

Paraplangia sinespeculo, a new genus and species of bush-cricket, with notes on its biology and a key to the genera of Phaneropterinae (Orthoptera: Tettigonioidea) from Madagascar

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Abstract

Madagascar is a well-known hotspot of biodiversity. However, many Orthoptera, and especially the Tettigonioidea, belong to little-studied groups. Here we describe a new genus and species of bush-cricket reared from field-collected eggs. *Paraplangia sinespeculo* gen. nov., sp. nov. belongs to Phaneropterinae and shares diagnostic characteristics with members of the tribe Amblycoryphini and its African subtribe Plangiina stat. nov. *Paraplangia*, which has a chromosome number of 31 X0, differs from other African members of the tribe and subtribe such as *Eurycorypha* and *Plangia*, which both have 29 X0. In addition to morphology, we describe the male calling song, female acoustic response, and mating behavior. As calling song, the male produces two series of short syllables. At the end of the second series the female responds with signals of similar duration and spectral composition as the male sounds (peak about 8-9 kHz). To make future identification easier, a key to all genera of Phaneropterinae found in Madagascar is presented.

Key words

Amblycoryphini, bioacoustics, chromosomes, duetting, *Orophus*

Introduction

The island of Madagascar is well known for its richness of endemic species. It is considered to be a very important hotspot of biodiversity due to several factors. Madagascar is a very large island, which is large enough to minimize the risk of extinction once a species has established. It is close enough to the mainland to receive occasional continental immigrants, but is far enough to allow a long, independent evolution of the fauna (MacArthur and Wilson 1967). Madagascar was formerly part of a continent (for a review see Vences et al. 2009). It separated from Gondwana about 135 million years ago (e.g. Briggs 2003, Yoder and Nowak 2006, McIntyre et al. 2017), so parts of its fauna and flora may be of Gondwanan origin. Then, for some time Madagascar and India drifted north-eastwards together, until their connection also broke (about 90 million years ago) and Madagascar remained isolated in

the Indian Ocean. It was, however, never very far from Africa, and even non-flying mammals seem to have crossed this channel several times (Ali and Huber 2010). Therefore, the time at which the Malagasy taxa diverged from their closest relatives varies greatly, and there are many publications dealing with this question for different groups of animals and plants. However, even more groups, especially insect groups, are still nearly completely unstudied.

One of these groups is bush-crickets (katydids; Tettigonioidea). Most studies on this group in this region were conducted before 1914, when the last comprehensive paper appeared (Carl 1914). Only very recently have some papers on selected groups been published (Massa 2017a,b,c,d, Ünal and Beccaloni 2017). There are no published data on the biology of any taxon (except some observations in Ünal and Beccaloni 2017). At present, four subfamilies of Tettigonioidea are represented by several species each in Madagascar, and Listroscolidinae is represented by a single species (all data according to Cigliano et al. 2018, abbreviated OSFO). The four more common subfamilies have quite different biogeographic patterns in terms of their Malagasy fauna. Pseudophyllinae and Meconematinae are represented with relatively few species each and only endemic species or genera are known. All Pseudophyllinae (except the phyllophorine-like genus *Aspidonotus*) belong to the tribe Simoderini which consists of species that occur exclusively in Australia and Madagascar. If this tribe was confirmed as a monophyletic unit, it would be a strong indication for a Gondwanan origin of the group. The subfamily Conocephalinae has many species in Madagascar and most genera are endemic, but there are also a few endemic species of the widespread genera *Conocephalus* and *Ruspolia* and even non-endemic species [*Conocephalus maculatus* (Le Guillou, 1841) ("Madagasian Region" Pitkin 1980), *Pseudorhynchus hastifer* (Schaum, 1853) and the swarm-producing (see Bailey and McCrae 1978) *Ruspolia differens* (Serville, 1838)]. Most conocephaline genera belong to the tribe Euconchophorini, which is endemic to Madagascar and some surrounding islands. Gorochov (1988) considered this group of short-winged species as a sister group to all other world-wide distributed Conocephalinae. However, in a

recent molecular study (Hemp et al. 2015) the Euconchophorini representative appeared basally to the studied Agraeciini from Africa, India and Australia, but within Conocephalinae. In any case, a member of this Agraeciini/Euconchophorini-complex seems to have arrived in Madagascar relatively long ago.

The largest Malagasy subfamily is Phaneropterinae (at present ca. 40 species; Table 1). Madagascar has a few species in common with continental Africa (*Phaneroptera sparsa*, *Tylopsis bilineolata*, *T. irregularis*, and *Eurycorypha cereris*), and several genera have species which are endemic to Africa as well as to Madagascar – most of them also with endemics on other islands in the Western Indian Ocean (*Eurycorypha*, *Plangia*, *Parapyrrhicia*, *Trigonocorypha*). One genus with one endemic species to Madagascar has most of its species distributed in Asia (*Holochlora*). Thus, two thirds of the 22 phaneropterine genera are endemic to Madagascar. Most phaneropterine species are long-winged. There have probably been several independent colonization events of Madagascar, mostly from Africa [as with the flying mammals (bats), although some of which seem to have come directly from Southeast Asia; Bates et al. 2006]. For genera endemic to Madagascar, the closest relatives are expected to be found in Africa.

Considering the low intensity of research, the number of species and genera known at present is certainly only a small percentage of that actually occurring there or which had, sadly, occurred there in the past (see Goodman and Jungers 2014). Therefore, one of the authors (KGH) seized the opportunity to rear nymphs of an unidentified species from Madagascar. After these animals molted successfully to adults, they had to be identified (see key below) and, not completely unexpectedly, they were identified as belonging to a new genus and species. Since they lived for quite some time in the laboratory, we were able collect data which were not previously known from any other Malagasy bush-cricket, and which are hopefully a starting point for similar studies *in situ*.

Methods

The animals were held in plastic containers, differing in size depending on the size of the animals, and fed with *Taraxacum officinale*, replaced daily.

Measurements.—Total body length, lateral aspect, refers to the mid-line length of the insect from fastigium verticis to tip of abdomen including the subgenital plate. In females, the ovipositor is not included in the measurement of the body length. Measurements of ovipositor are taken laterally in a straight line from tip to base disregarding the curvature.

To obtain the mass data, living animals and spermatophores were weighed to the nearest 2 mg (balance Tanita Professional Mini 1210– 100).

Acoustics.—The male calling song was recorded in the laboratory using a digital bat detector (Pettersson D1000X) with a sampling rate of 100 kHz. Duets were recorded in stereo using a Sony ECM-121 microphone (frequency response relatively flat up to 30 kHz according to own tests) and an Uher M645 microphone connected to a personal computer through an external soundcard (Transit USB, “M-Audio”; 44.1-kHz sampling rate).

Song measurements and spectrograms were obtained using Amadeus II and Amadeus Pro (Martin Hairer; <http://www.hairersoft.com>). Oscillograms of the songs were prepared using Turbolab (Bressner Technology, Germany). All recordings were made

at temperatures between 22 and 25 °C. The singers were caged in plastic tubes or gauze cages with microphone fixed or hand-held at distances between 5 (duet) and 80 cm.

