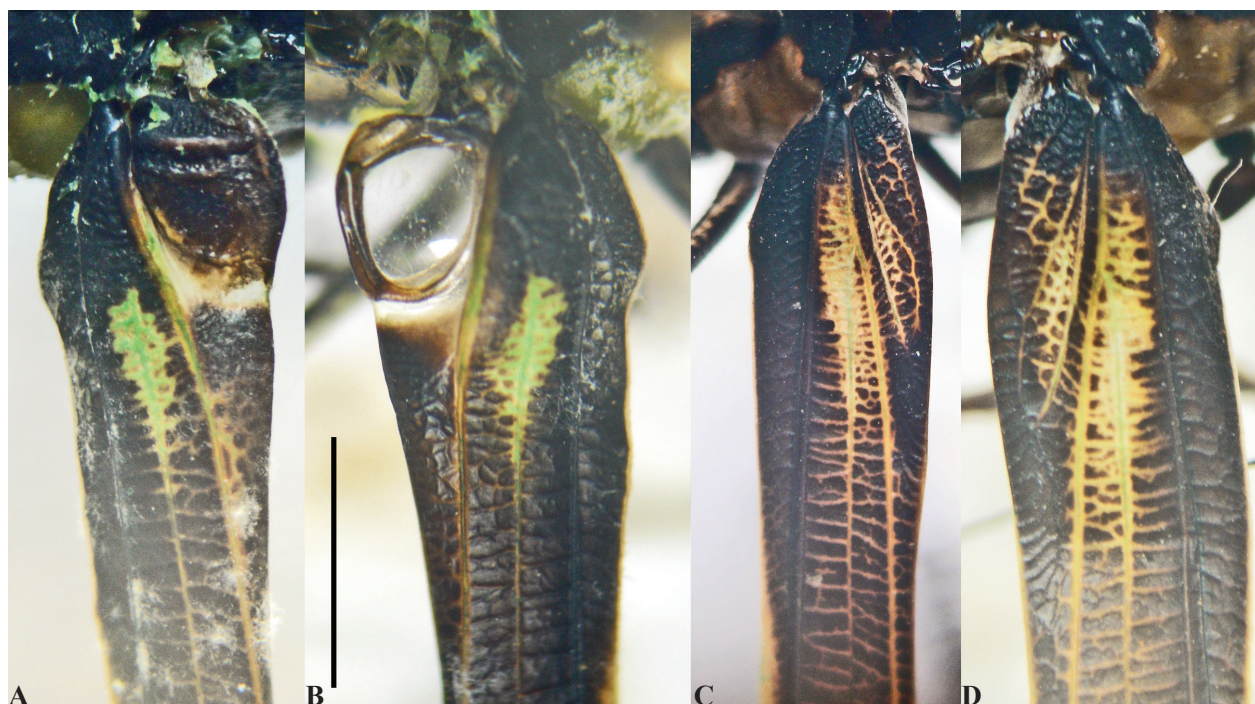


Figure 29. *Dioncomena flavoviridis* sp. nov. **A.** Base of male left tegmen; **B.** Base of male right tegmen; **C.** Base of female left tegmen; **D.** Base of female right tegmen. Scale bar: 5 mm.

hemisyllable are much smaller. The HF-syllable is also produced during an opening movement. Here the amplitude of the movement is larger than in the other syllables of the combination and the speed of the movement slower, but always the same part of the file seems to be used. Even the few loud isolated impulses are produced during the opening movement of the tegmina but with the teeth situated farer away from the articulation than that used for the other parts of the combination.

E Auditory organs

The tympanic membranes near to the auditory sensillae in the fore tibia are exposed, naked, and show no obvious modifications. However, the major input to the hearing organs is via the auditory spiracles in the prothorax, es-

pecially for higher sound frequencies (reviewed e.g. by Strauß 2019; Römer 2020). The large acoustic spiracles are permanently open, and continue into the prothoracic auditory bullae, the first parts of the auditory (acoustic) trachea (Bailey 1990). The outer parts of auditory trachea run without obvious change in diameter from the bullae to the sensory organs in the tibiae (Fig. 33). In *Dioncomena*, these bullae are very large – as in many phaneropterids –, but even the space before the openings is enormously enlarged due to the inflated paranota (Figs 34, 35) in many species. This structure is called prebulla. These prebullae show an impressive size variation in *Dioncomena*, also depending on the sex (Fig. 35, Table 2). While this variation is easily recognizable with the naked eye, it is much more difficult to quantify. Calculating relative pronotal width (overall width / overall length) gives only a first clue (Table 2), the scatter probably resulting from differently shaped pronota. Combining visual impression and measurements, prebullae are most distinct in the males of the *D. jagoi*-group, *D. grandis* and *D. nitens*. In females, only *D. flavoviridis* sp. nov. approaches or even surpasses the size of the male prebulla (Fig. 35A). The males of the other species have smaller prebullae, while they are completely missing in the females of some species.

However, not only the interspecific, but also the intra-specific variability may be quite large as can be seen in the data of *D. ornata* (Table 2, Fig. 35C, D), the only species with a relatively large number of populations studied.

Surprisingly, prebullae were discovered in a series of other East Africa phaneropterids, but always in males only. They are very pronounced in all species of the genus *Kefalia* which is morphologically similar to *Dioncomena* (Table 2, Fig. 35E). However, prebullae were found also in genera with uncertain relationship [*Merumontana*

Table 1. Data on stridulatory file and size (as hind femur length) in *Dioncomena* species.

