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Bioacoustics and systematics of *Mecopoda* (and related forms) from South East Asia and adjacent areas (Orthoptera, Tettigonioidea, Mecopodinae) including some chromosome data

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Abstract

Bush-crickets (or katydids) of the genus *Mecopoda* are relatively large insects well-known for their sounds for centuries. Bioacoustic studies in India and China revealed a surprisingly large diversity of sound patterns. We extend these studies into the tropics of South East Asia using integrative taxonomy, combining song analysis, morphology of sound producing organs and male genitalia as well as chromosomes, to get a better understanding of the phylogeny and evolution of this widespread group. Besides the closely related genus *Eumecopoda*, the genus *Mecopoda* contains some isolated species and a large group of species which we assign to the *Mecopoda elongata* group. Some species of this group have broad tegmina and stridulatory files with different tooth spacing patterns and produce continuous, often relatively complicated, trill-like songs. The species of another subgroup with narrower wings have all similar files. Their songs consist of echemes (groups of syllables) which differ in syllable number and syllable repetition rate and also in echeme repetition rate. Our results show that South East Asia harbours a large and certainly not yet fully explored number of *Mecopoda* species which are most easily and clearly identified by song. Based on the data, five new forms are described: *Mecopoda mahindai* Heller **sp. nov.**, *Mecopoda paucidens* Ingrisch, Su & Heller **sp. nov.**, *Mecopoda sismondoi* Heller **sp. nov.**, *Mecopoda niponensis vietnamica* Heller & Korsunovskaya **subsp. nov.**, *Eumecopoda cyrtoscelis zhantievi* Heller **subsp. nov.** In addition, some taxonomic changes are proposed: *Eumecopoda* Hebard, 1922 **stat. rev.**, *Paramecopoda* Gorochov, 2020, **syn. nov.** of *Eumecopoda* Hebard, 1922, *Mecopoda javana* (Johansson, 1763) **stat. nov.** (neotype selected) with *M. javana minahasa* Gorochov, 2020 **stat. nov.**, *M. javana darevskyi* Gorochov, 2020 **stat. nov.**, *M. javana buru* Gorochov, 2020 **stat. nov.**, *Mecopoda macassariensis* (Haan, 1843) **stat. rev.**, *Mecopoda ampla malayensis* Gorochov, 2020 **syn. nov.**, *Mecopada ampla javaensis* Gorochov, 2020 **syn. nov.**, *Mecopoda fallax aequatorialis* Gorochov, 2020 **syn. nov.**, the last three are all synonyms of *Mecopoda himalaya* Liu, 2020, *Mecopoda yunnana* Liu 2020, **stat. nov.**

Key words: Neotype *Gryllus javanicus*, new species, song, stridulation

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Introduction

Insects of the order Orthoptera are well-known for their sounds. Obviously, even in ancient times people were aware of these songs and liked to have singing insects as pets in their houses. Most of the old poems proving this interest may refer to crickets, but as early as 400 b.c. it is documented that Greek people had bush-crickets as pets and were sad when the singer died (Kevan 1978). Of course, it is unknown which species was involved. In Far East Asia, singing insects were—and are—also kept as pets, and here members of the genus *Mecopoda* are preferred species. Kevan (1978) presents a Chinese picture of a presumed *Mecopoda* painted in the 17th century as example of these singing insects. And also the first naturalists like Annandale (1900) noticed that people liked to have *Mecopoda* as singing pets. This tradition seems to have survived even into our days. Rentz *et al.* (2006) wrote about *Mecopoda*: "Their raucous stridulations are easily heard over the traffic and other metropolitan noises. They are frequently kept alive in cages in Asian countries as pets for the sound of singing males".

Bush-crickets (or katydids) of the genus *Mecopoda* Serville, 1831 are large insects (tegmen length between 35 and more than 70 mm) and they are found from Pakistan in the West and Japan in the North to the Solomon Islands in the South East. The scientific study of *Mecopoda* songs started not before 1990 when Sismondo analyzed song interactions of a *Mecopoda* species in Singapore. During this study he discovered several morphologically indistinguishable „song species" in South East Asia, all called *Mecopoda elongata*. Taxonomists had long before known about the morphological variation of this species (see e.g. Annandale 1900), and they were puzzled by the enormous variability. At first they established new species, mainly based on coloration or geographic origin, but finally they recognized that they could not find clear differences between the groups (e.g., Karny 1924). A morphometric study on the genital variation of five sympatric Indian *Mecopoda* species showed differences but failed to obtain a significant distinction (Dutta *et al.* 2018). Only in the last years scientists (Liu Yf *et al.* 2019 and Liu Cx *et al.* 2020) began to separate the different species in China, based on their calling songs. Liu Cx *et al.* (2020; 20 March) presented also details of their stridulatory organs. Recently, Gorochov (2020; December) published descriptions of many new forms from South East Asia, often based mainly on wing shape, with few details of variability and of the stridulatory organs, and without any data on acoustics or genetics.

Here we extend the previous bioacoustical studies to South East Asia. We analyze species-specific song patterns and then look for morphological correlates, especially in the stridulatory organs. However, this will probably be only a first step to understand the diversity of the genus *Mecopoda*. The Natural History Museum (formerly British Museum of Natural History) houses around 14 boxes with *Mecopoda elongata* sensu lato from many areas of the species' huge range, and a similar situation may be found in many large European museums.

Material and methods

Morphology

Besides specimens from own collections we obtained photographs from types and sonotypes (specimens with sound recordings available) deposited in several museums. We asked for scaled photos of the stridulatory files on the lower side of the left tegmen and of the mirror area at the base of the right tegmen. We determined the length of the file as direct connection between both ends and measured the inter-tooth distances as the mean between each eleven teeth (ten intervals) starting at the anal end (see Results). Length and width of the mirror area were measured as shown in Fig. 1.

In the studied specimens of the new species, the following measurements were taken (in mm): pronotum length; tegmina: length and maximum width; hind femora length; ovipositor length.

Acronyms / Depositories. ANIC Australian National Insect Collection, Canberra; IZCAS Institute of Zoology, Chinese Academy of Sciences, Beijing; LSUK, Linnean Society, London; MfN Museum für Naturkunde, Berlin; MNHN Museum national d'Histoire naturelle, Paris; NHM, Natural History Museum. London; NBC Naturalis Biodiversity Center, Leiden; NMED Naturkundemuseum Erfurt; NMPC National Museum Prague, Collectio, Prague; UUZM Uppsala University, Museum of Evolution, Zoology Section, Uppsala; ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn; ZIN Zoological Institute, Russian Academy of Sciences, Saint Petersburg; CH Collectio Heller; CI Collectio Ingrisch in ZFMK Bonn; OSF Orthoptera Species File (Cigliano *et al.* 2021).

Cytotaxonomy analyses

In the present cytogenetic study, 5 *Mecopoda* species were used: *M. sismondoi* **sp. nov.** (CH7704—SE Asia), *M. mahindai* **sp. nov.** (CH7843—Sri Lanka), *M. niponensis* (Haan, 1843) (CH7674—China), *M. himalaya* Liu, 2020 (CHLi-05—China) and *M. javana* (Johansson, 1763)(CH7725—Sri Lanka).

Somatic hepatic caeca were dissected, incubated in a hypotonic solution (0.9% sodium citrate), fixed in ethanol-acetic acid (3:1, v/v). The fixed material was squashed in 45% acetic acid followed by removal of coverslips using the dry ice technique and air-drying. Constitutive heterochromatin was revealed by the technique as described by Sumner (1972). Chromosomes were classified on the basis of the criteria proposed by Levan *et al.* (1964). At least ten mitotic metaphase samples per male were analyzed. Karyotypes were reconstructed by arranging homologous chromosomes in order of decreasing size.

The chromosome number in male (2n) and chromosome morphology (FN = Fundamental Number, the number of chromosome arms including the X chromosome) for each species are shown under the respective species.

Bioacoustics

The song recordings are partly own unpublished data (samples available in OSF or bio.acousti.ca), partly taken from the literature or bio.acousti.ca and evaluated all in the same way. For making the original recordings, many different microphones and tape recorders were used. Later all recordings were digitized. Since the songs always contained strong audio components, an audio frequency range of microphones was sufficient, and distorting effects of the microphone on the temporal pattern are not to be expected. However, the complete frequency range (studied up to 70 kHz), may only be covered in *M. niponensis, M. himalaya* and *M. sismondoi* **sp. nov.** The recordings of the last two species were made in the laboratory with a Racal store 4-D tape recorder using Brüel and Kjær microphones 4133 and 4135 and amplifier 2606 (frequency response flat up to 40 and 70 kHz respectively), distance microphone - animal 20–30 cm (recordings KGH). *M. niponenis vietnamica* **subsp. nov.** was recorded using a PC with ADC L-14440 (L-card, Russia) connected through an amplifier to the ¼-inch microphones, distance microphone—animal 7–10 cm (OK). Spectra were calculated analyzing 200 ms sections (10 ms for hemisyllables) of recordings sampled with 200/250 kHz, and using the mean of 512 point wide Hanning windows, overlapping by 100 pt. The stridulatory movements of *M. himalaya* and *M. sismondoi* **sp. nov.** were registered by an opto-electronic device (Helversen & Elsner 1977, modified as in Heller 1988). For the other species spectra were not calculated.

Song measurements were obtained using AUDACITY (http://audacity.sourceforge.net/), AMADEUS II and AMADEUS Pro (Martin Hairer; http://www.hairersoft. com). Oscillograms of the songs were prepared using TURBOLAB (Bressner Technology, Germany). Data are given as mean ± standard deviation, n=10 per series.

Bioacoustic terminology

Syllable is the sound produced during one cycle of movements, generated by opening and closing of the tegmina, each uni-directional movement generating a **hemisyllable**; **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 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). A first-order assemblage of syllables is called **echeme** (=chirp; short series of syllables, its length typically given in number of syllables) or **trill** (long series of syllables, its length typically given in seconds). However, there is no clear border between both (broken trill, trill segments).

Results

A. Taxonomic history and old names

The genus *Mecopoda* is based on the species *Mecopoda maculata* Serville, 1831 (present status see Tab. 1), but it includes species described much earlier. In the first revision of subfamily Mecopodinae, Redtenbacher (1892) listed *Mecopoda* with six species. They were placed in three groups: hind femora with spines/tubercles at the upper side (*M. cyrtoscelis* Karsch, 1888, now genus *Eumecopoda*), fastigium verticis anteriorly rounded [*M. elongata* (Linnaeus, 1758)] or with transverse keel (*M. dilatata* Redtenbacher, 1892; *M. divergens* Redtenbacher, 1892; *M. platyphoea* Walker, 1870; *M. walkeri* Kirby, 1891).

TABLE 1. *Mecopoda elongata* and its former ten synonyms (see text for details).

	Gryllus (Tettigonia) elongatus Linnaeus. 1758		type female, LSUK London Linnean Society, type locality India
1	*Gryllus javanus* Johansson, 1763	separate species	neotype designated, type (female) lost[1], type locality Indonesia, Java
2	*Gryllus (Tettigonia) ferruginea* Stoll, 1813	nomen dubium	description insufficient, no type, only figure of a female, type locality Bengal
3	*Gryllus (Tettigonia) rufa* Stoll, 1813	nomen dubium	description insufficient, no type, only figure of a female, type locality ‚Oostindie' (Indonesia)
4	*Locusta scalaris* Thunberg, 1815	nomen dubium	type female, UUZM Uppsala, type locality unknown
5	*Mecopoda maculata* Serville, 1831	synonym of *javana*	type female, MNHN, Paris ?[2], type locality Indonesia, Java
6	*Mecopoda virens* Brullé, 1835	synonym of *elongata*	type female, MNHN, Paris ?[2], type locality India, Malabar & Bombay
7	*Locusta (Mecopoda) macassariensis* Haan, 1843	separate species	type male, NSC Leiden, type locality Indonesia, Sulawesi
8	*Decticus tenebrosus* Walker, 1869	separate species	syntypes females, NHM, London, type locality Philippines (lectotype Storozhenko & Paik 2007)
9	*Mecopoda elongata* variety *burmeisteri* Karny, 1924	nomen nudum	no type specimen nor type locality
10	*Mecopoda elongata* variety *servillei* Karny, 1924	nomen nudum	no type specimen nor type locality

[1] specimen not in the collection of the Linnean Society (Marshall 1983) nor in Uppsala (Catalogue UUZM). Johansson was a student of Linnaeus.

[2] at least not marked as type in Paris (Desutter 26.4.2019 in litt.)

E. cyrtoscelis was relatively fast split off as a separate genus together with several early described species. From the third group one species (known to Redtenbacher only from literature) is suggested to belong to *Eumecopoda* (Hebard 1922), while for the remaining three (two from Borneo, one from Sri Lanka) no new data were published from 1900 until now (Gorochov 2020; except a misidentification from Pakistan; Panhwar *et al.* 2016; see below). The single species of the second group, *M. elongata*, had already at Redtenbacher's time many synonyms whose number increased by naming so-called varieties. *M. niponensis* was removed from its synonymy with *elongata* in the 1990ies, but only in 2019 new species in this group were described (Liu Yf *et al.* 2019). *M. elongata* was considered to have a huge range and was mentioned in many faunistic, morphological and even physiological and bioacoustical papers (Beier 1966, OSF, see *sismondoi, himalaya* below).

From the bioacoustical studies (Sismondo 1990; Nityananda & Balakrishnan 2006) it became obvious that under the name *M. elongata* several different species were combined, with sometimes up to four species occurring syntopically. The species are morphologically quite similar, but show enormous differences in calling song pattern. So *M. elongata* in its pre-2019 version is a complex of many species which only for China (Liu Yf *et al.* 2019; Liu Cx *et al.* 2020) has now been (partly) resolved taxonomically. As a first step to solve this problem globally the status of the old synonyms has to be studied. Liu Cx *et al.* (2020) already showed that some of them have to be considered as nomina dubia, based on unidentifiable nymphs. From the 10 synonyms existing at that time (mid of 2020; Tab. 1) Gorochov (2020) discussed some but did not drew any taxonomical consequences except of (1) restoring the status of the Philippine form *M. tenebrosa* as a valid species, (2) considering *M. maculata* as valid subspecies of *elongata* and (3) treating *M. macassariensis* Haan, 1843 as subspecies of *M. fallax* He, 2019.

The genus *Mecopoda* is based on the species *Mecopoda maculata*, its type specimen being a brown female from the island of Java (MNHP Paris). Its identification to species level may be difficult and it would be at best replaced by a neotype. However, there is an older name, also based on a brown female from Java, that is *Gryllus javanus*. Its type specimen is obviously lost (see below). To secure the stability of the genus *Mecopoda*, we will establish a neotype for *M. javana* from the island of Java (Indonesia), the terra typica, and consider *M. maculata* as a junior synonym of this species. Following this concept, we will below list and treat all forms (Tab. 1) accepting

Gorochov's proposal of *M. tenebrosa* as valid species, considering *M. maculata* as synonym of *javana* and recognising *M. macassariensis* as valid species different from *M. fallax*.

The oldest synonym (Tab. 1: 1) is based on a very poor description and its type seems to be lost. We establish a neotype for the species from the island of Java (Indonesia), the terra typica. The next two names (2,3) are based on drawings of female specimens. From these pictures it is impossible to understand to which of the different syntopic species the name may apply. They are thus considered as nomina dubia. For the remaining five names at least theoretically type specimens should exist. The types of *Locusta scalaris* (4) are in Uppsala (photos in OSF). However, since with present knowledge females cannot be safely identified and there is no information of the type locality, the name has also to be considered as nomen dubium. The type specimens of the next two synonyms (5,6) should be in Paris. However, they do not seem to be marked as types (Desutter-Grandcolas in litt.). In Java at least two *Mecopoda* species occur (see Results), and from the color we assume that *Mecopoda maculata* is a synonym of *M. javana.* For *Mecopoda virens* (6) the situation is similar. In India up to four species occur sympatrically. However, as long as the status of *Mecopoda elongata* is not solved, *M. virens* may be treated as synonym of *M. elongata*. The status of *Locusta (Mecopoda) macassariensis* Haan, 1843 (7) is discussed below. *Decticus tenebrosus* Walker, 1869, finally, represents a species from the *M. minor* subgroup (Liu Cx *et al.* 2020), judging from the shape of the tegmina. The two names (9, 10) introduced by Karny (1924) were intended as replacement names for alphabetically named morphological varieties of Burmeister (1834) without taxonomic background. They must be considered as nomina nuda. The status of the Linnean *Mecopoda elongata* remains unclear. In India several „song species“ (Nityananda & Balakrishnan 2006) have been recorded and no attempt was made to clarify which of them may be the ‚true' *elongata*, e.g. by defining a neotype. However, since none of the Indian song types was rediscovered in East (Liu Yf *et al.* 2019; Liu Cx *et al.* 2020) and South East Asia (this paper), we assume that the *Mecopoda* species from India are different from that now known from the more Eastern areas and that *M. elongata* is a species endemic to India.

The status and the relationships of the three island forms described by Gorochov (2020) is difficult to evaluate. From morphology they clearly belong to the *confracta* group which also contains *M. javana,* and we will treat them provisionally as subspecies of *javana* until more information is available.

M. javana minahasa Gorochov, 2020 **stat. nov.** (type locality Sulawesi)
M. javana darevskyi Gorochov, 2020 **stat. nov.** (type locality Flores)
M. javana buru Gorochov, 2020 **stat. nov.** (type locality Buru, Maluku Islands)

B. Bioacoustical, morphological and chromosomal data

As described in the introduction, the morphological characters usually helpful to differentiate species in Orthoptera do not work well in *Mecopoda.* This is even true for male genitalic structures. The shape of male subgenital plates (Fig. 2) and cerci is quite similar between species. Even *Eumecopoda* species do not show clear differences (Fig. 2). Possibly in the length of the minute styli and in the size and distance of the two cercal teeth small differences exist (Fig. 3–4), but with present knowledge they are not sufficient for safe identification. The length and width of the tegmina differs between species (e.g., Fig. 5) but is diagnostic only for some of them. On the other hand, the shape of the mirror cells in the forewings is largely diagnostic for some species groups (see Fig. 1, Tab. 2) but not for species. In song, however, the specimens can be placed in several clearly separated groups assumed to represent species. We have tried to analyze all sound recordings of *Mecopoda* and *Eumecopoda* species available in literature, our collections and at bio.acousti.ca and OSF (Tab. 3–4). In many specimens we could study the stridulatory organs in addition to song recordings. We excluded data from Eastern Asia (China, Japan and Korea; well-known from previous studies; see Liu Yf *et al.* 2019, Liu Cx *et al.* 2020) and India (Bangladesh, India, Pakistan; taxonomically a black spot due to the unsolved status of *M. elongata*), but used the information from there for comparison. Based on the temporal pattern of the song (Fig. 6–10), the data sets (individual specimens or means of several specimens; Tab. 3–4, 7) belong to nine groups. Four of them (*M. niponensis continentalis* Gorochov 2020*, M. himalaya, M. fallax, E. cyrtoscelis*) represent species whose songs had already been known, three were described without acoustic data (*M. javana, M. stridulata stridulata* Gorochov, 2020; *M. angusta* Gorochov, 2020) and three represent new species described below together with two new subspecies. In addition, another new species, *Mecopoda paucidens* Ingrisch, Su & Heller **sp. nov.**, is described based on morphology only.

TABLE 2. Dimensions of stridulatory organs and coloration in identified *Mecopoda* specimens.

species	specimen	ratio mirror length/width	colouration green/brown	number of file teeth	length of file (mm)
M. elongata **group**					
niponensis **subgroup**					
ampla	holotype *ampla ampla*	1.37		132	6.2
fallax	CI3254538	1.35	green	110	5.4
fallax	Liu *et al.* 2020	1.44		110	5.2*
himalaya	CI3254643	1.31		95	5.4
himalaya	Liu *et al.* 2020	1.33		90	5.6*
himalaya	CRTmeceloM01	1.34	brown	73	3.4
himalaya	CH3740	1.36	green	78	5.3
himalaya	CI3254539	1.39	green	74	5.0
himalaya	NHMUK010210933	1.47	green	86	4.6
himalaya	CH3737	1.47	green	79	5.3
himalaya	holotype *ampla javaensis)*	1.28	green	95	5.6
himalaya	holotype *ampla malayesis*	1.29	green	98	6.2
himalaya)	holotype *fallax aequatorialis)*	1.28		90	5.5
macassariensis	holotype	1.44	green	92	5.7
niponensis niponensis	lectotype	1.39	green	116	5.3
niponensis continentalis	CH7674	1.34	green	107	6.1
niponensis continentalis	Liu *et al.* 2020	1.47		105	5.2*
niponensis vietnamica **subsp. nov.**.	Vietnam	1.43	green	115	5.8
stridulata stridulata	holotype	1.46	greyish brown	115	5.8
stridulata stridulata	CRTmeceloM02	1.35	(green)	119	4.3
stridulata stridulata	CRTmeceloM03	1.47	green	126	4.6
stridulata latiuscula	holotype	1.56	brown	110	5.5
prominens	holotype	1.09	greyish brown	139	7.0
confracta **subgroup**					
confracta	Liu *et al.* 2020	1.67		90	4.8*
mahindai **sp. nov.**	CH7843	1.60	brown	104	5.6
sismondoi **sp. nov.**	holotype	1.73		88	4.5
sismondoi **sp. nov.**	CH3746	1.77	brown	82	4.6
sismondoi **sp. nov.**.	CH3738	1.79	brown	81	4.6
javana	neotype	1.50	brown	104	5.8
javana (Sri Lanka*)*	CH7725	1.63	brown	93	4.9
javana (Bali*)*	NHMUK010210932	1.62		95	4.9
M. dilatata	OTRmecdilS01	1.64	brown	68	4.4
M. angusta.	CH3697	1.43	brown	59	3.2
M. angusta.	CH3758	1.44	brown	63	3.5
M. angusta.	CH3674	1.46	brown	73	3.1

......continued on the next page

TABLE 2. (Continued)

species	specimen	ratio mirror length/width	colouration green/brown	number of file teeth	length of file (mm)
Eumecopoda cyrtoscelis zhantievi **subsp. nov.**	topotype		brown	64	2.9
c. cyrtoscelis	Sänger & Helfert 2007		brown	61–75	3.3
cyrtoscelis	Rentz el al. 2006		brown	70	1.8

* data from Liu *et al.* 2020.