Acoustical terminology.—Tettigonioids produce their songs by repeated opening and closing movements of their tegmina. The sound resulting during one cycle of movements is called a syllable; opening and closing hemisyllables can often be differentiated (Ragge and Reynolds 1998). Syllable duration: time period measured from the first impulse to the last; syllable period: time period measured from the first impulse to the first impulse of the next syllable; impulse: a simple, undivided, transient train of sound waves (here: the damped sound impulse arising as the effect of one tooth of the stridulatory file). Typically, after some time the same or a similar pattern of syllables and pauses is repeated. This grouping, often separated from the next by a silent interval, is called a song unit.

Chromosomal analysis.—*Paraplania sinespeculo* (two males CH8239, CH8240) and *Orophus* cf. *tessellatus* (Saussure, 1861) [Costa Rica; obtained from <https://www.saltatoria.info/arten%C3%BCbersicht-a-z-species-a-z/orophus-tesselatus/>] (one male CH7705 and one female CH7707) were used for chromosomal analyses. Preparations were obtained from testes and ovaries, incubated in hypotonic solution (0.9% sodium citrate), fixed in ethanol: acetic acid (3:1), and crushed in 45% acetic acid. C-banding was carried out using the method of Summer (1972) and the silver staining method (AgNO₃) for localization of the nucleolus organizer regions (NORs) was performed as previously reported (Warchałowska-Śliwa and Maryńska-Nadachowska 1992). Fluorescence *in situ* hybridization (FISH) with ribosomal 18S rDNA and telomeric (TTAGG)_n DNA probes were conducted following the protocol described by Warchałowska-Śliwa et al. (2009). Chromosomes were studied with a Nikon Eclipse 400 microscope with a CCD DS-U1 camera and NIS-Elements BR2.

Results

The specimens of the new species were identified using the key given below (based on Karsch 1889, Brunner von Wattenwyl 1891, Carl 1914, Ragge 1980, OSFO). See also Table 1 for additional data. Using Ragge’s (1980) key for all African Phaneropterinae with open tympana (excluding Madagascar) one would end up with *Plangia*.

Key to the genera of Phaneropterinae of Madagascar and the islands in the western Indian Ocean

- 1 Fore coxa without spine 2
- Fore coxa with spine 4
- 2 Occurring in Madagascar 3
- Occurring in Mauritius only *Arantia* (two species)
- 3 Tegmen shorter than 30 mm (observed 25), hind wings not longer than tegmina *Paracosmophyllum atrodelineatum*
- Tegmen longer than 30 mm (observed 37), hind wings longer than tegmina *Nesoscirtella polita*
- 4 One or both tympana of the fore tibia closed 5
- Both tympana of the fore tibia open 6
- 5 Both tympana closed *Tylopsis* (two species)
- Only anterior tympanum closed *Holochlora* (*mauritiana* Mauritius, *biloba* Madagascar)

6	Side keels of the pronotum modified (crenulated or serrate or with tubercles etc.) (possibly all members of Trigonocoryphini).....	7
–	Side keels of the pronotum smooth or indistinct.....	11
7	Hind wings hidden under (shorter than) tegmina.....	8
–	Hind wings longer than tegmina.....	9
8	Male supra-anal plate not modified..... <i>Cosmozoma</i> (4 species)	
–	Male supra-anal plate enlarged and three-lobed..... <i>Sikoriella (bimaculata)</i>	
9	Side keels with 4 large tubercles.....	<i>Polygamus</i> (2 species)
–	Side keels of pronotum crenulated or with small, irregular and indistinct tubercles.....	10
10	Side keels of pronotum dark, crenulated..... <i>Trigonocorypha (maxima)</i>	
–	Side keels of pronotum not dark, with small, irregular and indistinct tubercles.....	<i>Megotoessa insulana</i>
11	Tegmina narrow [ratio length/width >3.8; observed (3.8 M.p.*-) 4.3–7.0].....	12
–	Tegmina broad (ratio length/width <3.8; observed 2.1–3.6).....	18
12	Hind wings less than half of the length of the tegmina.....	
–	Hind wings longer than tegmina.....	13
13	Dorsal side of fore tibia rounded.....	14
–	Dorsal side of fore tibia flat or furrowed.....	15
14	Margins of pronotum rounded (=side keels indistinct).....	
–	Margins of pronotum evident (=side keels smooth but distinct)..... <i>Parapyrrhicia</i> (5 species)	
15	Tegmina long (>25 mm; observed 29–46 mm).....	16
–	Tegmina quite short (<25 mm; observed 14–21 mm).....	17
16	Tegmina long (>32 mm; observed 34–46 mm).....	
–	Tegmina short (<32 mm; observed 29 mm)... <i>Agennis (parallelinervis)</i>	
17	Last tergite of male unmodified, ovipositor short (4.0–4.7 mm), tegmina unicolored.....	<i>Phanoptera (sparsa)</i>
–	Last tergite of male modified, ovipositor long (7.5–8.0 mm), tegmina bicolored.....	<i>Xenodoxus</i> (2 species)
18	Male subgenital plate with long, up- and recurved appendices.....	
–	Male subgenital plate without large appendices.....	19
19	Fastigium verticis narrower than scapus.....	20
–	Fastigium verticis as wide or wider than scapus.....	21
20	Occurring in Madagascar, tegmina wide (ratio length/width = 3).....	
–	Occurring on the Seychelles, tegmina narrow (ratio length/width = 3.5).....	<i>Pelerinus rostratus</i>
21	Eyes elongate, fastigium verticis at least twice as broad as scapus.....	
–	Eyes circular or oval, fastigium verticis less than twice as broad as scapus.....	22
22	Fore femora ventrally armed, ventral edge of ovipositor evenly rounded.....	23
–	Fore femora ventrally unarmed, ventro-posterior edge of ovipositor slightly curved, its dorsal ending bent frontally (horizontal)..... <i>Paraplangia</i> gen. n.	
23	Legs flattened laterally.....	<i>Plangia</i> (3 species)
–	Legs not flattened laterally.....	<i>Madagascarantia (albolineata)</i>
*	Only <i>Mimoscudderia paulyi</i> Massa, 2017 with unusually wide tegmina.	

Tribe Amblycoryphini Brunner von Wattenwyl

Brunner von Wattenwyl (1891) combined several genera in Amblycoryphini using the key character “fastigium as wide or wider than scapus”. This may well be a convergently evolved character, but as long as no better grouping is available, it is useful for placing and finding similar genera. The group included and still includes (even after the splitting by Cadena-Castañeda 2014, 2015) African and American genera which were separated in Brunner von Wattenwyl (1891)’s key but not by Cadena-Castañeda (2014). According to the preliminary molecular tree (Mugleston et al. 2013), *Amblycorypha*, the type genus, is deeply nested among New World genera from different tribes. In other molecular studies, *Eurycorypha* and *Plangia* are closely related (Mugleston 2016), with *Isopsera* nearby (Liu Cx unpubl.). *Indogneta* Ingrisch & Shisodia, 2002, which also has a broad fastigium, certainly belongs to Isopserae (see Kang et al. 2014), and *Isopsera* has ant-like nymphs like *Eurycorypha*.

We also include *Corycomina* Karsch, 1896 because of its similarity to some *Eurycorypha* (*E. flavescens* was considered as member of *Corycomina* Karsch, 1896; see Massa 2017c).

