Short Communication
Journal of Orthoptera Research 2019, 28(1): 1-2

Yellow-winged digging grasshopper, *Acrotylus longipes* (Acrididae: Oedipodinae), confirmed in Croatia

Dora Papković[1], Antun Jelinčić[2]

1 Petrova 12, 10000 Zagreb, Croatia.
2 Ćire Truhelke 15, 10000 Zagreb, Croatia.

Corresponding author: *Dora Papković* (dora.tosamja@gmail.com)

Academic editor: *Daniel Petit* | Received 21 October 2018 | Accepted 4 December 2018 | Published 13 February 2019

http://zoobank.org/E7E8AFE8-21F8-4947-A921-690700E7F67C

Citation: Papković D, Jelinčić A (2019) Yellow-winged digging grasshopper, *Acrotylus longipes* (Acrididae: Oedipodinae), confirmed in Croatia. Journal of Orthoptera Research 28(1): 1–2. https://doi.org/10.3897/jor.28.30736

Abstract

We present the first confirmed record of the threatened yellow-winged digging grasshopper, *Acrotylus longipes* (Acrididae: Oedipodinae), from Croatia, from the island of Mljet, in Blace Bay. The yellow-winged digging grasshopper was found on sandy dunes covered with psammophytic vegetation characteristic of this type of habitat. Previously, only two localities of this species were reported from Croatia, both from photographs. This confirmed locality opens the possibility of a wider distribution of this species on similar habitats throughout Croatia.

Key words

Adriatic island, geographic distribution, Mljet, new record, Vulnerable

Introduction

The yellow-winged digging grasshopper, *Acrotylus longipes* (Charpentier, 1845), is a xerophilic and thermophilic species of the Acrididae family, subfamily Oedipodinae (Bounechada et al. 2006). The species inhabits coastal and riverine sand dunes in the Mediterranean, from the Canary Islands to Ukraine (Hochkirch et al. 2016). In addition to the Mediterranean area, the species has also been reported from similar habitats inland in the Balkans, from the Pannonian Plain on the border of Serbia and Romania, and from Macedonia, close to the border with Greece (Grebenschikov 1947).

In Croatia, the species is known only from two localities, Zaton in Dubrovnik Area and the island of Šolta, both recordings being doubtful as they are based solely on photographs (Skejo et al. 2018). In Italy, the grasshopper is also found living in highly disturbed sandy habitats (Fontana and Kleukers 2002). In addition to its coloration, the species is adapted to sandy conditions by alternating use of its legs so just three of them are touching the hot sand at a time, and it can also dig itself into the sand on cold or windy nights (Fontana and Kleukers 2002).

Since its subpopulations are severely fragmented, the species was listed on the IUCN Red List as Vulnerable (VU) in the 28 countries of the European Union EU28 and Near Threatened (NT) in Europe (Hochkirch et al. 2016). The largest threats to their habitats are river regulations and the development of tourism, which could lead to further fragmentation of habitats and a more pronounced edge effect (Hochkirch et al. 2016, Fontana and Kleukers 2002).

Methods

Blace Bay is located in the south-east part of the island of Mljet (Fig. 1; 42°41′29″N, 17°44′32″E), one of the southernmost Croatian Adriatic islands. D.P. and A.J. visited Blace Bay on August 28th, 2018, between 17:00 and 18:00. It was a hot and sunny day with a temperature of 34 °C. Specimens of *A. longipes* were recorded in notable abundance here (about 40 specimens were observed in one hour). The species was identified by diagnostic characters in the field from the keys of Harz (1975), Massa et al. (2012), and Willemse et al. (2018), and compared to *A. patruelis* and *A. insubricus*.

Results and discussion

On the habitat of the species on the island of Mljet.—Blace is a small bay with a narrow passage to the open sea. Therefore it is protected from the heavy impact of waves and wind which allows unobstructed sedimentation of sand. The silicate sand stretches along the coast for about 500 m. This sand contains vegetation from the classes *Ammophiletea* Br.-Bl. et Tx. ex Westhoff, et al. 1946 and *Cakiletea maritimae* Tx. et Preising in Tx. ex Oberd 1952 (Alegro et al. 2004). The soil formed from this sand can be classified as arenosol and represents the very first stage of soil development from this substrate. Because the Adriatic coast is mostly karstic, this type of habitat is rare and the psammophytic vegetation that is present on the sandy shores is fragmented and exists only in a few localities in Croatia. Mljet contains the largest contiguous area covered with this type of vegetation. Mljet includes Blace, Mala Saplunara and Velika Saplunara Bays (Alegro et al. 2004).