TABLE 3. Song parameters of *M. himalaya.*

source	country of origin	T (ºC)	echeme period (ms)	single syllable period (ms)	echeme repetition rate (Hz)
* + Liu *et al.* 2020	China: Yunnan	ca. 22	41.9±0.5		23.9/-
	China: Yunnan	ca. 25	53		18.9/32.4
*CH3737	Malaysia, peninsular	>28	25.9±0.3	17.9±0.3	25.3/55.9
*CH3740	Malaysia, peninsular	26	39.6±0.5	22.2±0.9	32.5/45.0
Kostarokas & Römer 2015	Malaysia, peninsular		30.8±0.6		
Krobath *et al.* 2017	Malaysia, peninsular				
Siegert *et al* 2013	Malaysia, peninsular		29.1		34.4/-
*Riede CRTmeceloM01	Malaysia, Sabah	ca. 20	27.3±0.5	19.4±0.5	36.6/51.5
Tan & Wahab 2018	Brunei	-	25	-	40/-
*Sismondo	Indonesia, Sumatra	-	36.0±0.5	22.1±0.7	27.8/45.2
	Indonesia, Sumatra	-	31.8±0.8	-	31.4/-
*Ingrisch 3254541	Indonesia, N Sumatra	25	30.4±0.5	19.5±1.4	32.9/51.3
*Ingrisch 3254646	Indonesia, W Sumatra	25	32.4±2.7	21.2±0.6	30.8/47.2
*Korsunoskaya 2008	Indonesia, Java	-	38.1 ± 0.1	22.9±0.4	26.2/43.7
*Ingrisch 3254643	Indonesia, Java	25	31.9±1.37	17.5±0.9	31.3/57.1
*Ingrisch 3254644	Indonesia, Java	23	36.8±1.2	23.3±0.7	27.2/42.9
*Ingrisch 3254645	Indonesia, W Java	24	35.7±0.5	22.6±1.3	28.0/44.2
*Ingrisch 3254539	Thailand	24,5	38.0±0.5	21.2±1.0	26.6/47.2
*Ingrisch 3254540	Thailand	19	40.5±0.5	-	24.7/-

* this paper

The stridulatory files in *Mecopoda* (and many other Mecopodinae; see Willemse 1977) differ from that commonly found in Tettigonioidea in one important aspect. As in most bush-crickets, at the basal end of the file the teeth become more or less continuously smaller ending in nearly uncountable pegs. In many species, the file ends also on the anal/distal end with very small teeth. In contrast, teeth in *Mecopoda* become only slightly smaller at the distal end, compared to the middle of the file, ending with relatively large teeth directly at the edge of the tegmen (see e.g. Liu Cx *et al.* 2020). The files of different species of *Mecopoda* (Fig. 11–12) can thus easily be compared taking the last tooth at the anal end as fix point.

The stridulatory apparatus at the base the right tegmen, called mirror area, is quite complicated and seems to be unique among katydids. There are no vestiges of a stridulatory file on the underside of this tegmen, similar to the situation in many Pseudophyllinae (Chamorro *et al.* 2014). However, there are large glossy cells resembling the well-known harp and mirror in crickets (e.g., Bennet-Clark 1989). The largest cell, called mirror, is not completely visible from above (see Fig. 1) but is partly covered by a heavily sclerotized structure (called overmirror by Gorochov 2020) which protects the thin glossy membrane but leaves enough space for its vibrations. The exact acoustical function of the different cells is unknown.

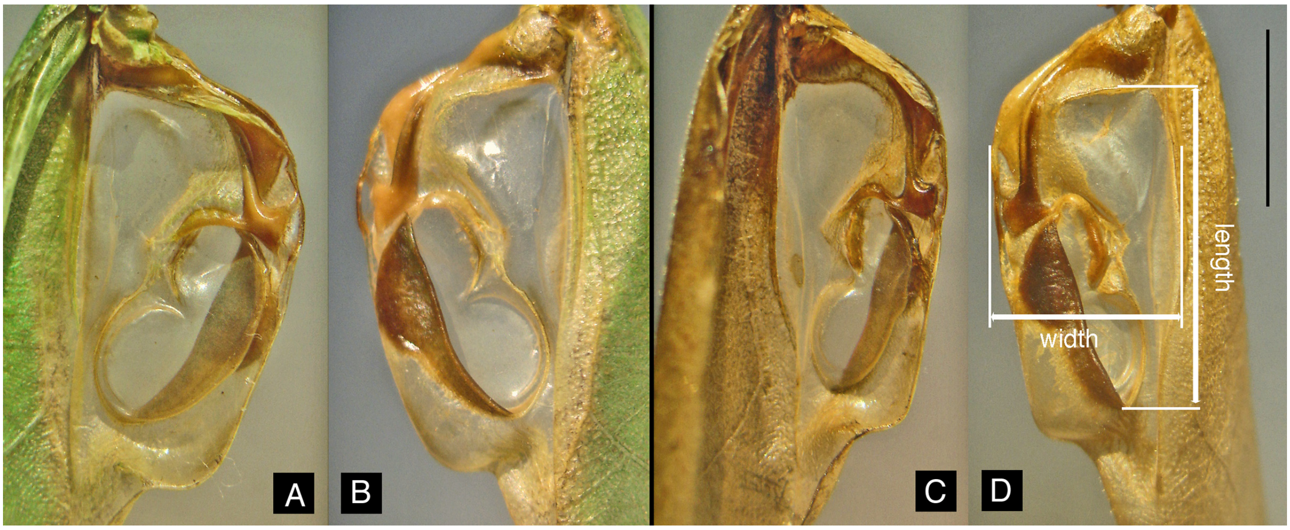

FIGURE 1. Mirror cells in the right male tegmen, viewed from the lower (A, C) and upper (B, D) side. **A–B** *Mecopoda himalaya* (CH3411), a member of the *niponensis* subgroup, **C–D** *M. sismondoi* **sp. nov.** (CH3688), *confracta* subgroup. Note the pretzel-shaped mirror in both species. Scale 5 mm.

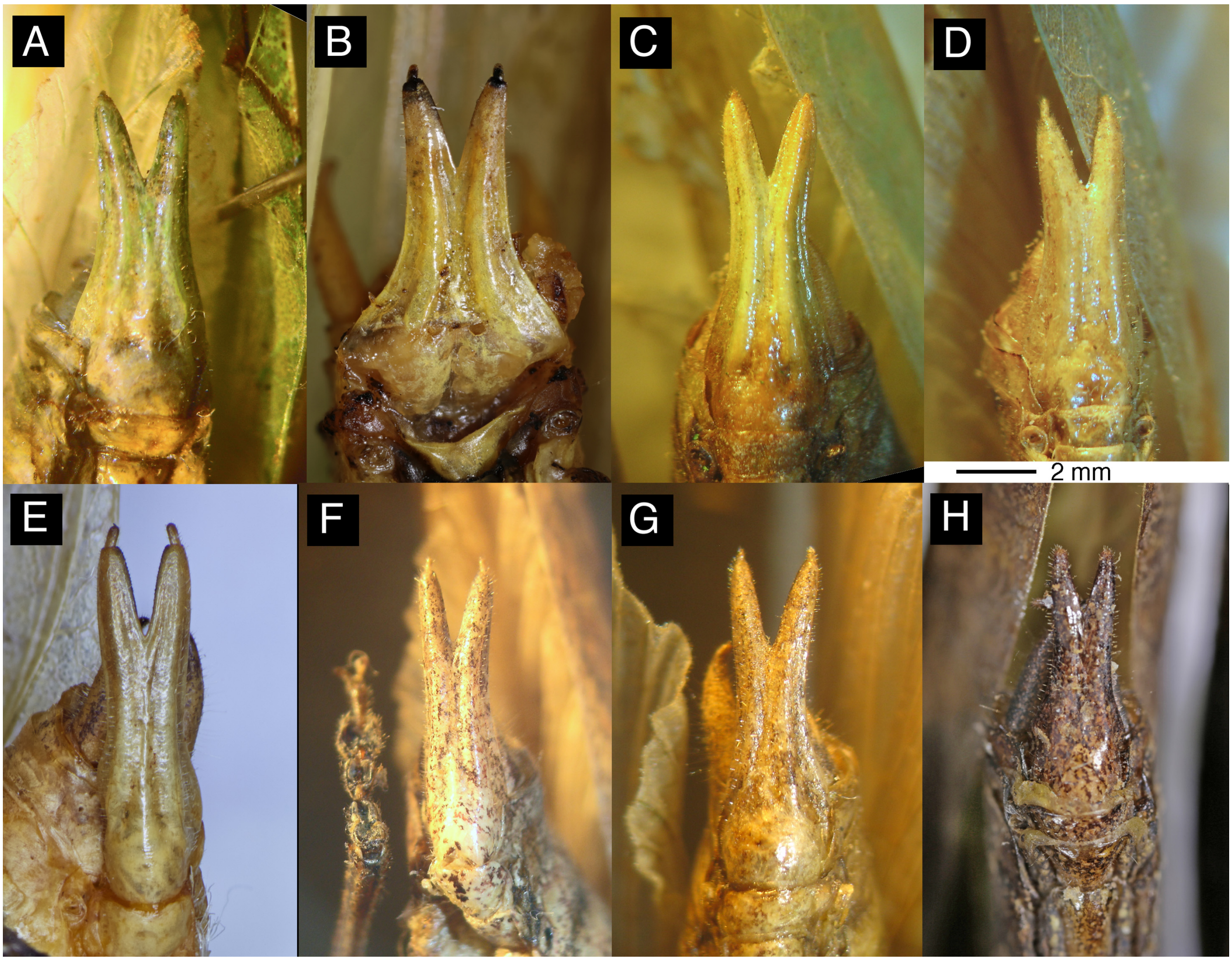

FIGURE 2. Male subgenital plates in *Mecopoda* and *Eumecopoda*. **A** *M. niponensis continentalis* (CH7674), **B** *M. niponensis vietnamica* **subsp. nov.** (holotype), **C** *M. himalaya* (CH3737), **D** *M. sismondoi* **sp. nov.** (CH3738), **E** *M. javana,* neotype, **F** *M. javana,* Sri Lanka, **G** *M. mahindai* **sp. nov.**, **H** *E. cyrtoscelis zhantievi* **subsp. nov.** Scale 2 mm.

TABLE 4. Song parameters in the *confracta* subgroup.

species/source	country of origin	T (ºC)	chirp duration (ms)	chirp period (ms)	syllables number in a chirp	syllable/double-syllable period	SRR (Hz)
confracta							
*CH7680+Liu *et al.* 2020	e.g. China, Yunnan	27	200	400	9	25	40
sismondoi							
*CH3746	Malaysia	28	297.9±52.4	1975.2±72.4	11.7±1.6	24.4±0.7	41.0
*CH3738	Malaysia	22	358.2±12.7	2626.2±61.6	14.8±0.4	23.4±0.8	42.7
*Sismondo S (84A)	Singapore	-	360.8±21.1	2045±40.1	10.6±0.5	24.9±0.6	40.2
*CH7704	South East Asia	20	368.8±33	3120±75	12.8±0.9	29.6±1.7	33.8
Hartbauer *et al.* 2012	Malaysia	26–27	273 (250–350)	2020±80	13–20	16–18	53–60
Hartbauer *et al.* 2006	Malaysia	27	200–300	1990 (1800–2300)			
Korsunovskaya 2008	Indonesia, Sumatra	-	393±7.7	3000±50	17	25	40
javana							
*neotype 3261437	Indonesia, Java	25	108.0±1.6	254.7±13.6	4	25.3±0.9	39.5
*Ingrisch 3254649	Indonesia, Java	23	95.9±12.4	247.8±14.1	4.2±0.4	27.5±1.1	36.4
*Ingrisch 3254650	Indonesia, Java	25	102.7±14.4	269.8±6.6	4.8±0.4	27.1±1.8	36.9
*Sismondo N1	Indonesia, Bali	27	117.7±2.2	270±7.8	5	24.6±0.5	40.7
*Sismondo N2	Indonesia, Bali	27	169.8±7.7	249.1±8.6	5.9±0.3	21.5±0.5	46.5
*Sismondo N3	Indonesia, Bali	28,5	137.5±7.7	230.6±10.3	5.3±0.5	20.4±1.0	49.2
*Helfert&Saenger in NHM	Sri Lanka	28	123.6±1.6	281.1±1.8	4	20.7±1.2	48.3
*Helfert&Saenger in NHM	Sri Lanka	28	97.8±2.4	281.1±3.6	4	19.0±1.2	52.6
*CH7725	Sri Lanka	27	194.8±13.4	282.7±12.4	4	20.1±0.9	49.8
Korsunovskaya 2008	Cambodia	-	123.8±2.3	309	4	22–29	34–45
Korsunovskaya 2008	Cambodia	-	167.8±33.6	341.5	3	25.4–29.8	33.8–39.4
mahindai							
*holotype CH7843	Sri Lanka	22	333.2±5.9	1051.4±58.0	3	123.2±2.4	8.1
"chirper"							
Nityananda & Balakrishnan 2006	India	26	109	483	10	10	100

* this paper

In all species of the *Mecopoda elongata* group, except for the *confracta* subgroup, the mirror area is wider than in *M. dilatata, M. angusta* and *Eumecopoda* (length/width<1.5; Tab. 2; Fig. 1, 11) and has a special pretzel-shaped structure while it is more roundish in the others (compare Fig. 13 A–P to O–N). The relative width seems also to be a good criterion to recognize members of the *confracta* subgroup although there is a certain overlap around 1.5 relative width.

The carrier frequencies of the song were studied in *M. niponensis vietnamica* **subsp. nov.**, *M. himalaya* and *M. sismondoi* **sp. nov.** only. As might be expected from the complicated structure of the mirror, all three species had very broad spectra as is also known from other studies of *Mecopoda* (Nityananda & Balakrishnan 2006, Kostarakos & Römer 2015, Liu Cx *et al.* 2020). In the three species, a relatively narrow but strong peak was situated between 5 and 10 kHz (Fig. 14). This component has the largest range. *M. n. vietnamica* **subsp. nov.** and *M. himalaya* had broad secondary peaks in the ultrasonic range (*M. n. vietnamica* **subsp. nov.** 20 and 40 kHz in chirp, around 50 kHz in trill, even stronger than the main peak; *M. himalaya* between 20 and 30 kHz), whereas *M. sismondoi* **sp. nov.** had a second narrow peak between 15 and 20 kHz and a strong broad range between 25 an 80 kHz with a weakly pronounced peak between 65 and 70 kHz. This difference between *M. himalaya* and *M. sismondoi* **sp. nov.** can also be seen in previous studies (Siegert *et al.* 2013; Kostarakos & Römer 2015; as species with chirp and trill respectively). No large differences were seen between opening and closing hemisyllables, except that the second peak (and the higher components) in *M. sismondoi* **sp. nov.** was much weaker during closing. In both species frequencies below the peak (see Siegert *et al.* 2013) were weaker or nearly absent in closing hemisyllables.

Comparison of the chromosomes of five *Mecopoda* species revealed differences between their karyotypes, including the number of chromosomes (2n), the morphology of the chromosomes, the Fundamental Number of chromosome arms (FN) and C-banding patterns (Fig. 15). All analysed species show the same sex determining system X0 (male) as well as the bi-armed (metacentric/submetacentric) X chromosome which is in size similar to the first pair of autosome. Regardless of the number of chromosomes in the set, autosomes can be divided into two size groups: 2 long (pairs 1, 2), and 12, 11 or 9 (depending on species) medium/small pairs gradually decreasing in size.

The standard karyotypes of *M. sismondoi* **sp. nov.** and *M. mahindai* **sp. nov.** were characterized by a chromosome number of 2n = 29 (males) and three acrocentric pairs of chromosomes, but they differ in the morphology of the X chromosome (submetacentric or metacentric, respectively). In the males investigated of *M. niponensis continentalis* and *M. himalaya* the chromosomal number was reduced to 2n = 27; in both species all thirteen pairs of autosomes are bi-armed (meta-/submeta-/subacrocentric). The lowest chromosome number, 2n = 23, FN = 46, was found in *M. javana* **stat. nov.**, the karyotype of this species shows only bi-armed chromosomes. C-banding revealed some discrete differences in number and distribution of constitutive heterochromatin blocks (C-bands) between the five species analysed. All species have paracentromeric blocks, which vary in size between different chromosomes and species. Additionally, in *M. mahindai* **sp. nov.** interstitial C-bands occur in one arm of the bi-armed first pair of autosomes and the X chromosome and in acrocentric pairs two and three. Generally, distal bands were observed in both arms of the first pair of autosomes and the X chromosome and in some medium/small pairs. The second pair in *M. sismondoi* **sp. nov.** and *M. mahindai* **sp. nov.** exhibited heteromorphism in terms of C-bands size between homologue chromosomes in the paracentromeric region in *M. sismondoi* **sp. nov.** respectively interstitially located in *M. mahindai* **sp. nov.**

C. Specific Part

Mecopoda Serville, 1831

Taxonomic remarks. Gorochov (2020) included the genus *Eumecopoda* and his new *Paramecopoda* as subgenera in *Mecopoda* based on their morphological similarity and because „the subgeneric position of some species is somewhat problematic“. However, the latter problem cannot be solved by downgrading, and all *Eumecopoda* species (including *Paramecopoda)* are characterized by falcate tegmina (see also below under *Eumecopoda*). Until genetic data are available we consider the two groups as separate genera.

Eumecopoda genus **stat. rev.**

Generic characters (after Liu *et al.* 2020).

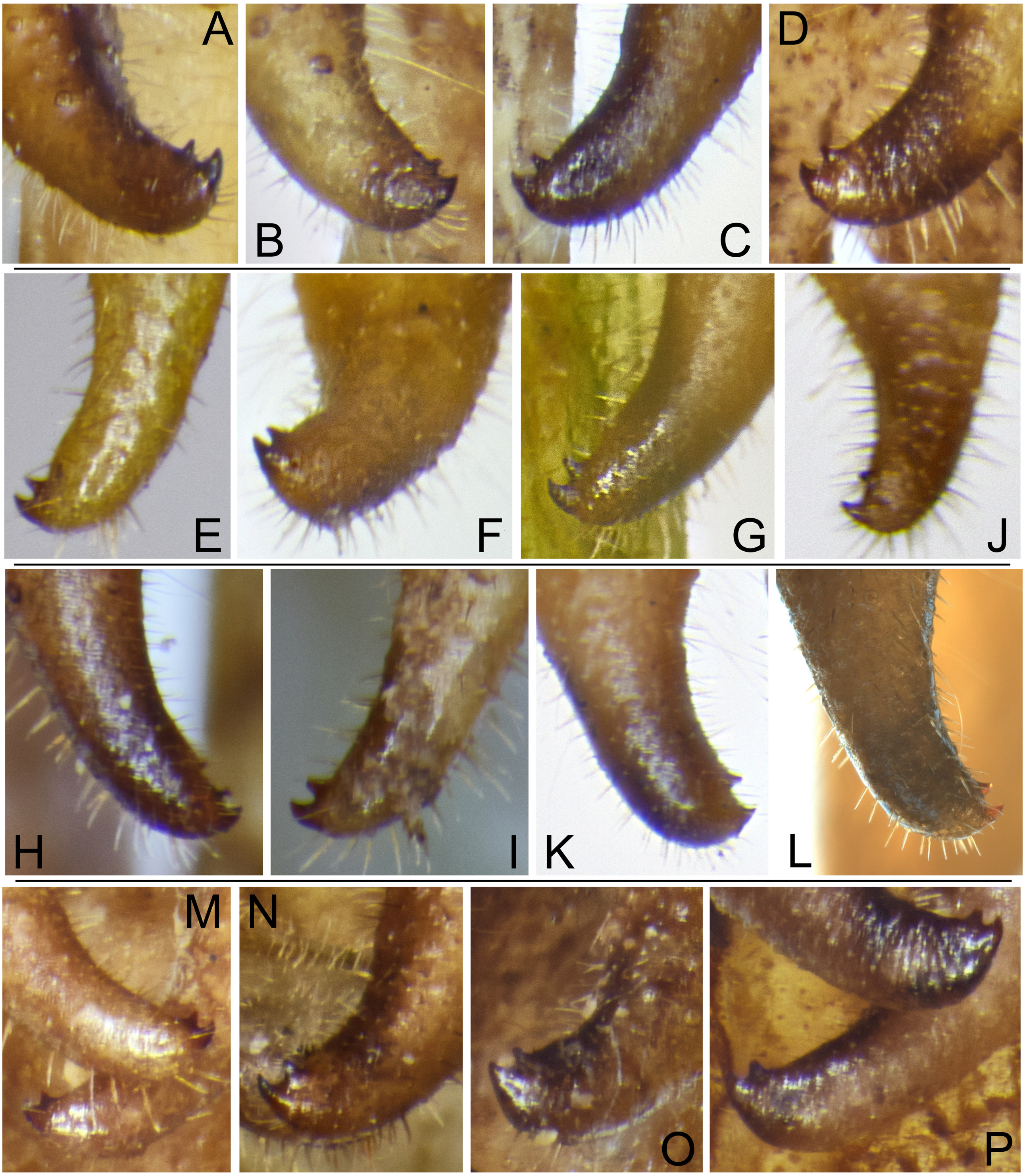

FIGURE 3. Apical area of male cerci of specimens from Java (A–G, J–K) and Borneo (H–I, M–P). **A–D:** *M. javana* from Palabuan Ratu (A 3261437 neotype; B 3261432; C 3261435; D 3261436); **E–I:** *M. himalaya* group (E 3261440 Gunung Salak; F 3261448 Bogor; G, 3254643 P. Ratu; H, 3261454 Sarawak near Batu Niah, I 3261461 Nanga Ngungun); **J:** unknown group from Palabuan Ratu forest (3261434 large species); **K–L:** *M. paucidens* (K 3261458 Gunung Lawu, L type from Timor); **M:** *M. himalaya* from Sabah (CRTmeceloM01); **N–P:** *M. s. stridulata* from Sabah (N CRTmeceloM02 from Poring; O OTRmeceloS15 and P OTRmeceloS16 from Matunggong).

