

# Complex songs and cryptic ethospecies: the case of the *Ducetia japonica* group (Orthoptera: Tettigoniodea: Phaneropteridae: Phaneropterinae)

KLAUS-GERHARD HELLER<sup>1</sup>, SIGFRID INGRISCH<sup>2</sup>, CHUN-XIANG LIU<sup>3</sup>, FU-MIN SHI<sup>4</sup>, CLAUDIA HEMP<sup>5</sup>, ELŻBIETA WARCHAŁOWSKA-ŚLIWA<sup>6</sup> and DAVID C.F. RENTZ<sup>7</sup>

<sup>1</sup>Grillenstieg 18, D-39120 Magdeburg, Germany

<sup>2</sup>Zoological Research Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany

<sup>3</sup>Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, P.R. China

<sup>4</sup>College of Life Sciences, Hebei University, Baoding 071002, P.R. China

<sup>5</sup>University of Würzburg, Dept. Animal Ecology and Tropical Biology (Zoology III), 97074 Würzburg, Germany

<sup>6</sup>Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, 31-016 Kraków, Poland

<sup>7</sup>Adjunct Professor, School of Marine and Biological Sciences, James Cook University, Smithfield, Queensland 4870, Australia

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In many groups of animals, especially insects, genital morphology is species distinctive. This is true of bush-crickets or katydids (Tettigoniodea). The calling songs produced by males are species distinctive and do not change significantly during the early stages of speciation. Their patterns are usually relatively simple. We present an example where none of these assumptions is true. Since the last revision of the genus *Ducetia* in 1961, one widespread species, *Ducetia japonica* (Thunberg, 1815) has been thought to be morphologically uniform. It is represented by tens of specimens from south and eastern Asia and Australasia on both sides of Wallace's Line. The male genitalic appendages vary little over the extent of its range. In contrast, the calling songs differ considerably from place to place. Examination of the stridulatory organs of both sexes (located on the first set of wings) reflects the differences in song. The teeth, which produce the sound, differ in shape, number, and size. We present details of the song patterns and the stridulatory organs that produce them. As a result, some synonyms are re-established, and new species are described. Chromosomal information is presented for two species. The origins and the distribution and expansion of the group are detailed. Duets between courting pairs have played an important role in the evolution of this song structure where efforts to trick eavesdropping rivals are common.

**ADDITIONAL KEYWORDS:** acoustic female – bioacoustics – bush-crickets – calling song – duet – katydids – Orthoptera – Phaneropterinae – response – speciation.

## INTRODUCTION

Communication usually precedes mating in most organisms with the function to locate each other and to exchange information about mate quality. Over long

distances, various groups employ a variety of mechanisms to facilitate encounters. Moths, for example, employ pheromones, butterflies rely on colour and colour patterns and cicadas, and many orthopteroid insects (crickets, grasshoppers, and katydids), utilize sound (see, e.g., Greenfield, 2002). At close range, tactile stimuli, usually produced by specific structures, become more important (Eberhard, 1985). The quality of these signals can be attributed to the Darwinian fitness of the senders and receivers, and this maintains

\*Corresponding author. E-mail: [heller.volleth@t-online.de](mailto:heller.volleth@t-online.de)  
[Version of Record, published on 1 April 2017; <http://zoobank.org/> urn:lsid:zoobank.org:pub:33EAAB15-651F-46E8-BC61-63BBF8840452]

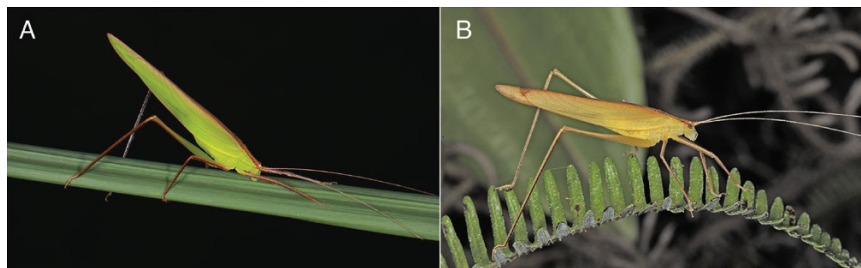
the coherence of gene pools. Mismatches occur when the signals are different (sender–receiver mismatch; see, e.g., Panhuis *et al.*, 2001). In the extreme, males and females do not recognize one another and do not mate. As a result, no offspring are produced, and if they are typically from two different populations, they would be considered as reproductively isolated and, therefore, be considered as two distinct species.

In the majority of insects, distinctive differences can be found in the morphology of the male and female genitalic organs – the structures used for the latest step in the exchange of signals between males and females. These structures are a sort of ‘lock and key’. If the structures do not fit, a successful mating will most likely not occur. There are some groups where the genitalia are remarkably similar from species to species. Inevitably, these groups rely on other parameters to achieve recognition. Some examples are lacewings (Neuroptera: Chrysopidae) that communicate by vibratory signals (Henry, 2006) and acridine grasshoppers that utilize species-specific courtship songs (Helvesen & Helvesen, 1994). These examples may indicate a more widespread phenomenon. They can only be studied in live animals and may be the result of ‘hidden genetic diversity’ (e.g., Jaiswara *et al.*, 2012).

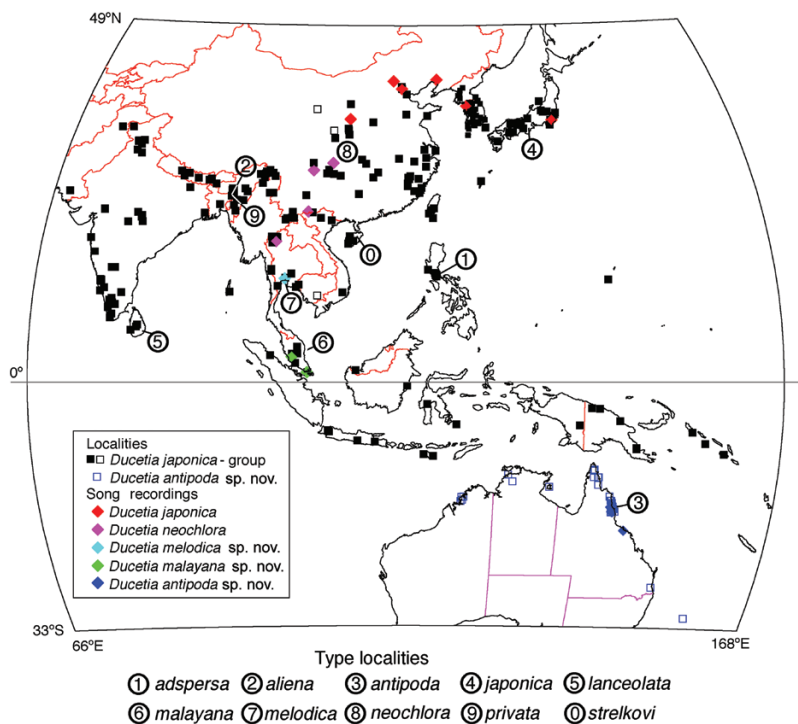
This sort of species diversity is not well documented in the tettigonioid Orthoptera (bush-crickets or katydids, in this manuscript called ‘bush-crickets’, but see Nityananda & Balakrishnan, 2006 for a rare exception). Walker (1964) discovered several examples in crickets (Grylloidea). According to Heller (2006), closely related, allopatric tettigonioid species differ typically in the morphology of their genitalia but differ only little in their calling songs. In the last few years, some allopatric species have been described, which differ in song but not in genitalia. In Europe, these are flightless, mostly locally distributed species (Kleukers, Ode & Fontana, 2010; Orci, Szövényi & Nagy, 2010; Iorgu, 2012) belonging to the subfamily Phaneropterinae. With few exceptions in all species of the group, females respond acoustically to the male song (review Heller *et al.*, 2015). These studies suggest that speciation may sometimes start from song differences.

In fully winged tettigonioids, capable of flight, Nityananda & Balakrishnan (2006) observed different song ‘forms’ of a winged species, *Mecopoda elongata*, occurring sympatrically in India, while in the same year Forrest, Lajoie & Cusick (2006) described two species of the genus *Amblycorypha* which occur sympatrically in parts of their ranges but differ only in song. These two species are relatively widespread with more or less continuous ranges covering more than 1500 km in diameter. Walker, Forrest & Spooner (2003) had previously described a similar example in *Amblycorypha*. It seems logical to conclude that, in these species, the first link of the chain of signals is sufficient for coexistence without the need for obvious changes in the structure of the genitalia. Interestingly, the North American species of *Amblycorypha* also belong to the subfamily Phaneropterinae as do the short-winged species mentioned above. The group contains species with quite simple to very complex songs with *Amblycorypha* belonging to the latter (Heller *et al.*, 2015).

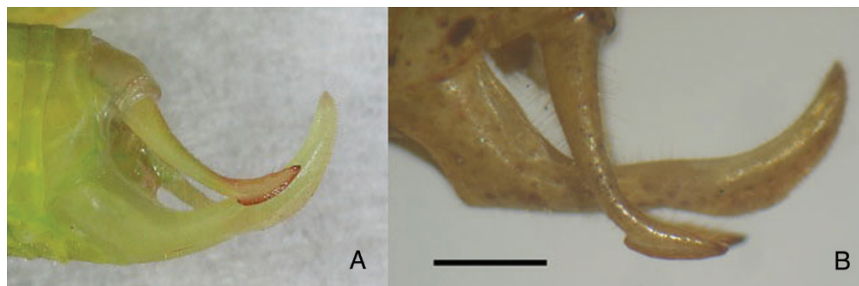
Here, we present acoustic data on another phaneropterine species or species complex of Phaneropterinae with complex song belonging to *Ducetia* Stål (see Heller *et al.*, 2015 for song complexity in phaneropterines). The genus has a very large geographic range covering tropical Africa, Asia, Australia, and Oceania (Ragge, 1961) and contains fully winged species and species with reduced hindwings as well as with reduced forewings. Some individual *Ducetia* species are very widespread. *Ducetia japonica*, the species studied here, is a long-winged species (Fig. 1) and one of the most widespread tettigonioid species in the world found from Japan to Australia (5000 km) and Pakistan to the Solomon Islands (10 000 km; Fig. 2). It is a medium-sized bush-cricket (length of the fore wings  $27 \pm 5$  mm; Ragge, 1961) with two colour morphs, green or brown (Fig. 1), and everywhere in its range, it is easily recognized and diagnosed by a long internoventral ridge of the male cerci (Fig. 3) and by unique tegminal venation. Similar to species of the above-mentioned genus *Amblycorypha*, it also has a long, complex song that is known from some published CDs (Rentz, 1996; Ichikawa *et al.*, 2006; Kim, 2009). Within China an



**Figure 1.** Male of *Ducetia antipoda* sp. nov., a member of the *D. japonica* group. (A) green morph in typical resting or defensive posture, (B) yellow-brown morph abroad at night.



**Figure 2.** Distribution map in Hammer equal area projection. Black squares – localities of specimens identified as *Ducetia japonica* s.l. (filled exact locality, open province/country only), blue squares – localities of specimens identified as *D. antipoda* sp. nov., coloured diamonds – localities where the different song types have been recorded. The numbers indicate the type localities of the forms currently considered as members of the *D. japonica* group.



**Figure 3.** Male cercus (A) and subgenital plate (B) of *D. antipoda* sp. nov. and *D. malayana* sp. nov. (CH3768; scale 1 mm).

unexpected variation in the calling song pattern has been described (Shi, Yang & Du, 2003, following observations of Yang, Chang & Lu, 2000). Using published and new data, we have first documentation of song variation of this complex throughout its huge range (at least in the North–South extension: Japan to Australia) and present data on female acoustical behaviour.

#### MATERIAL AND METHODS

Specimens of *D. japonica* group examined (all males except otherwise mentioned; CH, Collection Heller; FS, file studied; SR, song record): CH4147 FS, SR,

AUSTRALIA: Queensland, Atherton Table Land, Malanda near Malanda Falls (17°22'S, 145°36'E), 1 November 1997, leg. K.-G. Heller; CH4146 SR, 48 FS, AUSTRALIA: Queensland, near Daintree (Cape Tribulation), National Park: Lync Haven (16°10'S, 145°25'E), 31 October 1997, leg. K.-G. Heller; CH7908–7913, 7915–7934 FS, SR, AUSTRALIA: Queensland, Mt. Molloy, Bakers Rd 3.8 km from Hwy (16°40'S, 145°16'E), 385 m, 27 July 2014, coll. D.C.F. Rentz & Claudia Hemp + lab-reared F1 generation; CH7670 FS, SR, CHINA: Yunnan, Honghe, pass north of Jinping (22°51'N, 103°13'E), 1957 m, 19–20 August 2013, leg. Liu Chunxiang; C\_Liu SR, CHINA: Beijing suburbs, September 2015, leg. Liu Chunxiang; C\_Liu SR, CHINA,

Liaoning Province, Panjing, Gaosheng, Xibin, September 2015, leg. Liu Chunxiang; CH7373 INDONESIA: Sulawesi, S-Sulawesi, Rantepao, Makale, 16 September 1992, leg. Harald Beck; INDONESIA, Java, Gunung Salak, 20 March 1993, leg. Sigfrid Ingrisch; CH3653 SR, CH3771–2, 8–28 March 1981, CH3661 FS (tegmina of several specimens only), CH3768–9, 12–19 April 1981, CH3678 SR, CH3696 (tegmina only), CH3799, CH3802, CH3807, CH3816 (female), CH3819–20, 28 February–24 April 1984, CH3675 SR, CH3824, 30 April 1989, CH3417 4 March–5 April 1992, CH3484 (female) 5–8 November 1997, MALAYSIA: Selangor, Ulu Gombak Field Study Centre (20 km north-west of Kuala Lumpur; 3°20'N, 101°45'E), 260 m, leg. K.-G. Heller & M. Volleth; CH7422, SOUTH KOREA: Seoul Nowon-gu Chung-Gye 4 Dong Mt. Bulamsan, 4 × 2011, leg. Howon Rhee; CH7420–21, SOUTH KOREA: Seoul Nowon-gu Danghyunbach, 28 September 2011, leg. Howon Rhee.