Species	Hind femur (length; mm)	File (length; mm)	Teeth n	Remarks on file	Source
<i>flavoviridis</i>	19.8	1.6–1.68	39–42		
<i>jagoi</i>	17.3	1.5	45–50–53		Ragge 1980
<i>magombera</i>	18.75	1.3	50		
<i>sanje</i>	17.2	1.4–1.5	49–53		
<i>grandis</i>	19.7	1.6 (1.5–1.7)	81 (75–90)	3-parted	Ragge 1980
<i>scutellata</i>	20.4	ca. 1.5	41	3-parted	Hemp 2017
<i>ornata</i>	16.7	1.2 (1.1–1.3)	92 (80–100)	3-parted	Ragge 1980
<i>zernyi</i>	19.5	1.05	43	3-parted	Ragge 1980
<i>tanneri</i>	16.4	0.98	37		Ragge 1980
<i>versicolor</i>	15.75	1.0	54–55		
<i>ngurumontana</i>	16	1	32		
<i>takanoi</i>	18.5	1.2	60		Massa 2021
<i>bullia</i>	18.6	1.2 (1.05–1.3)	49 (45–55)		Ragge 1980
<i>nitens</i>	15.8	ca. 1	33		Ragge 1980

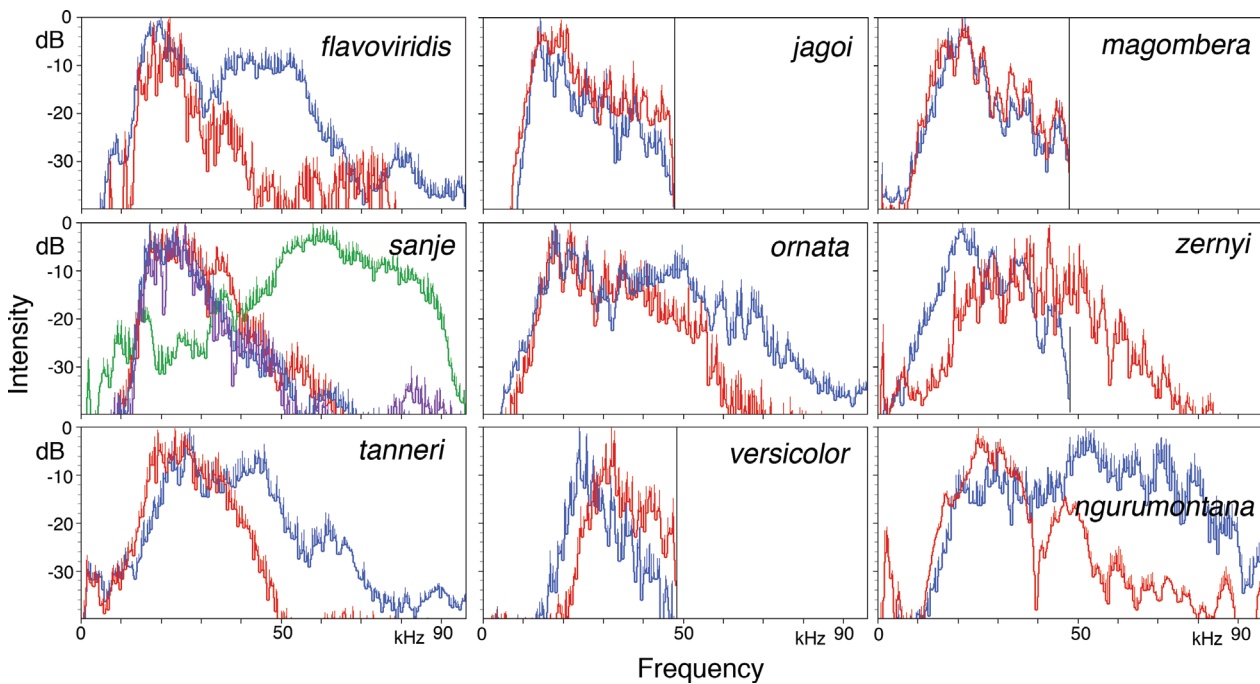


Figure 30. Power spectra of the male calling songs of the *Dioncomena* species studied. Asterisks in the respective color mark the positions of the analysed sounds, for *D. flavoviridis* sp. nov. in Fig. 23, for *D. jagoi* in Fig. 20, for *D. magombera* sp. nov. in Fig. 25, for *D. sanje* sp. nov. see Figs 26, 29 (dense combination: blue and violet, high frequency syllable: green, gappy combination: red), for *D. ornata* in Fig. 27, for *D. zernyi* in Fig. 25E (song), Fig. 21M (ticks), for *D. tanneri* in Fig. 25, for *D. versicolor* sp. nov. in Fig. 25, for *D. ngurumontana* sp. nov. in Fig. 23.

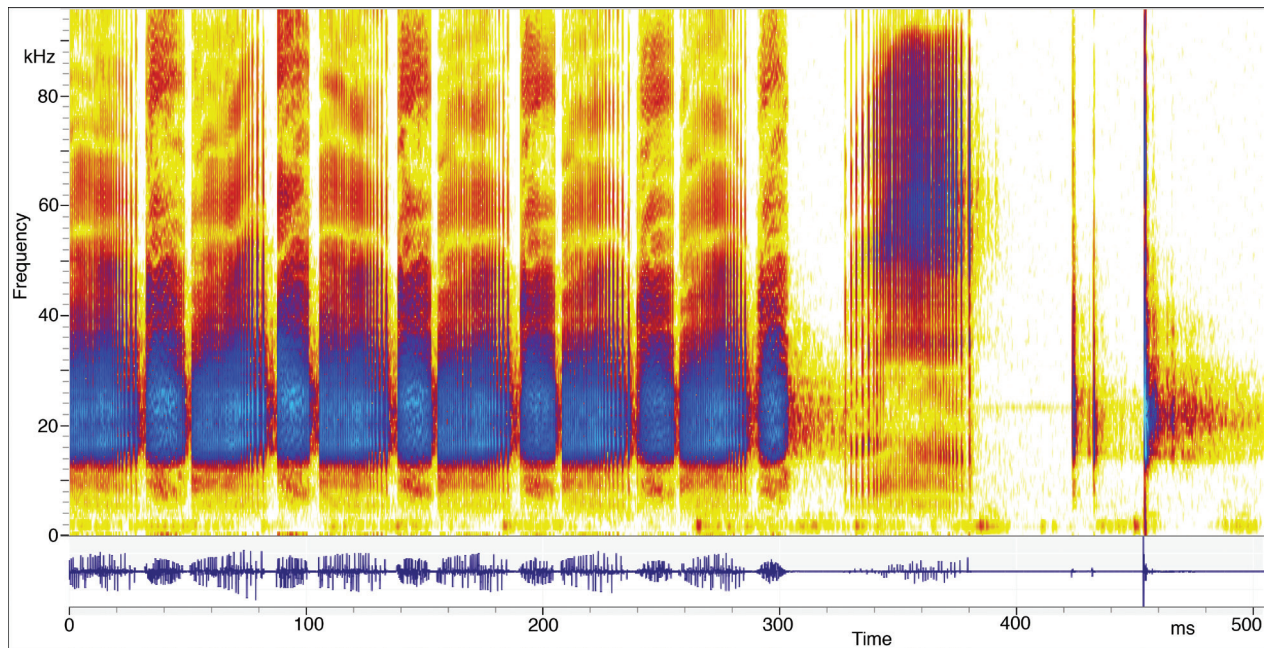


Figure 31. Sonogram of second half of the dense sound combination of *Dioncomena sanje* sp. nov. with HF-syllable.