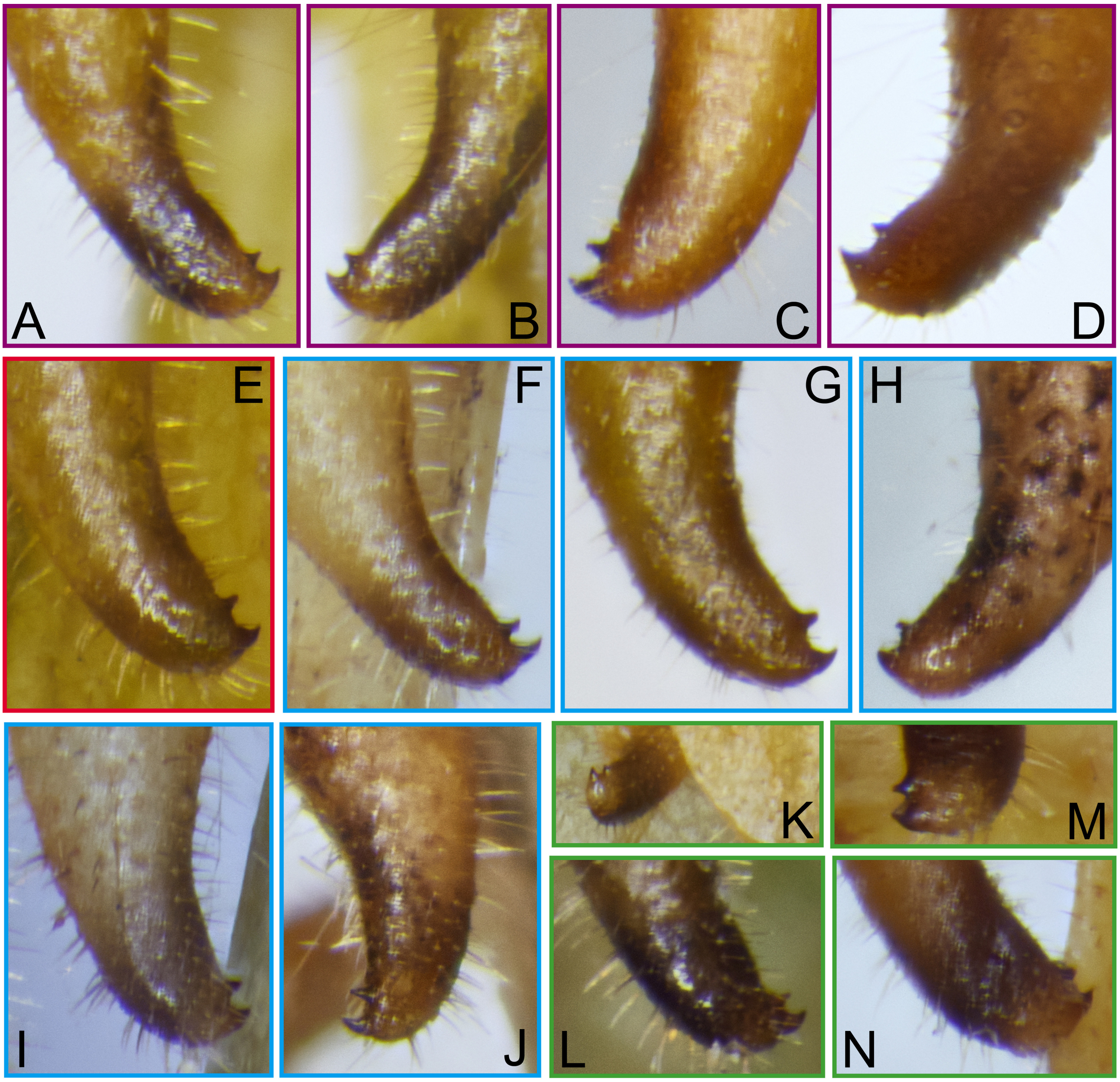

FIGURE 4. Apical area of male cerci of specimens from Thailand. **A–D:** *M. fallax* (**A–B** 3254538 NamNao left and right cercus; **C** 3261689 Khao Lak; **D** 3261441 Sok); **E:** *M. himalaya* (3254539 Monkrating); **F–I:** *confracta* subgroup (**F** 3261445 Chiang Mai in town; **G** 3261455 do. near Huei Khaeo Waterfall, **H** 3261456 do. Doi Suthep in mountain; **I** 3261452 Phrao district; **J** 3261444 Khao Yai); **K–N:** unknown subgroup (**K** 3261447 Khao Chong; **L** 3261449 Nan not voucher for song; **M–N** 3261442 Khao Sok right and left cercus).

Diagnostic characters. Large-sized species (habitus see e.g., fig. 4 in Liu *et al.* 2020). Fastigium verticis widened anteriorly. Head sulcate, with or without transverse lateral apices. Disc of pronotum flat, with truncate anterior and obtusely angular posterior margins, and distinct lateral carina. Tegmina surpassing apices of posterior femur. Prosternum bispinose. Male cerci with incurved apices, at tip with two minute acute teeth (Fig. 3–4) as in many other mecopodine genera. Male subgenital plate elongate, with styli and distinct apical notch. Ovipositor robust, elongate, sword-like.

Redescription. Head. Fastigium verticis widely truncated and 1.5–3 times wider than scapus. Thorax. Pronotum elongated and broadened backward. Male pronotum narrowest in the beginning of prozona, broadened backward after the first transverse sulcus. Disc of pronotum flat with the exception of distinct depression around the sulcus. Legs robust and long. Anterior coxa armed with a spine. Anterior femur longer than pronotum. Anterior and median femora with indistinct tiny spines on ventro-anterior margin; posterior femora with a few small spines near apex on ventro-posterior margin. Each tibia with fine spines on each margin. Tympana on the fore tibiae fully open on both sides, tibia widened at and abruptly constricted below tympana. Female pronotum similar to that of male in general, but less broadened backward especially in the ending of metazona. Wings. Male tegmina well developed, extending beyond abdominal apex and surpassing apex of hind femur. Large and often complicated mirror cells near base of the right tegmen (Fig. 13). Number of stridulatory teeth between 44 and 139 (see Fig. 11), the lowest number observed in *M. paucidens* **sp. nov.** and the highest in *M. prominens* Gorochov, 2020. Female tegmina also well developed extending beyond apex of abdomen, but distinguished from male tegmina by length and shape.

Key to species (partly after Redtenbacher 1892)

1 fastigium verticis rounded, no transverse keel; gap between fastigium frontis and fastigium verticis closed or separated by a fine suture; mirror on right male tegmen pretzel-shaped (Fig. 1, Fig. 13 A–P) . . . . *Mecopoda elongata* group
1’ fastigium verticis blunt, with transverse keel; gap between fastigium frontis and fastigium verticis distinct; Fig.14); mirror on right male tegmen in shape roundish (Fig. 13 O–N) 2
2 male subgenital plate broad with a small caudal incision (Fig. 17 A) . . . . *Mecopoda angusta*.
2’ male subgenital plate long and fork-like (Fig. 17 B, C). 3
3 body small, tegmina short (see Tab. 5; only one male known; Sumatra). . . . . *Mecopoda kerinci* Gorochov, 2020
3’ larger. 4
4 gap between fastigium frontis and fastigium verticis wide, deep . . . . *Mecopoda dilatata*
4’ gap between fastigium frontis and fastigium verticis subtle . . . . *Mecopoda divergens*

TABLE 5. Dimensions of *Mecopoda* species not belonging to the *elongata* group ([1]own data; [2]Gorochov 2020; [3]Redtenbacher 1892).

species	sex	pronotum length	tegmen length	tegmen width	hind femur length	ovipositor length
angusta[1/2]	male	7.5–8/ 6.7–7.3	57–60/51–57	13.3–14/-	42.5/38–42	
	female	7.5–9/8.2	56–74/60	14–15.7/-	40–51/45	28–33/31
kercini[2]	male	6.2	37	14	34.5	
	female					
dilatata[2]	male	8.6–9	65–70		50–54	
	female	7.8–9.6	59–77		45–58	29–33
divergens[3]	male					
	female	7	55		42.5	27.5

Mecopoda elongata group

We use the name *Mecopoda elongata* group despite some uncertainties about the identity of *M. elongata* itself, since all Indian and thus topotypical *Mecopoda* species possess the characteristic pretzel-shaped mirror on the right male tegmen (Nityananda & Balakrishnan 2006).

For the subgroups we follow the structuring proposed by Liu *et al.* 2020 (*niponensis, confracta, minor* subgroups)

Subgroup *niponensis* (Haan, 1843)

Member of this species group are characterized by wide tegmina, long files and wide mirrors compared to the *confracta* subgroup (Fig. 1), and have long-lasting, trill-like songs (see measurements in Liu Cx *et al.* 2020). In the song of many species regular changes between soft and loud parts are observed. Typical members are *M. niponensis*, *M. fallax* and *M. himalaya*. However, in morphology species of the *minor* subgroup (see below) are quite similar and can at present be separated only by the beginning of the song or by genetics (Liu *et al.* in prep).

Mecopoda niponensis (Haan, 1843)

The species can morphologically be separated from all other congeneric species by its short and wide tegmina (Fig. 5 A; see measurements in Liu Cx *et al.* 2020). Also its trilling calling song, studied in China (Liu YF *et al.* 2019; Liu Cx *et al.* 2020), Japan (Ichikawa *et al.* 2006; Yamamoto 2006) and Korea (Kim 2009), shows a characteristic amplitude modulation (see Fig. 6–7), clearly different from other *Mecopoda* species.

However, we have a specimen from Vietnam at hand in which morphology and song pattern disagree. The trilling song of this animal shows the typical *niponensis* pattern, but it has unusually long and narrow tegmina. With a length/width ratio of 3.43 it is just outside the range (2.19–3.36) given by Liu Cx *et al.* (2020) for *niponensis.* More important, the tegmen length (55 mm) is far outside the range of *niponensis* (34–49 mm, Liu Cx *et al.* 2020; 40–43 mm in Korea, Storozhenko *et al.* 2015). Since it has additional song components not known from *niponensis*, and was found outside the known range of the species, we consider it as member of a new subspecies (see below).

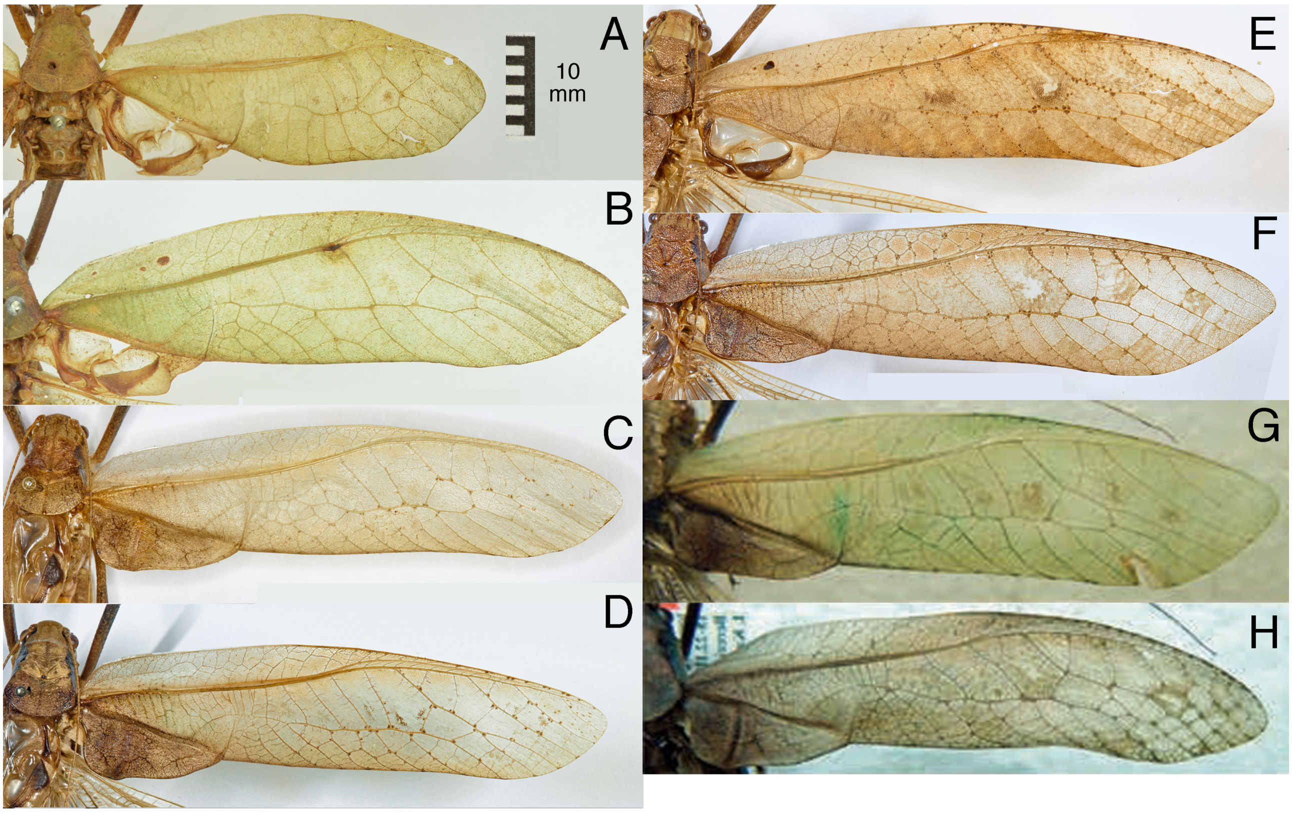

FIGURE 5. Male tegmina in selected *Mecopoda* species. **A** *M. niponensis niponensis*, lectotype, **B** *M. macassariensis*, lectotype, **C** *M. javana*, neotype, **D–H:** Species from Borneo: **D** *M. s. stridulata*, CRTmeceloM02, **E** *M. himalaya*, CRTmeceloM01, **F** *M. himalaya*, OTRmeceloS11, **G** *M. himalaya* (from Gorochov 2020: *fallax aequatorialis* **syn. nov.**), **H** *M. stridulata stridulata* (from Gorochov 2020). Right tegmen (A, B, E); left tegmen in mirror-inverted position (C–D, F–H). Scale 10 mm (for A–C only).

Mecopoda niponensis niponensis (Haan, 1843)

Lectotype male, here designated; labels (1) cotypus, (2) Museum Leiden, *L. (Mecopoda) niponensis* d. H., Det: de Haan (hand-written), (3) Museum Leiden, *Mecopoda elongata* L., det. C. de Jong, 1937. Stridulatory organs studied.

In the description of the species, de Haan (1843) obviously used a male and a female, probably both labeled as cotypes. We formally designate the male as lectotype although the female cotype seems to be lost. The stridulatory file has 116 teeth with the largest inter-tooth intervals between middle and anal third (Fig. 11–12). *M. marmorata* Liu, 2019 (Fig. 12) is similar to *M. niponensis* in file structure and basic pattern of the song (Liu *et al.* 2020), but not in genetics (Liu *et al.* 2019; Liu Cx in prep.).

Measurements (in mm): length of pronotum 7.1, tegmen length 39.1, tegmen width 15.4 (widest in the middle).

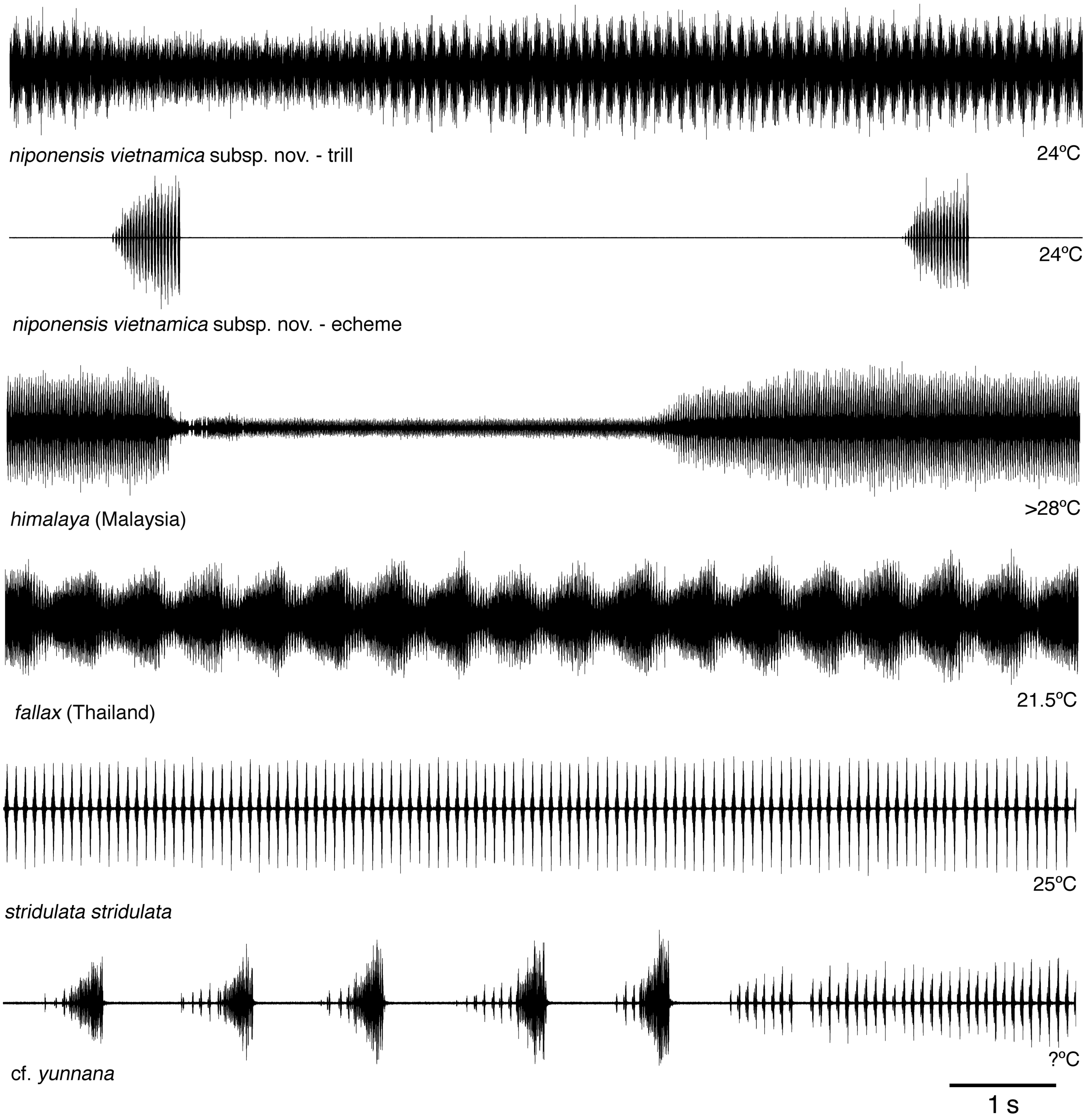

FIGURE 6. Oscillograms of the calling songs of species of the *Mecopoda niponensis* subgroup and of *M.* cf. *yunnana*. Overview (12 s sections).

Mecopoda niponensis continentalis Gorochov, 2020

Recording; male CH7674, CHINA: Yunnan, Honghe, Dai Yao Jinping Miao, Maandi (22°52'N, 103°13'E), 1900 m, 20 viii 2013, leg. Liu Chun-Xiang (song, stridulatory organs, chromosomes).

Other material (stridulatory files studied): 13 males, CHINA, Fukien (=Fujian), Kuatun (2300m) 27.40ºN, 117.40ºE, 11–15 ix 1938, leg. J. Klapperich; 1 male, CHINA, Fukien (=Fujian), Kwangtseh, 17 viii 1937, leg, J.Klapperich (ORT2002_1833-9, 1845, 1849–50, 1984; ZFMK).

For comparison with *M. n. vietnamica* **subsp. nov.**, we present an oscillogram of the song of the subspecies *continentalis* from China (Fig. 7). For the stridulatory file, see *M. n. vietnamica* **subsp. nov.** below.

Chromosomes: 2n = 27, FN = 54; pairs 1, 2 and 5–13 metacentric, 3 and 4 subacrocentric, X chromosome metacentric (Fig. 15).

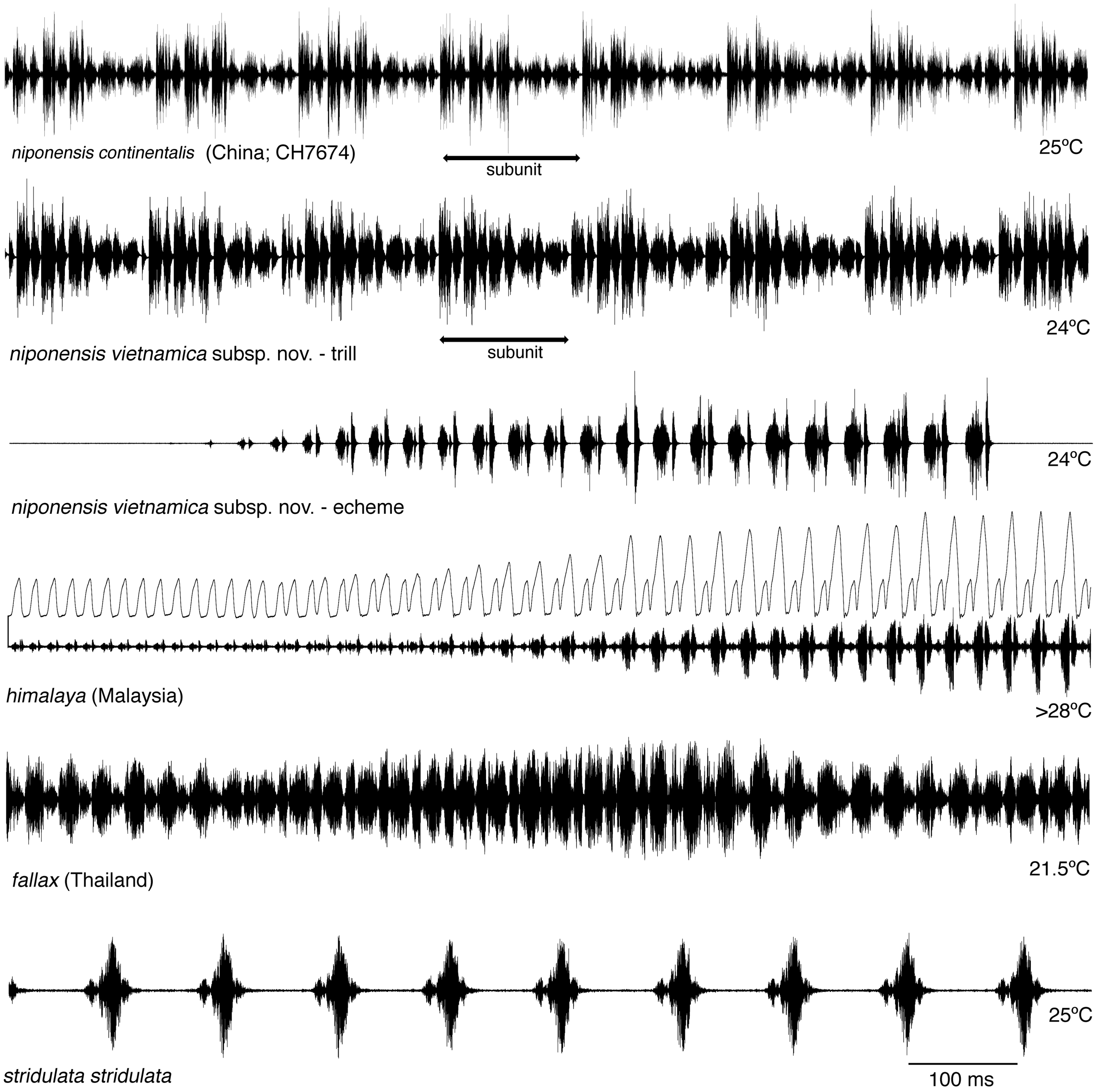

FIGURE 7. Oscillograms of the calling songs of species of the *Mecopoda niponensis* subgroup. Details (1 s sections). In *M. himalaya* synchronous registration of movement of left tegmen and sound (upper line: upward deflection indicating opening, downward closing; lower line: sound).