In addition, we examined the holotypes of *Ducetia adpersa* Brunner von Wattenwyl, 1878, in Museum für Naturkunde (MfN, Berlin) and of *Phanoptera aliena* Walker, 1869, *Steirodon lanceolatum* Walker, 1859, *Phanoptera neochlora* Walker, 1869, and *Phanoptera privata* Walker, 1869, in the Natural History Museum ([NHM], London), all considered to be synonyms of *D. japonica* by Ragge (1961).

See Supporting Information for more data of the new species.

Sound records of all species are deposited at SysTax and Orthoptera Species File Online (OSFO) and/or published on CDs (see Table 1). Sound files of one song unit of each species can also be found in SI6.

## BIOACOUSTICS

The song recordings are partly own unpublished data (samples available in OSFO and SysTax), partly taken from published CDs or the Internet (Table 1) and evaluated all in the same way. For making the recordings, many different microphones were used. The song is completely in the audible range, and thus, effects of the microphone on the temporal pattern are not to be expected (see also 'Results' section). Recordings covering the frequency range up to 50 kHz were made using a digital Bat Detector (Pettersson D1000×) with a sampling rate of 100 kHz. Male–female duets were recorded using two microphones, one close to a singing male and the other close to a virgin female sitting in a separate cage.

Song measurements and sonograms (FFT size 128 points, Hanning window, sound sampling rate = 100 000 Hz) 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).

## TERMINOLOGY

**Syllable** is the sound produced during one cycle of movements (opening and closing of the tegmina); **syllable duration** is the time period measured from the first impulse to the last; **syllable period** is the time period measured from the first impulse to the first impulse of the next syllable (reciprocal value: syllable repetition rate [SRR]); **impulse** is a simple, undivided,

**Table 1.** Data of song recordings (per country, from the North to the South)

Species	Geographic origin	Lat. N	Long. E	T (°C)	Source
<i>japonica</i>	Japan (assumed near Tokyo)	35.4	139.8	23	Ichikawa <i>et al.</i> (2006)
<i>japonica</i>	Japan			?	Kansatsuki (2015)
<i>japonica</i>	Korea, Incheon	37.46	126.65	28	Kim (2009)
<i>japonica</i>	China, Liaoning, Xibin	41.2	22.1	25	Unpublished
<i>japonica</i>	China, Hebei	41	115	28	Wu (2010)
<i>japonica</i>	China, Beijing	39.9	116.4	21–23	Unpublished
<i>japonica</i>	China, Shaanxi, Guanzhong	35.6	108.4	24	Shi <i>et al.</i> (2003)
<i>neochlora</i>	China, Chongqing, Beibei	29.5	106.3	24	Shi <i>et al.</i> (2003)
<i>neochlora</i>	China, Sichuan, Meigu	28.5	103.5	24	Shi <i>et al.</i> (2003)
<i>neochlora</i>	China, Yunnan	22.85	103.217	25	Unpublished
<i>neochlora</i>	Thailand, Chiang Mai, Hang Dong ex ovo	18.79	99	21–23	Own data in OSFO
<b><i>melodica</i> sp. nov.</b>	Thailand, Bangkok	13.75	100.5	24–28	Own data in OSFO
<b><i>malayana</i> sp. nov.</b>	Malaysia, Kuala Lumpur	3.333	101.75	20–25	Own data in OSFO
<b><i>malayana</i> sp. nov.</b>	Singapore	1.8	103.8	?	Sismondo 1983–1986
<b><i>antipoda</i> sp. nov.</b>	Australia, Daintree	–16.167	145.417	20	Own data in OSFO
<b><i>antipoda</i> sp. nov.</b>	Australia, Mt. Molloy	–16.67	145.267	20–23	Unpublished
<b><i>antipoda</i> sp. nov.</b>	Australia, Yungaburra	–17.27	145.55	25	Rentz (1996)
<b><i>antipoda</i> sp. nov.</b>	Australia, Malanda	–17.367	145.6	20	Own data in OSFO

transient train of sound waves (here the damped sound impulse arising as the effect of one tooth of the stridulatory file being struck by the scraper).

In all species, after some time, the same pattern of syllables and pauses is repeated. Such a portion of the song is called **song unit**. The duration of one unit was measured from beginning of the first syllable to end of the last syllable.

## RESULTS

### GENERAL MORPHOLOGY

In external morphology, all specimens studied here are uniform as also described by Ragge (1961) for the *D. japonica* specimens seen in his revision of the genus *Ducetia*. *Ducetia japonica* differs from all other *Ducetia* species by the venation of the forewings and especially by the peculiar structure of the male cerci. According to Ragge (1961), they have a long ‘internoventral ridge at the apex’ (Fig. 3) and differ in this character also from all *Ducetia* species described later (see Kang, Liu & Liu, 2014) except *Ducetia strelkovi* Gorochoy, Storozhenko & Kostia, 1994. The single known male of this species from Hainan differs by wing characters (Gorochoy, Storozhenko & Kostia, 1994). For *D. japonica*, Ragge (1961) explicitly noted that ‘there is generally very little geographic variation’. For a detailed description, see SI2 under *Ducetia antipoda* sp. nov. Specimens differ, however, by hidden details of the stridulatory organs that can be seen only after opening the tegmina (see below).

### DISTRIBUTION

Localities where specimens determined as *D. japonica* have been found are distributed over a huge area extending from Pakistan in the West to the Solomon Islands in the East and from Northern China in the North to northern Australia in the South (Fig. 2; for reference, see Table 2). In addition, we provide data from several museums (National Institute of Genetics: Entomological Specimens of Museum of Nature and Human Activities, Hyogo Pref., Japan; Zoologisches Forschungsinstitut und Museum Alexander Koenig: Orthopteroidea; National Museum of Nature and Science, Japan; Ibaraki Nature Museum, Arthropod collection; National Museum of Nature and Science, Japan: Insect Specimens of Omogo Mountain Museum; National Museum of Nature and Science, Japan: Gunma Museum of Natural History, Insect Specimen; all via GBIF = Global Biodiversity Information Facility). All personal data were evaluated. The list of localities is certainly not complete for such a widespread species but gives an idea of the area covered.

**Table 2.** References to localities shown in Fig. 2.

Author(s)	Year	Area
Asana, Makino & Niyama	1938	India
Bey-Bienko	1954	East Asia
Brunner von Wattenwyl	1878	Whole range
Buzzetti & Devriese	2008	Myanmar
Gupta & Shishodia	2009	India
Han, Liu & Shi	2015	China
Ingrisch & Garai	2001	Nepal
Ingrisch & Shishodia	2000	India
Jin & Xia	1994	China
Kang <i>et al.</i>	2014	China
Karny	1921	Philippines
Karny	1923	South East Asia
Kim & Kim	2001	Korea
Kim & Puskas	2012	Korea
Koide	2013	Guam
Kulkarni & Shishodia	2004	India
Kulkarni & Shishodia	2005	India
Mandal, Mandal & Hazra	2007	India
Matsumura & Shiraki	1908	Japan
Nagar, Swaminathan & Mal	2015	India
Prabakar	2015	India
Ragge	1961	Whole range
Shishodia	2000	India
Shishodia	2006	India
Shishodia	2007	India
Shishodia & Barman	2004	India
Shishodia & Gupta	2009	India
Shishodia & Kulkarni	2002	India
Shishodia <i>et al.</i>	2003	India
Shishodia, Chandra & Gupta	2010	India
Sultana, Wagan & Panhwar	2012	Pakistan
Thakur <i>et al.</i>	2004	India
Willemse	1953	Indonesia

According to Childebaev & Storozhenko (2004), *D. japonica* is not found in Kazakhstan as erroneously indicated by Kang *et al.* (2014).

### TAXONOMY

The different song types (see below) indicate clearly that *D. japonica* as presently understood is not a homogeneous, extremely widespread species, but a complex of several distinct species. The complete number of these species and their ranges are still largely unknown, but several can already be recognized. Also the study of the stridulatory organs revealed large differences between some specimens. While naming these forms, one has to consider whether one or more of the synonyms of *D. japonica* have to be restored. Fortunately, the nominate species was described from an area – Japan – where according to the present

knowledge no confusion is to be expected. So the northern form retains the name *D. japonica* with the synonym *Ducetia quinquenervis* (Haan, 1842) from the same country.

For the specimens from central/southern China to North Thailand the name *Ducetia neochlora* (Walker, 1869) seems to be appropriate. Walker (1869) states for the types ‘China Presented by G.T. Laye, Esq.’. In Walker’s catalogues (1869, 1870a, b) of insects in the British Museum, the same note appears for several species, but also as ‘Lay’ under *Caloptenus sinensis* Walker, 1870. Probably these notes refer always to George Tradescant Lay, a traveller, missionary, naturalist, plant collector, interpreter, and diplomat (Mason, 2005–2014). In science, he seems to be known mainly as a collector of plants (Anonymous, 2000–2015). Between 1836 and 1839 he was missionary in Macao and between 1841 and 1845 British diplomat in Guangzhou, Fuzhou, and Xiamen, so mainly active in central/southern China. He also presented the holotypes of *Acridium saturatum* Walker, 1870, and *C. sinensis* Walker, 1870 (both junior synonyms of *Eucoptacra praemorsa* (Stål, 1861), type locality Hong Kong), to the British Museum. This species seems to be found mainly in southern China (see map in OSFO), supporting the idea that the type of *D. neochlora* has also come from the South of China. Some other species found by G.T. Lay with locality ‘China’ are too widespread to give an indication where in China they might have been found (*Gryllotalpa africana*, *Ruspolia lineosa*). The stridulatory file of the holotype of *D. neochlora* agrees quite well with that of specimens from Chongqing in China (Shi *et al.*, 2003).

*Ducetia adspersa* Brunner von Wattenwyl, 1878, and *Ducetia lanceolata* (Walker, 1859), both formerly considered as synonyms, differ considerably in the structure of stridulatory file from all other forms of *D. japonica* (see Fig. SI1) and are considered as valid species.

The holotypes of the two species *Ducetia aliena* (Walker, 1869) and *Ducetia privata* (Walker, 1869) both come from Sylhet, Bangladesh, although found by different collectors. They have similar stridulatory files differing from the files of the species studied here. For the moment, we will consider them as belonging to a single separate species.

At present, we will leave *Phaneroptera suturalis* Heer, 1849, as an unresolved synonym under *Scudderia septentrionalis* (Serville, 1838). According to Rehn & Hebard (1914: 277), the description of *P. suturalis* does not fit to any North American phaneropterine. The authors assume that its type locality ‘Neu Georgien’ might be an island of the Solomon Islands, not part of North America as assumed by the author, and that it belongs to the genus *Ducetia* from which only

*D. japonica* is known from there. However, the type is probably lost (at least not marked in the collection of Heer at the ETH, Zürich). Heer described many beetles from ‘Neu Georgien’, and all checked ones came from North America (Eastwood, personal communication 15 September 2015).

#### *DUCETIA JAPONICA* (THUNBERG, 1815)

*Locusta japonica* Thunberg, 1815. Mémoires de l’Académie Impériale des Sciences de St. Pétersburg 5: 282. Type locality: Japan. Type material lost.

*Synonym: Locusta (Phaneroptera) quinquenervis* (Haan, 1842).

*Distribution:* Japan, Korea, and northern China (Fig. 2).

#### *DUCETIA NEOCHLORA* (WALKER, 1869)

##### STAT. REV.

*Phaneroptera neochlora* Walker, 1869. Catalogue of Dermaptera Saltatoria, p. 342, Lectotype male. China (Ragge, 1961). Two male paralectotypes, same data as lectotype. British Museum (NHM).

*Distribution:* Central and southern China, northern Thailand (see Fig. 2).

*Diagnosis:* Song unit of calling song consisting of three phases, the last two alternatingly repeated several times. Differs from the structurally similar calling song of *melodica* sp. nov. most notably by high SRR (c. 50 Hz) in the second phase (Table 3; see ‘Bioacoustics’ section for details).

#### *DUCETIA ALIENA* (WALKER, 1869) STAT. REV.

*Phaneroptera aliena* Walker, 1869. Catalogue of Dermaptera Saltatoria, p. 347.

*Type locality:* Silhet (=Sylhet, Bangladesh).

*Synonym: Phaneroptera privata* Walker, 1869, Catalogue of Dermaptera Saltatoria, p. 344.

*Type locality:* Silhet (=Sylhet, Bangladesh).

*Diagnosis:* Stridulatory file short, occupying only two-thirds of tegmen width (see Fig. SI1A–C; Table 4).

#### *DUCETIA ADSPERSA* BRUNNER VON WATTENWYL, 1878 STAT. REV.

Monographie der Phaneropteriden, p. 110.