Subtribe Plangiina Cadena-Castañeda, 2015, stat. n. (formerly genus group Plangiæ)

When splitting up Amblycoryphini, Cadena-Castañeda (2015) listed the similarities between Amblycoryphini s.s. and his Plangiæ. They had all generic characters in common except the eye shape. We consider this single trait to be insufficient for excluding *Plangia* and *Monteiroa* from the tribe, especially since Plangiæ obviously do not have any similarities to other phaneropterine genera, but share e.g. nymphal properties with *Eurycorypha*, the largest genus of the tribe (see Hemp in preparation). Despite some doubts, we retain the group as a subtribe and include *Madagascarantia* Massa, 2017, which is a sister genus to *Plangia*, *Pseudoplangia* Massa, 2014, and *Paraplangia* gen. n.

After having seen photos of one of the syntypes of *Plangia albolineata* (described as *Turpilia albo-lineata*), it turned out that *Madagascarantia bartolozzii* is conspecific with this species. Since *Madagascarantia* is considered as generically distinct from *Plangia*, we propose the following taxonomical corrections.

Madagascarantia albolineata (Brunner von Wattenwyl, 1878), comb. n.

syn. n. *Madagascarantia bartolozzii* Massa, 2017

Paraplangia Heller, gen. n.

<http://zoobank.org/F80FFF6B-DDAB-4836-8F16-045E6EC76F27>
urn:lsid:Orthoptera.speciesfile.org:TaxonName:502224

Type species of the genus.—*Paraplangia sinespeculo* sp. n., here designated.

Description.—Large size, short head, wide round eyes, fastigium verticis as wide as or slightly wider than scapus of antennae, in contact with fastigium frontis, fronto-genal carinae very indistinct. Antennae shorter than tegmina. Pronotum without lateral carinae, length shorter than height, two small pits at two-thirds point on midline; prozona hardly separable from metazona, anterior margin straight, posterior margin rounded, with evident lateral excisions where wings are inserted. Prothoracic spiracle slit-like, very

Table 1. List of the known phaneropterine species from Madagascar and some islands in the Western Indian Ocean together with some selected measurements. Abbreviations: Mad = Madagascar, Mau = Mauritius, Com = Comoros, Sey = Seychelles, B.v.W. = Brunner von Wattenwyl. Measurements in mm (taken from original sources).

Species	Distribution				Length of		Width of	Ratio width tegmen/	Ratio length/width
	Mad.	Mau.	Com.	Sey.	pronotum	tegmen	tegmen	length pronotum	of tegmen
<i>Agennis parallelinervis</i> B.v.W., 1891	•				4.8	29	4.5	0.9	6.4
<i>Anchispora appendiculata</i> B.v.W., 1891	•				6.2	46	13	2.1	3.5
<i>Arantia (Arantia) dentata</i> Saussure, 1899		•			7.5	48	10	1.3	4.8
<i>Arantia (Euarantia) mauritiana</i> Saussure, 1899 ^a		•			8.5	60	19	2.2	3.2
<i>Cosmozoma coelebs</i> Carl, 1914	•				9	62	18	2.0	3.4
<i>Cosmozoma doenitzi</i> Karsch, 1889	•				6	37	11.5	1.9	3.2
<i>Cosmozoma sikorae</i> B.v.W., 1891	•				5	30	10	2.0	3.0
<i>Cosmozoma vespertilio</i> Carl, 1914	•				10	65	21	2.1	3.1
<i>Cosmozoma voluptaria</i> B.v.W., 1891	•				8.2	43	17	2.1	2.5
<i>Eucatopta heringi</i> Karsch, 1889	•				3.5	12.5	3	0.9	4.2
<i>Eurycorypha brevipennis</i> Karsch, 1889	•				5	21	10.2	2.0	2.1
<i>Eurycorypha brunneri</i> Brancsik, 1893	•				5.5	35	14	2.6	2.5
<i>Eurycorypha cereris</i> (Stål, 1857)	•				5	28	9	1.8	3.1
<i>Eurycorypha prasinata</i> Stål, 1874	•			•	5	30	10	2.0	3.0
<i>Holochlora biloba</i> Stål, 1874 ^b	•	•?			8	52	14	1.8	3.7
<i>Holochlora mauritiana</i> Massa, 2017		•			7.2	48.1	12.2	1.7	4.0
<i>Madagascarantia albolineata</i> (B.v.W., 1878)	•				9	48	18	2.0	2.7
<i>Megotoessa insulana</i> Karsch, 1889	•				9	47	18	2.0	2.6
<i>Mimoscudderia modesta</i> Carl, 1914	•				5	39	7.5	1.5	5.2
<i>Mimoscudderia paulyi</i> Massa, 2017	•				4.7	45.6	12.1	2.6	3.8
<i>Mimoscudderia picta</i> Carl, 1914	•				5.5	41	7	1.3	5.9
<i>Mimoscudderia spinicercata</i> Massa, 2017	•				4.5	34.2	6.8	1.5	5.0
<i>Nesoscirtella polita</i> Carl, 1914	•				6	37	11	1.8	3.4
<i>Paracosmophyllum atrodelineatum</i> B.v.W., 1891	•				6.5	25	9.5	1.5	2.6
<i>Paraphylloptera relictata</i> Carl, 1914	•				6	39	13	2.2	3.0
<i>Paraplangia sinespeculo</i> sp. n.	•				6.5	42.5	11.7	1.8	3.6
<i>Parapyrrhicia dentipes</i> Saussure, 1899	•				5	34	–	–	
<i>Parapyrrhicia insularis</i> Chopard, 1958			•		4.5	23.5	5.5	1.2	4.3
<i>Parapyrrhicia longipodex</i> Massa, 2017	•				4.2	26.6	4.2	1.0	6.3
<i>Parapyrrhicia madagassus</i> (Karsch, 1889)	•				5	28.5	6.5	1.3	4.4
<i>Parapyrrhicia virilis</i> Carl, 1914	•				5	35	–	–	
<i>Pelerinus rostratus</i> (B.v.W., 1878)				•	6	38	11	1.8	3.5
<i>Phaneroptera sparsa</i> Stål, 1857 ^c	•				3.4	17	2.8	0.8	6.1
<i>Plangia guttatipennis</i> Karsch, 1889	•				6	27.5	8	1.3	3.4
<i>Plangia ovalifolia</i> Bolívar, 1912	•?			•	4.5	29	10	2.2	2.9
<i>Plangia segonoides</i> (Butler, 1878)	•				8	42.5	18.4	2.3	2.3
<i>Polygamus macropterus</i> Carl, 1914	•				9	61	16	1.8	3.8
<i>Polygamus punctipennis</i> Carl, 1914	•				6	50	12.5	2.1	4.0
<i>Sikoriella bimaculata</i> Carl, 1914	•				5	28	10	2.0	2.8
<i>Symmetroraggea depravata</i> Massa, 2017	•				4	26.3	5.4	1.4	4.9
<i>Symmetroraggea dirempta</i> (Karsch, 1889)	•				4.5	29	4.5	1.0	6.4
<i>Trigonocorypha maxima</i> Carl, 1914	•				6	53	15	2.5	3.5
<i>Tylopsis bilineolata</i> (Serville, 1838) ^d	•				3.5	20	3.5	1.0	5.7
<i>Tylopsis irregularis</i> Karsch, 1893 ^e	•				4	30.6	3.5	1.1	8.7
<i>Xenodoxus annulatus</i> (B.v.W., 1891)	•				3	17.5	2.5	0.8	7.0
<i>Xenodoxus nobilis</i> Carl, 1914 ^f	•				2.75	20	3.6	1.3	5.6

^a status doubtful, perhaps error in type locality (see Hollier and Heads 2015)

^b not *biloba* B.v.W. = *Holochlora indica* Kirby

^c data Ragge 1956

^d data B.v.W. 1878

^e data from foto in OSFO

^f data Massa 2017a

long, reaching nearly up to metanotum. Ventral edge of paranota rounded. Tegmina much wider than pronotal length. Right tegmen of male without clearly defined mirror. Hind wings longer than tegmina.