Sjöstedt, 1912 (Table 2, Fig. 35E) and in some species of *Ivensia* Bolivar, 1890] or even placed in other tribes [Atlasacris Rehn, 1914 (Table 2, Fig. 35G)]. Some other species were also checked and no prebullae were found [from OSF: *Arostratum oblitum* Massa, 2015 ♂, ♀, *Pronomapyga grandis* Rehn, 1914 ♂, ♀, *Pro. graueri* Rehn, 1914 ♂, ♀, *Gabonella cothurnata* (Bolivar, 1906) ♂, ♀, *Poecilogramma annulifemur* Karsch, 1887 ♂, ♀, *Poe. cloetensi* (Griffini, 1908) ♂, ♀), *Poe. striatifemur*

Karsch, 1887 ♂, ♀, *Pardalota asymmetrica* Karsch, 1896 ♂, ♀, *P. haasi* Griffini, 1908 ♂, ♀, *P. karschiana* Enderlein, 1907 ♂, ♀, *P. reimeri* La Baume, 1911 ♂, ♀, *P. superba* Sjöstedt, 1913 ♂, ♀, *P. versicolor* Brunner von Wattenwyl, 1878 ♂, ♀; from specimens in Collectio Hemp: *Odonturoides hanangensis* Hemp, 2009 ♂, ♀, *O. insolitus* Ragge, 1980 ♂, ♀, *Monticolaria meruensis* Sjöstedt, 1910 ♂, ♀, *M. manyara* Sjöstedt, 1910 ♂, ♀, *M. kilimandjarica* Sjöstedt, 1910 ♂, ♀].

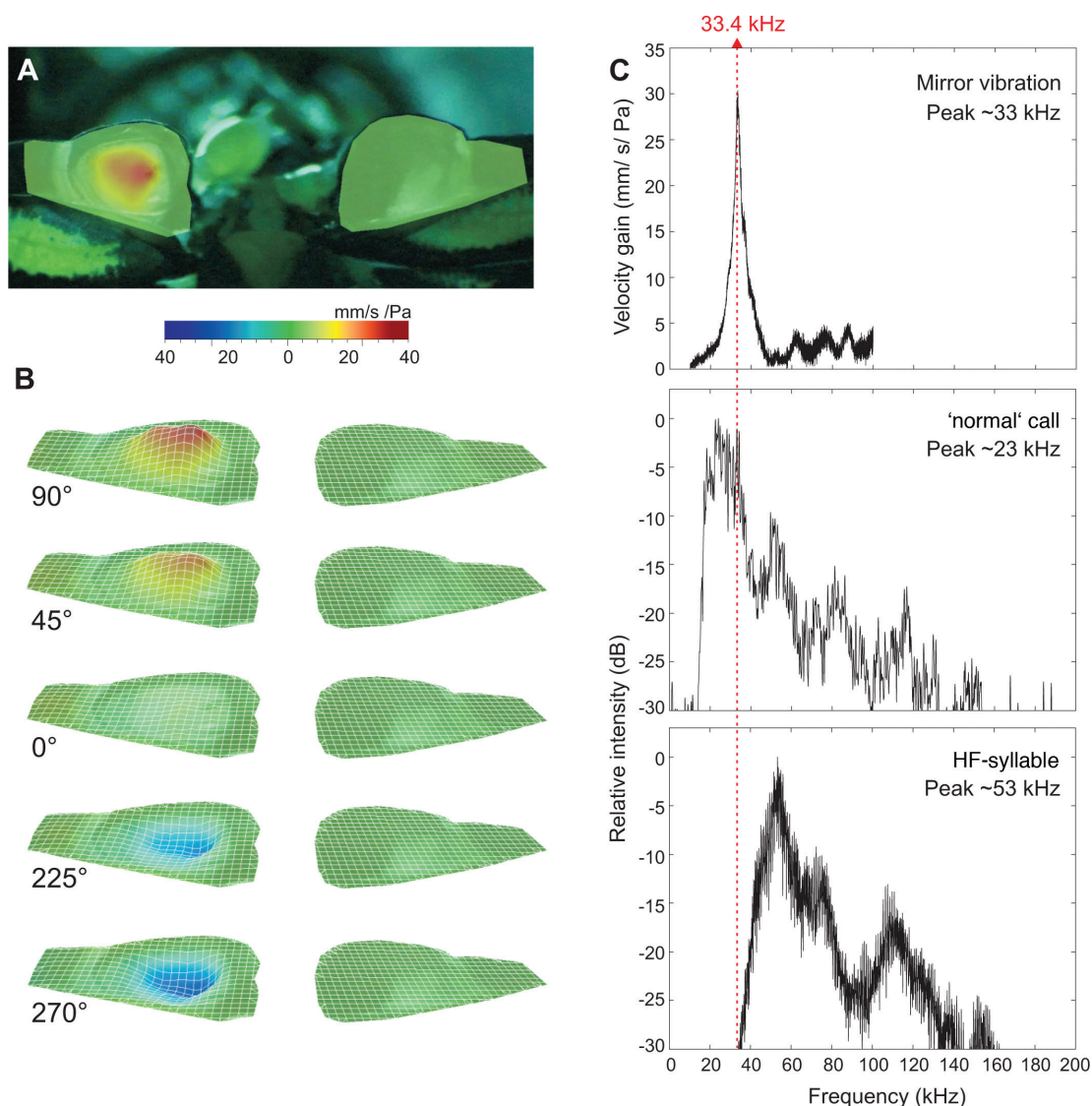


Figure 32. Forewing vibrational response in *Dioncomena sanje* sp. nov. A. Displacement of forewings in response to acoustic stimulus. The left wing is completely damped and probably not involved in sound radiation B. Deflection through phases of one oscillation C. Top panel: velocity gain of the mirror of the right wing as recorded through laser Doppler vibrometry. Middle panel: relative intensity of a section of the 'normal' call. Bottom panel: relative intensity of the HF-syllable. Note the mismatch of natural frequency of the mirror and the peak frequencies of the either of the call types.