**Table 3.** Characteristics of song units of species in the *Ducetia japonica* group

Species	Structure (different phases and typical number of repetitions)	Structure of song Phase A (duration; repetition rate of elements at end of part)	Structure of song Phase B (duration; repetition rate of elements)	Structure of song Phase C (duration; repetition rate of elements)	Number of specimens evaluated
<i>japonica</i>	AB	19–110 s; 6–14 Hz	2.7–7.5 s; 0.9–3.3 Hz		7
<i>neochlora</i>	A(BC) <sub>3–8</sub>	35–75 s; 4–9 Hz	1.5–6 s; 52–71 Hz	1–6 s; 10–13 Hz	4
<b><i>melodica</i> sp. nov.</b>	A(BC) <sub>5–9</sub>	19–24 s; 13–14 Hz	0.5–2 s; 17–22 Hz	0.4–1.9 s; 8.5–10 Hz	1
<b><i>malayana</i> sp. nov.</b>	A	1–2.6 s; 11–14 Hz			4
<b><i>antipoda</i> sp. nov.</b>	ABC	21–47 s; 2.6–4.1 Hz	2.5–4.5 s; 5.7–9.4 Hz	3–13 s; 3.2–5.7 Hz	12

**Table 4.** Characteristics of stridulatory files

Species	Source/specimen, origin (scanning electron microscope, SEM)	The number of teeth in distal part	The number of teeth in proximate part
<i>japonica</i>	Kim (2009): Korea, SEM	4 (9)	61
<i>japonica</i>	CH7421–2: Korea ( <i>n</i> = 2)	6	57–60
<i>japonica</i>	Wu (2010): China, Hebei	6	66
<i>japonica</i>	Shi <i>et al.</i> (2003): China, Shaanxi, SEM	10	71
<i>neochlora</i>	Shi <i>et al.</i> (2003): China, Ya'an, SEM	10	66
<i>neochlora</i>	holotype, China	4	74
<i>neochlora</i>	Shi <i>et al.</i> (2003): China, Beibei, SEM	5	72
<i>neochlora</i>	CH7670: China, Yunnan	7	68
<i>neochlora</i>	Ingrisch: Thailand, Chiang Mai, Hang Dong ex ovo	9–10	65–68
<b><i>melodica</i> sp. nov.</b>	Ingrisch: Thailand, Bangkok ( <i>n</i> = 2)	10–12	55–56
<b><i>malayana</i> sp. nov.</b>	CH3661a,b, 3675: Malaysia, SEM ( <i>n</i> = 3)	9–10	57–65
<b><i>antipoda</i> sp. nov.</b>	CH4147: Australia, Malanda	12	45
<b><i>antipoda</i> sp. nov.</b>	CH4148: Australia, Daintree	12	51
<b><i>antipoda</i> sp. nov.</b>	CH7913, 7915: Australia, Mt. Molloy ( <i>n</i> = 2)	13–15	37–38
<i>adspersa</i>	holotype, Philippines, Manila	7+	21
<i>aliena</i>	holotype, Bangladesh, Sylhet	15	56
<i>privata</i>	holotype, Bangladesh, Sylhet	12	<i>c.</i> 60 (estimated)
<i>lanceolata</i>	holotype, Sri Lanka	10	118
<i>javanica</i>	Ingrisch: Java, Tretes	15	25

*Type locality:* Manila, Philippines.

*Diagnosis:* Number of teeth on the stridulatory file is distinctly lower (fewer than 30, in the proximal part fewer than 25) than in any other species of the *D. japonica* group. There are no large teeth at the distal end of the file (see Fig. SI1A–C, Table 4). Mirror at the base of the right tegmen without triangular expansion of the posterior–internal angle as in *D. japonica* and some other species of the group. Minute internal tooth at the tip of the male cercus is compressed, not conical as in *D. japonica*.

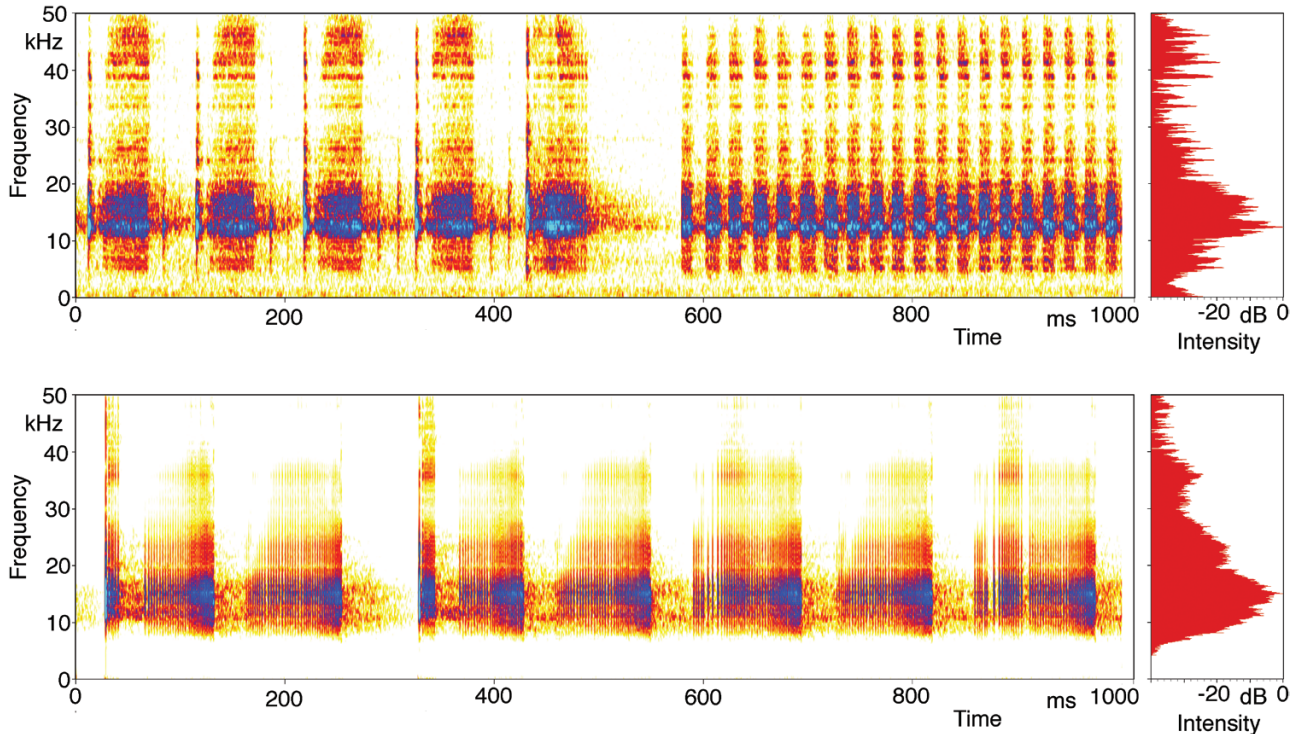
*DUCETIA LANCEOLATA* (WALKER, 1859)

STAT. REV.

*Steiroidon lanceolatum* Walker, 1859, Ann. Mag. nat. Hist. (3) 4: 222.

*Type locality:* Sri Lanka (lectotype Ragge, 1961)

*Diagnostic comment:* Number of teeth on the stridulatory file is distinctly higher (above 100) than in any other species of the *D. japonica* group (see Fig. SI1A–C, Table 4).



**Figure 4.** Sonogram (right) and power spectrum (left) of the calling song of *D. neochlora* (China, Yunnan) and *D. antipoda* sp. nov. (Australia, Mt. Molloy).

Distribution: Sri Lanka and possibly southern India. The description of a stridulatory file with about 150 teeth in *D. japonica* (Nagar, Swaminathan & Mal, 2015) from South India (Rajendra Nagar, personal communication 07 November 2015) supports a close relationship between this Indian specimen and *D. lanceolata* (c. 130 teeth).

***DUCETIA ANTIPODA* RENTZ & HELLER  
SP. NOV.**

(FIGS 1–3, SI2A–H, MAPS SI2, TABLE SI2. SONG FIGS 4, 11–12. STRIDULATORY ORGANS FIGS 13, 15, AND 17).

urn:lsid:Orthoptera.speciesfile.org:TaxonName:496315

*Ducetia japonica*: Tepper, 1892; Ragge, 1961 [partim]; Rentz & Balderson, 1979, 1989; Rentz, 1996, 2010. Not of Thunberg, 1815.

Holotype male. Label 16.48°S 145.38°E (GPS) QLD. Kuranda 335 m (Top of the Range) 19 Butler Dr 1–15 December 2012 DCF Rentz' (depository Australian National Insect Collection, CSIRO, Canberra). For list of paratypes, see SI2.

The type locality is a simple to complex mesophyll to notophyll vine forest on moderately to poorly drained metamorphics (Regional Ecosystem 7.11.1 EPA, 2007). The type was found at night singing from a low native shrub.

*Diagnosis*: Song unit of calling song consists of three phases each presented once, the last one consisting of a very long (3–13 s) sequence of mostly widely (c. 10–30 ms) separated impulses, thus differing from all other known species of the *D. japonica* complex (Table 3; see 'Bioacoustics' section for details).

*Description*: Stridulatory file with fewer than 55 teeth in the proximal part and more than 11 teeth in the distal part (Table 4). Otherwise morphologically similar to *D. japonica*. See text SI2 for details.

*Habitat*: *Ducetia antipoda* sp. nov. is a common inhabitant of edges, especially along roadway margins in tropical northern Australia. Adults can be found in the wet season (October–May), but they become less common as the habitat dries out. It frequents grasses, both native and introduced. This bush-cricket can also be found on herbs and some shrubs up to 1.5 m. The species is inactive during the day where it assumes a distinctive posture (Fig. 1). It also assumes this posture when it is under threat. Both sexes emerge after dark to feed and mate. It is a common food of the predatory listroscolid katydid, *Hexacentrus mundurra* Rentz, which lives in the same habitat. The females deposit their flat eggs between top and bottom layers of stiff leaves (in the laboratory, e.g., in *Quercus* leaves), as described as a



typical method of phaneropterines (Ingrisch, 2001; Rentz, 2010).

*Chromosomes*:  $2n = 29$  (male), 30 (female); sex determination system X0 (male), XX (female). The karyotype is quite similar to that of *D. japonica* (own data from specimens from North Korea). For details, see SI5.

*Etymology*: The name confers the Australian distribution of this species, roughly compared to the range of the other members of the *D. japonica* group. The word is based on Greek ἀντίποδες (opposite feet), used as a noun in apposition.

*Distribution*: Northern Australia from Western Australia in the West to Queensland in the East, reaching New South Wales in the South (see Fig. 2, list of paratypes in SI2, Figs SI2, Map 1, 2).

#### *DUCETIA MALAYANA* HELLER SP. NOV.

(FIGS 2, 3. SONG FIG. 10. STRIDULATORY ORGANS FIGS 13, 14, 17.)

urn:lsid:Orthoptera.speciesfile.org:TaxonName:496316

*Holotype*: Male (in ethanol). Label 1 'MALAYSIA: Selangor, Ulu Gombak Field Study Centre (20 km to Kuala Lumpur, 3°20'N, 101°45'E), 260 m a.s.l., 8–28 March 1981, leg. K.-G. Heller & M. Volleth'. Label 2 '3653'. Label 3 '16 March 1981 tape recorder symbol, handwritten (depository: MfN, Berlin).

*Paratypes (in ethanol or dried)*: 8 males, 2 females, same locality as holotype, but various dates (1981–1997) and collectors. Collection Heller.

*Diagnosis*: Song unit of calling song consisting of only one short (*c.* 2 s) phase, thus differing from all other known species of the *D. japonica* complex (Table 3; see 'Bioacoustics' section for details).

*Description*: Morphologically similar to *D. japonica* (and *D. antipoda* sp. nov. except for the stridulatory file). See SI3 and description of *D. antipoda* sp. nov. in SI2 for details.

*Habitat*: Similar to *D. antipoda* sp. nov. Not found in undisturbed or disturbed forests, but typically only in rural habitats.

*Etymology*: Name referring to the location of the type locality on the Malay Peninsula. Adjective, following *Ducetia* in gender.

*Distribution*: At present only known from the type locality and from Singapore, but probably widespread in Malaysia and adjacent regions.

#### *DUCETIA MELODICA* HELLER & INGRISCH SP. NOV.

(SONG FIG. 9. STRIDULATORY ORGANS FIGS 13, 15, 17.)

urn:lsid:Orthoptera.speciesfile.org:TaxonName:496317

*Material examined*: Holotype (male): Thailand, Bangkok, Lardprao, northern suburbs of Bangkok (near Poonsiri Village, about 13°50'N, 100°35'E), 5–8 June 1988, leg. S. Ingrisch (depository: Museum Koenig, Bonn, ZFMK).

*Paratypes*: same data as holotype – 2 males (1 ZFMK, 1 coll. Ingrisch).

*Diagnosis*: Song unit of calling song consisting of three phases, the last two alternatingly repeated several times. It differs from the structurally similar calling song of *D. neochlora* most notably by a relatively low SRR (*c.* 20 Hz) in the second phase and three-parted syllables in the third phase (Table 3; see 'Bioacoustics' section for details).

It differs morphologically by the male stridulatory apparatus having the dorsal side of the stridulatory area of the left tegmen vaulted, the stridulatory vein with a distinct angular fold separating the narrow teeth from the large teeth, the mirror on the right tegmen having the posteriointernal angle nearly rectangular and not projecting, and just behind the scraper and before the mirror with a vertically elevated lamellar projection that may serve as a secondary scraper (see Fig. 17C).

*Description*: General habitus, tegminal venation with five direct branches of radius and shape of male cerci with apical area widened and with a lamella along ventral margin as in *D. japonica* (as described, e.g., in Ragge, 1961). See text SI3 for details.

*Habitat*: Fallow land (seasonally flooded), roadside vegetation, and gardens. Sings in bushes at night.