Fore coxae armed, fore femora unarmed, several spinules positioned ventrally on fore tibiae, furrowed proximally, rounded distally, dorsal side rounded or flat or very slightly furrowed (rounded and slightly furrowed on left and right leg of the same specimen), without dorsal spurs. Tympana open on inner and outer side. Mid femora ventrally with 1-2 spinules, mid tibiae with about ten spinules. Hind femora armed ventrally, lower genicular lobe with spine on both sides. Hind tibiae armed ventrally and dorsally, furrowed on all sides. Hind tibiae longer than femora.

Meso- and metasterna with two lobes each, rounded.

Female.—Ovipositor short, curved, but not evenly; ventro-posterior edge of the lower valve only slightly curved, without teeth, dorso-posterior edge sharply bent inwards, this part and distal half of the upper valve serrated. Proximal quarter of right tegmen (dorsal area) with transverse veins bearing small teeth.

Diagnosis.—*Paraplantia* differs from most African and Malagasy phaneropterine genera with open tympana by its fastigium. Being about as wide as scapus, the fastigium is wider than in most genera, but clearly narrower than in *Eurycorypha* and *Monteiroa*. Its width is similar to that of *Plangia* and *Madagascarantia*. These two genera, however, have evenly curved ovipositors. In *Paraplantia*, the fore femora are also unarmed [a character occasionally found within otherwise armed genera: e.g. *Arantia* (Hemp and Massa 2017), but used by Brunner von Wattenwyl (1891) to differentiate genera], which is not observed very often in large species. The paranota are relatively narrow for Plangiina, only about two thirds as wide as high. *Paraplantia* has other unusual characters, like a stridulatory file with relatively few teeth of varying size, which is quite different from that known in *Plangia* and *Madagascarantia*. Its right male tegmen lacking a glossy mirror is not known in any of the similar genera.

Derivatio nominis.—Para, Greek = nearby; *Plangia*, another Plangiina genus. *Paraplantia* feminine.

Paraplantia sinespeculo Heller, sp. n.

<http://zoobank.org/03B56614-F8D3-40C1-8652-EFE6F2C80077>

urn:lsid:Orthoptera.speciesfile.org:TaxonName:502225

Material examined and depository.—Holotype ♂, allotype ♀ and 1 paratype ♂. All pinned, original labels "MADAGASCAR: Mitsinjo Forest Reserve, near Moramanga (18°57'S, 48°13'E), 1 i - 31 xii 2014, coll. Giesse". "Holotype *Paraplantia sinespeculo*" [red handwritten label]. Holo- (CH8239) and allotype (CH8241) in Museum für Naturkunde, Berlin, Paratype (CH8240) in Collectio Heller. One hind leg of CH8240-1 separate in pure ethanol in Collectio Heller.

Sound files are deposited at OSFO and bio.acousti.ca (see also Suppl. materials 1, 2).

Measurements.—(In mm) Males. Body length: 27.5–28.2; pronotum length: 6.8–7.4; pronotum height: 6.9–7.0; hind femur: 19.5–20.0; hind tibiae: 21.9–23.5; tegmina: 43.2–43.8; length of hind wings: 46.4–46.6; tegmina width: 14.3–14.7. Female. Body length: 29.9; pronotum length: 7.8; pronotum height: 7.0; hind

femur: 20.9; hind tibiae: 22.0; tegmina: 43.6; length of hind wings: 47.6; tegmina width: 17.2; ovipositor 13.0.

Diagnosis.—As for genus (sole species).

Description.—Male. Habitus and color: Large bush-crickets, predominantly green with a weak yellow mid line on head and pronotum (Fig. 1; not visible in dried specimens). Anterior (costal) edge of tegmen in basal half to two thirds with white spots. Head, pronotum and thoracic sternites (Fig. 2) as for genus.

The stridulatory area of the left tegmen green, with distinct but not elevated stridulatory vein (Fig. 3A), of right tegmen weakly green or white, with several irregular veins, without glossy mirror (Fig. 3B). The stridulatory vein beginning at the distal end with a series of ca. 15 small teeth, increasing slowly in size. At the same place, the file starting to be elevated above the tegmen level. Having reached the highest point, there are ca. 10 widely spaced large teeth. After five of them, tooth size and spacing continuously decrease again. The file then ends in about 10 small to very small teeth (Fig. 3D).

Fore coxae armed with a long spine. Fore femora unarmed, fore tibiae with 2–3 inner ventral spines and 3 distal ones, superiorly mainly flat (see above). Mid femora with 2 very small spinules, mid tibiae ventrally with about 7 spines each on outer and inner side. Hind femora distally with about 7 outer and 2–4 inner ventral spines, hind tibiae straight, longer than femora, in cross-section square, with many spines on all four edges (about 15 on each ventral, about 25 on each dorsal side).

Abdomen.—Subgenital plate long, tapering into a deeply incised caudal part, bearing long styli (Fig. 4A). Cerci relatively long, slightly in-curved at tip, with a short, strong, hook-like outer and a rounded inner spine (Fig. 4A–B). No sclerotized titillator.

Female.—Color and general habitus like male. Ovipositor as described for genus (Fig. 5A–B). Subgenital plate short, triangular and at apex slightly incised, side sclerites with strong and incurved lower edge (Fig. 4C), probably the anchor point for the male cerci during mating.

Derivatio nominis.—Sinespeculo (Latin = without mirror). To be treated as noun in the nominative singular.

Eggs.—Mature eggs were taken from the female after her death and preserved in ethanol. They show the flat, ovoid shape, typical for phaneropterines (length 5.7 ± 0.2 mm, width 2.75 ± 0.06 mm, $n = 4$; Fig. 1B). The collector wrote "we found the eggs under leaves".

Nymphs.—The specimens were obtained as relatively small nymphs (probably stage 2 or 3). At that time they were nearly completely green with few brown markings (not looking like the small nymphs of *Plangia saticsaerulea*; see Hemp in preparation). Soon they showed a yellow midline running from head to mid of abdomen and they developed a brown pattern at the back of the abdomen, similar to that seen in older *Eurycorypha* nymphs (Hemp in preparation; Fig. 1C–E). The pronotum had a middle keel like the adults in *Tropidonotacris* Chopard, 1954 (Hemp et al. 2014) or *Pelecynotum* Piza, 1967 (OSFO). The males became adult at 9th and 13th May, the female slightly later, at 20th May. The female died on 30th June due to an infection with Nematomorpha and all were prepared.