The two bullae of the *Dioncomena* are also coupled via a membrane or 'septum' in males but not in females (Fig. 33A–F). The surface area of this connection in one micro-CT scanned male of *D. sanje* sp. nov. is $\sim 0.56 \text{ mm}^2$ (Fig. 33G, H).

Discussion

Little was known at present on the biogeography, phenology, biology and the bioacoustics of species of the genus *Dioncomena*, a genus with mostly colorful species first depicted alive in Naskrecki and Guta (2019) and Hemp (2021).

A species recently described by Massa (2021) occurs in riverine and thus wet forest in Zambia while another species described from Zambia, *D. nitens*, was also collected from riverine forests in northern Zambia on the border with Tanzania and thus are probably

restricted to riverine forests along rivers. *D. bulla* is recorded from southern Malawi, specimens in the British Museum coming from near the towns of Blantyre and Thyolo and the Mt Mulanje area (Ragge 1980). While the areas around Blantyre and Thyolo are almost completely deforested, today this species very likely is restricted to the forest reserve of Mt Mulanje in the north-west of Malawi (Fig. 36). Nothing is known about their bioacoustics and whether they are found aggregated or not, so an assignment of these species to any of the above-mentioned groups or to new groups is not possible.

The remaining known species of *Dioncomena* occur in Tanzania, Kenya and Uganda (except for *D. grandis*) and as outlined above can be divided into three groups on the basis of their habitat, their distribution, their behavior, their morphology, and their color pattern: the *ornata*-, *jagoi*-, and *tanneri*-group.

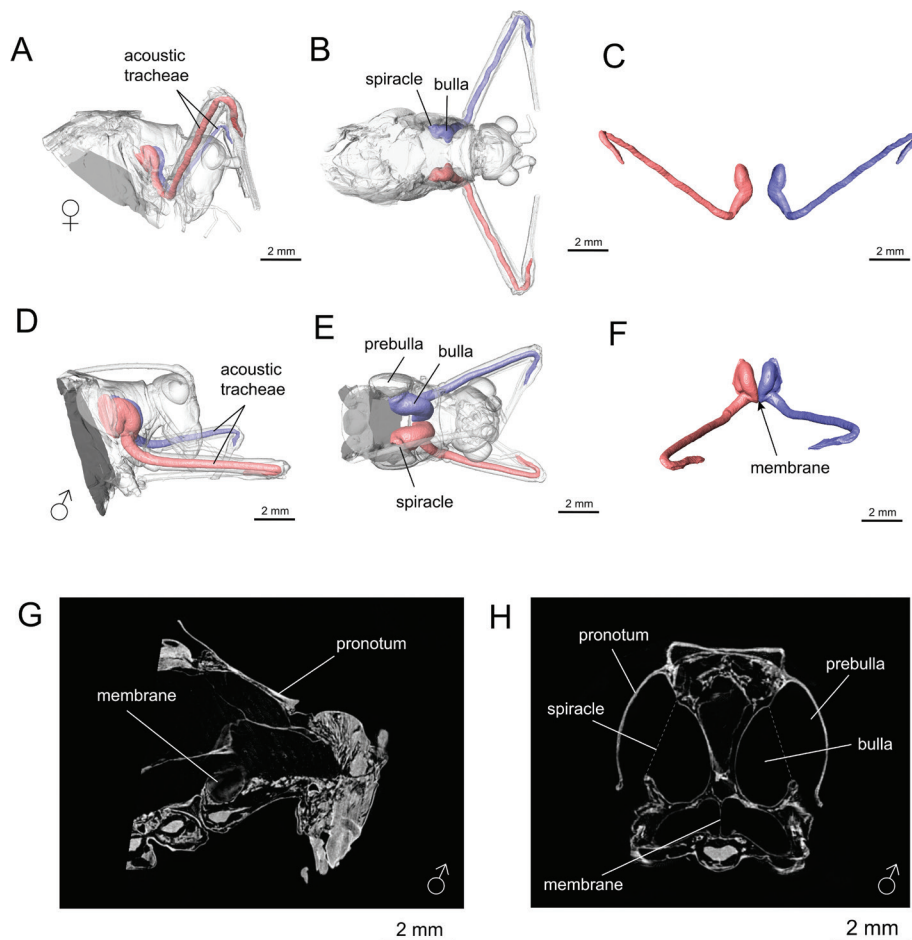


Figure 33. Outer parts of the auditory tracheae in *D. sanje* sp. nov. A–C. Female auditory tracheae in lateral (A), dorsal (B), and anterior (C) axes; D–F. Male auditory tracheae in lateral (D), dorsal (E), and anterior (F) axes; G. Male head and thorax (sagittal-section) showing membrane which connects the two bullae; H. Male thorax (cross-section) at the point of the membrane in G.