Mecopoda niponensis vietnamica Heller & Korsunovskaya subsp. nov.

Holotype: VIETNAM: Tân Phú District, Dong Nai, Cát Tiên National Park, 128 m a.s.l.,11°26' N, 107°26' E. 13 vi 2019, leg. N. Sevastianov. ZIN. Song and stridulatory organs studied.

Diagnosis. Differs from the nominate subspecies by longer tegmina, from other *Mecopoda* species by the characteristic amplitude modulation in the trill (see Fig. 6–7) and from the Vietnamese species *M. ampla* and *M. prominens* in file structure (see Fig. 11–12).

Morphology. As nominate subspecies, but with longer tegmina (see above).

Song. The recorded specimen had an unusually variable song containing two elements. It produced trill-like series, quite similar to the song of the continental subspecies (Fig. 6) and to that known from other parts of its range (for details see Liu Cx *et al.* 2020). These series last for many minutes and have a relatively complicated structure.

Within a song unit, the low-amplitude beginning and ending phases consist of repeated simple syllables, while the high-amplitude climax is composed of many repeated subunits. In the recorded specimen the subunits consisted of five to six syllables with a characteristic amplitude pattern (Fig. 7). In other parts of its range like Japan and Korea (*n. niponensis*) one subunit seems to have typically only three syllables (Ichikawa *et al.* 2006; Kim 2009). Besides the trills, the specimen produced also occasionally long series of echemes before the trill. In the frequency spectrum, the ultrasound components were even stronger than the peak in the audible range (Fig. 14).

Stridulatory file. Like specimens of the nominate subspecies, also the Vietnamese specimen has a long file carrying about 115 teeth (Fig. 11 B) like *M. n. niponenis*. The inter-teeth distances start anally with 50 µm and reach their maximum of about 80 µm between the 30th and 40th tooth (Fig. 12). In the file of the lectotype of *M. n. niponenis* the inter-tooth distances are slightly smaller but there is some variability in this character. The file of the *M. n. continentalis* specimen (105 teeth) photographed by Liu Cx *et al.* (2020) is similar to *M. n. vietnamica* n. ssp, but has the maximum around the 50th tooth. Another Chinese specimen of *M. n. continentalis* (Fig. 11 A; CH7674, 107 teeth) is between the lastly mentioned and *M. n. vietnamica* **subsp. nov.**, and the specimen from Fujian (*M. n. continentalis*; 115 teeth) is similar to the lectotype of *M. n. niponenis* (Fig. 12).

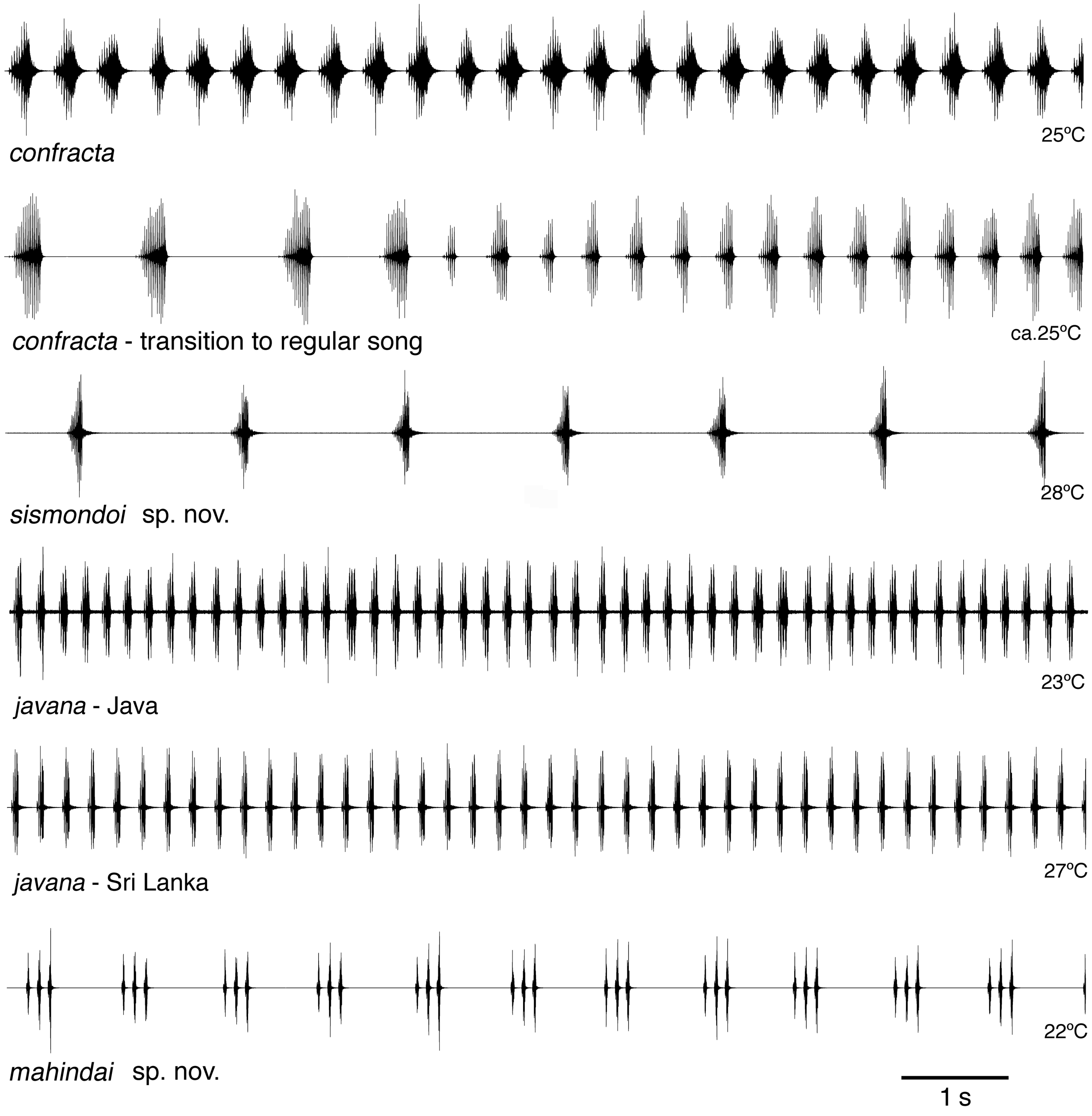

FIGURE 8. Oscillograms of the calling songs of species of the *Mecopoda confracta* subgroup. Overview (12 s sections).

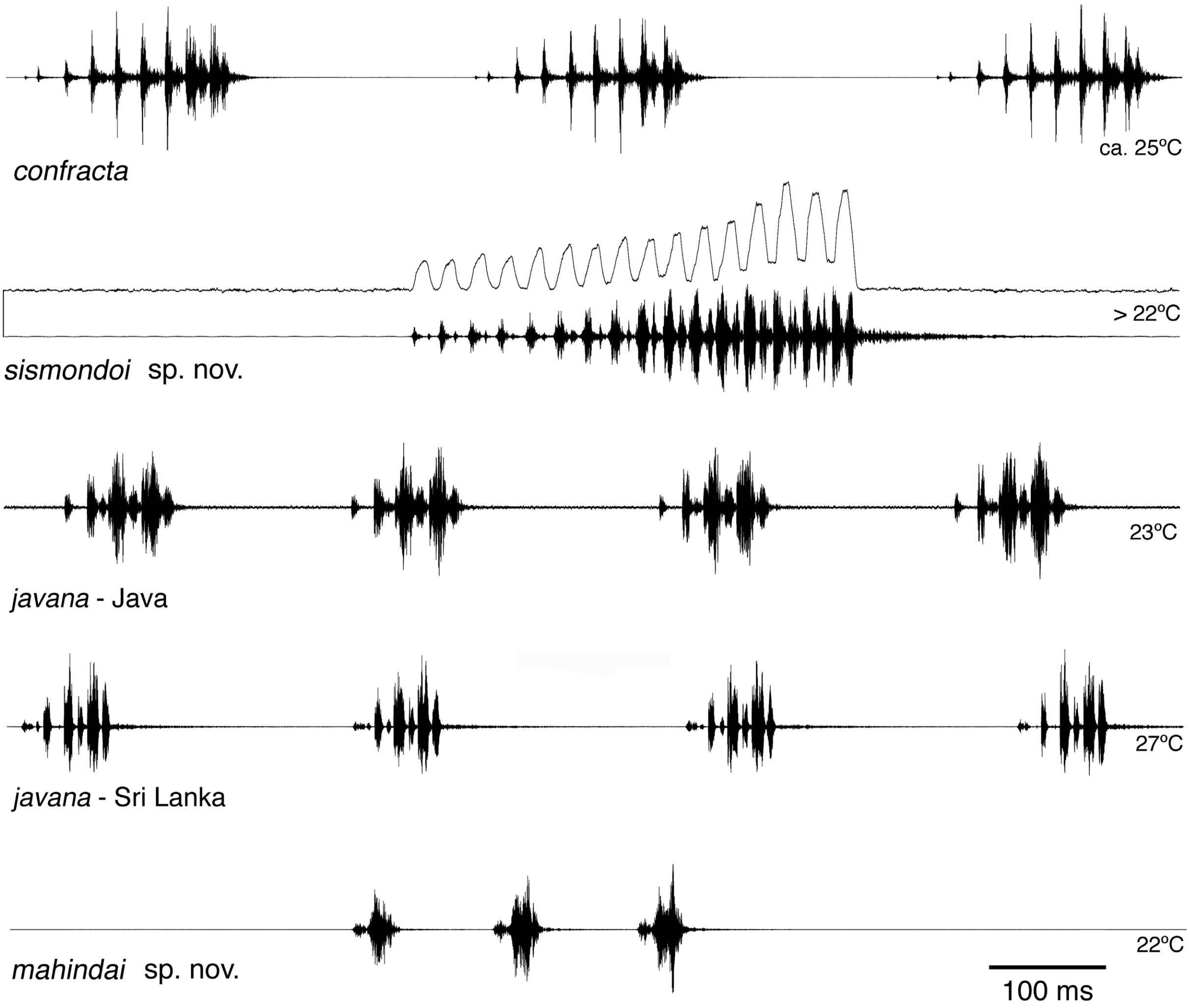

FIGURE 9. Oscillograms of the calling songs of species of the *Mecopoda confracta* subgroup. Details (1 s sections). In *M. sismondoi* **sp. nov.** synchronous registration of movement of left tegmen and sound (upper line: upward deflection indicating opening, downward closing; lower line: sound).

Distribution. Vietnam.

Measurements (length in mm). Pronotum 9.0, tegmina 55, hind femur 51.7.

Mecopoda himalaya Liu, 2020

Mecopoda ampla malayensis Gorochov, 2020 **syn. nov.**
Mecopada ampla javaensis Gorochov, 2020 **syn. nov.**
Mecopoda fallax aequatorialis Gorochov, 2020 **syn. nov.**

The species was described in 2020 from two males in Yunnan, China, but it is obviously quite widespread. Its characteristic song was first recorded in 1985 by Sismondo on Sumatra, and later by others in several localities in Thailand, Malaysia, Brunei and Indonesia (see below). Also the stridulatory file with relatively few teeth seems to be unique (but see below for the Sulawesian species *M. macassariensis*).

Song recordings and stridulatory organs: THAILAND: 3254539 (CI), Tak Ban Mae Salit, Monkrating resort (17°30'N, 98°5'E), 700–800 m a.s.l., 18 ix 1989, leg. S. Ingrisch. MALAYSIA, peninsular: CH3737, CH3740, Selangor, Ulu Gombak Field Study Centre (20 km nno Kuala Lumpur) (3°20'N, 101°45'E), 260 m, 8–28 iii 1981 and 12–19 iv 1981, leg. K.-G. Heller & M. Volleth (both songs and stridulatory organs). MALAYSIA, Sabah: CRT-meceloM01 (ZFMK), Mt. Kinabalu NP, Poring, 04.10.1993, 500–700 m a.s.l., leg. K. Riede. INDONESIA: Java:

2534643 (CI) Indonesia West Java Palabuan Ratu, Samudra beach (6°58’S, 106°30’E), 2 iii 1995, leg. S. Ingrisch. NHMUK010210933, Sumatra: Brastagi [probably Berastagi, 3° 11′N, 98° 31′E], 17 ii 1985, leg E. Sismondo.

Song only. THAILAND: 3254540 (CI) Thailand Nan Doi Phukha, guesthouse near “Pass” (19°15’N, 101°10’E), 1500 m a.s.l., 5 x 1991, leg. S. Ingrisch. INDONESIA: 3254644-5 (CI) Indonesia Java Bogor, Kebun Raya (6°35’S, 106°47’E), 250 m a.s.l., 15 ii 1995, leg. S. Ingrisch (both song). 3254541 (CI) Indonesia North Sumatra Pematang Siantar (2°59’N, 99°0’E), 400 m a.s.l., 2 iii 1993, leg. S. Ingrisch. 3254646 (CI) Indonesia West Sumatra Maninjau (0°18’S, 100°15’E), 400 m a.s.l., 13 iii 1995, leg. S. Ingrisch.

Stridulatory organs only. THAILAND: Male, Surat Thani Prov. (Malay Peninsula), ~40 km WSWof Phanom Town, environs of Khao Sok NationalPark, secondary-primary forest, 20–28 July 1996, A. Gorochov (holotype of *Mecopoda ampla malayensis*). INDONESIA: Male, “Java merid. 1500′ 1891 H. Fruhstorfer”, “104-98”, “Mecopoda elongata № 42” (holotype of *Mecopoda ampla javaensis*). Male, Indonesia, West Sumatra Prov., environs of Harau Valley National Park, equator, 24–26 November 1990, A. Gorochov (holotype *Mecopoda fallax aequatorialis;* relative mirror width 1.28).

Other material: Males CH3742, CH3489, MALAYSIA: Pahang, Krau Game Reserve (study area) bei Kuala Kerau, Kuala Lompat near Temerloh (3°43’N, 102°16’E), 28 iii–12 iv 1981 and 18–21 iii 1992, leg. K.-G. Heller & M. Volleth. Males CH3741, CH3750, CH3754, CH3755, CH3756, MALAYSIA: Selangor, Ulu Gombak Field Study Centre (20 km nno Kuala Lumpur) (3°20’N, 101°45’E), 260 m, 8–28 iii 1981 and 28 ii–24 iv 1984, leg. K.-G. Heller & M. Volleth. Seven pairs of male tegmina CH3411, CH3412, CH3413, CH3657, CH3659, CH3660, CH3691 (2) from the same localities. Females (assumed to belong to *himalaya* because of large size and green coloration): CH3743, MALAYSIA: Pahang, Krau Game Reserve (study area) near Kuala Kerau, Kuala Lompat near Temerloh (3°43’N, 102°16’E), 28 iii–12 iv 1981, leg. K.-G. Heller & M. Volleth. CH3745, CH3749, MALAYSIA: Selangor, Ulu Gombak Field Study Centre (20 km nno Kuala Lumpur) (3°20’N, 101°45’E), 260 m, 8–28 iii 1981, leg. K.-G. Heller & M. Volleth.

Literature data on song: Korsunoskaya 2008 (INDONESIA: Java), Kostarokas & Römer 2015, Krobath *et al.* 2017, Siegert *et al.* 2013 (all MALAYSIA), Liu Cx *et al.* 2020 (CHINA), Tan & Wahab 2018 (BRUNEI).

The most detailed study of the song was undertaken by Krobath (2013; Krobath *et al.* 2017) under the name ‚trilling species of the *Mecopoda* complex‘. At intervals of many minutes, the males produce calling bouts which last several minutes and start with an alternation between soft and loud trilling parts and end in a continuous long loud trill (Krobath 2013; Krobath *et al.* 2017). The stridulatory movements differ between soft and loud parts. When singing softly, the males make simple to-and-fro movements (single syllables), but during the loud part they alternate between long and short syllables (echemes), as it can be seen in the wing movement recordings (Fig. 7). Period data are given in Tab. 3. However, the males are heating up during singing by up to eight degrees (Erregger *et al.* 2017) with the effect that all time parameters may change during the song. Impulses are produced during both opening and closing of the tegmina (Fig. 7). Opening and closing hemisyllables differ slightly in spectral composition (Fig. 14).

The stridulatory file of *himalaya* has less teeth (73–98) than that of *niponensis* and *fallax* (Tab. 2, see also Fig. 12). The inter-tooth distances start anally with 60 µm and reach their maximum (between 80 µm and 100 µm) always around the 30th tooth (except one specimen from Thailand with obvious irregularities; Fig. 12).

Considering the large range, local variation in file structure as well as in mirror dimensions and other morphological structures are to be expected and do exist (see above listed synonyms). The status of these forms will be established after the relationship to *M. macassariensis* is solved.

Chromosomes (from holotype): 2n = 27, FN = 54; pair 1 metacentric, pairs 4–14 metacentric or submetacentric, 2 and 3 subacrocentric, X chromosome metacentric (Fig. 15).

Measurements (in mm): CH3737, 3740: pronotum length 9.5; tegmen length 62–65; tegmen width 15–16; hind femora length 46.0–46.5.

Mecopoda macassariensis (Haan, 1843) stat. rev.

Holotype male, RMNH.INS.1256442 (Indonesia, Sulawesi, Makassar). NBC.

From its broad mirror area (length/width = 1.44), the species belongs to the *niponensis* subgroup. In tooth number (93) and inter-tooth distances it is very similar to *M. himalaya* (Fig. 11, 12). Since *M. himalaya* is quite widespread, both names could refer to the same species with *macassariensis* having priority.

However, even species with quite similar files can have very different songs (see below; *M. fallax* and *M. s. stridulata*). Since wrong combining is more difficult to restore than wrong splitting, we remain on the safe side and consider at the moment *M. macassariensis* as a species endemic to Sulawesi. Data on its song are urgently needed.

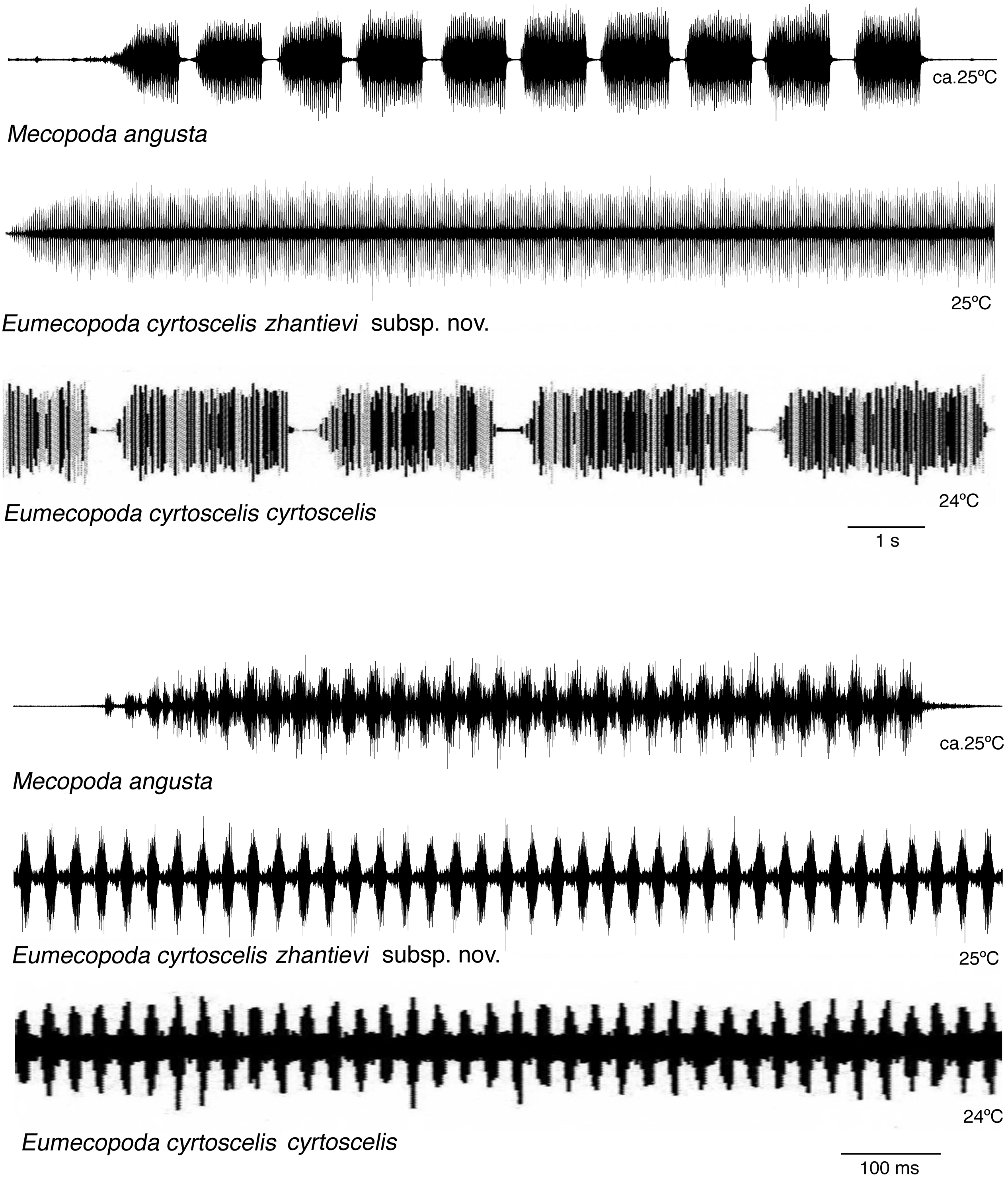

FIGURE 10. Oscillograms of the calling songs of *Mecopoda angusta* and *Eumecopoda cyrtoscelis*. Overview (12 s sections) and details (1 s sections). Figures of *Eumecopoda c. cyrtoscelis* based on figures in Helfert & Sänger (2007), all sound recordings the figures are made from seem to be lost (Römer, email 2019/10/23).