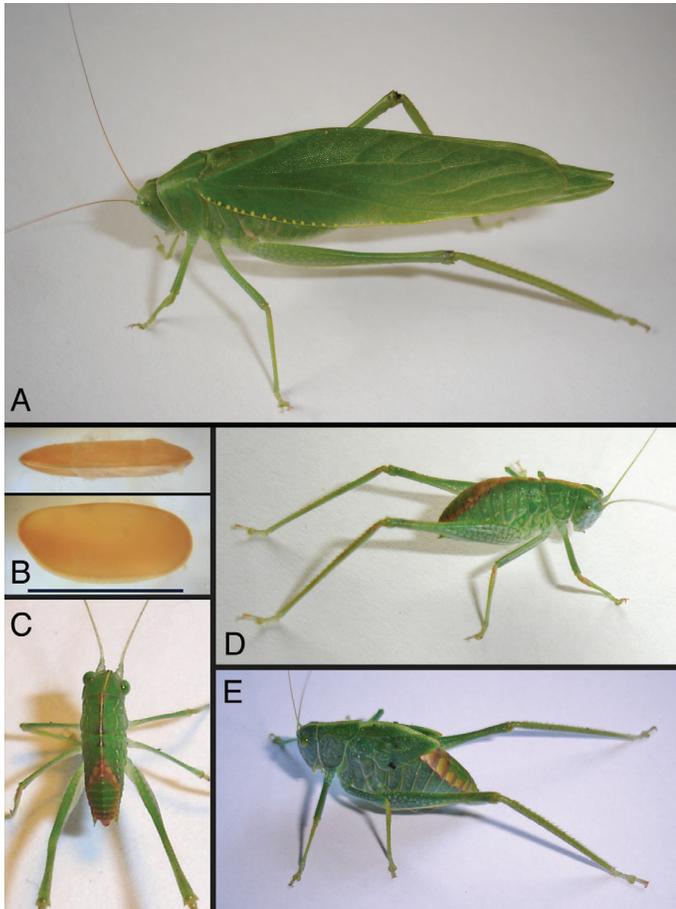


Fig. 1. Habitus. A. Adult male; B. Egg (lateral and ventral view, scale 5 mm); C. Nymph, 3rd March; D. Nymph, 30th March; E. Female nymph, 10th May, 10 days before imaginal molt.

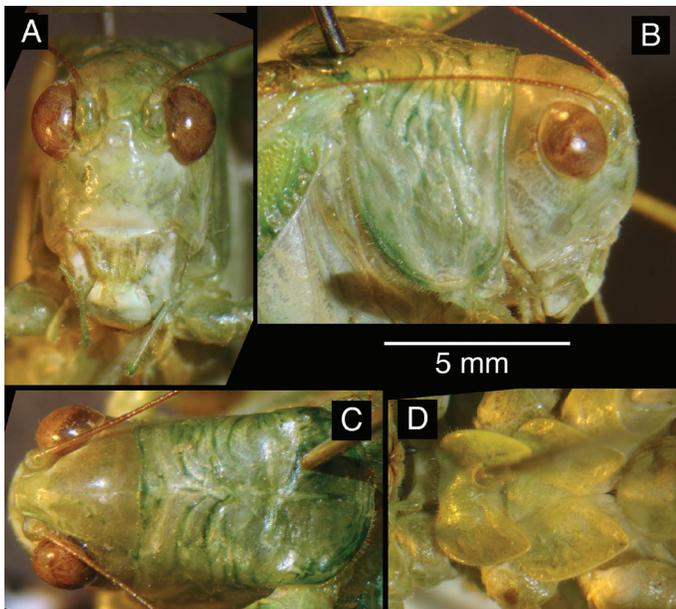


Fig. 2. Head and pronotum. A. Face (head frontal); B. Pronotum lateral; C. Fastigium verticis and pronotum dorsal; D. Meso- and metasterna, head to the left.

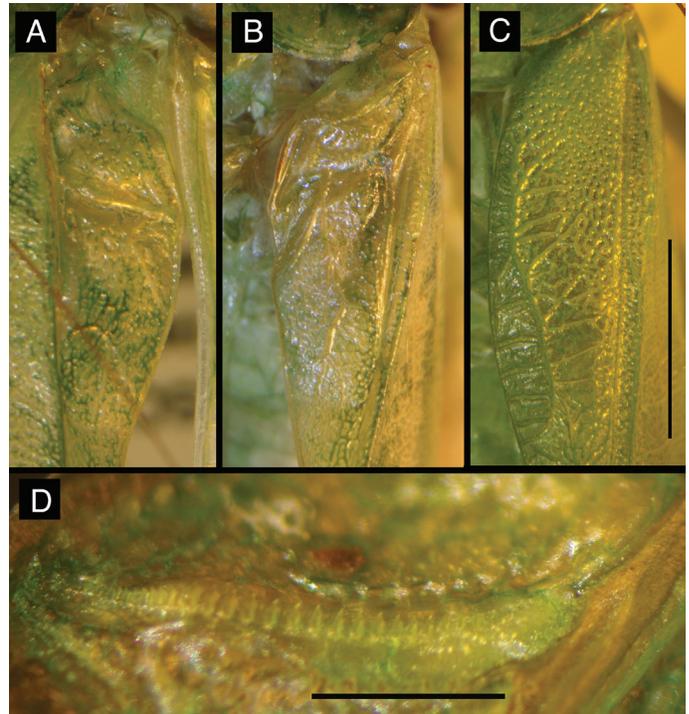


Fig. 3. A, B. Left and right, respectively, stridulatory areas in male and C. Female tegmina (scale 5 mm); D. Male stridulatory file (distal end to the left; scale 1 mm).

Acoustics.—The male calling song consisted of song units, repeated in interval of many minutes as long as the female did not respond. Each song unit (163 recorded) contained two series of syllables, the first with 10.7 ± 1.0 syllables (mean \pm SD; range 8–12; $n = 21$), the second only with 4.2 ± 0.9 (range 3–5; Fig. 6). The second series started 9.3 ± 0.7 s (range 8.3–10.7 s) after the beginning of the first and both series were separated by a silent interval of 4.2 ± 0.4 s (range 3.7–5.3 s). The intervals between the syllables ranged from 400 to 619 ms (487 ± 66 ms), measured in the second half of the first series. In amplitude modulation, both series were decrescendo or without change in loudness. The syllables were very short, less than 5 ms (Fig. 7A), consisting of few, often hardly separable impulses.

Like in most phaneropterines (Heller et al. 2015), the female that was ready to mate reacted to the male song with its own acoustic signals. It always answered after or at the end of the second series. The first response syllable of its response was registered 2.7 ± 0.6 s after the beginning of the second male series (range 1.7–4.2 s; $n = 74$) and 0.55 ± 0.33 s after a male syllable (range 0.04–2.8 s; $n = 73$). The female response was quite variable; the simplest answer consisted of one impulse, but she could also make two impulses at relatively large intervals, long (about 8) series of impulses with short intervals or mixtures with many impulses at varying intervals (Fig. 6B–C; see Suppl. materials 1, 2: duets 1 and 2).