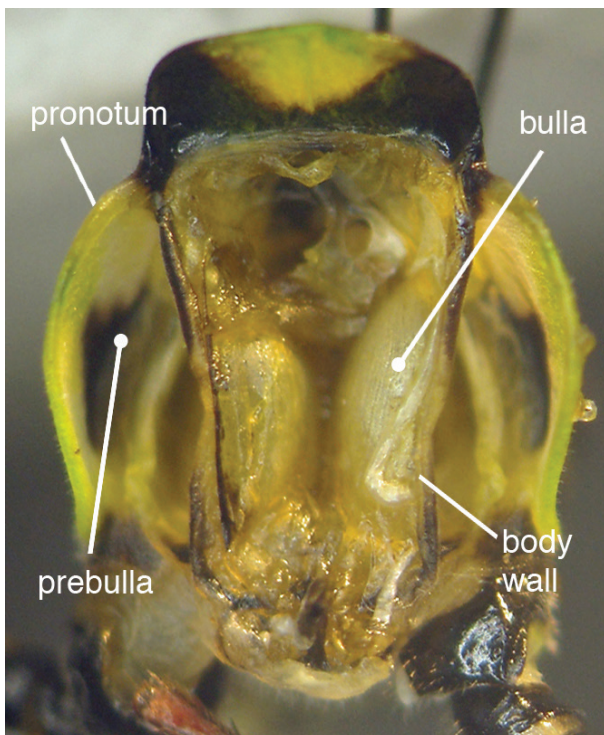


Figure 34. Auditory tracheae in pronotum of male *Dioncomena sanje* sp. nov. from behind, abdomen removed.

The *ornata*-group is comprised of *D. ornata*, a species widely distributed throughout forested areas in Tanzania with records also from forests in southern Kenya (Ragge 1980), *D. zernyi* with a distribution in southern Tanzania (Ragge 1980; Hemp 2021) and *D. grandis* with records in the border area between Mozambique and Zambia. *D. ornata* and *D. zernyi* have a posteriorly produced 9th abdominal tergite covering parts of the 10th abdominal tergite, in *D. grandis* the 9th tergite is only very slightly produced (images in Naskrecki and Guta 2019). In contrast to *D. ornata* and *D. grandis* the last tergites are hairy in *D. zernyi* and the color pattern differs between *D. ornata* and *D. grandis* on the one side and *D. zernyi* on the other. Both, *D. ornata* and *D. zernyi* are dwellers of forest clearings and show aggregation behavior – several individuals often found closely together on single bushes or the herb vegetation while on other suitable patches nearby no individuals were seen. These two species were not found syntopically up to now. Naskrecki and Guta (2019) state for *D. grandis* that it is relatively abundant along forest edges, thus this species occurs in analogue habitats. *D. scutellata* has a conspicuously flap-like 10th abdominal tergite which is unique for *Dioncomena* being very different from the 10th abdominal tergite of *D. ornata* and *D. zernyi*. Thus, and also since *D. ornata* and *D. scutellata* occur sym-

Table 2. Expansion pronotal lobes (prebullae) in males and females of *Dioncomena* species and similar genera. Relative width (of pronotum) = pronotal width / pronotal length.

Species	Male			Female			Aggregation behaviour	Source
	Pronotal lobes inflated							
Pronotal lobes inflated	praebullae	rel. width	n	praebullae	Rel. width	n		
<i>D. flavoviridis</i> sp. nov.	yes	1.15–1.33 (mean: 1.28)	3	yes	1.09–1.16 (mean: 1.13)	6	–	
<i>D. jagoi</i>	yes	1.03–1.15	2	yes	1.11–1.13	2	–	
<i>D. magombera</i> sp. nov.	small	0.97–1.02 (mean: 1.0)	3	no		6	–	
<i>D. sanje</i> sp. nov.	yes	1.03–1.17 (mean: 1.08)	6	small	0.98–1.16 (mean: 1.09)	6	-	
<i>D. ornata</i> East Usambara	yes	0.92–1.1 (mean: 1.01)	6	small			+	
<i>D. ornata</i> West Usambara	yes	0.98–1.15 (mean: 1.18)	6	small				
<i>D. ornata</i> Uluguru (Kimboza)	yes	1.08–1.12 (mean: 1.1)	6	small			+	
<i>D. ornata</i> Nguru	yes	1.02–1.17 (mean: 1.08)	3	small				
<i>D. ornata</i> coast	yes	1.0–1.15 (mean: 1.05)	6	small			+	
<i>D. ornata</i> Zanzibar	yes	1.05–1.17 (mean: 1.1)	6	small				
<i>D. zernyi</i>	small	0.89–1.1 (mean: 1.01)	6	small			+	
<i>D. ngurumontana</i> sp. nov.	small	0.93–1.07 (mean: 1.0)	3	no		6	+	
<i>D. tanneri</i>	no	0.9–1.07 (mean: 0.96)	6	no		6	+	
<i>D. versicolor</i> sp. nov.	small	0.88–0.96 (mean: 0.94)	3	no			+	
<i>D. bulla</i>	yes	1.15						
<i>D. grandis</i>	yes	1.1 (n = 2)						
<i>D. nitens</i>	yes	1.26						
<i>D. scutellata</i>	yes	1.14					?	
<i>D. takanoi</i>	yes	0.96					?	
<i>D. ugandana</i>	yes	1.09–1.15		small	1.05–1.17 (mean: 1.13)	4		
<i>Kefalia grafika</i> Hemp, 2019	yes	1.17		no				
<i>Kefalia laeta</i> Hemp, 2019	yes	1.59		no				
<i>Kefalia omorfa</i> Hemp, 2019	yes	1.39		no				
<i>Atlasacris peculiaris</i> Rehn, 1914	yes	1.25		very slightly	?			OSF
<i>Atlasacris brevipennis</i> Massa, 2015	yes	1.11		?	?			Massa 2015
<i>Ivensia breviala</i> Ragge, 1980	yes	1.37		?	?			OSF
<i>Ivensia longispina</i> Ragge, 1980	slightly/no	1.18		?	?			OSF
<i>Ivensia parva</i> Ragge, 1980	yes	1.5		?	?			OSF
<i>Ivensia scaura</i> Ragge, 1980	slightly/no	1.16		?	?			OSF
<i>Meruterrana elegans</i> Sjöstedt, 1912	yes	1.52		no	0.94			
<i>Arostratum oblitum</i> Massa, 2015	(very) slightly			?				Massa 2015

patrically, the relationship of *D. scutellata* to any of the here mentioned groups is unclear. Only if more individuals were found, the songs studied and the color pattern of living individuals compared more about the relationship of this species to other groups may be encountered. A common character between *D. ornata*, *D. grandis*, *D. zernyi*, and *D. scutellata* is a three-parted stridulatory file. Both, *D. ornata* and *D. scutellata*, are distributed throughout coastal and lowland habitats while *D. ornata* is also found at submontane to montane elevations (e.g. in the West Usambara and the Uluguru Mountains). The only two known males of *D. scutellata* were found in the East Usambara Mountains (Kwamgumi Forest Reserve) and the Pugu Hills near Dar es Salaam thus suggesting a coastal/lowland forest distribution.