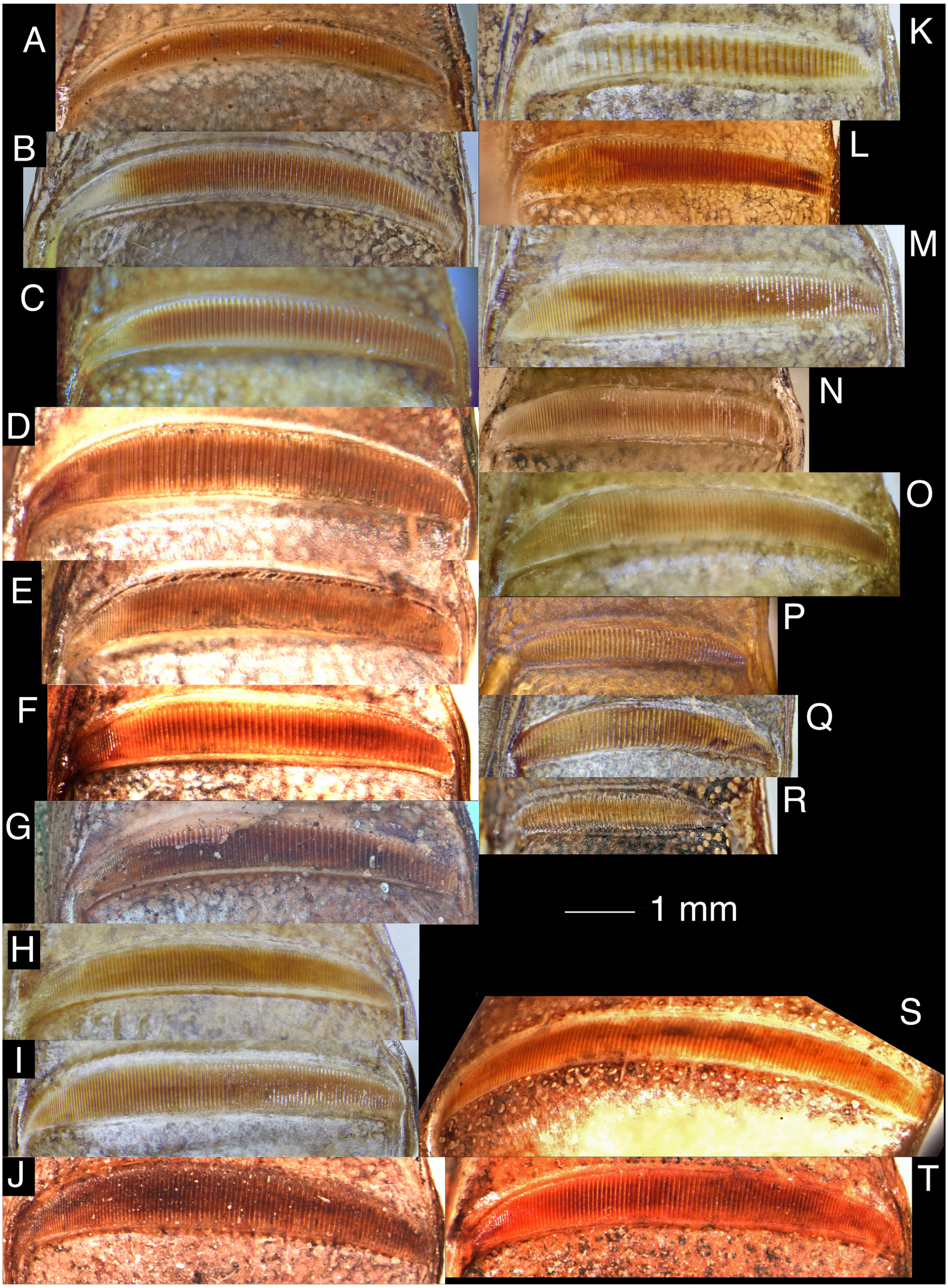

FIGURE 11. Stridulatory files in *Mecopoda* and *Eumecopoda*. **A** *M. niponensis niponensis,* lectotype, **B** *M. niponensis vietnamica* **subsp. nov.**, holotype, **C** *M. himalaya*, CH3737 (Malaysia), **D** *M. himalaya* (=*M. ampla malayensis*, holotype), **E** *M. himalaya* (=*M. ampla javaensis*, holotype), **F** *M. himalaya* (=*M. fallax aequatorialis, holotype), ***G** *M. macassariensis*, holotype, **H** *M. fallax*, Thailand, **I** *M. stridulata stridulata*, CRTmeceloM02 (Borneo), **J** *M. stridulata stridulata,* holotype, **K** *M. paucidens* **sp. nov.**, (Java), **L** *M. sismondoi* **sp. nov.**, holotype, **M** *M. javana*, neotype, **N** *M. javana,* Sri Lanka, **O** *M. mahindai* **sp. nov.**, holotype, **P** *M. angusta*, CH3697, **Q** *M. dilatata*, ORT 2005/413 (Borneo), **R** *E. cyrtoscelis zhantievi* **subsp. nov.**, holotype, **S** *M. prominens,* holotype, **T** *M. ampla ampla,* holotype. Scale 1 mm.

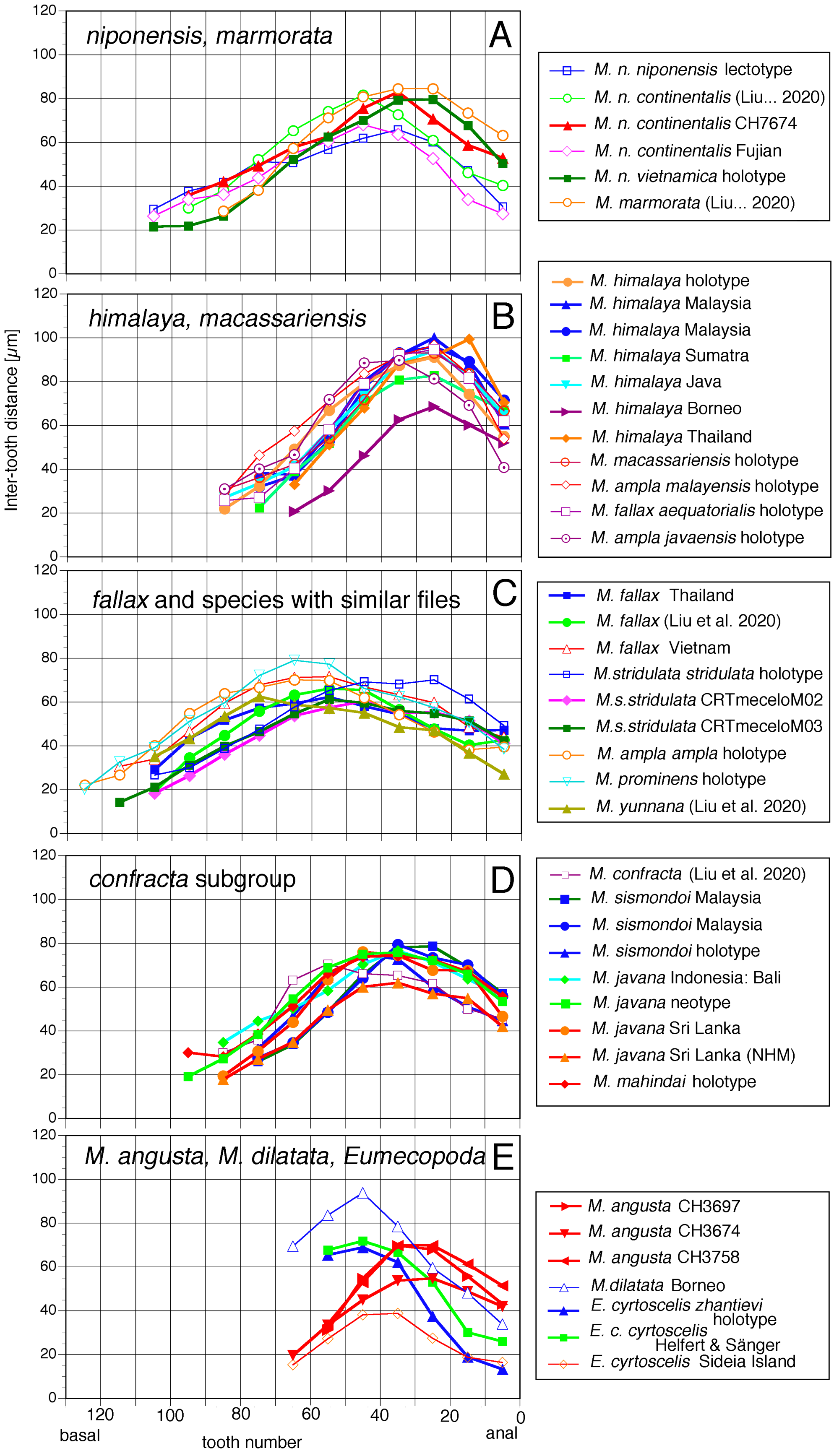

FIGURE 12. Inter-tooth spacing in stridulatory files of *Mecopoda* species. Thick lines and filled symbols indicate specimens with known song. **A–D:** *M. elongata* group: **A** *M. niponensis* subgroup and *M. marmorata* , **B** *M. himalaya* and *macassariensis,* **C** *M. fallax* and species with similar files, **D** *M. confracta* subgroup, **E** other *Mecopoda* and *Eumecopoda* species.

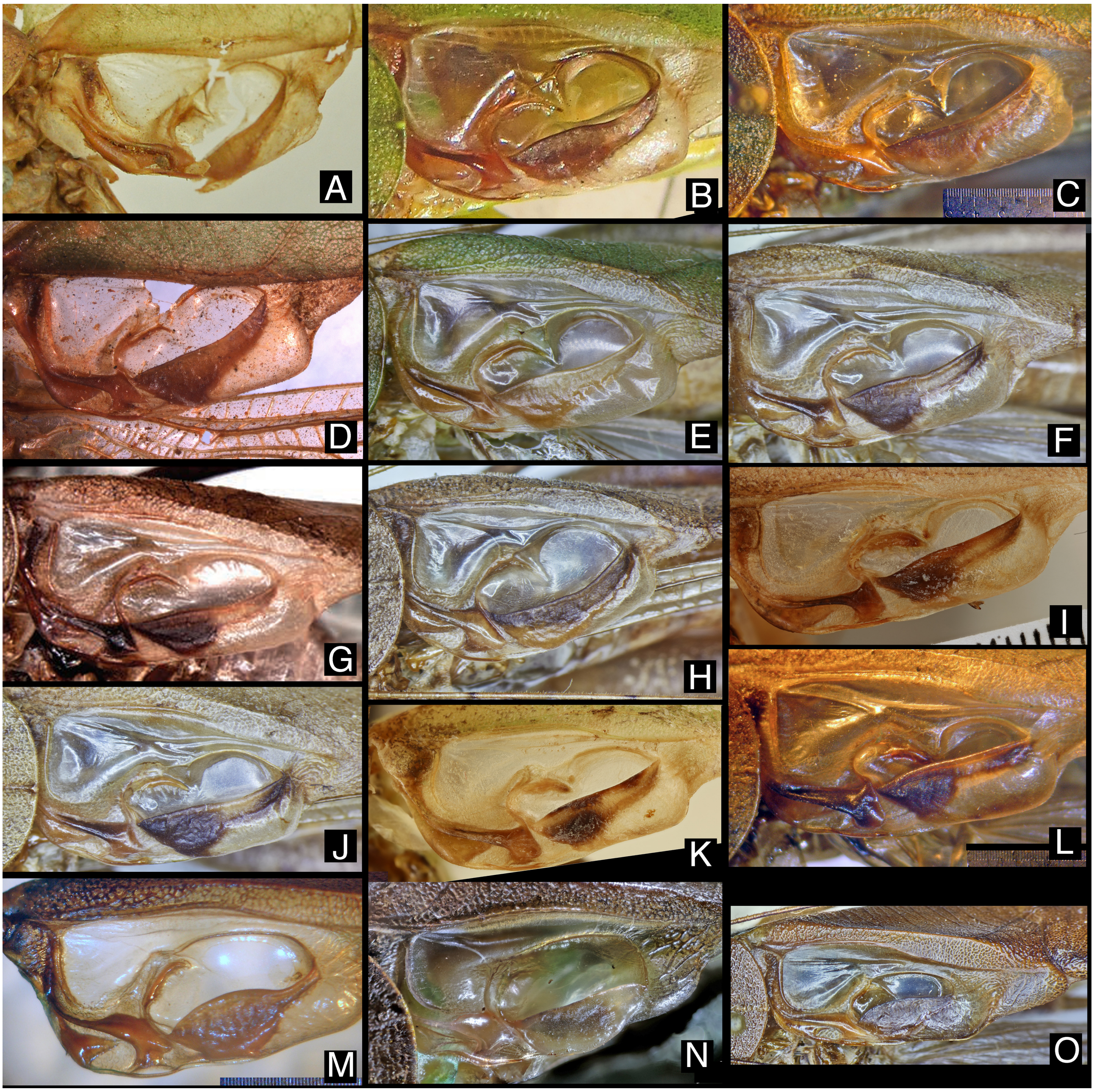

FIGURE 13. Mirror area in the right male tegmen of *Mecopoda* and *Eumecopoda* species. **A–K:** *elongata*-group: **A–G** *niponensis*-subgr.: **A** *M. niponensis niponensis*, lectotype, **B** *M. niponensis vietnamica* **subsp. nov.**, holotype, **C** *M. himalaya,* Malaysia (CH3737), **D** *M. macassariensis*, holotype, **E** *M. fallax*, Thailand (CI 3254538), **F** *M. s. stridulata* (CRTmeceloM02), **G** *M. s. stridulata* (from Gorochov 2020), **H** *niponensis*-subgr.?: *M. paucidens* **sp. nov.**, Java; **I–L:** *confracta*-subgr.: **I** *M. sismondoi* **sp. nov.**, holotype, **J** *M. javana*, neotype, **K** *M. javana*, Sri Lanka, **L** *M. mahindai* **sp. nov.**, holotype; **M** *M. angusta, (*CH3674), **N** *Eumecopoda cyrtoscelis zhantievi* **subsp. nov.**, **O** *M. dilatata*, Borneo.

Mecopoda fallax He, 2019

Recordings: THAILAND: 3254538 (CI), Phetchabun, Nam Nao 1000 m a.s.l., 13 ix 1989, leg. S. Ingrisch (song and stridulatory organs). MALAYSIA: CHX066, MALAYSIA: Pahang, Krau Game Reserve (study area) bei Kuala Kerau, Kuala Lompat near Temerloh (3°43'N, 102°16'E), 28 iii–12 iv 1981, leg. K.-G. Heller & M. Volleth (song only). VIETNAM: one specimen from Vinh Phu, Hoa Binh and Gia Lai Provinces, leg. A. Gorochov; stridulatory file only.

The species was described from China (Liu Yf *et al.* 2019, Liu Cx *et al.* 2020), but is obviously more widespread.

The long lasting trilling song of *M. fallax* (Fig. 6) is composed of quite short song units (less than one second) which are repeated without intervals. Within these units regular changes in amplitude are observed (Fig. 7). The duration of one unit was 0.3–0.8 s in China (T=24–29ºC; Liu Yf *et al.* 2019, Liu Cx *et al.* 2020), 0.7 s in Thailand (T=21.5ºC) and 0.2 s in Malaysia (T=27ºC).

M. fallax has a long stridulatory file carrying about 110 teeth (Fig. 11 E). Concerning the inter-tooth distances, the file is relatively homogenous. The distances start anally around 40–50 µm, reach the maximum at about 60–70 µm and become smaller than 40 µm only very near to the articulation (Fig. 12).

It will be interesting to study the songs and the relationships between the two Vietnamese species *M. prominens* and *M. ampla* and the widespread *M. fallax*. All three have with quite similar files (Figs. 11–12) and occur in Vietnam.

Mecopoda stridulata stridulata Gorochov, 2020

Recordings: male, ZFMK CRTmeceloM02, MALAYSIA, Sabah, Mt. Kinabalu NP, Poring, [6⁰03' N, 116⁰43'E], 07 vi 1993, 500–700 m a.s.l., leg. Hoffmann. Song and stridulatory organs studied. Male, ZFMK CRTmeceloM03, 9 vi 1993, other data as before. Song and stridulatory organs studied.

Other specimens studied. All MALAYSIA, Sabah (Borneo): 1 male (3261450), Kota Kinabalu, 9.viii.1984, (secondary vegetation), CI [additional label "Stridulation = gleichmässiges Zwitschern" (stridulation=uniform chirping)]. 3 males, OTRmeceloS15-17 (ZFMK), Matunggong, 19 viii 1992, coll. K. Riede.

Our specimens were identified on base of male 3261450 which has a file in structure nearly identical to that of the holotype of *Mecopoda stridulata stridulata.* The song of this specimen was described as ‚uniformly chirping' fitting well to the recordings mentioned above. The specimens with this song, however, differ slightly in file structure.

Song. The long lasting calling song (recording of M2 lasting 136 s, of M3 89 s) consists of single isolated syllables, produced with an SRR of 8.3 Hz (Figs. 6–7; T = 20ºC). Within the syllable, a short (10 ms) and soft part is followed by a much louder and longer (20 ms) part. This second part had a resonant structure with the strongest component sweeping upwards from 7.3 to 8.3 kHz. The fundamental at 2.5 kHz was clearly visible, but the second strongest harmonic was at 10 kHz.

Additional description. Morphologically the Bornean species differs from *M. himalaya* by the following, although weak, morphological characters: the pair of teeth at the end of the male cercus are of nearly identical size and are clearly spaced from each other instead of having the apical tooth markedly larger than the preapical tooth and both teeth inserted rather close to each other. Further on, the styli at tip of the male subgenital plate are thin and short but less shortened than in the latter species.

Male cerci not very stout at base, narrow apical area little curved mediad and provided at end with two small acute teeth of rather equal size that are markedly spaced from each other (Fig. 3 L–O). Stridulatory file long (5.0–5.8 mm), with about 106–126 teeth. Subgenital plate moderately wide, narrowed from base towards midlength; divided into two lobes in apical area; apical incision about 0.26–0.28 times the length of the subgenital plate; styli short and thin. There are brown and green color variants.

Remarks. From the dimensions of the stridulatory organs the species belongs to the *Mecopoda* subgroup *niponensis.* It differs in song clearly from all other species of the subgroup and also from *M. yunnana* by producing very short song units (single syllables), separated by short silent gaps from the preceding and following syllables (Figs. 6–7). Concerning the inter-tooth distances, the file is relatively homogenous (Figs. 11 F, 12) like that of *M. fallax* and *M. yunnana* [using fig. 5l (*M. minor*) in Liu *et al.* 2020 for comparison instead of the smaller fig. 5m (*M. yunnana*) following the description of the sizes in the text]. The distances start anally at around 40–50 µm, do not exceed about 70 µm in the middle of the file and become smaller than 40 µm only near to the articulation (Fig. 12). In song, *M. s. stridulata* differs clearly from *M. fallax*, but its SRR is quite similar to the rhythm in the trill phase of *M. yunnana*. *M. yunnana*, however, seems to produce fast syllable groups (Liu Cx *et al.* 2020). Further bioacoustic and genetic studies have to confirm that *M. s. stridulata* really belongs to the *niponensis* subgroup.

Measurements (5 males). Body w/wings: male 61–66 (63.8±2.3); body w/o wings: male 27–34 (29.8±2.7);

pronotum: male 6.5–8.5; tegmen: male 45–54 (50.8±3.4); hind femur: male 40–43; tegmen width: male 12–13 (12.2±.4) mm.

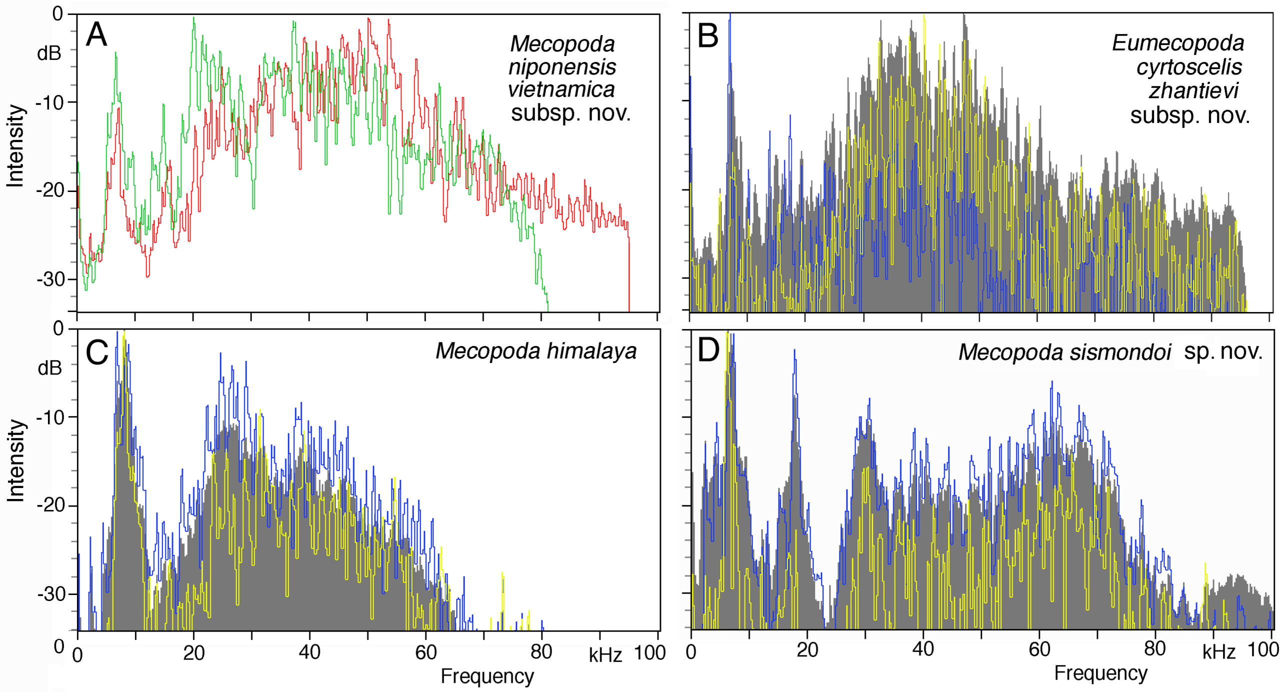

FIGURE 14. Power spectra of the calling songs of *Mecopoda* species. In A, red line trill, green line chirp; in B–D, grey area opening and closing hemisyllable together, blue line opening hemisyllable only, yellow line closing hemisyllable only (for *Eumecopoda* opening/closing assumed).

Subgroup *confracta* Liu, 2020

According to Liu Cx *et al.* (2020), the species of this group „have mediate-width long tegmina, comparatively short files and the narrowest mirror. The file is widest in basal quarter, from which teeth are gradually narrower toward both ends. The songs are discontinuous and each song unit consists of numerous simple syllables“. The authors included the two newly described species *Mecopoda confracta* and *M. synconfracta* sp. n. (China), but listed also *Mecopoda*_“S” (Malaysia) with song and file data and *Mecopoda*_“N” (Bali) (Sismondo 1990) as group members. In addition and based on file structure, they added an unidentified *Mecopoda* species from Vietnam and an otherwise undescribed ‚*Mecopoda elongata*‘ from India. From song structure also the „chirper“ in Nityananda & Balakrishnan (2006) belongs to the group. In our material specimens with a ratio larger than 1.5 (length/width of mirror area) always belonged to the *confracta* subgroup.