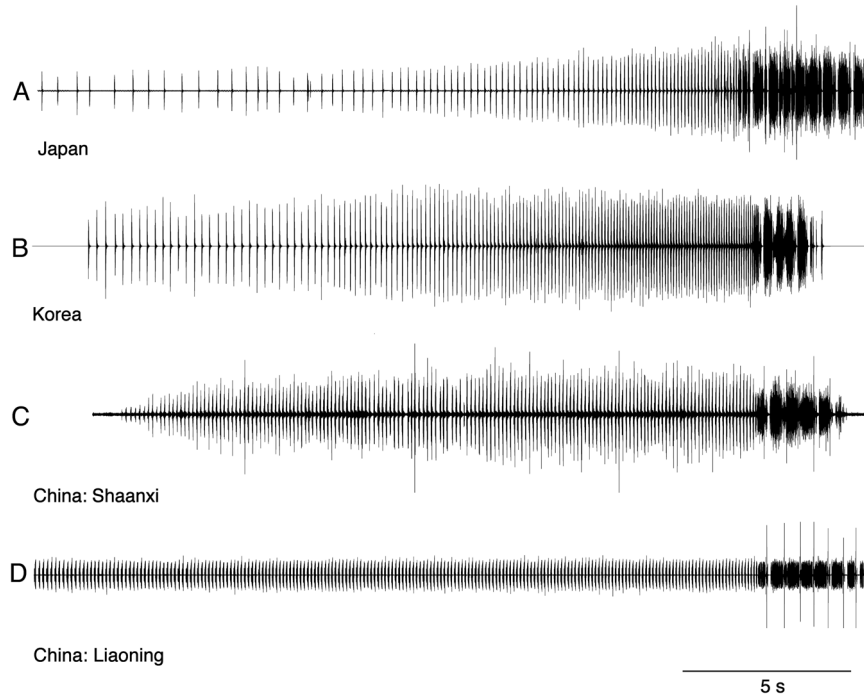
*Distribution*: At present only known from the type locality.

*Etymology*: Named after the melodious stridulation that gave the stimulation to collect the specimens thought to belong to a common species. Latin adjective (= melodic), following *Ducetia* in gender.

#### BIOACOUSTICS

##### *Spectral composition*

The calling songs of all recorded specimens showed broadband spectra with a peak between 11 and 15 kHz. In the ultrasonic range (above 20 kHz), only weak components were observed, and the various parts of a song unit did not differ in frequency composition (Fig. 4).



**Figure 5.** Oscillograms of the northern type of the calling song (*Ducetia japonica s.s.*), review of one (mostly complete) song unit.

The female response of *D. antipoda* sp. nov. had a broad peak between 10 and 20 kHz (studied only in the audio range)

#### *Amplitude pattern of male calling song*

Most recorded songs of specimens of the *D. japonica* group consisted of long-lasting song units with durations of up to 100 s. However, the structure of these units differed considerably between regions. Along a line from the North to South (East), five different types were recognized. In addition, some forms also have short songs with unknown function (observed in Thailand, Malaysia, and Australia).

In all song types, syllables with a peculiar amplitude modulation were observed. These sound elements always started with a single impulse (or very few, densely packed), which was followed by series of much softer impulses (see, e.g., Fig. 10E). They are probably produced by one complete closing movement of the tegmina. The single impulse results from the contact of one large tooth at the distal end of the file with the scraper and the softer ones from contacts of the smaller teeth (see below, stridulatory organs).

A. Northern type (Japan, Korea, and northern China) – *D. japonica s.s.* (Figs 5, 6)

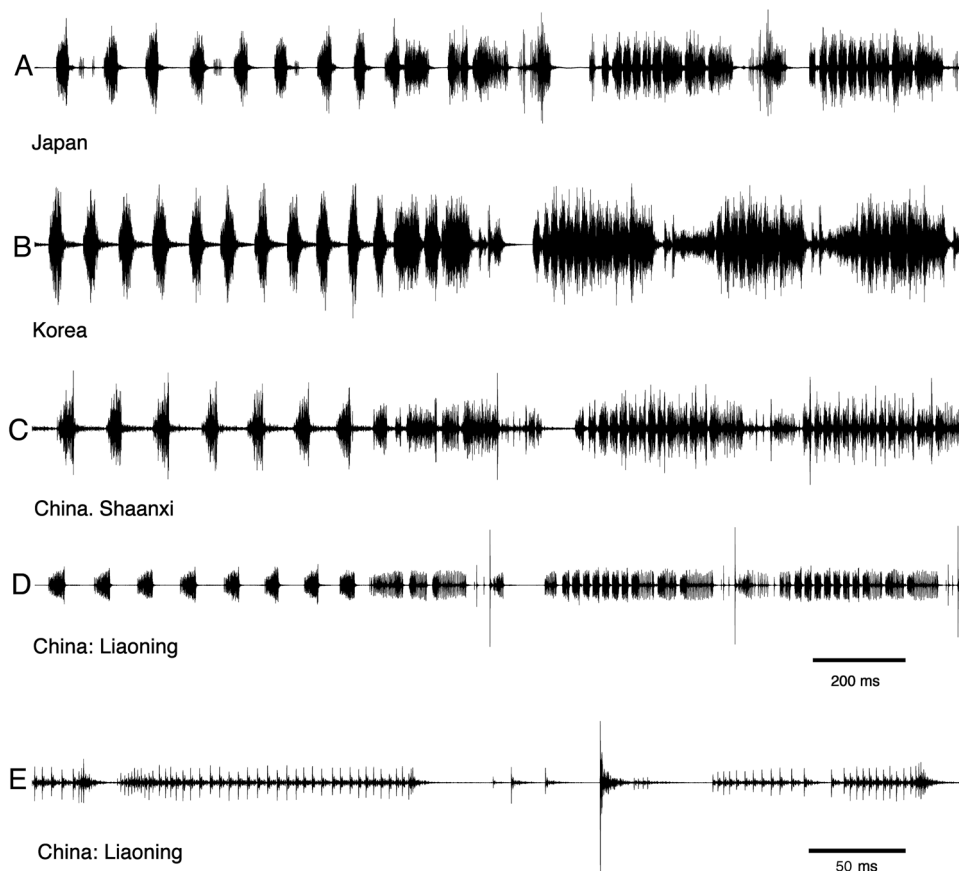
Each song unit consisted of two parts. During the beginning of the long first part, the syllables are mostly

produced in a quite slow rhythm (e.g., 2–6 Hz), which often increases more or less continuously until it reaches an SRR of around 10 Hz. This part lasted about 20 s or longer. After a quite short relatively irregular ‘switching’ phase (about 0.5 s), the second part started, which consisted of a series of long subunits. Without recordings of the stridulatory movement, the structure of these subunits is difficult to describe in terms of syllable composition. At the beginning, there was a series of short impulse groups (repetition rate about 50 Hz), followed by some much longer impulse groups that were repeated at a correspondingly slower rate. After a short interval, one of the peculiar syllables (see above; in some recordings difficult to recognize) was inserted. After four to ten of such subunits, the whole song unit ended with one or two softer, irregularly shaped subunits.

The following three song types (B–D) have one prominent similarity; they all show series of syllables with the peculiar amplitude modulation (see above) and present them in about the same rhythm. However, in other characters, they differ clearly.

B. North–central type (central/southern China to northern Thailand) – *D. neochlora* (Figs 7, 8)

A song unit of this song type did not seem to consist of a fixed number of parts but was made up from three phases, some of which could be repeated several times. As in Type A, it started with isolated syllables (or small groups of up to four syllables, internal SRR, c. 15 Hz;



**Figure 6.** Oscillograms of the northern type of the calling song (*Ducetia japonica s.s.*), transition from first to second part.

amplitude modulation sometimes as seen in Phase 3), which were produced with an increasing rate (3–5 Hz). This first part is followed by a series of short and densely packed syllables (SRR, *c.* 50 Hz) of variable duration (*c.* 1–5 s). After this second part (and phase), a slower (SRR = 10 Hz) series of longer syllables with a peculiar amplitude modulation was observed (phase three), again lasting about one to several seconds. These syllables always started with a single (or very few, densely packed; echoes) impulse that was followed by a series of much softer impulses. The combination of second and third phases is repeated several (up to eight) times, ending with Phase 3 or an irregular version of it, slowed down or broken by intervals. The duration of one complete song unit was quite variable, ranging from 25 to 90 s. Sometimes one song unit followed immediately after another. In Thailand (Chiang Mai), additionally short (6–8), isolated syllable groups (SRR = 11 Hz) were observed, possibly representing a prephase of Phase 1.

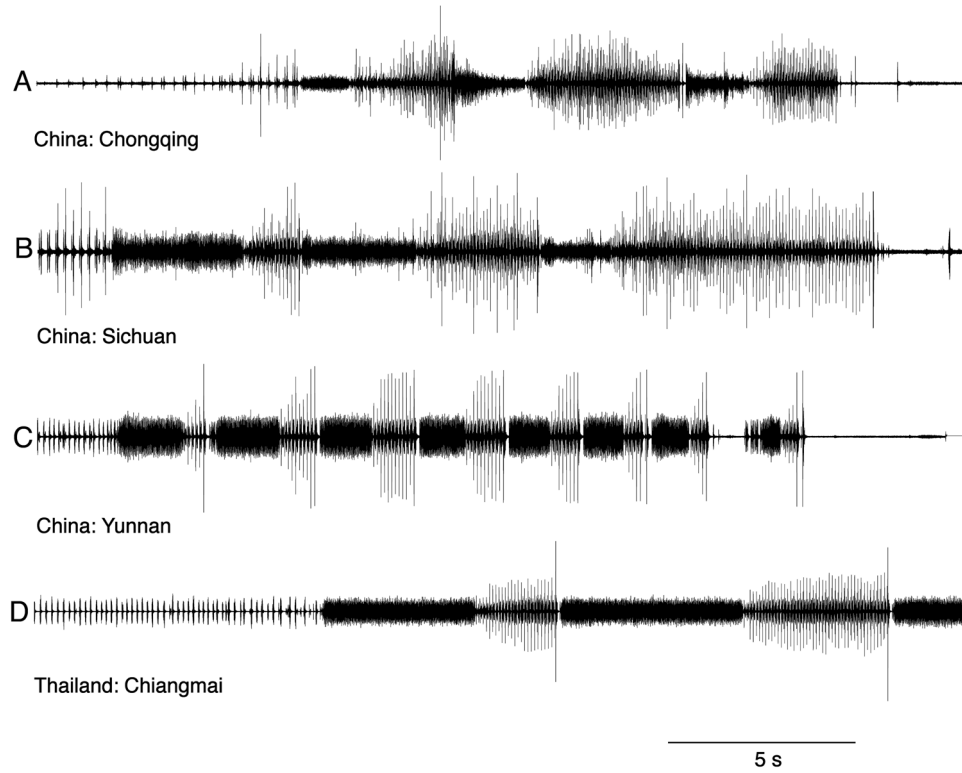
C. Central part (Central Thailand) – *D. melodica* sp. nov. (Fig. 9)

This song type shows similarities, but also distinct differences to Type B. The song started (Phase 1) with a

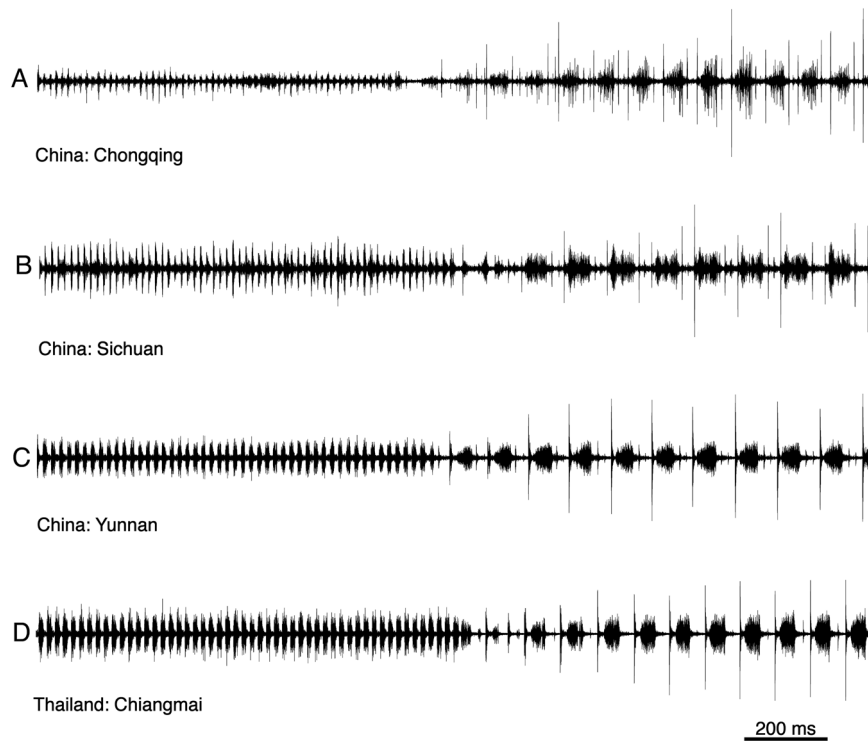
sequence of syllables (SRR, *c.* 10 Hz) presenting the peculiar amplitude modulation as described for the third phase of Type B. After about 15–20 s, the soft impulse groups became continuously shorter for about 1 s, ending with quite short syllables presented with a rate of about 20 Hz (Phase 2). Two seconds later, these short syllables changed, but only for about half a second, to longer, triparted syllables (Phase 3). This alternation between Phases 2 and 3 occurred several times for about 15 s, before the song unit ended.