The other specimens known from Tanzania are restricted to mountain ranges of the Eastern Arc Chain and form the other two groups – lowland/submontane and montane species – with each group characterized by a color pattern typical for the species of each group. The *jagoi*-group (*D. jagoi*, *D. flavoviridis* sp. nov., *D. magombera* sp. nov., *D. sanje* sp. nov., and probably *D. ugandana* sp. nov. from Uganda) consists of species restricted to lowland and submontane elevations along the Eastern Arc chain with a contrasting color pattern of black and green or yellow with males sometimes having a turquoise tinge (Fig. 1). Also, as far as it can be judged from dried specimens, *D. ugandana* sp. nov., belongs to this group. In all species medially on the pronotum a black stripe is pres-

ent solid black or divided into parallel lines with greenish or yellowish color between them but always running to the posterior margin of the pronotum. All studied species of the *jagoi*-group occur in closed forest and were never found to reach high abundancies at a certain locality, as observed e.g. in *D. ornata*.

The montane *tanneri*-group on the other hand does not show conspicuously inflated pronotal lobes, only slightly inflated in the males of some of the species and not at all in females. Individuals of these species are often found clustered and maybe due to montane elevations they also depend on open situations within forests to be able to bask and thus gain enough warmth for development. Therefore the radius addressing a female partner with the song must not be as large as in species occurring in closed forest with a low density sitting far apart as in the *jagoi*-group with partly strongly inflated pronotal lobes. The montane group is comprised of *D. tanneri* endemic to the West Usambaras, *D. ngurumontana* sp. nov., endemic to the Ngurus, and *D. versicolor* sp. nov., endemic to the Uluguru Mountains. In terms of their color pattern, only slightly inflated pronotal lobes, and occurring on clearings and open forest paths as well as exhibiting aggregation behavior they could be related to the *ornata*-group, however with an adaptation to montane elevations. As in the *tanneri*-group, males of the *ornata*-group also can have slightly, but also distinctly inflated pronotal lobes with differences between the single populations from small prebullae to considerably inflated ones (Table 2).

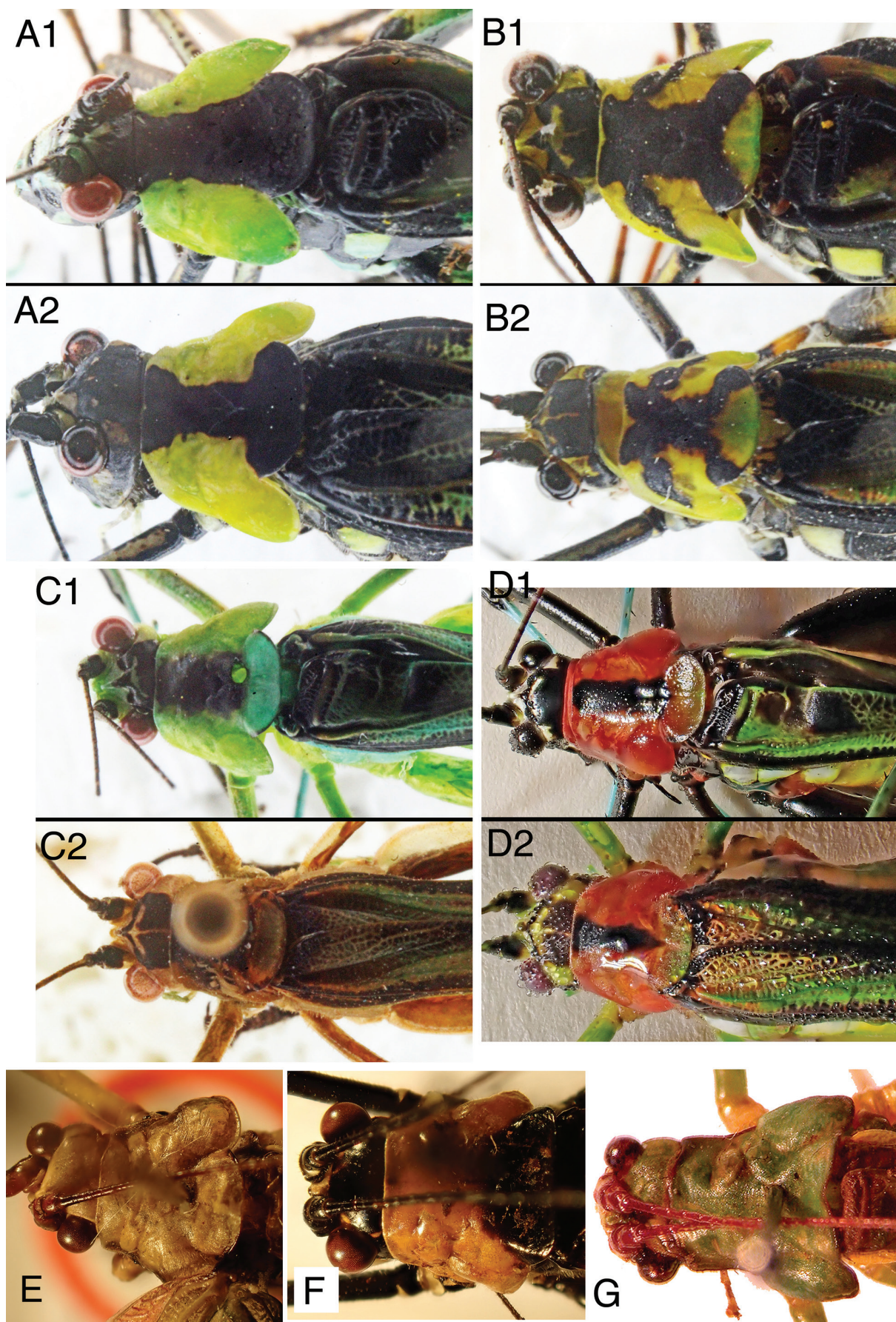


Figure 35. Dorsal view of pronotum in *Dioncomena* and related genera, indicating different degrees of widening. **A.** *D. flavoviridis* sp. nov.; **B.** *D. sanje* sp. nov.; **C.** *D. ornata*, Amani; **D.** *D. ornata*, Jozani, Zanzibar; **E.** *Kefalia laeta* Hemp, 2017; **F.** *Meruterrana elegans* Sjöstedt, 1912; **G.** *Atlasacris brevipennis* Massa, 2015 (photo OSF); 1 male, 2 female.