The carrier spectrum of male and female song is relatively narrow-banded with its maximum at about 8.4 ± 0.7 kHz ($n = 3$; range 10 db below peak 7.3–10.2 kHz) in the male and 8.7 ± 0.2 kHz ($n = 3$; range 10 db below peak 6.9–10.9 kHz; Fig. 7) in the female.

Mating behavior.—Both males (body mass 1178 mg and 1236 mg) copulated with the female (body mass 2536 mg, 2528 mg) at an interval of 3 days (21st and 24th June). They mated in the morning



Fig. 4. Subgenital plate and cerci. A. Male subgenital plate and cerci, ventral; B. Male cercus, dorso-lateral view (dorsum to the left); C. Female subgenital plate with lateral sclerites, ventral view.

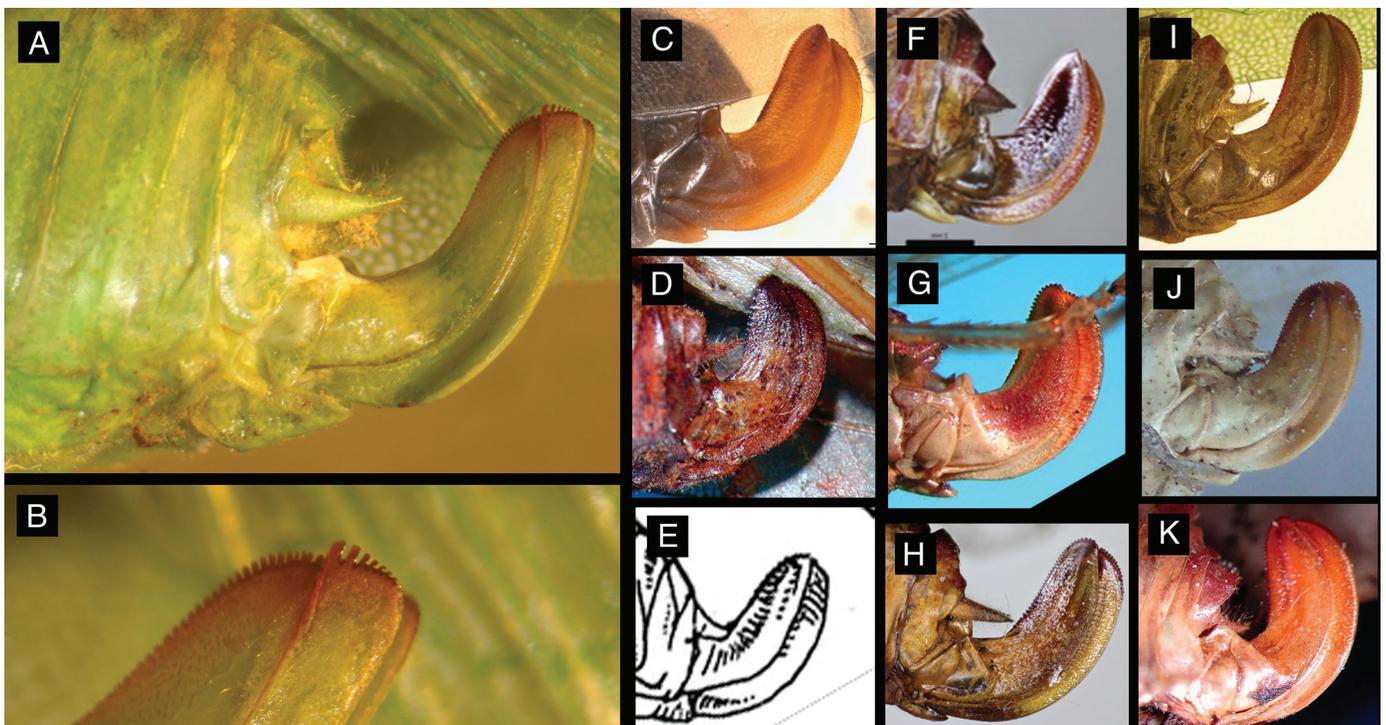


Fig. 5. A, B. Ovipositor of *Paraplantia sinespeculo*; and other Plangiina for comparison; C. *Plangia graminea* (Serville, 1838); D. *P. guttati-pennis* Karsch, 1889; E. *P. karschi* Chopard, 1954; F. *P. multimaculata* Hemp, 2017; G. *P. nebulosa* Karsch, 1890; H. *P. satsiscaerulea* Hemp, 2017; I. *P. variacantans* Hemp, 2017; J. *Madagascarantia albolineata* (syntype); K. *Pseudoplantia laminifera* (Karsch, 1896). Sources OSFO: D, E, G, J, K; Hemp 2017; C; Hemp et al. 2015; F, H, I.

(about 9:00–10:00; they were placed together the evening before, but did not mate) with mating durations of a few minutes and transferred spermatophores of 130 and 151 mg (mean of male loss and female gain), thus about 12% of the male body mass. They were slightly smaller than in *Plangia multimaculata* (17%; Hemp et al. 2015). Both spermatophylaces showed relatively irregularly formed central parts protruding anteriorly, in addition to the symmetrical lateral basal parts (Fig. 8).

Chromosomes.—Both analyzed species, the African *Paraplantia sinespeculo* and *Orophus* cf. *tessellatus* from Costa Rica, showed a dip-

loid chromosome number of $2n = 31$ karyotype in the male with an X0 and 32 in the female (*O.* cf. *tessellatus*) with XX sex determination system. Fifteen pairs of acrocentric chromosomes gradually decreased in size; the sex chromosome (X) was the largest element in the karyotype (Fig. 9A–D). After FISH with 18S rDNA, silver staining, and C-banding, the results demonstrated coincidence between the localization of major ribosomal genes and active NOR as well as the position of C-bands. In individuals of both species, a single large rDNA cluster per haploid genome was detected, located on the first pair of autosomes near the distal region (Fig. 9B – left corner) and active NOR (Fig. 9B) as well as C-band (Fig. 9A).