On the new record of Acrotylus longipes.—We found a notable abundance of *A. longipes* jumping between sedges (*Cyperus capitatus*) and other plants (Fig. 2). Altogether, about 40 specimens

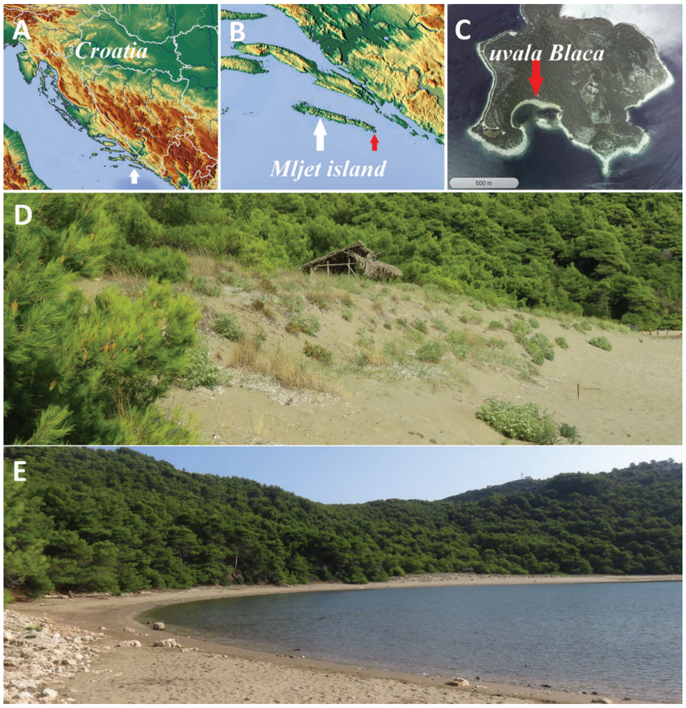


Fig. 1. Images of the study site: **A–C.** The location of Blace Bay in Croatia in the southeast of the island of Mljet; **D.** The psammophytic vegetation where the species was found; **E.** Blace Bay.

Fig. 2. *Acrotylus longipes* male specimen in its natural sandy habitat. **A.** Lateral view; **B.** Dorsal view.

were observed of both males and females. Because of its fine, cryptic coloration as an adaptation to the structure of the sand, it is barely visible on the sand surface, especially for potential predators. The insect is mostly visible when jumping. The yellow-winged digging grasshopper is distinguishable from other *Acrotylus* species, as its common name proposes, by its yellow, rarely orange, hind wings. These hind wings lack a black band that is present in both *A. insubricus* and *A. patruelis*. Another helpful character is the long and slender legs lacking setae, while both *A. insubricus* and *A. patruelis* have legs with many setae. In Croatia, *A. patruelis* is known from the Adriatic part, while *A. insubricus* has been recorded on continental sands (Skejo et al. 2018).

The yellow-winged digging grasshopper was previously known from Croatia from two photographs, which were likely to represent this species – one from Zaton taken by F. Chladek (Biolib 2018), and one taken by D. Sule on Šolta island (Skejo and Sule 2015, Skejo et al. 2018). Those records were never confirmed, and the latter was published as *Acrotylus* cf. *longipes*. In conclusion, the knowledge on this species is scarce and here we contribute new knowledge of its geographic distribution. Although the records of this species in Croatia are few, it is assumed that its distribution could be wider. Since the Pannonian Plain where the species' presence was confirmed extends into north-eastern Croatia along the Drava River, there is a possibility of the presence of *A. longipes* there. This record confirms the species presence in Blace Bay and increases the possibility of a wider distribution of this species on the island of Mljet because of the abundance of sandy habitats suitable for this species.

Acknowledgements

We thank Josip Skejo for confirming the identification, checking the manuscript, and proofreading.

References

Alegro A, Biljaković M, Bogdanović S, Boršić I (2004) Psammo-halophytic vegetation on the largest sand area on the Croatian coast: the island of Mljet, southern Adriatic. Biologia 59: 435–445.