D. tanneri is a rare species in the West Usambara Mountains as is *D. versicolor* sp. nov. in the Uluguru Mountains. As in *D. ornata* populations found in submontane elevations, *D. tanneri* and *D. versicolor* sp. nov. only have one generation per year. In contrast to *D. ornata* where hatching of the eggs is very likely triggered by temperature and precipitation, *D. tanneri* seems to be fully adapted to a montane climate. Although eggs of *D. tanneri* laid in March 2021 were kept moist and were exposed to summer temperatures in the laboratory, nymphs did not hatch before September 2021 while *D. ornata* and *D. sanje* sp. nov. eggs hatched more or less 2 months later during the same time period and under the same climatic conditions.

Acoustics

Among bush-crickets, phaneropterines are well-known for their complicated songs. Their sounds may contain up to five syllable types and more than 1000 syllables per song unit (see Heller et al. 2015). However, species with these extremely complicated songs are not common. Species with more than 200 syllables per song unit, for example, are known only from six genera worldwide. Most *Dioncomena* species are above this value. They all have complex songs, strongly differing between the species (Fig. 18). Most of them have clearly structured songs with a starting, a middle and an end sequence, only *D. sanje* produces a continuous song lasting sometimes many minutes with two parts alternating. All species are diurnal, i.e. their songs are heard only during daytime (and sometimes at dusk). However, regular tick sounds – often for hours – were recorded in some species also at night (e.g. *D. jagoi*, *D. zernyi*, *D. ornata*).

Females respond very precisely at certain points of the male song (Figs 23–25) – an indication that these duets are very important for mate localization. However, what happens really before the sexes meet? Unfortunately, data from the behavior in the field do not exist. In the lab and without female contact males were observed to sit at one place for the whole day and sing. One could assume that the females approach a singing male silently – by day and night? – and start to respond (during daytime) when his song is loud enough and sufficient for her standards. In such a scenario the male ticking song could be used for a rough mate localization by the female. The last steps before the contact would have to be done by the male (strategy 3 in Spooner 1995).

During the production of the complicated songs the sounds produced during opening movements of the tegmina are louder than those during the closing movements. This was demonstrated by the recording of the stridulatory movement in *D. sanje* sp. nov., where the closing movement can sometimes even be completely mute. In the other species the sound production is not known in detail, but the structure of the file teeth suggest the same mechanism: the teeth are often curved with the tip towards the articulation (e.g., Fig. 2H) and/or the steep side of the teeth faces this direction (e.g., Fig. 2B). Sound production by opening wing movements (called ‘reverse stridulation’ by Mon-

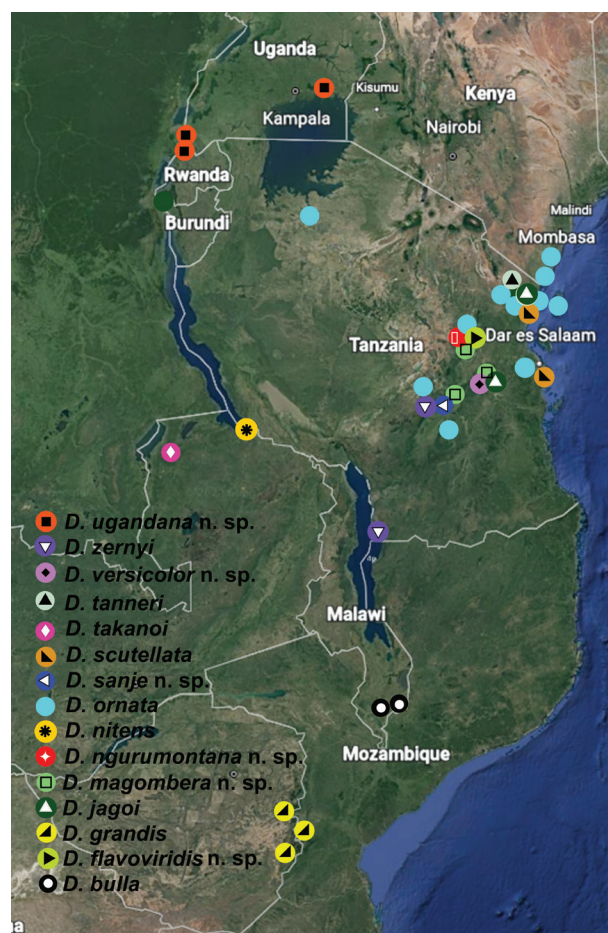


Figure 36. Distribution of *Dioncomena* species in East Africa. Locality data this paper, Ragge 1980; Hemp 2017; Massa 2021; Naskrecki and Guta 2019. Source: Google maps.

tealegre-Z 2012) is rare among Tettigonioidae and among phaneropterines documented only for *Phaneroptera* spp. Serville, 1831 and *Monticolaria kilimandjarica* (see Heller et al. 2015). The stridulatory files in *Dioncomena* are quite diverse. However, in no species lumps (or wing stoppers) as in *Ischnomela* Stål, 1873 (Montealegre-Z 2012) or a bend in the file like in *Phaneroptera* (Heller et al. 2021) are found, which were interpreted as a protection against ‘complete separation of the wings and subsequent erroneous wing overlapping during the ongoing cycle’ (Montealegre-Z 2012). However, another character of reverse stridulation, tooth spacing gradually increasing towards the anal margin of the wing (Montealegre-Z 2012), can be observed in several species, although it is not necessary for a pure-tone sound not found in *Dioncomena*. Within the genus, the number of stridulatory teeth varies between 30 and 100. More surprising, not only the number of teeth differs by a factor of three, but also their arrangement shows huge differences. In *Dioncomena flavoviridis* sp. nov. the file bears ca. 50 uniformly spaced teeth (Fig. 2B), in *D. jagoi* and *D. magombera* sp. nov. the basal end of the file differs distinctly from the rest (Fig. 2A, C), and in the three species *D. ornata*, *D. grandis* and *D. zernyi* the file is divided into three parts of very different tooth density (Fig. 2E–G). Phaneropterines are well known for complicated files and in some cases the function of the file modifi-

cation is understood (e.g., genus *Acrometopa* Fieber, 1853; Hemp et al. 2018). In *Dioncomena*, however, the situation is more complicated. From the amplitude pattern alone the use of different file parts cannot be safely predicted. The stridulatory movement is known only in *D. sanje* sp. nov., a species with a relatively simple file. Nevertheless, using this file the males are able to produce syllable types with a widely different spectral composition (see Fig. 30).