D. South-central type (Malaysia, Singapore) – *D. malayana* sp. nov. (Fig. 10)

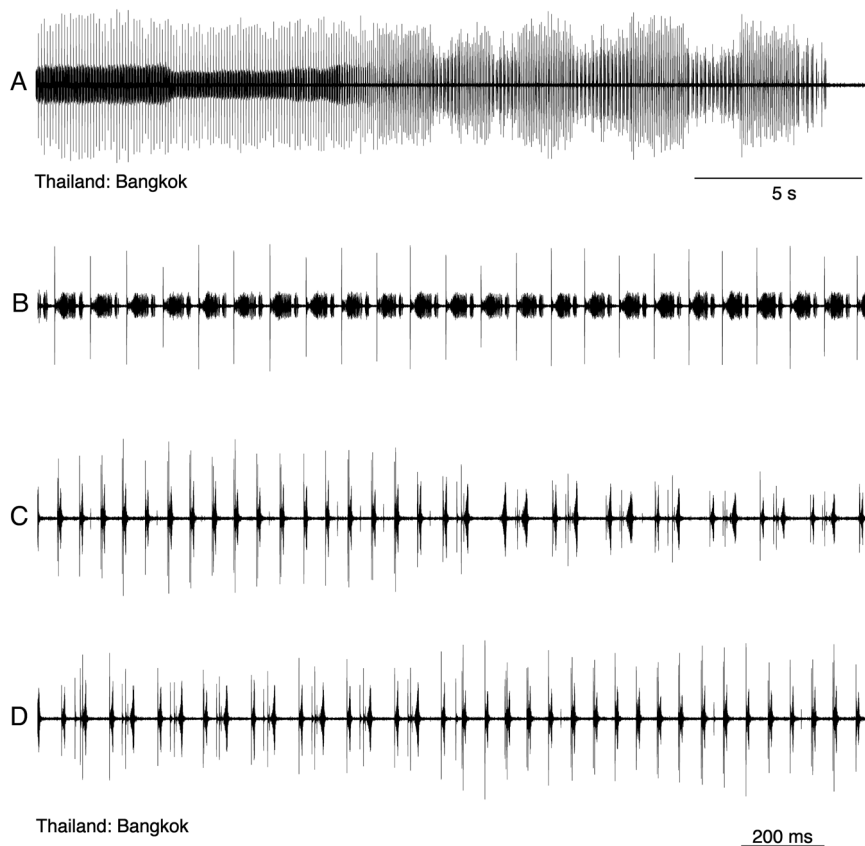
In Malaysia and Singapore, much simpler songs than in the other localities were observed than in the other localities. The longest song units consisted of dense sequence of 15–30 syllables (SRR, *c.* 10–15 Hz, differences probably related to different temperatures), increasing in amplitude. The syllables showed the peculiar amplitude modulation as described for the third phase of Type B. Often several (up to three) of such song units were produced directly one after another. Sometimes series of short, isolated syllables were observed between the long units. Additionally,



**Figure 7.** Oscillograms of the north-central type of the calling song (*Ducetia neochlora*), review of central parts of one song unit (Phases 1 to 3).



**Figure 8.** Oscillograms of the north-central type of the calling song (*Ducetia neochlora*), transition from second to third phase.



**Figure 9.** Oscillograms of the central type of the calling song (*Ducetia melodica* sp. nov.). (A) review, (B) Phase 1, (C) transition from Phase 2 to 3, (D) transition from Phase 3 to 2 (see text).

short (6–8 syllables), isolated syllable groups (SRR = 11 Hz) were heard. In many nights in the field catching bats (Heller & Volleth, 1989) or observing moths (Heller & Achmann, 1995), we (KGH) never noticed more complicated songs.

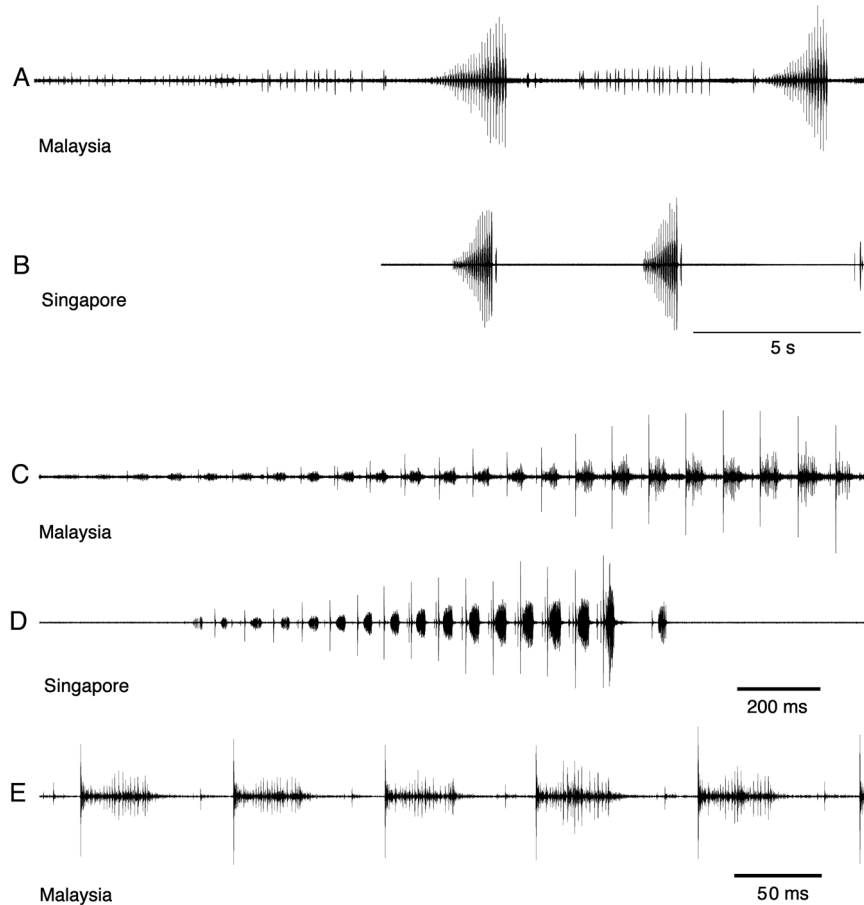
#### E. Southern type (Australia) – *D. antipoda* sp. nov. (Figs 11 and 12)

In this song type, a song unit consisted of a sequence of several parts each presented only once as in Type A. At the beginning, relatively long syllables were observed, presented at an SRR less than 2 Hz. Another animal started with syllables already (see below) combined to groups, but the syllables were softer and with more gaps than later. After about 15 s, the animals switched to a more complicated pattern consisting of syllable pairs or triplets. Such a group started with a short syllable of high amplitude, followed by two longer and softer ones, the second slightly longer than the first. These combined elements were repeated in a rhythm of 2–4 Hz for more than 15 s. During the next part, monomorphic syllables appeared with an SRR of 10 Hz. After some time (c. 10 s), these syllables became softer and more ‘gappy’, that is, single impulses could be recognized, until at the

end a nearly continuous sequence of impulses (periods 10–60 ms) was found. This last part varied distinctly in length (3–13 s observed). In addition to these long song units, the specimens often produced short sequences of syllables, in structure like the beginning of a long song.

#### Female response

Phaneropterine females typically respond acoustically to the male song (Heller *et al.*, 2015). The signals are produced by rubbing spines (shape: Shi & Jiang, 2002) on veins on the upper face of the left tegmen (Fig. SI2H) against the plectrum consisting of the anal edge of the right tegmen. In the *D. japonica* group, these response songs are known only from *D. antipoda* sp. nov. (Figs 11, Figs 12). Interestingly, the females did not respond after the male song or during gaps in the male song as is known from other species (see Heller *et al.*, 2015), but during the male sound production without any strict temporal relation to elements of the male song. The response songs were variable in duration (1 to c. 40 impulses) and were only observed during the final, ‘gappy’ part of the male song. Sometimes they even continued after the end of the male song and



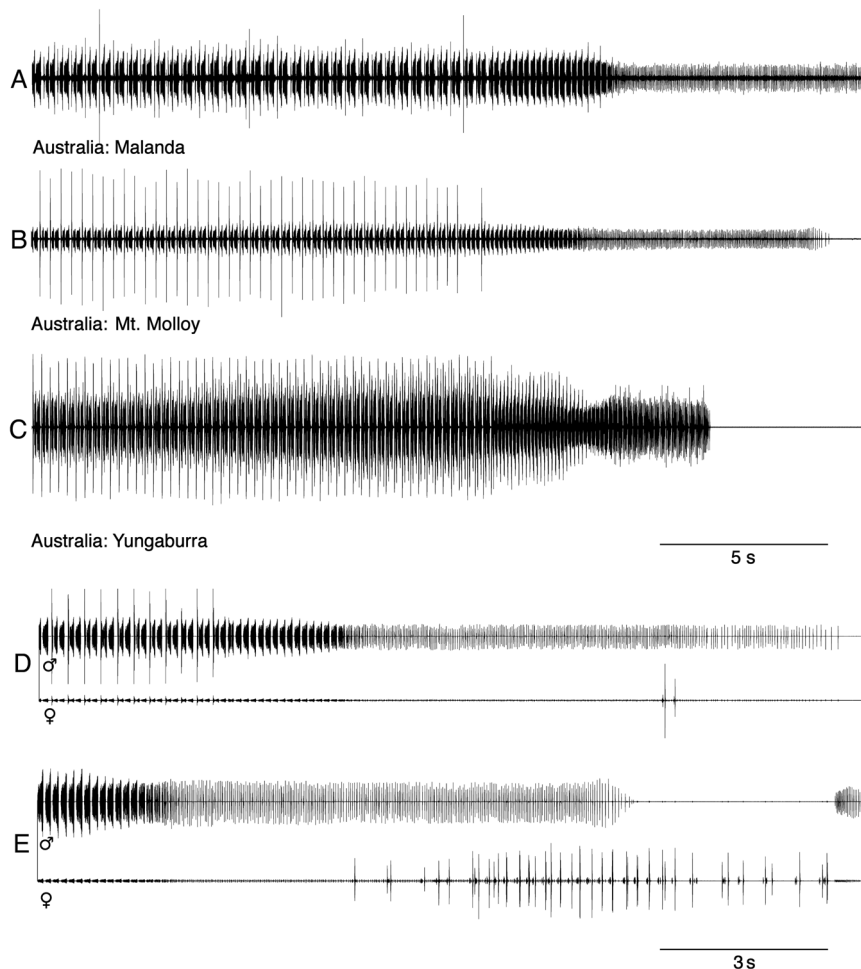
**Figure 10.** Oscillograms of the south-central type of the calling song (*D. malayana* sp. nov.). (A, B) review, (C–E): final parts.

were occasionally followed by a series of male impulses (see Fig. 11).

#### *Morphology of stridulatory organs*

The stridulatory file is found at the lower side of the left tegmen. The right tegmen does not even carry a rudimentary file (checked in specimens of *D. antipoda* sp. nov., *D. japonica*, and *D. malayana* sp. nov.). All studied files in the *D. japonica* group (except *D. adspersa*) showed a similar basic structure (Figs 13, SI1C). At the distal end near to the edge of the tegmen, the files started with a few small or knob-like teeth (sometimes missing), which became rapidly larger. After a (short) series of quite large teeth, the size of the teeth changed more or less abruptly to smaller ones, which were typically similar to each other in the remaining part of the file. This proximate part occupied about 55–85% of the file length. Photos of such files were already published by Shi *et al.* (2003) and Kim (2009). Shi *et al.* (2003) noted that in the part with the large teeth geographical differences were observed. In our material, the lowest

number of large teeth were found in *D. neochlora* (holotype; from China, Beibei, Chongqing), but the numbers in typical *D. japonica* from Korea and northern China are only slightly higher. In *D. neochlora* from southern China and *D. malayana* sp. nov. from Malaysia typically six to eight teeth were found, while in the Australian *D. antipoda* sp. nov. and *D. melodica* sp. nov. from Thailand about 12 large teeth were found, and a smaller number of teeth in the proximate part than in the other species. So the morphological variation does not completely agree with the song types – possibly more cryptic species are present, especially in *D. neochlora*. However, even files with similar dimensions may differ in the degree of bending, which is associated with the change of the size of the teeth (Fig. 15). However, there are not enough data to understand the variation in the file characters and their connection to the song type. Data from isolated specimens from other parts of the range of the *D. japonica* group (e.g., Indonesia: Java; Fig. 16) indicate that the variability of the file in the *D. japonica* group is not completely covered with our sample.



**Figure 11.** Oscillograms of the southern type of the calling song and of two-channel recordings of male–female duets (*Ducetia antipoda* sp. nov.), review of endings of song units without (A–C) and with (D, E) female response (two different females to the same male, all from Mt. Molloy).

In other *Ducetia* species (*Ducetia javanica*; Fig. 16), the teeth in the distal part are not larger than in the proximate, but smaller as also in *D. adspersa* from the *D. japonica* group.

Other parts of the stridulatory organs like the mirror and the stridulatory field on the upper side of the right tegmen differ in shape between species (Fig. 17), but at present, we do not see any significant effects on the song.

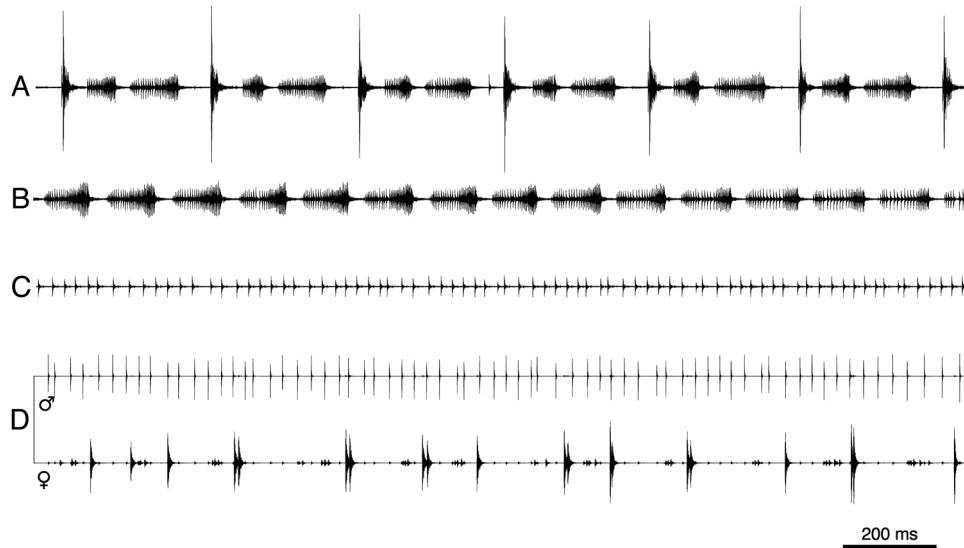
## DISCUSSION

The different forms of the *D. japonica* complex present an unusual combination of characters. Throughout their huge range, they are morphologically uniform but demonstrate very different calling songs, most of them being long and quite complex. Some are pure ethospecies differing in acoustic behaviour only, and others show small differences in their stridulatory organs as well. The variability of the male stridulatory file

suggests differences in song, and therefore, perhaps, additional species are involved. In other bush-cricket species, typically allopatric forms differ in genitalia but much less in song (Heller, 2006; Ciplak, Heller & Willemse, 2009). But from where, how, and when did the group spread over such distances and split up into several species?