Among this material there are at least three forms which differ clearly in song pattern from the previously described ones and from each other. Their songs differ mainly in three parameters, in echeme repetition rate (echeme period), in syllable repetition rate (syllable period) and in the number of syllables per echeme. For comparison, we present also data on the song of the Chinese species *M. confracta* (Tab. 4).

Concerning the structure of the stridulatory file, all species of the subgroup are relatively similar (Figs. 11 H–K, 12).

Mecopoda confracta Liu, 2020

Recording: CHINA, Yunnan, Jin Ping, 23 viii 2013, leg. K-G Heller & Cx Liu (paratype CH7680, collected as nymph)

For comparison, we present oscillograms of the song of this Chinese species (Figs. 8, 9) in the same scale as the other species. The recorded male typically started to sing with isolated echemes, changed to a slow and irregular rhythm and switched (Fig. 8) to the species-specific fast echeme repetition rate only after some minutes. For detailed data of the song of the species see Liu Cx *et al.* (2020).

Mecopoda sismondoi Heller sp. nov.

Holotype: male, labels: (1) Singapore [1°17′ N, 103°50′ E] 84 A, (2) Brit. Mus. 1985-242, (3) Molted to adult 28 I 84 gassed on 9 VI 84, (4) COLLECTED BY E. SISMONDO (5) SONG-RECORDED (6) The stridulation of this specimen has been recorded. Tape No. 568 Recording No 1, (7) NHMUK010210931. NHM. Song and stridulatory organs studied.

Paratypes; males CH3746, MALAYSIA: Selangor, Ulu Gombak Field Study Centre (20 km nno Kuala Lumpur) (3°20'N, 101°45'E), 260 m, 8–28 iii 1981, leg. K.-G. Heller & M. Volleth (song and stridulatory organs). CH3738, MALAYSIA: Selangor, Ulu Gombak Field Study Centre (20 km nno Kuala Lumpur) (3°20'N, 101°45'E), 260 m, 12–19 iv 1981, leg. K.-G. Heller & M. Volleth (song and stridulatory organs) (all CH).

Other material: Male CH7704, SOUTH EAST ASIA, exact locality unknown, obtained from breeder, 2013 (song, stridulatory organs, chromosomes). Males CH3751, CH3645, CH3739, MALAYSIA: Selangor, Ulu Gombak Field Study Centre (20 km nno Kuala Lumpur) (3°20'N, 101°45'E), 260 m, 12–19 iv 1981 and 28 ii–24 iv 1984, leg. K.-G. Heller & M. Volleth. Six pairs of male tegmina CH3656, CH3663, CH3666, CH3687, CH3688, CH3690 from the same locality.

The song of the species is described by Sismondo (1990) (SINGAPORE; as species S), by Korsunoskaya (2008) (INDONESIA: Sumatra) and by Hartbauer *et al.* (2006; 2012) (MALAYSIA).

Diagnosis. The species has a much slower echeme repetition rate than the other species of the subgroup (echeme periods about 3 s; Tab. 4).

Description. Morphologically no difference to other species of the *M. confracta* subgroup (Liu Cx *et al.* 2020).

Measurements (in mm): CH3738, 3746: pronotum length 8.0–8.7; tegmen length 55–57; tegmen width 13; hind femora length 42.0–44.5.

In peninsular Malaysia, the species is often found syntopically with *M. himalaya* (our data, Tan & Kamaruddin 2016). It is typically a little bit smaller than *himalaya* and often brown, whereas *himalaya* is more often green.

Chromosomes: 2n = 29, FN = 52; pairs 1 metacentric and 4–7, 9, 10, 12–14 metacentric/ submetacentric, 3 subacrocentric, 2, 8 and 11 acrocentric, X chromosome submetacentric (Fig. 15).

Derivatio nominis. Named in honour of Enrico Sismondo who discovered the song diversity of *Mecopoda,* collected and recorded the type specimens of *M. sismondoi* and analyzed and described the signal interactions in that genus (Sismondo 1990).

Mecopoda javana (Johansson, 1763) stat. nov.

Gryllus javanus Johansson, 1763
Mecopoda maculata Serville, 1831 syn. nov

Neotype, here designated: male, INDONESIA, West Java, Palabuan Ratu, Samudra beach, (6°58'S, 106°30'E), 3–6 iii 1995, coll. S. Ingrisch (CI 3261437 in ZFMK). Song and stridulatory organs studied.

The need to clarify the status of *M. javana* comes from observations showing that in South East Asia many morphologically similar species exist (see above) formerly united under the name *M elongata*. To secure nomenclature stability the status of the old names has to be clarified. *M. javana* has priority over *M. maculata* Serville, 1831, a species with type locality also on the island of Java and assumed to belong to the same species.

Qualifying conditions for neotype designation according to Art. 75.3.1–7 of the ICZN (1999):
1. The neotype is designated to clarify the taxonomic status of the species *M. javana*.
2. See diagnosis, description and bioacoustical data below.
3. See data of neotype
4. After the description, the holotype of the species was obviously never seen nor studied by any scientist. The author Johansson was a student of Linnaeus. The specimen, however, is not in the collection of the Linnean Society (Marshall 1983) nor in Uppsala (Catalogue UUZM). 80 years after the description, the species was mentioned again by de Haan (1843) who considered all specimens of the *Mecopoda elongata* group from South East Asia and China as belonging to this species except his new *macassariensis* and *niponensis*. Redtenbacher

(1892) and Karny (1920, 1924) considered all three as belonging to *M. elongata*. There is no indication that any of these orthopterologists had seen the type.

5. From Java at least two biological species (song types) are known, the mostly green species *M. himalaya* with a trilling song (see above) and a mostly brown species producing chirps (echemes). Since *M. javana* is described as greyish-brownish (cinereus, fuscescens) we considered the chirping species as *javana* and select a specimen with this song type as neotype.
6. The neotype comes from Java, the type locality (no further details given).
7. The neotype is deposited in Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFKM).

Other material. 3 males, INDONESIA, West Java, Palabuan Ratu, Samudra beach, (6°58'S, 106°30'E), 3–6.iii.1995, 3261432, 3261435, 3261436 (stridulatory organs studied), coll. S. Ingrisch (CI). Male, labels: (1) INDONESIA, Bali, Nusa Dua, [8° 48′ S, 115° 13′ E], 27.XII.1987, E. Sismondo, B.M. 1989-38, (2) MECOBA 2, (3) The stridulation of this specimen has been recorded. Tape No. 711 Recording No 3, (4) NHMUK010210932; (song and stridulatory organs).

Additional song recordings of two other males in bio.acousti.ca from Bali, Nusa Dua, made by Sismondo (species mentioned by Sismondo 1990 as species N) and from two males (specimens not collected) Ingrisch 3254649–50 (from type locality).

Other material from outside Indonesia. Male, labels: (1) SRI LANKA, Sinharadja Forest, III 1980, leg. K. Sänger & B. Helfert, B.M.1981-464, (2) kept in captivity killed 27 viii 1981, (3) The stridulation of this specimen has been recorded. Tape No. 400 Recording No, (4) NHMUK010210934 (Song and stridulatory organs). Male CH7725, SRI LANKA: Weddagala (near Rock View Hotel) (6°33'N, 81°20'E), 10 iii 2014, leg. K.-G. Heller, (song, stridulatory organs, chromosomes).

Diagnosis. The calling song of the species has a distinctly lower number of syllables per echeme than the other species of the group except *mahindai* (see below) and a higher echeme repetition rate than most other species of the group (Tab. 2). *M. javana* (specimen from Sri Lanka) has also a chromosome number (2n = 23) lower than known from any other species of the genus.

Description. General habitus of the genus.

Specimens collected in Java of brown color. Male cerci not very stout at base, narrow apical area moderately curved with internal apical tooth larger and stouter than pre-apical tooth. Subgenital plate with moderately long styli (longer than in "P. Ratu green" = *M. himalaya*).

Morphologically the new species differs from *M. himalaya*-group that occurs in Palabuan Ratu (South coast of Java) in the same locality by structure of the mirror and song, by the apical teeth of the male cerci arising from the end of the internal margin of the cercus. These teeth are moderately spaced and the apical tooth is stouter and larger than the pre-apical tooth, while in *M. himalaya*-group from Java arises nearly fully from the apical margin, the apical tooth is slightly less stout (than in *M. himalaya*), both teeth are closer together, and by the styli of the male subgenital plate that are although short longer than in *M. himalaya*-group (Fig. 2) and by the brown instead of mostly green color.

Song. The calling song consisted of long (from a few seconds to more than one and a half minute documented) sequences of echemes (Fig. 8, 9; parameters Tab. 4)

Measurements. 4 males, Java: Body w/wings: male 66–70 (67.3±1.9); body w/o wings: male 36–38 (37.3±1); pronotum: male 8.9–9.0 (9.0±0.1); tegmen: male 55–58 (56.6±1.6); hind femur: male 42–46 (43.4±1.9); anterior femur: male 10; tegmen width: male 13.0–15.2 (13.9±.9) mm. Male CH7725, Sri Lanka: pronotum 8.5; tegmen length ca. 50 (slightly damaged); tegmen width 12; hind femur 39 mm.

Literature data on song: Korsunoskaya 2008 (CAMBODIA)

Specimens with this song type have been found in two widely separated areas, in South East Asia (in several Indonesian islands and in Cambodia and Thailand; see below) as well as in Sri Lanka without obvious differences in morphology.

Chromosomes (CH7725): 2n = 23, FN = 46; pairs 1 and 4–11 metacentric, 2 and 3 subacrocentric, X chromosome metacentric (Fig. 15)

Based on chromosome number (see Discussion), a female from Thailand (Luanpirom *et al.* 1999) may also belong to this species. Uvarov (1927) mentions *Mecopoda elongata* from Sri Lanka (Museum Colombo); these specimens may either belong to *M. javana* or to *M. mahindai* **sp. nov.** (see below).

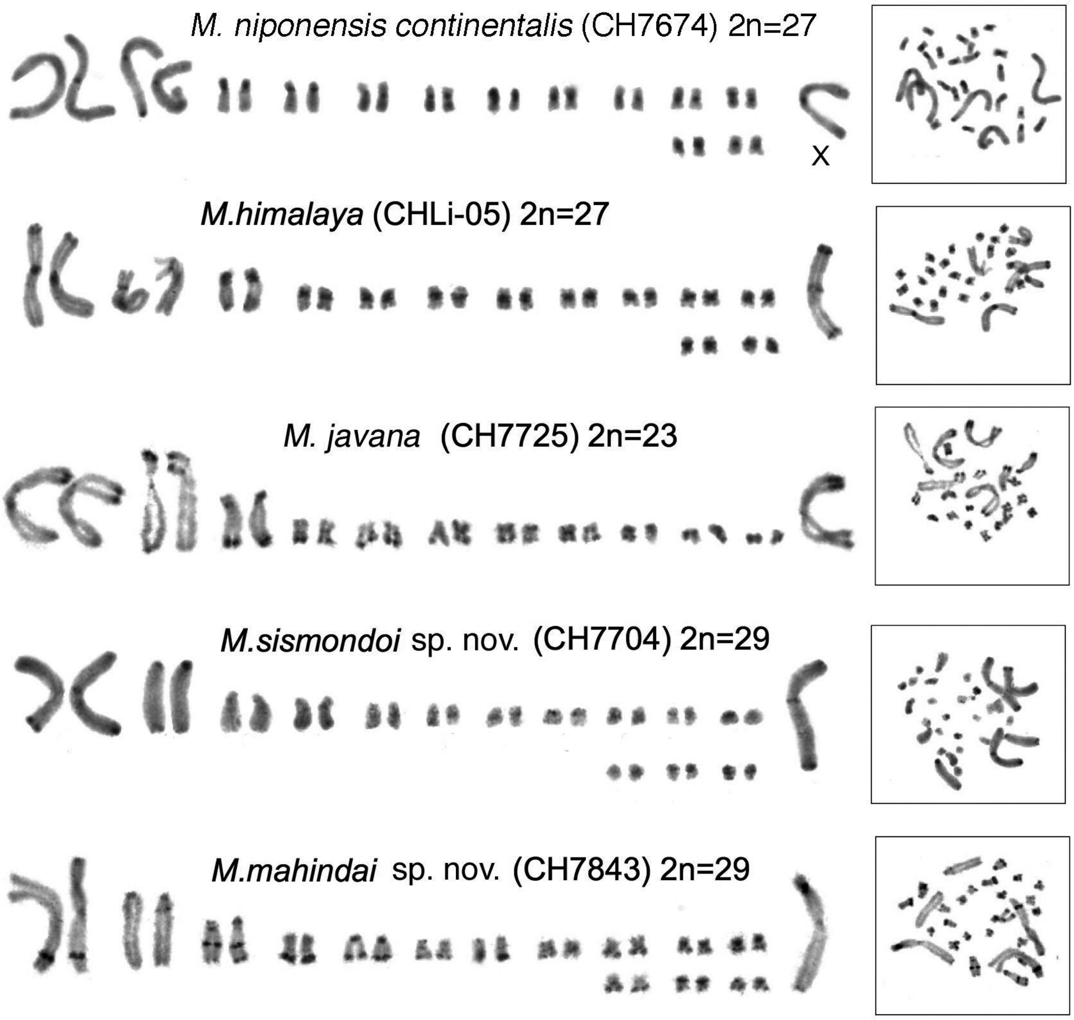

FIGURE 15. C-banded karyotypes (left side) and mitotic metaphase (right side) of five *Mecopoda* species with different chromosome number (2n). Karyotypes are reconstructed by arranging homologous chromosomes in order of decreasing size. X, sex chromosome.

Mecopoda mahindai Heller sp. nov.

Holotype male CH7843, SRI LANKA: Mihintale (8°21'N, 80°31'E), 100 m, 4 iii 2014, leg. K.-G. Heller. MfN. Song, stridulatory organs and chromosomes studied.

Diagnosis. The calling song of the species does not consist of a homogenous sequence of echemes as in all other known species of the group, but the very short echemes are grouped in small series of three echemes separated from the next series by a larger interval (Fig. 8, 9).

Description. Morphologically no difference to other species of the *M. confracta* subgroup (Liu *et al.* 2020).

Measurements (in mm): pronotum length 8; tegmen length 56; tegmen width 13.5; hind femora length 43.

Chromosomes: 2n = 29, FN = 52; pairs 1, 4 and 6–14 metacentric, 2, 3 and 5 acrocentric, X chromosome metacentric (Fig. 15).

Derivatio nominis. Name remembering to the Indian monk Mahinda who arrived in Mihintale, the type locality, according to religious myths traveling through the air, founding Buddhism in Sri Lanka. The insect was found on the stupa which was built to celebrate this event. Substantive in genitive.

Subgroup *minor* Liu, 2020

The species of this group are characterized by a complicated song „constituted by numerous discontinuous chirps at the beginning followed by continuous syllables" (Liu *et al.* 2020).

Included species and subspecies: *M. minor* (East Asia), *M. yunnana* (China; see below), *M. hainanensis* He, 2019 (China).

Mecopoda yunnana Liu 2020, stat. nov.

Mecopoda cf. yunnana

Unfortunately, we did not find specimens of this group for our study, but in bio.acousti.ca is a recording from Myanmar [probably from the city of Taunggyi (20° 47'N, 97° 02'E), as spoken in the recording] with the typical group-specific pattern (Fig. 6). It was made by Sismondo in 1985, but the corresponding specimen could not be localized in NHM.

In this recording the syllable repetition rate is ca. 12 Hz in the trill and 50 Hz in the chirp (recording temperature unknown). *M. minor minor* has 33 Hz in the trill (20–40 Hz in Liu Cx *et al.* 2020) and 60 Hz in the chirp (Liu Cx, unpublished), whereas *M. minor yunnana* shows a rhythm of 12.5 Hz (8–11 Hz; 14–18ºC; Liu *et al.* 2020) in the trill (possibly from syllable groups; no data for chirp).

The song of Sismondo's specimen is thus quite similar to that of *yunnana*, not surprising considering the proximity of the collecting localities. Compared to *minor minor*, however, the SRR during the trill is much slower, but similar during the chirp. The song differences between the subspecies thus cannot result from different temperatures, but are species-specific characters large enough to consider *yunnana* as a separate species.

Mecopoda species not belonging to the *M. elongata* group (ungrouped)

Mecopoda angusta Gorochov, 2020

Recordings: MALAYSIA: CH3697, Negeri Sembilan, Pasoh Forest Reserve (near Simbang Pertang north of Kuala Pilah) (2°57'N, 102°15'E), 29–31 iii 1992, leg. K.-G. Heller & M. Volleth (song and stridulatory organs), in ethanol, IZCAS. CH3674, Selangor, Templer Park near Kuala Lumpur (3°17'N, 101°39'E), 19 iii 1984, leg. K.-G. Heller (song and stridulatory organs), in ethanol. Male CH3758+CHX071, Selangor, Ulu Gombak Field Study Centre (20 km nno Kuala Lumpur) (3°20'N, 101°45'E), 200 m, 28 ii–24 iv 1984, leg. K.-G. Heller & M. Volleth (stridulatory organs). Song CHX071, same data, animal not collected.

Other material: Females. MALAYSIA: CH3744, Selangor, Ulu Gombak Field Study Centre (20 km nno Kuala Lumpur) (3°20'N, 101°45'E), 260 m, 8–28 iii 1981, leg. K.-G. Heller & M. Volleth. CH3790, same locality, 4 iii–5 iv 1992, leg. K.-G. Heller & M. Volleth.

Material used for comparison. *Mecopoda dilatata* Redtenbacher, 1892. Type series with three males under *M. dilatata* Redtb., 13846, Borneo, all NMW. Holotype male, labels: (1) type, (2) *Mecopoda dilatata* Redt, det. Redtenbacher, (3) Coll. Br. v. W. Borneo Grabovsky, (4) 13846, (5) II 13846. Second male from type series without labels. Third male with label Borneo. Male, labels (1) *Mecopoda dilatata* Redtenbacher, 1892 det. S. Ingrisch 1994, (2) SABAH Poring 15 IV 1991, leg K. Riede, (3) DORSA ORTmecdilS01 (4) Museum Koenig ORT 2005/413.

Mecopoda divergens Redtenbacher, 1892. Holotype female, NMW, labels: (1) *Mecopoda divergens* det. Redtenbacher, (2) Coll. Br. v. W. Indien Türk, (3) 2635, (4) 12 2635. Male, NMW, labels: (1) *Mecopoda divergens* det. Redtenbacher, (2) Coll. Br. v. W., (3) Java occident. Pengalengan, 4000' 1893 H. Fruhstorfer, (4) 20 286.

Within *Mecopoda*, *M. angusta* does not belong to the *elongata* group s.l. because the apex of the vertex is not rounded as in the *elongata*-related forms, but transversely and bluntly carinate. The fastigium verticis is met from below by a broad fastigium frontis, leaving a distinct gap in between (Fig. 16). These characteristics are shown by *M. dilatata, M. divergens* and *M. platyphoea* Walker, 1870 and probably also by *M. kerinci* (no information given in Gorochov 2020). From *M. dilatata, M. angusta* can be easily discriminated by its special subgenital plate. *M. divergens*, however, was known only by the female holotype with unknown origin. Fortunately it turned out that

Redtenbacher obtained and identified also a male collected one year (1893) after his description of the female. It has the typical mecopodine fork-like subgenital plate (Fig. 17). Finally, *E. platyphoea* (see under *Eumecopoda*) from Sri Lanka, known only from the brown female type and, after Kirby (1891), a green male, has broader tegmina and a shorter, thicker ovipositor than *M. angusta* (Fig. 18). It also has spines on the fore femora („Fore femora with three spines in one row towards the tips" Walker 1870) missing in *M. angusta*. The females from Pakistan, described under *M. platyphoea* by Panhwar *et al.* (2016), differ widely in the species-specific characteristics (see their figures 1a,c,e) and do not belong to this species. For other morphological details see Fig. 20.

Stridulatory vein with 59–73 teeth (Fig. 11 M; inter-tooth distances see Fig. 12).

Song. The calling song of *M. angusta* consists of series of 7–18 echemes (trill segments), each series (trill) lasting about 10 –15 s. The echemes had durations of 0.7–1.3 s with SRRs between 30 and 40 Hz (Fig. 10; Tab. 7). In the echeme structure the song is similar to that of *Eumecopoda c. cyrtoscelis* (Helfert & Sänger 2007; see below), but not to any known in *Mecopoda*.

M. angusta was known from two localities in peninsular Malaysia and from one locality in Sumatra, but is obviously more widespread.