Biolib (2018) *Acrotylus longipes*. https://www.biolib.cz/en/taxonimage/id177709/?taxonid=397066 [accessed 1 September 2018]

Bounechada M, Doumandji SE, Çiplak B (2006) Bioecology of the Orthoptera species of the Setifian Plateau, North-East Algeria. Turkish Journal of Zoology 30: 245–253.

Fontana P, Kleukers RMJC (2002) The Orthoptera of the Adriatic coast of Italy (Insecta: Orthoptera). Biogeographia 23: 36–53. https://doi.org/10.21426/B6110182

Grebenschikov O (1947) The occurrence of *Acrotylus longipes* (Charpentier, 1845) in Yugoslavia (Orthoptera, Acrididae). Physiological Entomology 22: 101.

Harz K (1975) Die Orthopteren Europas II./ The Orthoptera of Europe II. Dr. W. Junk B.V., The Hague, 939 pp. https://doi.org/10.1007/978-94-010-1947-7

Hochkirch A, Puskas G, Sirin D, Ivkovic S, Szovenyi G, Chobanov DP, Lemonnier-Darcemont M, Skejo J, Rutschmann F, Presa JJ, Kristin A, Willemse LPM, Kleukers R (2016) *Acrotylus longipes*. The IUCN Red List of Threatened Species 2016 (downloaded September 5th 2018). Available at: https://www.iucnredlist.org/species/15431174/70826598

Massa B, Fontana P, Buzzetti FM, Kleukers RMJC, Odé B (2012) Fauna d'Italia – XLVIII – Orthoptera. Calderini, Bologna, 563 pp.

Skejo J, Sule D (2015) Prvi doprinos poznavanju raznolikosti zrikavaca i skakavaca (Insecta: Orthoptera) Šolte // First contribution to the knowledge of crickets' and grasshoppers' diversity (Insecta: Orthoptera) on the Island of Šolta. Bašćina 24: 19–24.

Skejo J, Rebrina F, Szövényi G, Puskás G, Tvrtković N (2018) The first annotated checklist of Croatian crickets and grasshoppers (Orthoptera: Ensifera, Caelifera). Zootaxa 4533: 1–95. https://doi.org/10.11646/zootaxa.4533.1

Willemse LPM, Kleukers RMJC, Odé B (2018) The grasshoppers of Greece. EIS Kenniscentrum Insecten and Naturalis Biodiversity Center, Leiden, 439 pp.

Anaxipha hyalicetra sp. n. (Gryllidae: Trigonidiinae), a new sword-tailed cricket species from Arizona

Jeffrey A. Cole[1,2], David H. Funk[3]

1 Natural Sciences Division, Pasadena City College, 1570 East Colorado Boulevard, Pasadena, CA, 91106, USA.
2 Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA, 90007, USA.
3 Stroud Water Research Center, Avondale, PA, 19311, USA.

Corresponding author: *Jeffrey A. Cole* (jacole@pasadena.edu)

Academic editor: *Juliana Chamorro-Rengifo* | Received 28 September 2018 | Accepted 29 December 2018 | Published 11 April 2019

http://zoobank.org/53A484AD-2D25-4DB7-8C36-A9666237829C

Citation: Cole JA, Funk DH (2019) *Anaxipha hyalicetra* sp. n. (Gryllidae: Trigonidiinae), a new sword-tailed cricket species from Arizona. Journal of Orthoptera Research 28(1): 3–9. https://doi.org/10.3897/jor.28.30143

Abstract

A new *Anaxipha* species is described from a locality in southeastern Arizona adjacent to the border with Mexico. The species is unique among the North American fauna by virtue of the broad tegmina, distinctive male genitalia, and calling song phrased in an irregular chirp with a variable pulse train rate. The possibility that the behavioral repertoire of this species includes aggressive song as well as calling song is discussed.

Key words

aggressive song, calling song, mate recognition, Mexico, Neotropical, Sonora

Introduction

Anaxipha is a speciose genus of small crickets with a worldwide distribution (Walker and Funk 2014, Cigliano et al. 2018). The systematics of *Anaxipha*, and of the Trigonidiinae in general, are in a primitive state (Otte and Perez-Gelabert 2009). Regional systematic studies have revealed entire faunas of these crickets in recent years (Otte 2006, Otte and Perez-Gelabert 2009, Walker and Funk 2014), and numerous new species await description (e.g. Tan 2012, DHF unpublished data). A revision of the North American *Anaxipha* described two-thirds of the fauna as new to science (8 of 13 species; Walker and Funk 2014). All species known to date occur in the eastern portion of the continent (Walker and Funk 2014, Cigliano et al. 2018).