Except *D. sanje* sp. nov., most sounds produced by investigated *Dioncomena* males were relatively similar in the spectral composition (Fig. 30). The broad main peak was nearly always situated around 20 kHz. Some song parts had ultrasonic components in addition, only in *D. zernyi* and *D. ngurumontana* sp. nov. very broad-banded sounds were observed with peaks around 45 kHz. *D. sanje* sp. nov. males, however, produced a special type of syllables at certain points of their song. These HF-syllables have a peak at 60 kHz and only weak components with lower frequencies (Fig. 30, green curve; Fig. 31). They are placed after the dense sound combination and before the loud, short ticking sound which may trigger the female response. Possibly the HF-syllable helps the female to estimate the distance to the singing male as hypothesized for the HF-syllables in *Phaneroptera* (Heller et al. 2021). Surprisingly, the HF-syllables seem to be produced with exactly the same part of the file as the dense sound combination (Fig. 27B) which is much lower in frequency. In the phaneropterine *Gonatoxia helleri* Hemp, 2016 the males sing with different frequencies very likely by using differently structured parts of the file (Heller and Hemp 2017). The different frequencies are also not easily explained by the tegmen morphology, since as in *D. flavoviridis* sp. nov. (Fig. 29) and all *Dioncomena* species studied so far, the right tegmen bears only one large mirror cell. The mismatch of the natural frequency of the mirror and the peak frequencies of the either of the call types (in *D. sanje* sp. nov.) suggests that the apparent sharp tuning of the mirror is not being exploited during stridulation (i.e. matched to the tooth strike rate): a case of non-resonant stridulation. The observed tuning peak in the mirror may be the natural response of a membrane which acts to radiate all and any input frequencies or a vestigial trait of a resonantly calling ancestor.

Sounds at 20–30 kHz are certainly easily perceived by the animals since they are in the typical frequency range of tettigoniid signals. At higher frequencies the ears often become less sensitive. However, there are exceptions where the hearing threshold falls continuously until at least 40 kHz (see *Poecilimon elegans* Brunner von Wattenwyl, 1878 in Strauß et al. 2014). These special adaptations cannot be recognized from morphology and have to be studied neurophysiologically.

In some *Dioncomena* species (and some other species; see Table 2) the ears show unusual modifications, but they are probably not related to improved frequency sensitivity. The inflation of the pronotal lobes, the prebullae, have most likely evolved to increase the general auditory sensitivity and/or the directionality of the ears. The physiological function of these ears having huge auditory tracheae with left and right one touching each other are not well understood. A first detailed study was done by Ce-

liker et al. (2022), but they could not model the cross-talk between left and right ear. That this connectivity exists – similar to the situation in field crickets (Michelsen and Løhe 1995) – was already described in 2011 by Mohsin and Schul in a conference presentation. Improving sensitivity and/or the directionality would easily explain why mostly the males possess prebullae: to detect the short, rare and probably faint female signals.

But why are these structures not found in all *Dioncomena* species? Their presence in the closely related *Kefalia* (Grzywacz et al. in prep.) indicates that they evolved in the common ancestor of both, if not earlier. At least in *Dioncomena* the size of the lateral lobes is strongly correlated with the behavior and ecology of the species, i. e. the population density. The largest inflations of the pronotal lobes are found in species living scattered within closed forest while species living on clearings and along forests edges often found in clusters have less or not inflated pronotal lobes, especially in the females. Obviously the costs of such ears are not negligible (see Stumpner and Heller 1992; Lehmann 2012; Strauß et al. 2014) and the hearing sensitivity evolves towards an optimum but not a maximum. Unfortunately, hard data for this point are nearly completely missing (see Helversen et al. 2012) but from the variability seen in and between populations of *D. ornata* one could assume that here costs and benefits are nearly balanced.

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Supplementary material 1

***Dioncomena flavoviridis*, male calling song at 22 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 2

***Dioncomena flavoviridis*, male female duet at 23 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 3

***Dioncomena jagoi*, male calling song at 22 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 4

***Dioncomena ngurumontana*, male calling song at 21 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 5

***Dioncomena ngurumontana*, male female duet at 21 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

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Supplementary material 6

***Dioncomena ornata*, male calling song at 23 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 7

***Dioncomena ornata*, male female duet at 22 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 8

***Dioncomena sanje*, male calling song at 23 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Link: <https://doi.org/10.3897/dez.70.100804.suppl8>

Supplementary material 9

***Dioncomena sanje*, male calling song at 24 °C, sampling rate 192 kHz**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Link: <https://doi.org/10.3897/dez.70.100804.suppl9>

Supplementary material 10

***Dioncomena sanje*, male female duet at 21 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Link: <https://doi.org/10.3897/dez.70.100804.suppl10>

Supplementary material 11

***Dioncomena tanneri*, male calling song at 23 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Link: <https://doi.org/10.3897/dez.70.100804.suppl11>

Supplementary material 12

***Dioncomena versicolor*, male calling song at 23 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Link: <https://doi.org/10.3897/dez.70.100804.suppl12>

Supplementary material 13

***Dioncomena zernyi*, male calling song at 28 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z,
Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Link: <https://doi.org/10.3897/dez.70.100804.suppl13>

Supplementary material 14

***Dioncomena magombera*, male calling song at 23 °C**

Authors: Claudia Hemp, Fernando Montealegre-Z,
Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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