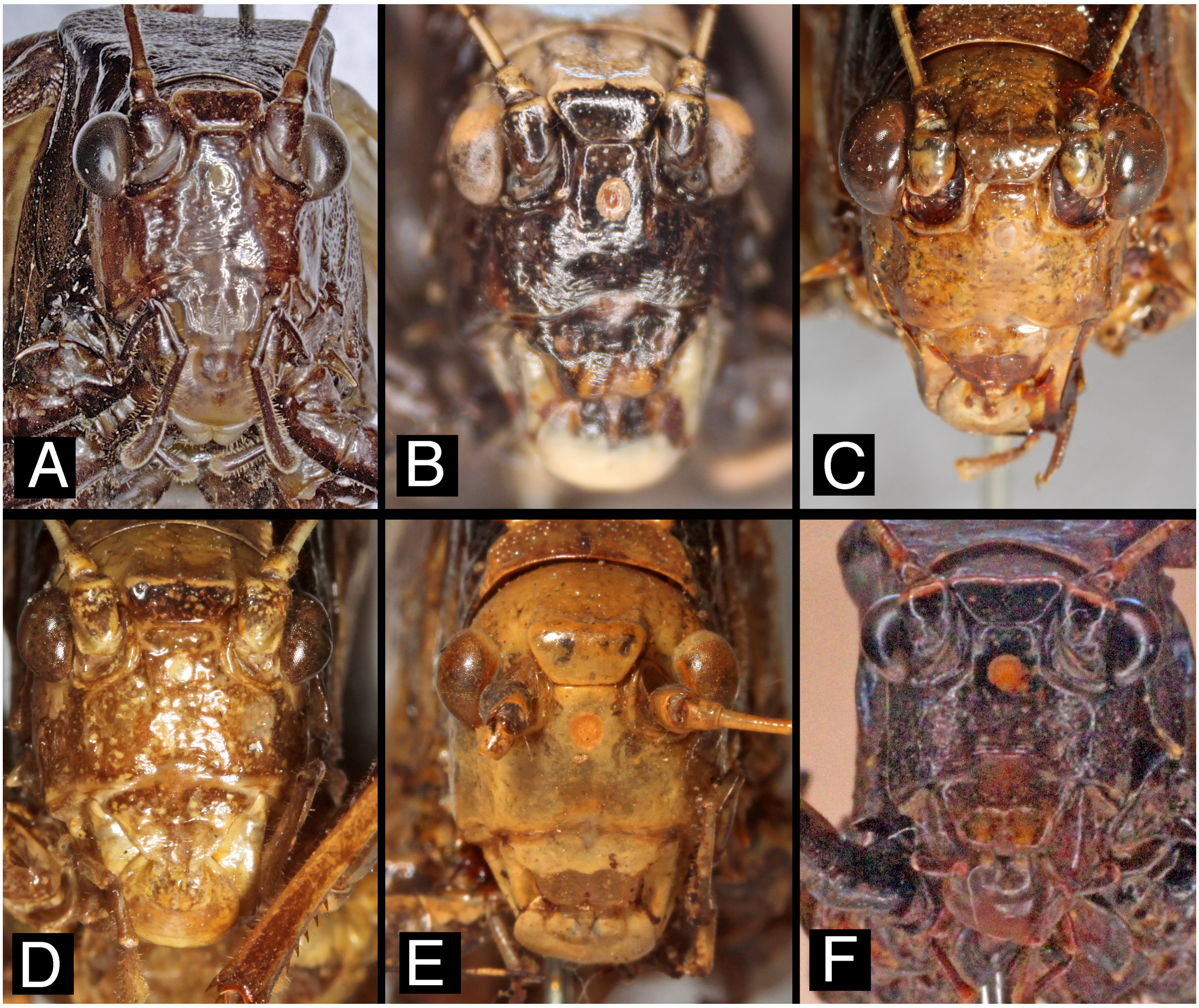

FIGURE 16. Frontal view of the head in *Mecopoda* and *Eumecopoda* species. **A** *M. angusta*, male, **B** *M. angusta,* female, **C** *M. dilatata*, male, syntype, **D** *M. divergens,* male, NMW, **E** *M. divergens,* female, holotype, **F** *E. cyrtoscelis zhantievi* **subsp. nov.**, male, holotype.

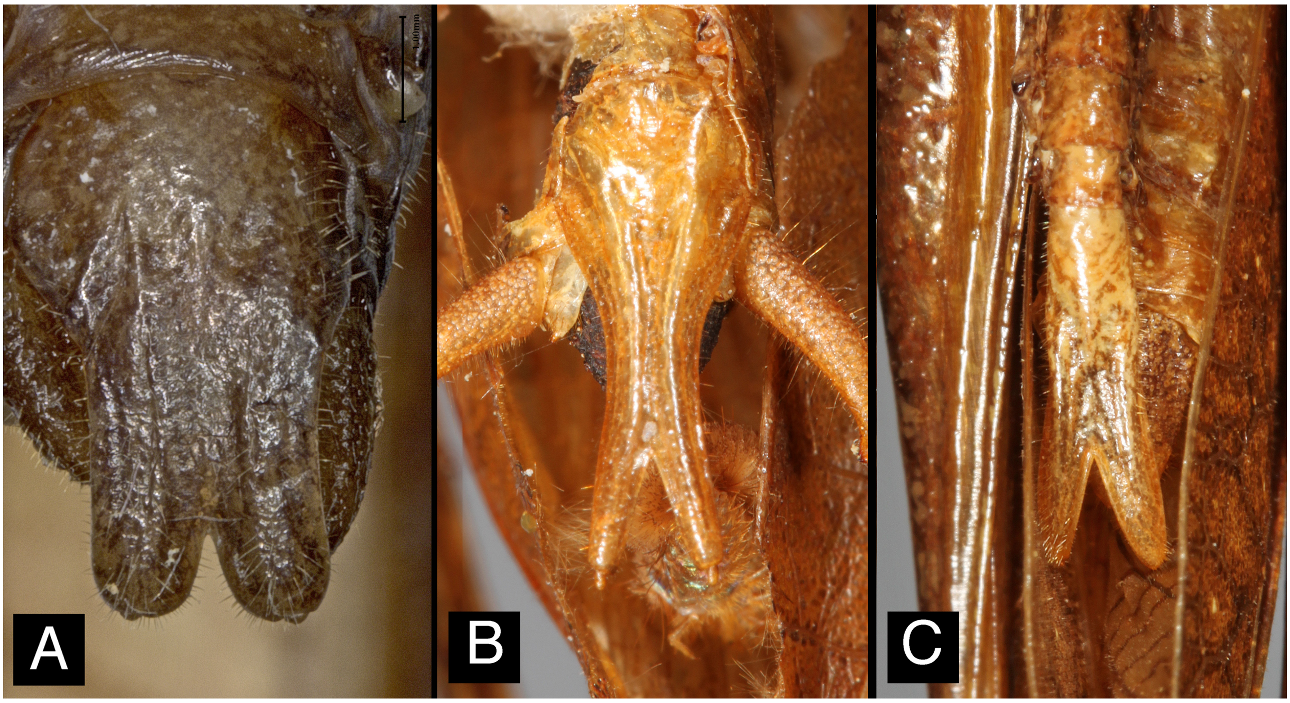

FIGURE 17. Male subgenital plate, ventral view, in *Mecopoda* species. **A** *M angusta* (CH3697), **B** *M. dilatata*, type, **C** *M. divergens*, NHW.

FIGURE 18. Ovipositor of **A** *Mecopoda angusta* (CH3744) and **B** *Eumecopoda platyphoea* **stat. nov.**, holotype. Scale 10 mm.

Genus *Eumecopoda* Hebard, 1922

(Fastigium verticis blunt, with transverse keel; gap between fastigium frontis and fastigium distinct; Fig. 16)

Paramecopoda Gorochov 2020, **syn. nov.**

The genus *Eumecopoda* was introduced by Hebard (1922) with *E. cyrtoscelis* Karsch, 1888 as type species. Hebard listed several supposed genus-specific characters. However, not all of them are diagnostic. Interestingly, the shape of the fastigium is described as looking as in *M. dilatata* and *M. divergens*, but Hebard did not mention these species. Also with regard to the distinct gap between fastigium frontis and fastigium verticis *E. cyrtoscelis* is similar to these species (Fig. 16). In *Eumecopoda* according to Hebard (1922) „the tips of the tegmina are somewhat falcate". This characteristic, however, is also seen in *M. platyphoea* (Fig. 19). Hebard mentions also the structure of the tympana in the fore tibiae, open in *Mecopoda* and partially closed in *Eumecopoda*. However, according to Griffini (1908), *E. cyrtoscelis* „has considerable variability in the structure of the tympani of the front tibiae, now almost concave, now rhymed, often differently made to the front side and the back side, being able to be in the open side and in this somewhat closed or even vice versa" (Griffini 1908, translated). A similar or even larger variation is seen in *M. dilatata*, where specimens with open tympana and with the condition as in *E. cyrtoscelis* have been found (Fritze 1900, Griffini 1908). Gorochov (2020) used this character to differentiate his new (sub)genus *Paramecopoda.* All *Eumecopoda* species (no information available for *E. walkeri)* seem to have femora supplied dorsally with blunt tubercles, a characteristic not found outside the genus and also not found in *Paramecopoda granulosa* (no information available for *M. platyphoea).*

We will use the character from Hebard's (1922) description „the tips of the tegmina are somewhat falcate" as differential character of *Eumecopoda* (see Fig. 19 und figs. 20–21 in Gorochov 2020) to unite a group of species similar to, but different from *Mecopoda.* Based on this definition, the genus *Eumecopoda* includes the Philippine species *E. reducta* Hebard, 1922, *E. walkeri* Kirby, 1891 and *E. granulosa* (Gorochov, 2020) **stat. nov.**, the four species *E. cyrtoscelis* Karsch, 1888, *E. moluccarum* Griffini, 1908, *E. superba* Bolívar, 1898 and *E. spinosa* (Gorochov, 2020) **stat. nov.** occurring around New Guinea (Fig. 21; Tab. 6), and *E. platyphoea* Walker, 1871 **stat. nov.** from Sri Lanka. Future studies have to show if this biogeographic pattern is reflected in phylogeny. *Mecopoda kerinci* with its single known male specimen may remain in *Mecopoda* for the moment.

Eumecopoda cyrtoscelis zhantievi Heller subsp. nov.

Holotype, male; CH8767, INDONESIA, NW Papua, Radja Ampat, isl. Waigeo [0°12'S, 130°50'E], XII.2017. leg. M. Berezin (from laboratory culture), MfN.

Paratypes. Female, CH8768, same data as holotype. Female, Collectio Helb, INDONESIA, West Papua, Wasai Prov., Waigeo Island, 7.2018, leg. V. Voitsekhovskii

Other material. 3 males, 3 females, Moscow State University; 1 male, 1 female, ZIN (data as holotype).

Material used for comparison. *Eumecopoda cyrtoscelis*, male, NEW GUINEA, Sideia Island, Sideia Mission, 2. Dec. 1968, leg. G. Hangay. ANIC (Rentz *et al.* 2006, Su, per email)

The specimens at hand are morphologically quite similar to that described in detail by Helfert & Sänger (2007) as *Eumecopoda cyrtoscelis cyrtoscelis*. However, they differ in song from the two populations studied there. Therefore we consider our specimens as belonging to a distinct island subspecies. The stridulatory files do not seem to differ.

The closely related species *E. superba* Bolivar, 1898 occurs also in NW Papua. The type locality „Hassam", given by Bolivar (1898) and not traceable in any gazetter, is obviously an error, since on the label of a (syn-?) type (see Paris 1994) in NMPC the word „Hattam" is given (Machackova & Fikacek 2014). Hatam or Hattam is the name of a language/tribe in NW Papua living on the mainland of New Guinea (https://en.wikipedia.org/wiki/Hatam_language) near (to the island of) Mansinam where the species was listed by Griffini (1908). The specimens of *E. superba* are clearly larger than ours and that from Helfert & Sänger (2007) (see Tab. 6). The distribution of *E. cyrtoscelis, E. superba, E. spinosa* Gorochov, 2020 and *E. moluccarum* (Griffini, 1908) around Northwestern New Guinea is given in Fig. 21.

Diagnosis. In the calling song of the species, trills with durations from several seconds to more than a minute were observed, clearly different from the much shorter segments of a „broken trill" (called „continuous (short) caller" by Römer in Helfert & Sänger 2007) observed in *Eumecopoda c. cyrtoscelis* by Helfert & Sänger (2007; fig. 32). In morphology, possibly some body relations like tegmen to femur in the female differ between subspecies (or populations) but there are too few data for safe conclusions.

Derivatio nominis. Named in honour of Prof. Dr. R. D. Zhantiev, Moscow State University, the pioneer of bioacoustics of insects (author of a book with same title in 1981 and of many papers before and after this date) in the USSR and Russia.

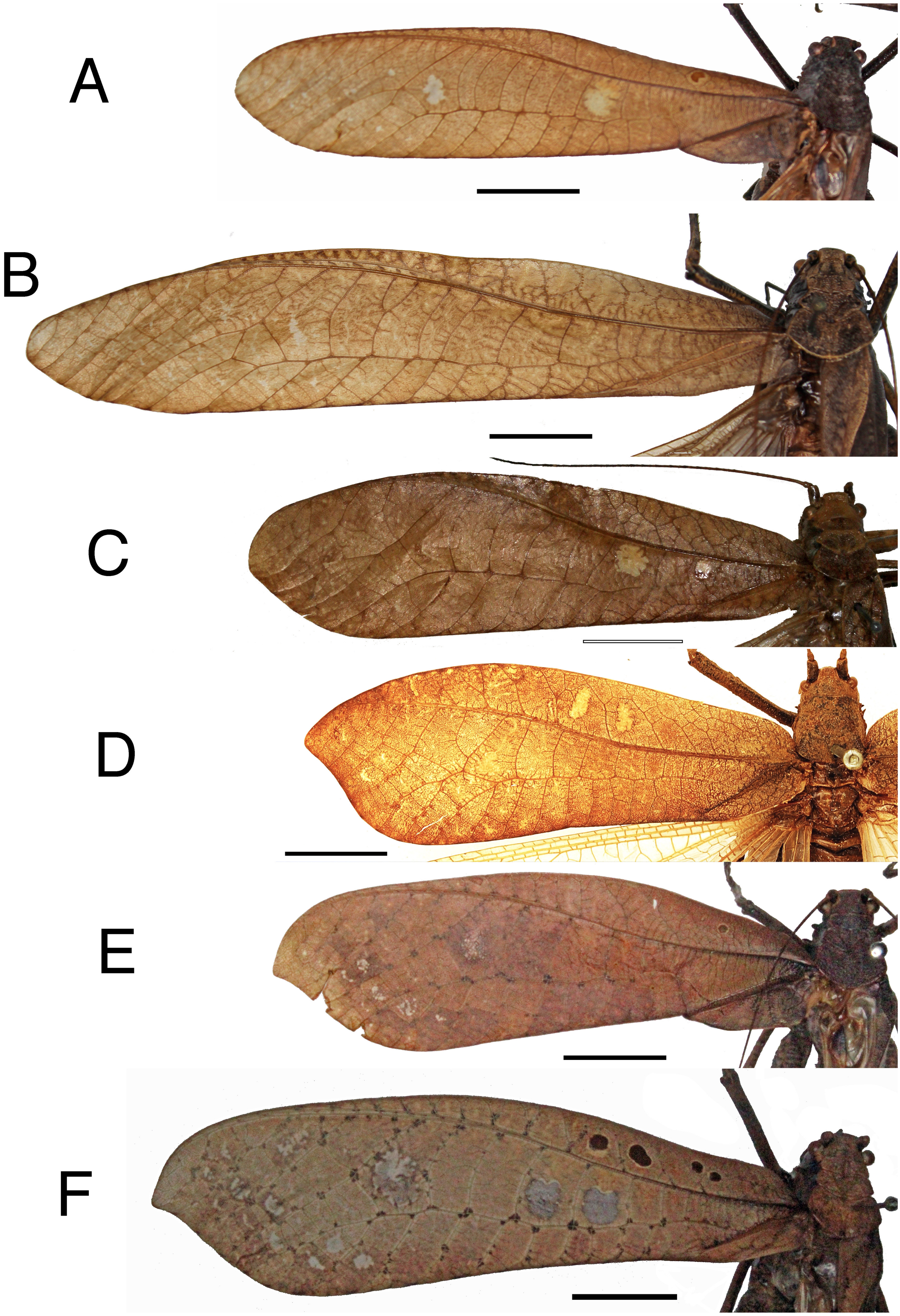

FIGURE 19. Tegmina in *Mecopoda* and *Eumecopoda* species. **A** *M. angusta*, male, **B** *M. angusta*, female, **C** *M. divergens*, female, holotype, photo without scale, size according to the description, **D** *E. platyphoea* **stat. nov.**, female, holotype, **E** *E. cyrtoscelis zhantievi* **subsp. nov.**, male, holotype, **F** *E. cyrtoscelis zhantievi* **subsp. nov.**, female, paratype. Scale 10 mm.

FIGURE 20. Morphological details of male *Mecopoda angusta* (CH3697). **A** pronotum dorsal view, **B** pronotum, lateral view, **C** cercus. Scale 1 mm.

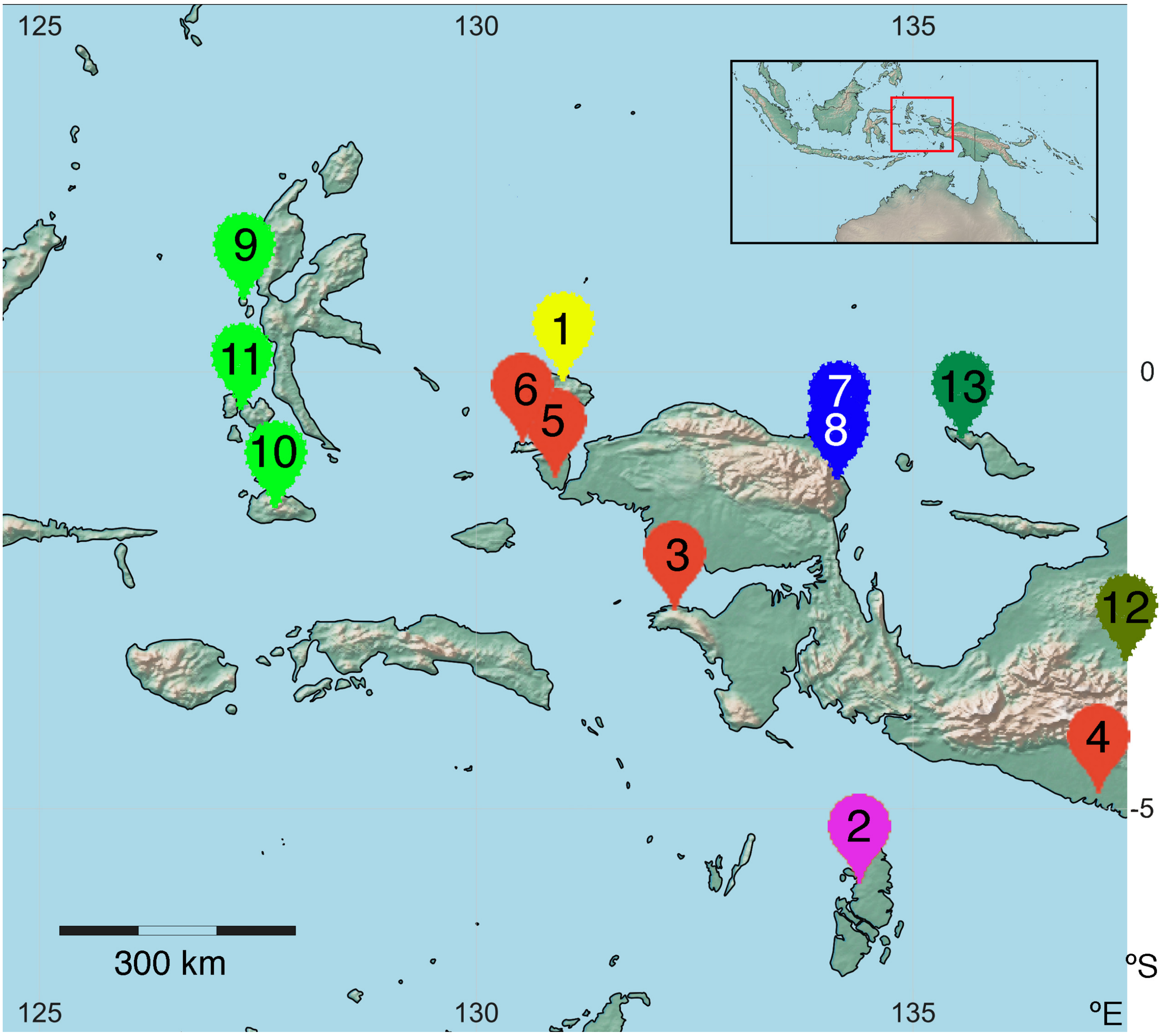

FIGURE 21. Distribution map of *Eumecopoda* species in and around Northwestern New Guinea. 1 type locality of *E. cyrtoscelis zhantievi* **subsp. nov.** , 2 type locality of *E. cyrtoscelis aru (*Gorochov 2020, Redtenbacher 1892, Willemse 1933), 3–6 *E. cyrtoscelis cyrtoscelis* (3 type locality, 4 Hebard 1922, 5, 6 Helfert & Sänger 2007), 7–8 *E. superba* (7 Griffini 1908, Gorochov 2020, 8 type locality), 9–11 *E. moluccarum* (9 type locality, 10 Hebard 1922, 11 Gorochov 2020), 12 type locality of *E. sp. spinosa* Gorochov 2020, 13 type locality of *E. spinosa supiori* Gorochov 2020. Map based on SimpleMappr (Shorthouse, 2010).

TABLE 6. Dimensions of *Eumecopoda* species of New Guinea and surroundings.

species	distribution	pronotum male/female	tegmina male/female	hind femur male/female	ovipositor	source
cyrtoscelis zhantievi **subsp. nov.**	NW Papua / culture	8 / 9	51,5 / 62	38 / 42.5	24	holotype/allotype
	NW Papua / culture	7.3 / 8.2	53 / 58.8	40 / 46	24.5	*dry (n=3)
	NW Papua / culture	7 / 8.7	50.8 / 62,5	37.2 /45.5	26	*alive (n-2)
	NW Papua / culture	7–8/7–9	51.5–56/56–67	37–43/42.5–47	24–26	range (all; n=7)
cyrtoscelis cyrtoscelis	NW Papua (2º41'S, 132º24'E)	- / -	- / 72	- / 57	26.5	Karsch 1888; holotype
cyrtoscelis cyrtoscelis	NW Papua, opposite Aru Islands	8,8 / 10,1	57.8 / 69.1	42 / 51.2	26.7	Hebard 1922
cyrtoscelis cyrtoscelis	NW Papua	7,9 / 9,3	56,2 / 66.9	39 / 49,5	29.4	*Helfert & Sänger 2007
				36.3–42.7 n=45 range males 45.6–52.5 n=48 range females		Helfert & Sänger 2007
					26.9–31.8 n=48	Helfert & Sänger 2007
cyrtoscelis karschi	Queensland	- / -	40 / -	43 / -	-	Kirby 1891; holotype
cyrtoscelis regina	Duke of York Islands	- / -	- / 65	- / 56	23	Kirby 1891; holotype
cyrtoscelis aru	Aru Islands	- / -	- / -	- / -	-	Gorochov 2020
cyrtoscelis moresby	East Papua	- / -	- / -	- / -	-	Gorochov 2020
cyrtoscelis with ssp.	New Guinea + islands	6,5 / 8,8	50–51/62–72	38 / 46–57	23–27	Redtenbacher 1892
superba	NW Papua	- / -	- / 72	- / 54	35	Bolivar 1898; syntypes
superba	NW Papua, Mansinam island	10,6 / 13,4	62 / 76	45 / 54	36	Griffini 1908
superba	NW Papua, Manokwari	11/12–13.5	61/71–74	55/51–56	35–38	Gorochov 2020
moluccarum	Halmahera, Ternate	8 / 10	55 / 70	43 / 53	30	Griffini 1908; syntypes
moluccarum	Obi Island	7.8–9.5/9.8–10.7	56–66/69–75	40–49/51–54	32	Hebard 1922
moluccarum	Halmahera, Bacan	7.5–10/.9.5–11	52–65/69–75	40–50/51–55	30–32.5	Gorochov 2020
spinosa spinosa	NW Papua	8–9/9–10.5	56–59/70–72	44–47/51–53	25–27	Gorochov 2020
spinosa supiori	NW Papua, Supiori Island	8/-	56/-	41.5/-	-	Gorochov 2020
spinosa tuberculata	Papua, Jayapura	9/11	67/79	47/59	31	Gorochov 2020

*mean

Measurements: see Tab. 6.