While engaged in general Orthoptera collecting in southeastern Arizona in 2013, the first author followed an unfamiliar calling song to discover an *Anaxipha* population. Apart from the highly disjunct locality, which is adjacent to the border of the United States with Sonora, Mexico, this *Anaxipha* immediately stood out as new to the North American fauna by virtue of the broad tegmina of males and the variable pulse train rate in the male calling song. Laboratory study revealed distinct genitalia and stridulatory file characteristics. No morphologically similar *Anaxipha* were found among specimens at the Academy of Natural Sciences of Drexel University (DHF pers. obs.). The species is described here as new.

Methods

Fieldwork was performed at dusk and at night during 15–16 July 2013, 23 July 2014, and 29–31 August 2014. Triangulation of calling songs, visual inspection, beating, and sweeping of vegetation were all employed to secure specimen series. Specimens are deposited at the Natural History Museum of Los Angeles County (LACM), at the Academy of Natural Sciences of Drexel University (ANSP), and at the University of Florida (UFL).

Habitus images (Fig. 1) were made at LACM using a digital microscope (model VHX-6000, Keyence Corp., Itasca, IL) with a 10× objective lens. With this microscope, a calibrated anchor point-based digital measurement function was used to obtain the following morphological measurements (in mm) for a subset of dried specimens deposited at LACM: body length (BL, measured from the front of the head to the end of the tegmina for males and to the end of the ovipositor for females), body width (BW, measured at the widest point of the tegmina immediately behind the hind trochanters), and hind femur length (HF). Measurements are reported as mean ± standard deviation (range) separately for each sex.

Male genitalia were removed from a pinned specimen that had been relaxed and cleared in hot 10% KOH. These were mounted in glycerin on a well slide and photographed using a trinocular microscope (Labophot, Nikon Inc., Melville, NY) equipped with a digital SLR (model T1i, Canon Corp., New York, NY) controlled with Canon EOS Utility software in Live View mode. Images taken at several focal points were composited in Adobe Photoshop CS3 software (Fig. 2A). Afterward, the genitalia were transferred to a genitalia vial with glycerin which now resides with the specimen.

The right tegmen of the above specimen was removed and slide-mounted in euparal. The tegmen was then photographed with the trinocular microscope (Fig. 2B). A single digital image was constructed from multiple fields using Adobe Photoshop. File counts were made from the photograph and, starting at the hind margin, a small red dot was added every 10th tooth to facilitate counting (Fig. 2C). Linear measurement was made from the first tooth (closest to hind margin) to the junction of the stridulatory vein and the harp vein. This measurement was expressed as length of cell 5 (sensu Otte 1994) and tooth density was estimated from this region in order to minimize errors attributable to straight-line measurement of the (slightly curved) stridulatory vein.

Songs were recorded in the field and in the laboratory using a digital linear PCM recorder with a built-in condenser microphone pair (model PCM-D50, Sony Corp., New York, NY). This device recorded .wav files at a 96 kHz sampling rate and a bit depth of 16 with a flat response range extending to 40 kHz. The temperature of laboratory recordings was controlled at 24.1 ± 0.7°C (Table 1). Temperature was measured with a digital thermal sensor (model Trail Pilot 2, Highgear USA, Inc., Fletcher, NC).

Recordings were visualized (Fig. 3) with Raven Lite v. 2.0 (Cornell Laboratory of Ornithology, available from http://www.birds.cornell.edu/brp/raven/RavenOverview.html) and analyzed using BatSound (Pettersson Elektronik AB 2001). The Pulse Characteristics feature of BatSound automatically extracted pulse durations, intervals, and peak frequencies from the .wav files. Oscillogram thresholds for pulse characteristics extraction were set between -18 and -10 dB, with higher values necessary to avoid higher noise floors. Noise below 2 kHz was attenuated with a Butterworth high pass filter in BatSound before analysis. Spectrogram settings for peak frequency measurement were a Hanning Window employing a 256 Hz fast Fourier transformation. Song terminology follows that of Walker and Funk (2014). Abbreviations for song characters are reiterated here for convenience and are graphically shown in Fig. 3:

PD	pulse duration
PI	pulse interval
PP	pulse period (=PD+PI)
PR	pulse rate (=1/PP)
Pdc	pulse duty cycle (=PD/PP)
PT	pulse train
PN	number of pulses per train
PTD	pulse train duration
PTI	pulse train interval
PTP	pulse train period (=PTD+PTI)
PTR	pulse train rate (=1/PTP)
PTdc	pulse train duty cycle (=PTD/PTP)
PTCF	pulse train carrier frequency

Statistical analysis was performed in R (R Core Team 2015). *Anaxipha* songs are complex, and our analysis considered 12 song characters. Besides those characters that are mathematically related (see abbreviations above), additional correlations may exist among characters. To find statistically independent variables for analysis, we explored song character data structure with maximum likelihood factor analysis. The number of components to extract was determined by examining a scree plot generated with the nFactors package (Raiche and Magis 2015). A distinct inflection point ("knee") in the plot of eigenvalues vs. components indicates the number of components to extract. The number of components output by the nFactors scree plot was then input into the factanal function, with rotation set to varimax. The output of this function consists of statistically independent factors, together with the magnitudes and signs of the contributions of the song characters to each factor. A MANOVA compared song character means between field and laboratory conditions.

Results

Anaxipha hyalicetra Cole & Funk, sp. n.

http://zoobank.org/1CF3949F-F602-4AEA-ACB6-FF1195B2766D
http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:505367
Fig. 1: habitus and morphology; Fig. 2: male genitalia, tegmina, and stridulatory file; Fig. 3: songs, recording 140723_11, available as Suppl. material 1.

Holotype.—1 male. USA. ARIZONA: Santa Cruz County; Peña Blanca Canyon, Coronado National Forest, 31.38230, -111.09251, elevation 1203 m. 23-VII-2014. J.A. Cole leg. Recording number 140814_00. Prepared with tegmina raised. Right antenna missing most of the flagellum, otherwise complete (Fig. 1A, B). Deposited in LACM.

Paratypes.—3 males, 1 female (pinned), same data as holotype (ANSP); 5 males, 1 female, same data as holotype (FSCA); 4 males, 2 females (pinned), 4 males (DNA vouchers SING0518, SING0519, SING0520, SING0521 in 100% ethanol), same data as holotype (LACM); 2 males (pinned), same locality as holotype collected 31-VIII-2014 (LACM); 5 males (pinned), 2 males (DNA vouchers SING0453, SING0454 in 100% ethanol), same locality as holotype collected 15-16-VII-2013, J.A. Cole and J.F. Limón leg. (LACM).

Measurements.—Males (n = 7): BL = 7.63 ± 0.24 (7.38 – 7.95), BW = 3.38 ± 0.18 (3.13 – 3.73), HF = 4.20 ± 0.14 (4.00 – 4.35); females (n = 2): BL = 7.31 ± 0.27 (7.11 – 7.50), BW = 1.95 ± 0.06 (1.91 – 1.99), HF = 4.25 ± 0.23 (4.08 – 4.41).

Hind wings.—No specimens among the type series are macropterous.

Seasonal occurrence.—Available records suggest early summer to midsummer adult activity. Individuals were common from 15–23 July in two consecutive years. By 31 August 2014, males were scarce, and no females were found. Males collected 23 July lived in captivity until 19 August.

Habitat.—The population resides in a north-south trending canyon. Within the canyon, individuals are most common in the creek bed at the canyon bottom but extend a short distance up the canyon walls into mixed woodland. During both July collecting events monsoon rains had recently fallen in the canyon and humidity was high. Crickets were found on catclaw acacia (*Senegalia greggii* (A. Gray)), on stems of pointleaf manzanita (*Arctostaphylos pungens* Kunth), on *Yucca*, on bunch grass, and on oak leaf litter. Like other North American *Anaxipha*, individuals perched within 1 m of the ground (Walker and Funk 2014). Acoustic activity was observed in the field from 19:41 to 22:05 h. In July and August, *A. hyalicetra* was sympatric with *Oecanthus californicus* Saussure, an arboreal chirping *Oecanthus rileyi* Group sp., *Gryllus ?personatus* Uhler, and two undescribed *Gryllus* species. *Cycloptilum* sp. and *Hoplosphyrum* sp. scaly crickets (Mogoplistidae) were found in the same habitat during the August 2014 collecting event.