All members of the *D. japonica* group are characterized by a long ventral ridge of the male cerci (Fig. 3). Most other *Ducetia* species do not have cercal ridges at all (Ragge, 1961). However, there is a group of species in East Asia, having one or even two cercal ridges (see Kang *et al.*, 2014). From these observations, it seems likely that the *D. japonica* group also originated somewhere in East Asia and spread from there into the North (Japan), West (India), and South (Australia).

In many parts of its range, *D. japonica* group species are the sole representatives of the genus and have obviously occupied these areas from the (South)



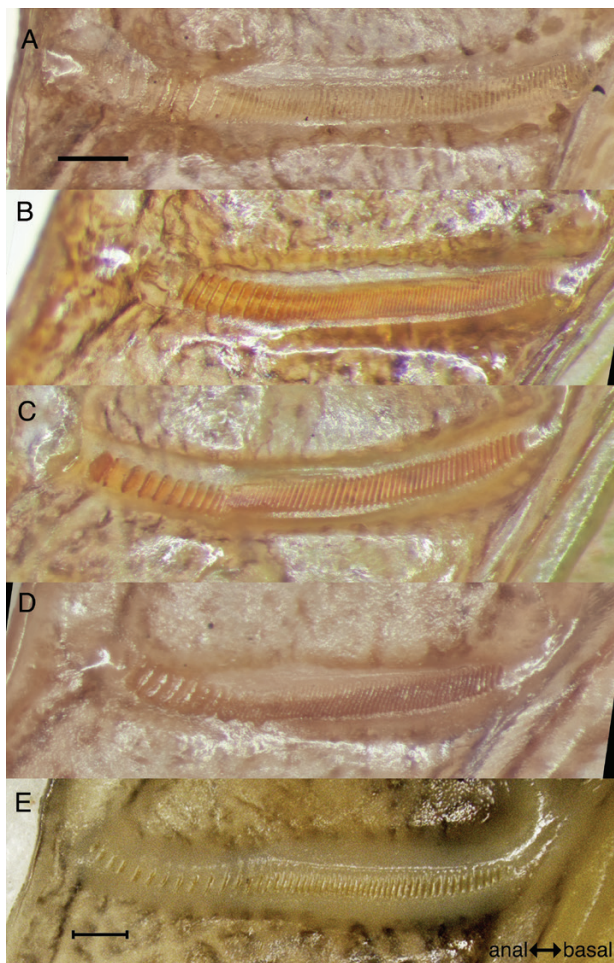
**Figure 12.** Oscillograms of the southern type of the calling song and of two-channel recordings of male–female duets (*Ducetia antipoda* sp. nov.), (A) second part, (B) transition to final part, (C) final part, (D) final part with female response.

East Asian core region of the Asian part of the genus. Probably during the process of range enlargement, some expanding populations changed their song pattern due to bottleneck situations or founder effects at or after arriving at new territories. Thus, the newly settled areas would have been inhabited by new song species. But why in the *D. japonica* group is the genitalic morphology so stable while the song seems to change so quickly? This strongly contrasts with the situation in other bush-crickets. Two characters of *D. japonica* can be invoked for explanation, separate or in combination.

Besides its acoustic communication (see below), another special character of the *D. japonica* group might be its excellent dispersal capabilities. It is very difficult to find proof for this, since to use the large range itself would be circular reasoning. In any case, both males and females have long fore and hind wings, and the species crossed Wallace's line, a well-known biogeographical border, and all the related lines (Simpson, 1977) without any noticeable difficulty and occurs in five of the eleven zoogeographic realms of the world (Holt *et al.*, 2013, Fig. 1, SI). It should be mentioned that these lines are also borders for many flying animals such as species of bats (Hall *et al.*, 2004) and birds (Lincoln, 1975). As an argument supporting good dispersal, one can mention that *D. japonica* group species are found on numerous islands. Combined with the information about its range, it can be considered as a kind of tettigonioid supertramp (see Diamond, 1974; Balke *et al.*, 2009). The occurrence on islands refers not only to Indonesia, but also to, for example, the Andaman and Nicobar

Islands, the Solomon Islands, or Lord Howe Island (see Fig. 2). However, the distribution on islands may be the result of different circumstances. At the time of the species' arrival, an island may have been connected with the mainland or another, larger island (e.g., Indonesian islands in the Pleistocene; Leonard *et al.*, 2015), or a species may have been introduced accidentally by man. Girard (1969) mentions aircraft transport for *D. japonica*. This is certainly not the reason for most island occurrences but could apply to Guam or Lord Howe Island. Plants can be imported to Lord Howe without a permit, and this may have provided a means for the incursion of the species there. On the other hand, Norfolk Island has habitats and a climate that would be suitable for *Ducetia* species, but there are no records of the genus from there (Rentz, 1988). Probably significant is the quarantine on importation of plants to the island. Guam is notorious for its introductions (recent list in Wikipedia, 2015), and *D. japonica* may have arrived recently (Koide, 2013; not mentioned by Vickery, Kevan & English, 1999) with a similar event having been also assumed for *Mecopoda elongata* (Kevan, 1987; see below). However, differences in mean body size as mentioned for the Solomon Islands (Ragge, 1961) do not support the idea of a recent introduction. Another problem concerns the identification of the species on islands. For example, *D. japonica* is mentioned from Bonin Island. However, from that island, Ishikawa (1987) described *Ducetia boninensis*, not discussing the older records of *D. japonica* (see Vickery *et al.*, 1999, who did not mention Ishikawa, 1987). On the other hand, *D. japonica* group species did not settle

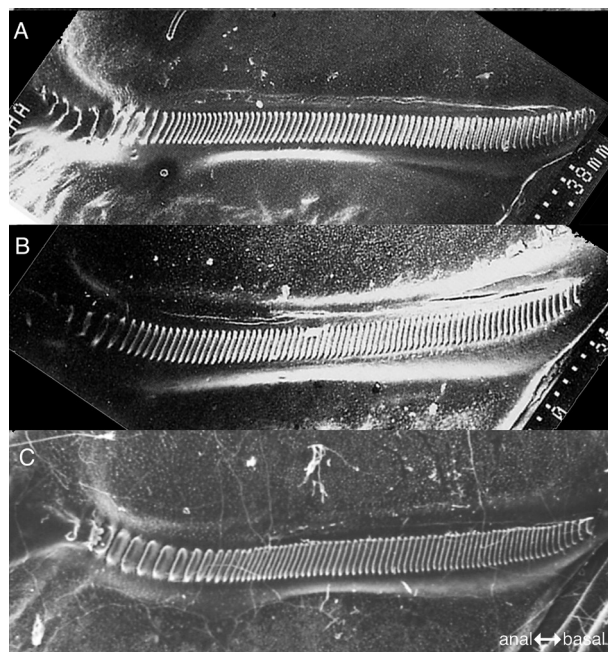




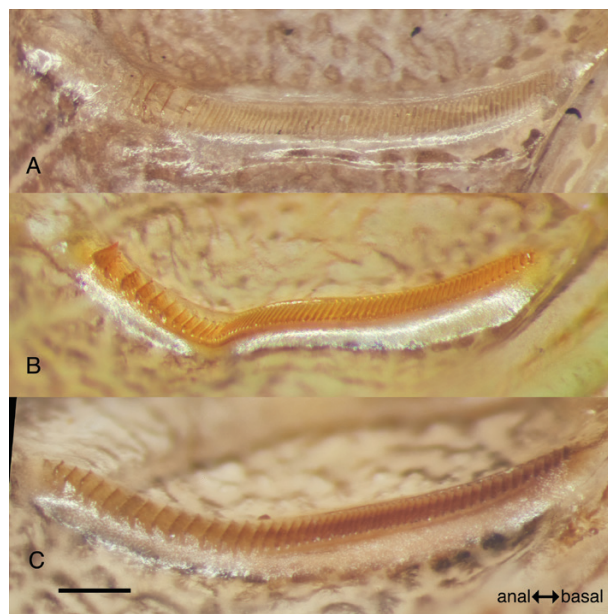
**Figure 13.** Stridulatory files. (A) *D. japonica*, Korea (CH7422), (B) *D. neochlora*, Thailand (Hang Dong 3254551), (C) *D. melodica* sp. nov., Thailand (holotype 3254547), (D) *D. malayana* sp. nov., Malaysia (CH3675), (E) *D. antipoda* sp. nov., Australia (CH7913). Scale 200 µm.

Micronesia except for the above-mentioned islands of Bonin (Vickery *et al.*, 1999) and Guam (Koide, 2013).

The distribution of the *D. japonica* group has surprising similarities to that of the *M. elongata* (Linnaeus, 1758) group (see map in OSFO, incomplete), also a complex of long-winged, morphologically very similar species differing mainly in song (e.g., Bugrov *et al.*, 2004; Nityananda & Balakrishnan, 2006; Kostarakos & Römer, 2015). *Mecopoda elongata* does not go so far to the North and the South and does not seem to be found on so many islands as the *D. japonica* group, but the core of the range is the same. Possibly the spreading of both complexes had similar reasons. A more detailed study of songs and genetics of both species groups, especially on the islands, could improve our knowledge about the spreading process(es) significantly. If the large range is based on recent, fast dispersal, genetic



**Figure 14.** Stridulatory files, scanning electron microscope pictures. (A) *D. japonica*, China: Shaanxi (from Shi *et al.*, 2003, modified; reproduced with permission), (B) *D. neochlora*, China: Chongqing (from Shi *et al.*, 2003 modified; reproduced with permission); (C) *D. malayana* sp. nov., Malaysia (CH3661b).

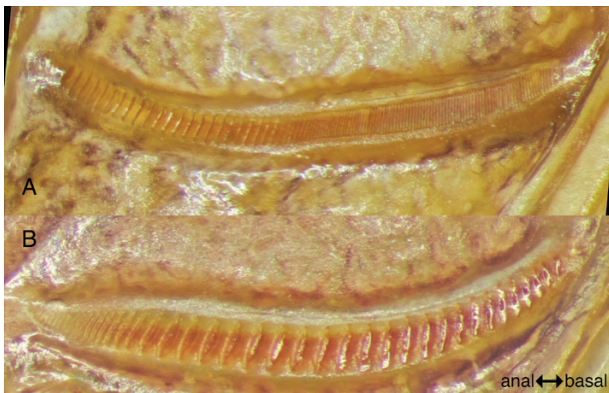


**Figure 15.** Stridulatory files, lateral view. (A) *D. japonica*, Korea (CH7422), (B) *D. melodica* sp. nov., Thailand (holotype 3254547), (C) *D. antipoda* sp. nov., Australia (CH7915). Scale 200 µm.

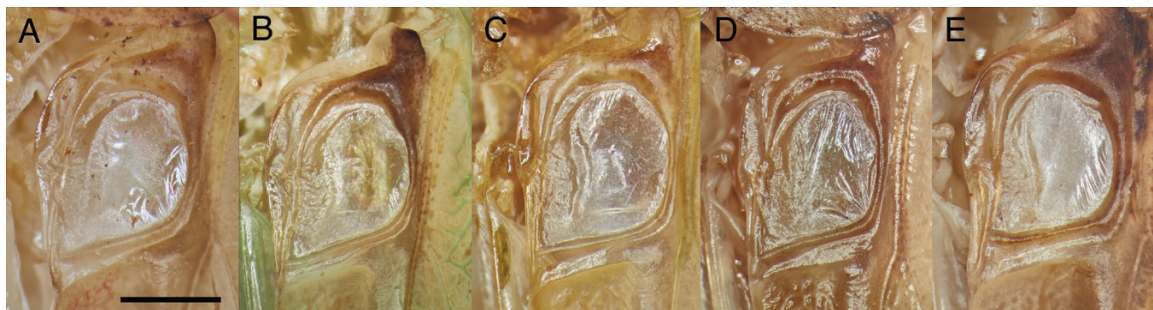
differences between the species of each group may be small as, for example, in species groups of the acridid subfamily Gomphocerinae, famous for its morphological and genetic similarity and the characteristic of species-specific songs (e.g., Vedenina & Mague, 2011).