Song. The calling song of the species consists of trills with durations from several seconds to more than a minute (Fig. 10; Tab. 7).

It should be noted that the stridulatory file of a male from Sideia Island (extreme SE New Guinea), identified as *E. cyrtoscelis* (Rentz *et al.* 2006), differs distinctly from our specimen and from that of Helfert & Sänger (2007; see Fig. 12).

Coloration. Dark brown.

TABLE 7. Song characteristics of *Mecopoda angusta* and *Eumecopoda cyrtoscelis.*

species/source	T (ºC)	duration of series/trill (s)	duration of echeme/trill segments (ms)	echeme number per series	syllable period (ms)	SRR (Hz)
M. angusta						
CHX066	24,5	13.1±1.2	1253±61	7.3±0.5	33.3±0.8	30
CH3674	26	14.6±1.1	704±96	17.7±0.5	25±0.7	40
CH3697	ca. 25	9.8±1.2	774±53	10±1.2	25.4± 0.7	39,4
E. c. cyrtoscelis						
Helfert & Sänger 2007	24	30–360	1351±443	-	27	37
E. c. zhantievi **subsp. nov.**						
topotype	25	ca. 6–60	-	-	24.8	40

D. File diversity of the *Mecopoda elongata* group in some regions of South East Asia

Since the structure of the stridulatory file seems to be the most important and at present even the only characteristic to identify collected specimens of the *Mecopoda elongata* group we compared larger series of this group from three different areas hoping to find species-specific differences.

a) Borneo

List of studied male specimens

3261443 (ZFMK) East Malaysia Sabah Mt. Kinabalu NP, Poring 500–700 m a.s.l., 1 v 1993, leg. K. Riede. 3261450 (ZFMK) East Malaysia Sabah Kota Kinabalu 9 viii 1984, leg. S. Ingrisch. 3261454 (CI) East Malaysia Sarawak Batu Niah 3 viii1984, leg. S. Ingrisch. 3261461 (CI) East Malaysia Sarawak Rajang-Nebenfluß, Nanga Ngungun (Langhäuser) 30 vii 1984, leg. S. Ingrisch. CRTmeceloM01 (ZFMK) East Malaysia Sabah Mt. Kinabalu NP, Poring 500–700 m a.s.l., 10 iv 1993, leg. K. Riede. CRTmeceloM02 (ZFMK) East Malaysia Sabah Mt. Kinabalu NP, Poring 500–700 m a.s.l., 7 vi 1993, leg. Hoffmann. CRTmeceloM03 (ZFMK) East Malaysia Sabah Mt. Kinabalu NP, Poring 500–700 m a.s.l., 9 vi 1993, leg. Hoffmann. Sarawak State (Borneo I.), Bako National Park on sea bank not far from Kuching City, primary forest on hills, 18–22 iii 2012, A. Gorochov, M. Berezin, E. Tkatsheva, I. Kamskov (holotype of *M. stridulata stridulata*; ZIN).

The data from Borneo (Fig. 22) indicate that all studied files can be attributed to two different file types, corresponding to *M. himalaya* and *M. stridulata stridulata*. However, according to the observations of Bugrov *et al.* (2004; KK song-2), in Borneo also a species of the *confracta*-subgroup occurs.

b) Indonesian Islands (Sumatra, Java, Bali, Timor)

List of studied male specimens

3254643, 3261432, 3261434, 3261435 3261437 (CI) Indonesia West Java Palabuan Ratu, Samudra beach, 2 iii 1995, leg. S. Ingrisch. 3261433, Indonesia West Sumatra Maninjau (0°18'S, 100°15'E), 400 m a.s.l., 13 iii 1995, leg. S. Ingrisch. 3261438, 3261439 (CI) Indonesia North Sumatra Pematang Siantar 400 m a.s.l., 2 iii 1993, leg. S. Ingrisch. 3261440 (CI) Indonesia West Java Gunung Salak, above Ciapus, Sukamandri 850–950 m a.s.l., 27 ii 1995, leg. S. Ingrisch. 3261448 (CI) Indonesia West Java Bogor, Botanical Garden 16 iii 1993, leg. S. Ingrisch.

3261458 (CI) Indonesia Central Java Gunung Lawu, Tawangmangu 1000 m a.s.l., 28 iii 1993, leg. S. Ingrisch. NHM, NHMUK010210933, Sumatra: Brastagi [probably Berastagi, 3° 11′N, 98° 31′E], 17 ii 1985, leg E. Sismondo. NHM, NHMUK010210932, Bali, Nusa Dua, 27 xii 1987, E. Sismondo. Rentz *et al.* 2006: Timor-Leste, Maubisse, 1431m, 1–10 vi 1965, leg. R.N. Ferreira (Rentz & Su, per email). Male, Java I., "Mecopoda elongata Fab. Java", "Brunner v. W. det." (holotype *M. stridulata latiuscula*; ZIN). Male, INDONESIA:"Java merid. 1500′ 1891 H. Fruhstorfer", "104-98","Mecopoda elongata № 42" (holotype *M. ampla javaensis*; ZIN).

The situation in the Indonesian islands is more complicated than in Borneo (Fig. 22). Most surprisingly, we found two specimens (black in Fig. 22) with a file type differing widely from all others known so far. They have to be considered as representatives of a new species (see below). Besides these, there are specimens with *himalaya* file type (red in Fig. 22) and from the *confracta*-subgroup (blue in Fig. 22) identified by their narrow mirror area. One of the files of the *confracta* groups differs strongly from the others.

c) Thailand

List of studied male specimen

3254538 (CI) Thailand Phetchabun Nam Nao 1000 m a.s.l., 13 ix 1989, leg. S. Ingrisch. 3254539 (CI) Thailand Tak Ban Mae Salit, Monkrating resort 700–800 m a.s.l., 18 ix 1989, leg. S. Ingrisch. 3261441 (CI) Thailand Surat Thani Khao Sok 150–180 m a.s.l., 22 i 1997, leg. S. Ingrisch. 3261442 (CI) Thailand Surat Thani Khao Sok 150–180 m a.s.l., 22 i 1997, leg. S. Ingrisch. 3261444 (CI) Thailand Nakhon Nayok Khao Yai National Park, near headquarter 700 m a.s.l., 15 x 1990, leg. S. Ingrisch. 3261445 (CI) Thailand Chiang Mai Amphoe Muang (city district) 10 ix 1989, leg. S. Ingrisch. 3261447 (CI) Thailand Trang Khao Chong 22 x 1991, leg. S. Ingrisch. 3261449 (CI) Thailand Nan Doi Phukha 1500–1600 m a.s.l., 4 x 1991, leg. S. Ingrisch. 3261452 (CI) Thailand Chiang Mai near Ban Pradu (10 km S of Phrao) 28 ix 1985, leg. S. Ingrisch. 3261456 (CI) Thailand Chiang Mai Doi Suthep-Pui 1300–1400 m a.s.l., 8 x 1991, leg. S. Ingrisch. 3262689, S- THAILAND, Phang-nga Prov., Thimung distr., 5 km S Khao Lak, 08°36'N, 98°15'E, 10–100 m., 1–14 viii 2014, leg. A. Skale (NMED).

Among the file types from Thailand specimens from two species of the *niponenesis* subgroup can be identified: specimens with *himalaya* file type (red in Fig. 22) and with *fallax*-like tooth distributions (lilac in Fig. 22), There are also files from specimens of the *confracta* subgroup (blue in Fig. 22) identified by their narrow mirror area. Also some unidentified specimen (green in Fig. 22) were found. At least part of them may possibly also belong to species of the *confracta* subgroup, but with unusually broad mirror areas.

Mecopoda paucidens Ingrisch, Su & Heller sp. nov.

Holotype, male, East Timor: Maubisse, elev. 1431 m [8°50'S, 125°36'E], 1–10 vi 1965, coll. R.N. Ferreira. ANIC. Other specimens studied: see below.

Diagnosis. The new species differs from all other species of the genus so far known by the narrow tegmen combined with the very low number of teeth on the male stridulatory file on underside of the left tegmen (Fig. 23). Member of the *M. elongata* group.

Description. General habitus of the genus. Medium sized species with narrow tegmina; tegmen moderately curved in midlength, its greatest width 11 mm. Subcosta attached to radius except at very base, it separates before the curvature that brings both veins close to the anterior margin of tegmen. Male: Stridulatory file with 44 (Timor) respectively 50 (Java) teeth. Cerci stout at base, markedly curved mediad and narrow in about apical third, in apical area on internal side with two minute spines. Subgenital plate moderately wide, narrowed from base towards midlength; divided into two lobes, apical incision about 0.28 times the length of the subgenital plate; styli narrow, moderately long, about 10:22 the length of the apical incision of the subgenital plate.

Measurements (1 male). Body w/wings: 73; body w/o wings: 33; pronotum: 8.8; tegmen: 61; hind femur: 56; tegmen width: 11 mm.

Other specimen studied: Indonesia: Central Java, Gunung Lawu, Tawangmangu, elev. 1000–1200 m (7°39'S, 111°7'E), 28 iii 1993, coll. S. Ingrisch, 3261458 (CI).

Male cerci not very stout at base but little stronger than in the other species from Java, narrow apical area moderately curved, at internal side just before and at the end with two minute acute black teeth, the apical tooth hardly larger than the preapical tooth.

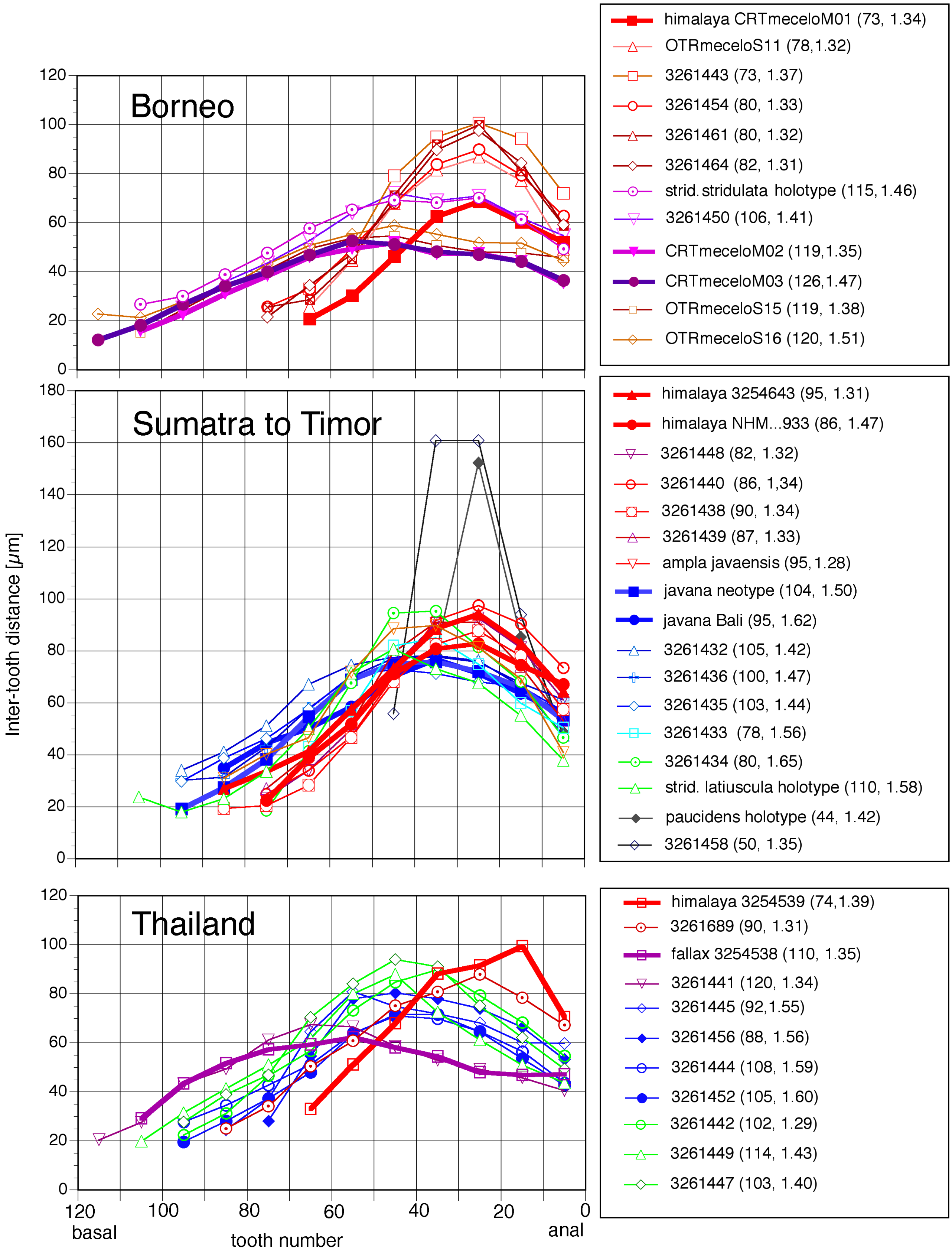

FIGURE 22. File diversity in *Mecopoda* in selected areas. **A** Borneo, **B** Indonesian islands Sumatra-Java-Bali-Timor, **C** Thailand. Inter-tooth spacing in stridulatory files. Thick lines indicate specimens with known song. Red/lilac lines presumed *niponensis* subgroup, blue presumed *confracta* subgroup, green unknown, black *paucidens*. In the legend after specimen ID the number of stridulatory teeth and relative width of the mirror cells (width/length; in brackets).

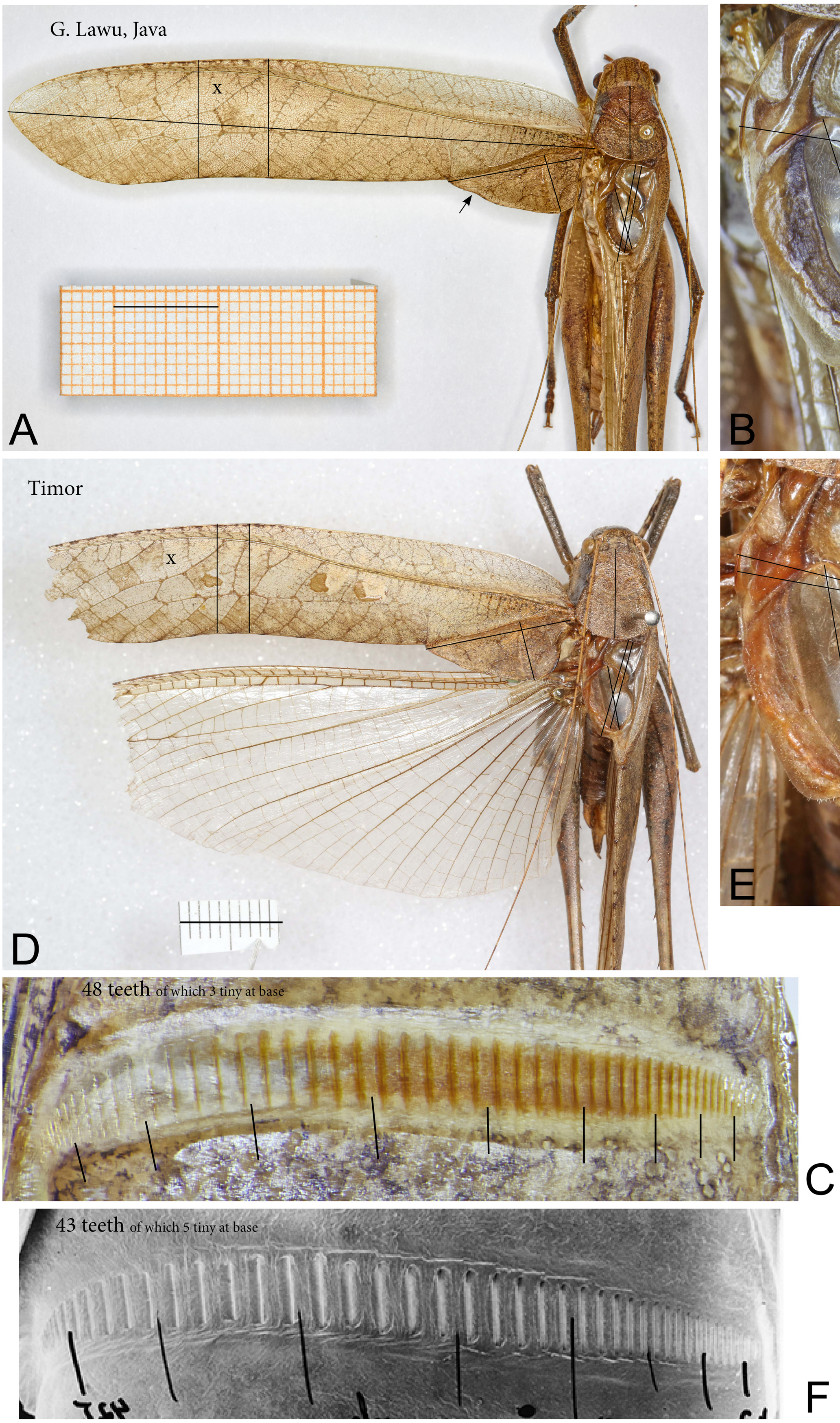

FIGURE 23. *Mecopoda paucidens* **sp. nov.**: habitus (A, D), mirror area of right tegmen (B, E), stridulatory file of left tegmen (C, F).—**A–C:** male from Gunung Lawu, Java; **D–F**: holotype male from Timor. The thin lines mark the measuring tracks (A–E) or the borders between bulks of five teeth (C, F).

Measurements (1 male). Body w/wings: 65; body w/o wings: 35; pronotum: 7.5; tegmen: 55; hind femur: 43; tegmen width:11.5 mm.

Song. Unknown.

Derivatio nominis. Named according to its stridulatory file which carries only relatively few (Latin pauci) teeth (Latin dens=tooth). Noun in apposition.

Discussion

According to our data and the information published in the last three years (Liu Yf *et al.*2019; Liu Cx *et al.* 2020; Gorochov 2020), *Mecopoda* is an astonishingly divers genus, in morphology as well as in acoustics. Considering the few areas which have been studied carefully, we have to assume that many species have yet to be described. Two countries seem to be especially important in this respect. India is well-known for the high diversity of *Mecopoda* species (Nityananda & Balakrishnan 2006) but even the species studied there have not yet been formally described. Based on old data, also the Philippines are known to harbour several *Mecopoda* and *Eumecopoda* species, but there are still only few data available (Tan *et al.* 2019). The *Mecopoda* species were assigned to *M. elongata* (e.g. Hebard 1922; Ballentes *et al.* 2006), but also to the ‚forms‘ *macassariensis* and *niponensis* (Karny 1921), neglecting the probably endemic *M. tenebrosa*. All these results require confirmation.

The problems in identifying *Mecopoda* species morphologically are now beginning to be solved. However, contrasting the minute and vague differences in morphology, especially in the *M. elongata* group, distinct clusters appear when comparing the calling songs. In the *niponensis* subgroup, one of these groups is formed by the widespread *M. himalaya* which has a very similar song from Yunnan to Java and Borneo (Tab. 3). *M. fallax* also has nearly identical songs from China to Malaysia. The more northern *M. niponesis* and the Bornean *M. s. stridulata* differ also clearly in song. All species of the subgroup have long lasting, uninterrupted songs. The situation in the *confracta* subgroup, however, is different. All species have songs consisting of echemes (groups of syllables, chirps), but, as far as we know, the number of syllables and the SRRs differ between areas (Tab. 4). To get an idea about the evolution of these pattern, we need to know more about the *minor* subgroup whose species seem to combine both song types, and about the phylogenetic relationships between the groups and species. Surprisingly, in spectral composition the songs of the species of the *Mecopoda elongata* group and of *Eumecopoda* do not show significant differences despite the dissimilar mirror shapes.

Compared to the morphological uniformity, *Mecopoda* is unexpectedly diverse in chromosome structure. The model chromosome number in most tettigoniids is 2n = 31 in males, with acrocentric chromosomes and X0 sex mechanism (e.g. Warchałowska-Śliwa 1998). The pattern of chromosome evolution in the species of the genus *Mecopoda* is interesting. The taxa examined in this study form three groups according to their karyotype; the first group contains species with chromosome number 2n = 29 (*M. sismondoi* **sp. nov.**, *M. mahindai* **sp. nov.**), the second group with reduced chromosome number 2n = 27 (*M. niponensis, M. himalaya*). The same chromosome number was also reported for *M. niponensis* from Japan (Hareyama 1932). The third group shows the next step in the reduction to 2n = 23 (*M. javana*). Interestingly, the occurrence of 24 chromosomes, probably in a female, has been previously noted in a species from Thailand (Luanpirom *et al.* 1999), identified as *Mecopoda elongata*, but probably a form identical or related to *M. javana*. All karyotypes are characterized by a distinct morphology of the chromosomes (FN = 54, 52, 46, respectively). In all cases, centric fusion, tandem fusion and/or pericentric inversion changed the basic karyotype. The results described herein, besides changes of chromosome number and morphology, involved some differences concerning the heterochromatin distribution obtained by C-banding.

Up to now, cytotaxonomic studies of the Mecopodinae are scarce. Karyological information is available only for two Australian species of *Austromecopoda* (Rentz *et al.* 2006), one African species of *Philoscirtus* (Hemp *et al.* 2015) and some Indian (Asana *et al.* 1938; Aswathanarayana & Aswath 1994), Japanese (Hareyama 1932) and Malaysian (Hewitt 1979, Bugrov *et al.* 2004) species belonging to the genus *Mecopoda*. Here the chromosome number was 2n = 29 or 27 in males. The chromosomes were characterized by a high level of differentiation among populations and a distinct morphology (FN = 32, 54, 56). They consisted of two to fourteen bi-armed autosomes (meta-/submeta-/subacrocentric) and a meta-/submetacentric X chromosome (Aswathanarayana & Aswath 1994, see review Warchałowska-Śliwa 1998, Bugrov *et al.* 2004). Our results corroborate previous studies that revealed that *Mecopoda* showed an advanced karyotype evolution.

Finally, a characteristic feature of the *Mecopoda* species complex is its extreme diversity of conspicuous songs. Since the seminal paper of Sismondo (1990) *Mecopoda* species have become model organisms for studies about acoustic communication, including chorusing behavior and synchrony entrainment (see Nityananda and Balakrishnan 2021, and references therein). Due to taxonomic uncertainties, preliminary names were used by physiologists and ethologists, such as *Mecopoda* sp. 'Two-part caller' (l.c.). Our integrative taxonomic approach will hopefully contribute to create a reliable and stable nomenclatural framework, which is necessary for a better understanding of these interesting species.

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