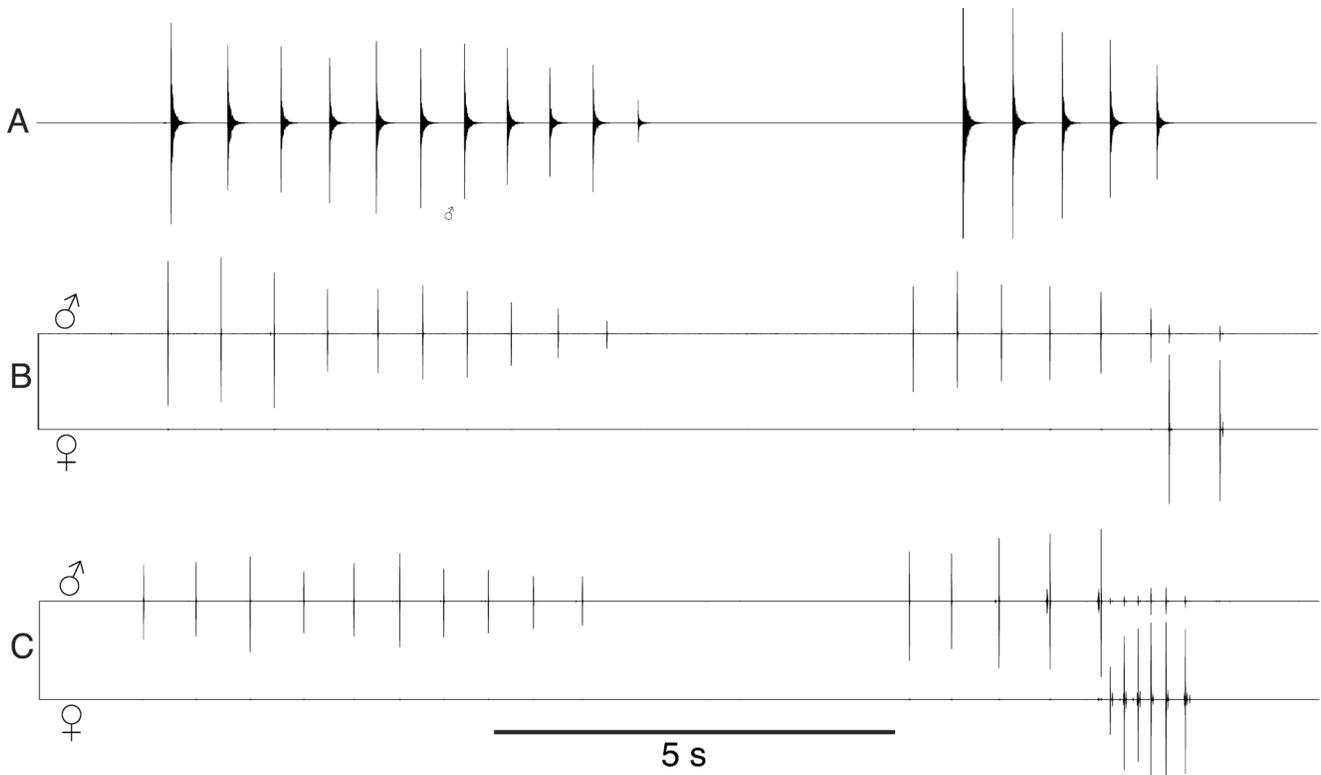


Fig. 6. Oscillograms of: A. the spontaneous male calling song, and B, C. of two-channel recordings of male-female duets (B: Female response with few impulses; C: With many impulses).

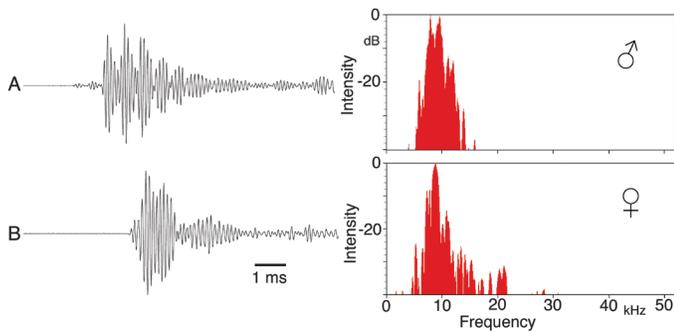


Fig. 7. Oscillograms of: A. A male syllable and; B. A female response together with power spectra (Hanning window, 512 points, mean of 12-ms-section of the song).

In contrast, in *Orophus cf. tessellatus*, FISH revealed a paracentromeric signal on the fourth pair of autosomes (Fig. 9D) coincident with thick C-bands (Fig. 9C) and active NOR (not shown). The signals produced by FISH with the $(TTAGG)_n$ probe were stronger in *O. cf. tessellatus* (Fig. 9D) than those observed in *P. sinespeculo* (hardly visible).

Discussion

Paraplangia sinespeculo belongs to a phaneropterine morphotype which is widespread in many tropical areas. Such medium to large species with long wings of intermediate width and white markings at the costal edge of the tegmina are found in central America (e.g. *Lamprophyllum*, *Philophyllia*; Fontana et al. 2008, and

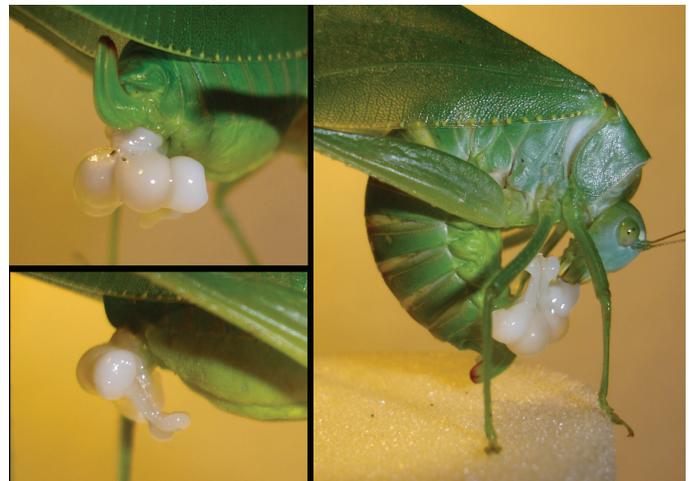


Fig. 8. Female with spermatophore after mating.

Syntechna; Cadena-Castañeda 2014), Australia (e.g. *Paracaedicia*; Rentz 2010), China (e.g. *Sinochlora*; Kang et al. 2014), and Africa (e.g. some *Arantia*; Hemp and Massa 2017). They are unlikely to be closely related and do not seem to possess any other special characters in common. Their specific ecological adaptations are unknown for all of them. They may live in trees with similar leaf shape or spend the day at special roosting sites where the shape of the tegmina essentially improves the camouflage among the leaves.

However, some morphological similarities may have been overlooked. Many species do not have any or have only weakly developed mirrors on the right wing (checked in OSFO for members

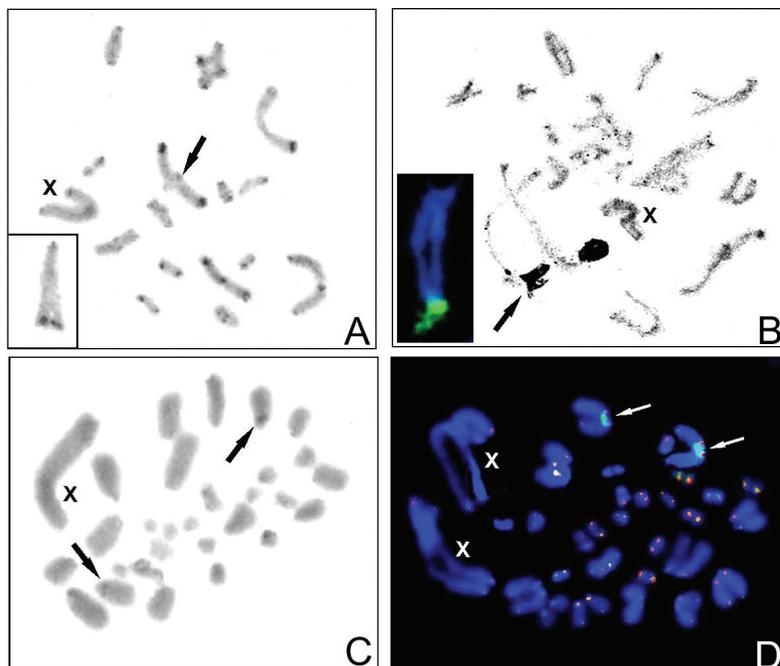


Fig. 9. Chromosomes of: A, B. *Paraplantia sinespeculo* and; C, D. *Orophus* cf. *tessellatus* stained using different techniques: C-banding (A, C), silver staining (B), and FISH with both 18S rDNA (green) and telomeric DNA (red) probes (B – left corner and D). Diakinesis and the insert in the left corner mitotic large chromosome (A), diplotene and FISH with 18S rDNA in the left corner mitotic chromosome (B): arrows and the insert chromosome demonstrated distally located thin C-band and single NOR coincide with cluster of 18S rDNA on the first pair of autosome. Arrows in spermatogonial (C) and female metaphases (D) indicate near paracentromeric located C-bands and 18S rDNA loci on the fourth pair of chromosomes. X indicates sex chromosome.