To reiterate, the genus *Ducetia* belongs to the phaneropterines, a tettigonioid subfamily where the females respond acoustically to the male song (Heller *et al.*, 2015). While most species have relatively simple songs like most other tettigonioids, there are a few genera with very complicated songs like *Amblycorypha* (e.g., Forrest *et al.*, 2006), *Polysarcus* (Heller, 1990), *Eurycorpha* (Hemp *et al.*, 2013), and others, and also *Ducetia* (for a review, see Heller *et al.*, 2015). Within the *D. japonica* group, at present, five species with different songs are known, which seem to occur allopatrically. Thus, species recognition may not be the main reason for the song differences. However, regarding distribution, several contact zones or even overlapping ranges are to be expected thus a present or past function in this context cannot be completely excluded. Four out of five species have relatively complex song patterns with several distinct

parts or phrases. In the Phaneropterinae, often some elements of the male calling song are used to trigger the acoustic female response (Heller *et al.*, 2015). These parts are typically characterized by a high amplitude (e.g., *Polysarcus denticauda*; Heller, 1990) and/or pauses in the male song before and/or after these marker elements (e.g., *Barbitistes* spp., Stumpner & Meyer, 2001). In many species, the males additionally produce soft single impulses or short series of impulses around the time where a female response can be expected (see, e.g., *Eurycorypha varia*; Hemp *et al.*, 2013), possibly to avoid the exploitation of the duet by eavesdropping rivals (Villarreal & Gilbert, 2014; Heller *et al.*, 2015). In the songs of the *D. japonica* group, there are no clearly visible, distinct marker sounds. Only in *D. japonica* s.s. could the relatively short ending of a long song unit (see Fig. 3) be possibly used in that function with a female response following shortly afterwards. Also in *D. malayana* sp. nov., a female ready to mate could simply respond after the loud end of the male song. In both species, at least occasionally, the male also produces a series of soft impulses at that time. In *D. antipoda* sp. nov., on the other hand, the male song ends with a long and soft series of impulses (Figs. 11, 12). Obviously the females respond during this phase and are probably difficult to detect acoustically by rivals. The male song of *D. antipoda* sp. nov. exceeds all other studied phaneropterines in the degree of covering the female response. The question as to how the singing male recognizes these responses has not been studied in detail for any species, but there is a hypothesis that the male singer may not be as disturbed by different directions of male and female sounds as the rival will be (see Heller *et al.*, 2015, for a review). In *D. neochlora* and *D. melodica* sp. nov., the female responses are not yet known. The songs of these species are so complex that predictions about response times are difficult. Here detailed behavioural studies are necessary. To understand the evolutionary changes of the songs, the actual interaction between the sexes has to also be observed in all species, that is, the



**Figure 16.** Stridulatory files. (A) *Ducetia japonica* group from Indonesia, Java, Salak (3258293). (B) *Ducetia javanica*, Indonesia, Java, Tretes (3254556).



**Figure 17.** Mirror of right tegmen. (A) *D. japonica*, Korea (CH7422), (B) *D. neochlora*, Thailand (Hang Dong), (C) *D. melodica* sp. nov., Thailand (holotype), (D) *D. malayana* sp. nov., Malaysia (CH3675), (E) *D. antipoda* sp. nov., Australia (CH7913). Scale 500  $\mu$ m.

reaction of each sex after it has heard the sound of the other. Phaneropterines are well known for their variability concerning which sex will move towards the singer or responder respectively (Spooner, 1968, 1995; Zhantiev & Korsunovskaya, 1986). Besides the anti-rivalry effect during duetting, song complexity may also be the result of female choice for some song parameters as assumed in Ephemeroptera, the only other group of tettigonioids with male–female duets (Pfau & Pfau, 2015).

For the production of these complicated songs not only are complex neuronal programs used (see Elsner, 1975 for examples from acridid Orthoptera), but also special modifications of the stridulatory file. Abrupt changes in the size and shape of teeth along the file, as in most species of the *D. japonica* group, are not uncommon among phaneropterines; however, there are not many examples for which the stridulatory movements and the effects of the tooth changes are known. In the excellent video clip of Kansatsuki (2015), it can be recognized that during the first part a *D. japonica* male makes relatively small movements using the middle part of the file. The male sits most of the time with slightly opened wings and closes the wings a little bit only for short moments. According to frame-to-frame observations, in the final part, the amplitude of movements is larger, and the male opens the tegmina to a larger extent and closes them more tightly. So the large teeth at the distal end are probably used only during the final part, coinciding with loud impulses and the special syllable type. From the shape of the teeth [steep side oriented towards the distal (anal) edge; Fig. 14], sound production during the closing movement is very likely. The number of the large teeth does not seem to be correlated with the number of recognizable loud impulses during the special syllables. Obviously the movement pattern of *D. japonica* is distinctly different from that of *Ectadia fulva* Brunner von Wattenwyl, 1893, which has a similarly structured file. *Ectadia fulva* uses its large teeth exclusively for a period of time (Heller *et al.*, 2015). In contrast, *Kuwayamaea sapporensis* Matsumura & Shiraki, 1908, another member of Ducetiini, which has a similar song to *D. japonica* group species, has a file in which the large teeth are situated near the proximal end (Kim, 2009) opposite to *D. japonica*. It will be a very interesting and fascinating area of research to understand the function of the complex files in phaneropterines and especially in *Ducetia*, where more species and song types are expected even when only the *D. japonica* group is considered.

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#### REFERENCES

- Anonymous.** 2000–2015. Lay, George Tradescant (1799–1845). Available at: <http://plants.jstor.org/person/bm000055412..>
- Asana JJ, Makino S, Niyama H.** 1938. A chromosomal survey of some Indian insects. 1. Morphology of the chromosomes in eight species of the Locustidae. *Journal of Faculty of Science, Hokkaido University* **6**: 221–234.
- Balke M, Ribera I, Hendrich L, Miller MA, Sagata K, Posman A, Vogler AP, Meier R.** 2009. New Guinea highland origin of a widespread arthropod supertramp. *Proceedings of the Royal Society B* **276**: 2359–2367.
- Bey-Bienko GYa.** 1954. *Phaneropterinae. Fauna of the USSR, Orthoptera Vol. II, No. 2.* Moskva-Leningrad. Israel Program for Scientific Translation, Jerusalem, 1965.
- Brunner von Wattenwyl C.** 1878. *Monographie der Phaneropteriden.* Brockhaus: Wien.
- Bugrov AG, Warchalowska-Sliwa E, Ito G, Tchernykh A, Maryati M.** 2004. Karyotype and C-banding patterns of the katydid *Mecopoda elongata* (L.) (Orthoptera, Tettigoniidae, Mecopodinae) from Amami Is. (Japan) and Borneo (Malaysia). *Caryologia* **57**: 25–29.
- Buzzetti FM, Devriese H.** 2008. On some Oriental Orthoptera, mostly from Myanmar (Insecta: Orthoptera: Ensifera, Caelifera). *Bollettino del Museo Civico di Storia Naturale di Verona Botanica Zoologia* **32**: 161–169.
- Childebaev MK, Storozhenko SYu.** 2004. An annotated list of the long-horned orthopterans (Orthoptera, Ensifera) of Kazakhstan. *Tethys Entomological Research* **9**: 213–228.
- Ciplak B, Heller KG, Willemse F.** 2009. Review of the genus *Eupholidoptera* (Orthoptera, Tettigoniidae): different genitalia, uniform song. *Zootaxa* **2156**: 1–77.
- Diamond JM.** 1974. Colonization of exploded volcanic islands by birds: the Supertramp strategy. *Science* **184**: 803–806.
- Eades DC, Otte D, Cigliano MM, Braun H.** 2015. *Orthoptera species file. Version 5.0/5.0.* Available at: <http://Orthoptera.SpeciesFile.org>.
- Eberhard WG.** 1985. *Sexual selection and animal genitalia.* Cambridge, MA: Harvard University Press.
- Elsner N.** 1975. Neuroethology of sound production in gomphocerine grasshoppers (Orthoptera: Acrididae) II. *Neuromuscular activity underlying stridulation. Journal of Comparative Physiology* **97**: 291–322.
- EPA.** 2007. Available at: <https://environment.ehp.qld.gov.au/regional-ecosystems/details/?re=7.11.1>.

- EPA = EnvironGlobal Biodiversity Information Facility (2014)  
 Ducetia japonicament Protection Authority (2007) Regional ecosystem descriptions.
- Forrest TG, Lajoie DR, Cusick D. 2006.** Calling songs, duets, and auditory tuning in two cryptic katydids (Tettigoniidae: Phaneropterinae: *Amblycorypha*). *Annals of the Entomological Society of America* **99**: 978–987.
- GBIF. 2014.** The study was partly funded by the National Natural Science Foundation of China (No. 31572308). Available at: <http://www.gbif.org/species/1690860>.
- Girard DH. 1969.** *List of intercepted plant pests, 1968 (pests recorded from July 1, 1967, through June 30, 1968)*. Hyattsville, MD: United States Agricultural Research Service.
- Gorochov AV, Storozhenko SYu, Kostia D. 1994.** Systematic notes on the Tettigoniidae of East Asia (Orthoptera). *Zoosystematica Rossica* **2**: 287–291.
- Greenfield MD. 2002.** *Signalers and receivers: mechanisms and evolution of arthropod communication*. Oxford: Oxford University Press.
- Gupta SK, Shishodia MS. 2009.** Insecta: Orthoptera. In: Director, Zoological Survey of India, ed. *Fauna of Pachmarhi Biosphere Reserve (Madhya Pradesh)*. Kolkata: Zoological Survey of India, Conservation Area Series, **39**: 213–246.
- Hall LS, Grigg GG, Moritz C, Ketala B, Saito I, Marni W, Abdullah MT. 2004.** Biogeography of fruit bats in Southeast Asia. *The Sarawak Museum Journal* **40**: 191–284.
- Han L, Liu HY, Shi FM. 2015.** The investigation of Orthoptera from Huagaoxi Nature Reserve of Sichuan, China. *International Journal of Fauna and Biological Studies* **2**: 17–24.
- Heer O. 1849.** *Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Zweiter Teil*. Leipzig: Verlag Wilhelm Engelmann.
- Heller KG. 1990.** Evolution of song pattern in east Mediterranean Phaneropterinae: constraints by the communication system. In: Bailey WJ, Rentz DCF, eds. *The Tettigoniidae. Biology, systematics and evolution*. Berlin, Heidelberg etc.: Springer, 130–151.
- Heller KG. 2006.** Song evolution and speciation in bushcrickets. In: Drosopoulos S, Claridge MF, eds. *Insect sounds and communication: physiology, behaviour, ecology and evolution*. Boca Raton, London & New York: Taylor & Francis, 137–151.
- Heller KG, Achmann R. 1995.** Ultrasound communication in the pyralid moth species *Symmoracma minoralis*. *Entomologia generalis* **20**: 1–9.
- Heller KG, Hemp C, Ingrisch S, Liu CX. 2015.** Acoustic communication in Phaneropterinae (Tettigoniidae) – a global review with some new data. *Journal of Orthoptera Research* **24**: 7–18.
- Heller KG, Volleth M. 1989.** [Bats of Malaysia. 1. Observations of the biology, morphology and taxonomy (Mammalia: Chiroptera)] (in German). *Senckenbergiana biologica* **69**: 243–276.
- Helversen Ov, Helversen Dv. 1994.** Forces driving coevolution of song and song recognition in grasshoppers. *Fortschritte der Zoologie* **39**: 253–284.
- Hemp C, Heller KG, Warchalowska-Sliwa E, Grzywacz B, Hemp A. 2013.** Biogeography, ecology, acoustics and chromosomes of East African *Eurycorypha* Stål species (Orthoptera, Phaneropterinae) with the description of new species. *Organisms Diversity & Evolution* **13**: 373–395.
- Henry CS. 2006.** Acoustic communication in neuropteroid insects. In: Drosopoulos S, Claridge MF, eds. *Insect sounds and communication: physiology, behaviour, ecology and evolution*. Boca Raton, London & New York: Taylor & Francis, 153–166.
- Holt BG, Lessard JP, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre PH, Graham CH, Graves GR, Jönsson KA, Nogués-Bravo D, Wang Z, Whittaker RJ, Fjeldså J, Rahbek C. 2013.** An update of Wallace's zoogeographic regions of the world. *Science* **339**: 74–78.
- Ichikawa A, Kano Y, Kawai M, Tominago O, Murai T, eds. 2006.** *Orthoptera of the Japanese Archipelago in Color (in Japanese)*. Sapporo: Hokkaido University Press (+ CD-ROM).
- Ingrisch S. 2001.** [Orthopterans with long antennae. Problems and solutions for care and breeding (native and tropical species)] (in German). *Arthropoda* **9**: 2–11.
- Ingrisch S, Garai A. 2001.** Orthopteroid insects from Ganesh Himal, Nepal. *Esperiana* **8**: 755–770.
- Ingrisch S, Shishodia MS. 2000.** New taxa and distribution records of Tettigoniidae from India (Orthoptera: Ensifera). *Mitteilungen der Muenchener Entomologischen Gesellschaft* **90**: 5–37.
- Iorgu IS. 2012.** Acoustic analysis reveals a new cryptic bush-cricket in the Carpathian Mountains (Orthoptera, Phaneropteridae). *ZooKeys* **254**: 1–22.
- Ishikawa H. 1987.** A new species of the genus *Ducetia* Stål (Orthoptera: Tettigoniidae Phaneropterinae) from Chichijima, the Bonin Islands, Japan. *Transactions of the Shikoku Entomological Society* **18**: 245–248.
- Jaiswara R, Balakrishnan R, Robillard T, Rao K, Cruaud C, Desutter-Grandcolas L. 2012.** Testing concordance in species boundaries using acoustic, morphological, and molecular data in the field cricket genus *Itaropsis* (Orthoptera: Grylloidea, Gryllidae: Gryllinae). *Zoological Journal of the Linnean Society* **164**: 285–303.
- Jin XB, Xia KL. 1994.** An index-catalogue of Chinese Tettigoniodea (Orthopteroidea: Grylloptera). *Journal of Orthoptera Research* **3**: 15–41.
- Kang L, Liu CX, Liu XW. 2014.** *Fauna Sinica. Insecta Vol. 57. Orthoptera, Tettigoniidae, Phaneropterinae*. Beijing: Science Press.
- Kansatsuki U. 2015.** *Ducetia japonica*. <https://www.youtube.com/watch?v=DdtkM207GgU>.
- Karny H. 1921.** Katydids (Tettigoniidae) of the Philippine Islands, collected by C.F. Baker. *Philippine Journal of Science* **18**: 607–617.
- Karny H. 1923.** On Malaysian katydids (Gryllacrididae and Tettigoniidae) from the Raffles Museum, Singapore. *Journal of the Malaysian Branch of the Royal Asiatic Society* **1**: 116–193.
- Kevan DKM. 1987.** The Orthoptera, s. str., and Grylloptera, or grigs, of Micronesia - a preliminary survey. In: Baccetti B, ed. *Evolutionary biology of orthopteroid insects*. Chichester, England: Ellis Horwood Ltd., 296–324.

- Kim JI, Kim TW. 2001.** Taxonomic review of Korean Phaneropterinae (Orthoptera, Tettigoniidae). *Korean Journal of Entomology* **31**: 147–156.
- Kim TW. 2009.** *Taxonomy and acoustic signals of Korean Tettigonioidae (Orthoptera: Ensifera) II (in Korean)*. Incheon: National Institute of Biological Reserves (+ CD).
- Kim TW, Puskás G. 2012.** Check-list of North Korean Orthoptera based on the specimens deposited in the Hungarian Natural History Museum. *Zootaxa* **3202**: 1–27.
- Kleukers RMJC, Ode B, Fontana P. 2010.** Two new cryptic *Leptophyes* species from southern Italy. *Zootaxa* **2506**: 26–42.
- Koide Y. 2013.** *Ducetia japonica*. <http://guaminsects.myspecies.info/eol/14892/nojs>.
- Kostarakos K, Römer H. 2015.** Neural mechanisms for acoustic signal detection under strong masking in an insect. *The Journal of Neuroscience* **35**: 10562–10571.
- Kulkarni PP, Shishodia MS. 2004.** Insecta: Orthoptera. In: *Fauna of Pench National Park (Maharashtra)*. Kolkata: Zoological Survey of India, Conservation Area Series **20**, 207–225.
- Kulkarni PP, Shishodia MS. 2005.** Insecta: Orthoptera. In: Mahabal AS, Mahabal AS, ed. *Fauna of Melghat Tiger Reserve*. Kolkata: Zoological Survey of India, Conservation Area Series **24**, 317–340.
- Leonard JA, den Tex RJ, Hawkins MTR, Munoz-Fuentes V, Thorington R, Maldonado JE. 2015.** Phylogeography of vertebrates on the Sunda Shelf: a multi-species comparison. *Journal of Biogeography* **42**: 871–887.
- Lincoln GA. 1975.** Bird counts either side of Wallace's Line. *Journal of Zoology* **177**: 349–361.
- Mandal SK, Mandal GP, Hazra AK. 2007.** Insecta: Orthoptera. In: Anonymous, ed. *Fauna of Kudremukh National Park (Karnataka)*. Kolkata: Zoological Survey of India, Conservation Area Series **32**, 15–25.
- Mason L. 2005–2014.** *Biographical Dictionary of Chinese Christianity*. Available at: <http://www.bdconline.net/en/stories/l/lay-george-tradescant.php>.
- Matsumura S, Shiraki T. 1908.** Locustiden Japans. *Journal of the College of Agriculture, Tohoku Imperial University* **3**: 1–80, pls. 1–2.
- Nagar R, Swaminathan R, Mal J. 2015.** Some common and less known Phaneropterinae (Orthoptera: Tettigoniidae; Phaneropterinae) with the description of a new species from India. *Zootaxa* **4027**: 301–340.
- Nityananda V, Balakrishnan R. 2006.** A diversity of songs among morphologically indistinguishable katydids of the genus *Mecopoda* (Orthoptera: Tettigoniidae) from southern India. *Bioacoustics* **15**: 223–250.
- Orci KM, Szövényi G, Nagy B. 2010.** *Isophya sicula* sp. n. (Orthoptera: Tettigonioidae), a new, morphologically cryptic bush-cricket species from the Eastern Carpathians (Romania) recognized from its peculiar male calling song. *Zootaxa* **2627**: 57–68.
- OSFO Orthoptera Species File Online = Eades et al. 2015.**
- Panhuis TM, Butlin R, Zuk M, Tregenza T. 2001.** Sexual selection and speciation. *Trends in Ecology & Evolution* **16**: 364–371.
- Pfau HK, Pfau B. 2015.** On the Bioacoustics of the Iberian Ephippigerini (Orthoptera, Tettigoniidae, Bradyporinae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **88**: 105–154.
- Prabakar D. 2015.** An updated checklist of Insecta: Orthoptera of Tamil Nadu with new distributional records. *Biolife* **3**: 263–290.
- Ragge DR. 1961.** A revision of the genus *Ducetia* Stål (Orthoptera: Tettigoniidae). *Bulletin of the British Museum (Natural History), Entomology Series* **10**: 171–208.
- Rehn JAG, Hebard M. 1914.** Studies in American Tettigoniidae (Orthoptera). I. A synopsis of the genus *Scudderia*. *Transactions of the American Entomological Society* **40**: 271–314, pls 9–11.
- Rentz DCF. 1988.** The orthopteroid insects of Norfolk Island, with descriptions and records of some related species from Lord Howe Island, South Pacific. *Invertebrate Taxonomy* **3**: 1013–1077.
- Rentz DCF. 1996.** *Grasshopper Country: the abundant orthopteroid insects of Australia*. Sydney: University of New South Wales Press (+ CD).
- Rentz DCF. 2010.** *A guide to the katydids of Australia*. Collingwood: CSIRO Publishing.
- Rentz DCF, Balderson J. 1979.** Catalogue of Australian Tettigoniidae. *CSIRO, Division of Entomology, Technical Paper* **15**: 1–24.
- Rentz DCF, Balderson J. 1989.** A discography of the recorded insect sounds in the Australian National Insect Collection, CSIRO, Canberra. *CSIRO, Division of Entomology, Report* **44**: 1–90.
- Shi FM, Jiang SN. 2002.** Comparative observations on female stridulatory spines of the genera *Ducetia* and *Kuwayamaea* (Orthoptera: Phaneropteridae)(in Chinese). *Acta Entomologica Sinica* **45** (Suppl.): 28–30.
- Shi FM, Yang PL, Du X. 2003.** A comparative study on the male songs of different geographical populations of *Ducetia japonica* (Thunberg) (Orthoptera, Phaneropteridae)(in Chinese). *Acta Zootaxonomica Sinica* **28**: 402–410.
- Shishodia MS. 2000.** Orthoptera (Insecta) fauna of Andaman and Nicobar Islands. *Records of the Zoological Survey of India* **98**: 1–24.
- Shishodia MS. 2006.** Insecta: Orthoptera: Tettigoniidae. In: Alfred JRB, ed. *Fauna of Nagaland*. Kolkata: Zoological Survey of India, State Fauna Series **12**, 89–93.
- Shishodia MS. 2007.** Insecta: Orthoptera: Tettigoniidae. In: Director, Zoological Survey of India, ed. *Fauna of Mizoram*. Kolkata: Zoological Survey of India, State Fauna Series **14**, 207–215.
- Shishodia MS, Barman RS. 2004.** Insecta: Orthoptera: Tettigoniidae. In: Alfred JRB, ed. *Fauna of Manipur, Part 2 (Insects)*. Kolkata: Zoological Survey of India, State Fauna Series **10**, 139–145.
- Shishodia MS, Chandra K, Gupta SK. 2010.** An annotated checklist of Orthoptera (Insecta) from India. *Zoological Survey of India, Occasional Paper* **314**: 1–366.
- Shishodia MS, Gupta S. 2009.** Checklist of Orthoptera (Insecta) of Himachal Pradesh, India. *Journal of Threatened Taxa* **1**: 569–572.
- Shishodia MS, Kulkarni PP. 2002.** Insecta: Orthoptera. In: Anonymous, ed. *Fauna of Eravikulam National Park*. Kolkata: Zoological Survey of India, 11–15.

- Shishodia MS, Mehta HS, Mattu VK, Thakur SK. 2003.** Orthoptera (Insecta) from Pong Dam Wetland, District Kangra, Himachal Pradesh, India. *Zoos' Print Journal* **18**: 1047–1048.
- Simpson GG. 1977.** Too many lines; the limits of the oriental and Australian zoogeographic regions. *Proceedings of the American Philosophical Society* **121**: 107–120.
- Sismondo E. 1983–6.** Recordings of *Ducetia japonica* by E. Sismondo. Available at: <http://bio.acousti.ca/node/12586>.
- Spooner JD. 1968.** Pair-forming acoustic systems of phaneropterine katydids (Orthoptera, Tettigoniidae). *Animal Behaviour* **16**: 197–212.
- Spooner JD. 1995.** Pair-forming phonotaxic strategies of phaneropterine katydids (Tettigoniidae: Phaneropterinae). *Journal of Orthoptera Research* **4**: 127–129.
- Stumpner A, Meyer S. 2001.** Songs and the function of song elements in four duetting bushcricket species (Ensifera, Phaneropteridae, *Barbitistes*). *Journal of Insect Behavior* **14**: 511–534.
- Sultana R, Wagan MS, Panhwar WA. 2012.** Distribution and incidence of Tettigonioida (Ensifera) Orthoptera from Sindh Pakistan. *Pakistan Journal of Entomology* **27**: 117–122.
- SysTax. 2015.** Database system for systematics and taxonomy. Available at: [http://www.biologie.uni-ulm.de/systax/daten/index\\_d.html](http://www.biologie.uni-ulm.de/systax/daten/index_d.html).
- Tepper JGO. 1892.** The Phaneropteridae of Australia and Polynesia. *Transactions of the Royal Society of South Australia* **15**: 77–113.
- Thakur SK, Shishadia MS, Mehta HS, Mattu VK. 2004.** Orthopteran diversity of Roper Wetland Punjab, India. *Zoos' Print Journal* **19**: 1697.
- Thunberg CP. 1815.** Hemipterorum maxillosorum genera illustrata plurimisque novis speciebus ditata ac descripta. *Mémoires de l'Académie Impériale des Sciences de St. Pétersburg* **5**: 211–301, pl. 3.
- Vedenina VY, Mogue N. 2011.** Speciation in gomphocerine grasshoppers: molecular phylogeny versus bioacoustics and courtship behavior. *Journal of Orthoptera Research* **20**: 109–125.
- Vickery VR, Kevan DKM, English ML. 1999.** Insects of Micronesia volume 5, no. 4 Gryllacridoidea, Rhaphidophorioidea and Tettigonioida (Grylloptera). *Micronesica* **32**: 11–83.
- Villarreal SM, Gilbert C. 2014.** Male *Scudderia pistillata* katydids defend their acoustic duet against eavesdroppers. *Behavioral Ecology and Sociobiology* **68**: 1669–1675.
- Walker F. 1859.** Characters of some apparently undescribed Ceylon insects. *Annals and Magazine of Natural History* **4**: 217–224.
- Walker F. 1869.** *Catalogue of the specimens of Dermaptera Saltatoria in the collection of the British Museum. Part II. Catalogue of Locustidae*. London: British Museum of Natural History.
- Walker F. 1870a.** *Catalogue of the specimens of Dermaptera Saltatoria in the collection of the British Museum. Part III*. London: British Museum of Natural History.
- Walker F. 1870b.** *Catalogue of the specimens of Dermaptera Saltatoria in the collection of the British Museum. Part IV*. London: British Museum of Natural History.
- Walker TJ. 1964.** Cryptic species among sound-producing ensiferan Orthoptera (Gryllidae and Tettigoniidae). *The Quarterly Review of Biology* **39**: 345–355.
- Walker TJ, Forrest TG, Spooner JD. 2003.** The *rotundifolia* complex of the genus *Amblycorypha* (Orthoptera: Tettigoniidae): songs reveal new species. *Annals of the Entomological Society of America* **96**: 433–447.
- Wikipedia. 2015.** Guam. Available at: [https://en.wikipedia.org/wiki/Guam#Ecological\\_issues](https://en.wikipedia.org/wiki/Guam#Ecological_issues).
- Willemsse C. 1953.** On a collection of Orthoptera from the Sumba Islands (Indonesia). *Verhandlungen der Naturforschenden Gesellschaft zu Basel* **64**: 89–104.
- Wu S. 2010.** [*Songs and stridulatory organs of common katydids and crickets from Hebei*] (in Chinese with English summary). Master thesis, Hebei University. Available at: <http://www.docin.com/p-700148231.html>.
- Yang P, Chang Y, Lu R. 2000.** Stridulatory character of *Ducetia japonica* Thunberg (in Chinese). *Journal of Guangxi Academy of Sciences* **16**: 138–141.
- Zhantiev RD, Korsunovskaya OS. 1986.** Sound communication in bush crickets (Tettigoniidae: Phaneropterinae) of the European part of the USSR (in Russian). *Zoologicheskij Zhurnal* **65**: 1151–1163.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Supporting Information 1.** Comparative figures of stridulatory organs of holotypes/lectotypes of all forms in the *D. japonica* group described in the 19th century (except Japanese *D. quinquenervis*; holotype of *Ducetia japonica* lost).

**Supporting Information 2.** Detailed description, measurements, and distributional data including list of paratypes of *Ducetia antipoda* Rentz & Heller, sp. nov.

**Supporting Information 3.** Morphological details and measurements of *Ducetia malayana* Heller, sp. nov.

**Supporting Information 4.** Detailed description including measurements of *Ducetia melodica* Heller & Ingrisch, sp. nov.

**Supporting Information 5.** Chromosomal data of *Ducetia antipoda* sp. nov. and *D. japonica*.

**Supporting Information 6.** Sound files.