of the above-mentioned genera; only the morphologically very diverse *Arantia* seems to also be variable in this character: *A. fasciata* has a large distinct mirror, while some other *Arantia* species have small and/or indistinct ones, and *A. mauritiana* does not have one at all; Hemp and Massa 2017). The mirror is an important structure for sound radiation and is considered as typical for bush-crickets (e.g. Montealegre-Z et al. 2017). However, its systematic distribution and size have never been studied in detail. In some species it is a typical 'mirror', a large, thin, transparent membrane covering a significant portion of the tegmen's width, while in others it is hardly discernible at all (for examples see e.g. fig. 5 in Heller et al. 2014). In Amblycoryphini (Old and New World species) and some other phaneropterines (see above), it is often, if not always, weakly developed or even missing. On the contrary, in many Poreuomenini, another African tribe which occurs together with Amblycoryphini and Phaneropterini (according to OSFO), it is large and transparent. Correlations with song characteristics are unknown. Unfortunately, in many descriptions of new species, even in recent ones, size and shape of the mirror are often not mentioned nor illustrated.

Amblycoryphini are well known for the complexity of their songs, as in the type genus *Amblycorypha* (e.g. Walker 2004). Some species can produce up to four different syllable types. This complexity results obviously from different neuro-muscular programs used for the stridulatory movements. The stridulatory files can differ in tooth number between species (Walker 2004), but do not show any irregularities (see front page of Science, Walker and Dew 1972). Also the song of another New World species, *Orophus conspersus* (Brunner von Wattenwyl, 1878), contains several different song elements (Taliaferro et al. 1999), produced with a simple file (see Cadena-Castañeda 2014). The calling songs of two African *Plangia* spe-

cies, however, are relatively simple (Hemp et al. 2015). They consist of short di- or tri-syllabic echemes or of single syllables, sometimes combined into small series. In contrast, *Paraplantia* males produce a relatively long song which is answered by the female at its end, suggesting that the latter evaluates the preceding syllable pattern. The very short syllables would seem to be suitable as trigger for a very fast female response (e.g. Heller et al. 2018), but there is no strict temporal correlation between the female response and any parameter of the male song. The female responded with a relatively long and variable delay of about 0.5 s after a syllable (mostly the last) of the second series of the male, so the female signal may be interpreted by eavesdropping male rivals as an additional male syllable. Also the carrier frequency and the intervals between additional female responses would fit into this pattern. However, the female sometimes produced quite fast response series with unknown function. The male file with its low teeth number and abrupt change in tooth density differs from all genera mentioned above.

Paraplantia has a relatively broad fastigium verticis. This character is generally rare in long-winged phaneropterines worldwide as well as in Africa (e.g. in *Monteiroa* and *Pseudoplantia*; Ragge 1980), but surprisingly frequent in Madagascar (genera *Eurycorypha*, *Madagascarantia*, *Plangia*, *Paraplantia*). It is unknown if the reasons are phylogenetic, biogeographical, ecological or accidental. In any case, the commonness is not based on a Malagasy radiation. All these genera are currently included in Amblycoryphini. Surprisingly, they also share a flat (only in some *Plangia* and a few *Eurycorypha* very slightly sulcate; own unpublished observations) or rounded dorsal surface of the fore tibiae, which is also uncommon among Phaneropterinae. In the amblycoryphine genera *Amblycorypha* and *Orophus*, fore and middle tibia are dorsally sulcate (Brunner von Wattenwyl 1878). In size, habitus

of adults and nymphs, and shape of the male subgenital plate, *Paraplangia* shows surprising similarities to *Gonatoxia* (Hemp in preparation), but differs in width of fastigium and structure of the tympana.

Representatives of the two Amblycoryphini genera examined in this study, *Paraplangia* and *Orophus*, have a karyotype including 31 (male) or 32 (female) acrocentric chromosomes with X0 (male) and XX (female). This chromosome number coincides with previous studies, which revealed that more than 50 genera of phaneropterines found in the Palaearctic region, South America, East Africa and India are characterized by such basic/ancestral karyotypes (e.g. for review see Warchałowska-Śliwa 1998, Hemp et al. 2014). It should be noted that this chromosome number, morphology (except for the bi-armed X chromosome) and sex determination system was found also in Canadian specimens of *Amblycorypha oblongifolia* (De Geer, 1773; Beaudry 1973). However, this plesiomorphic chromosome number is reduced to 29 (X0) in the African genera *Plangia* (Hemp et al. 2015) and *Eurycorypha* (Hemp et al. 2013 and unpublished data Warchałowska-Śliwa) as a result of a tandem fusion between two pairs of autosomes. Additionally, in comparison to *Paraplangia* and *Orophus* with an ancestral acrocentric X chromosome, pericentric inversions modified the position of the centromere and changed the morphology of the X chromosome from acrocentric to bi-armed in *A. oblongifolia* and some species of *Plangia* and *Eurycorypha*. In the Amblycoryphini chromosomes described in this paper as well as in that of *Eurycorypha* and *Plangia* (Hemp et al. 2013, 2015, respectively) one 18S rDNA FISH locus (per haploid genome) coincides with a single active NOR and C-band segment, independently from the number of chromosomes in the set. However, in these species, different patterns of the location of rDNA/NOR were observed. The single 18S rDNA loci revealed by FISH are located distally on the largest autosome in the Malagasy *Paraplangia* ($2n = 31$, present study) and the African *Plangia* ($2n = 29$, Hemp et al. 2015), but were found in the paracentromeric region of a medium-sized chromosome in the Costa Rican *Orophus* ($2n = 31$; present paper) and in an interstitial region on a short autosome in African species of *Eurycorypha* (Hemp et al. 2013). The cytogenetic study presented here constitutes another step to better understanding of chromosome organization and the evolution of Phaneropterinae species and genera.

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Supplementary material 1

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Data type: WAV file

Explanation note: Male-female-duet 1 (2-channel-recording) with female response consisting of few impulses (microphone male UHER M645, female SONY ECM-121, T=25°C).

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Supplementary material 2

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Data type: WAV file

Explanation note: Male-female-duet 2 (2-channel-recording) with female response consisting of many impulses (microphone male UHER M645, female SONY ECM-121, T=25°C).

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