Diagnosis.—*A. hyalicetra* has a unique combination of morphological characters among the North American *Anaxipha* fauna. The

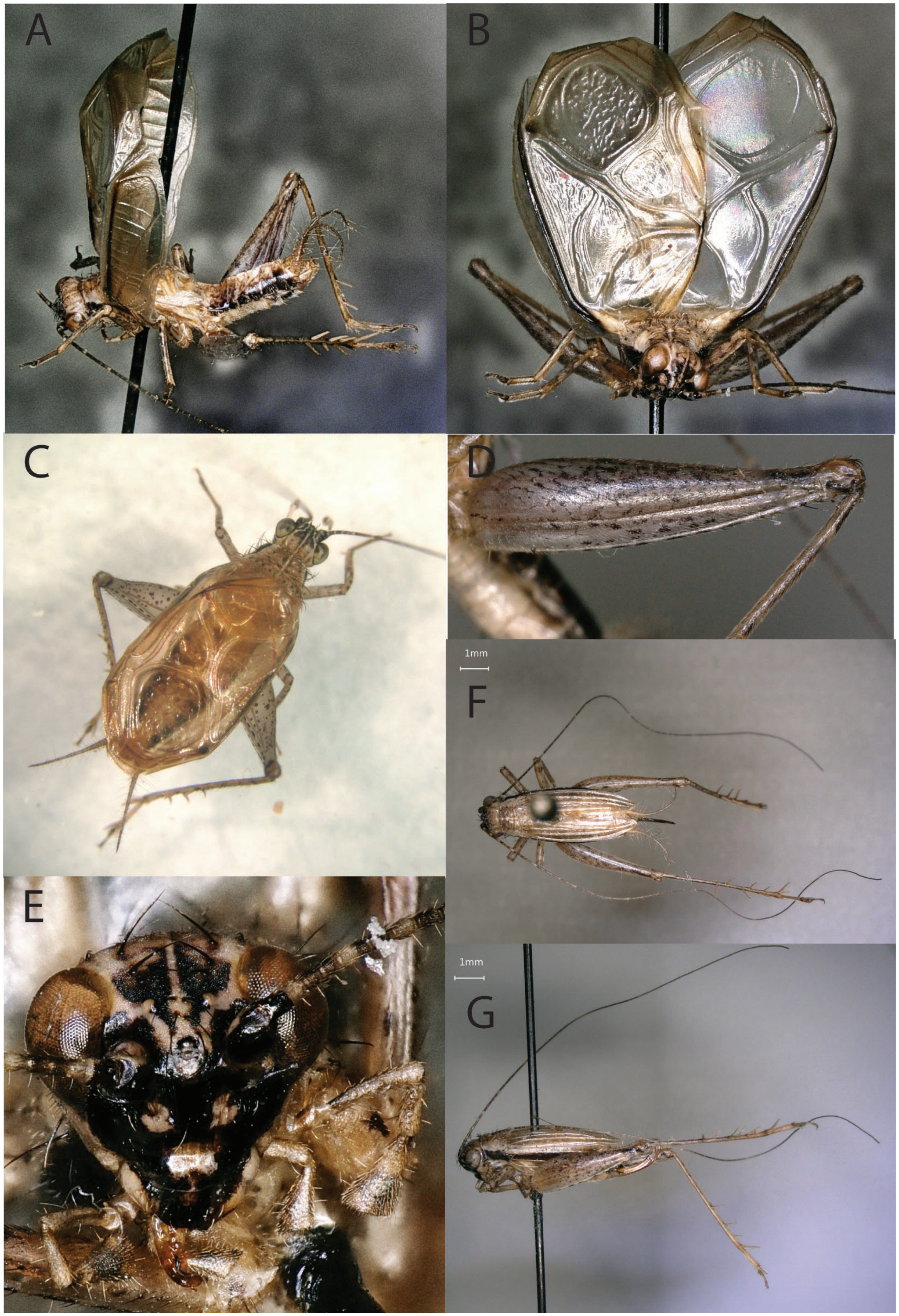


Fig. 1. A. Holotype male, dorsolateral view; **B.** Holotype male, anterior view; **C.** Paratype male, living habitus; **D**. Holotype male, left hind femur; **E.** Holotype male, face; **F.** Paratype female, dorsal view; **G.** Paratype female, lateral view.

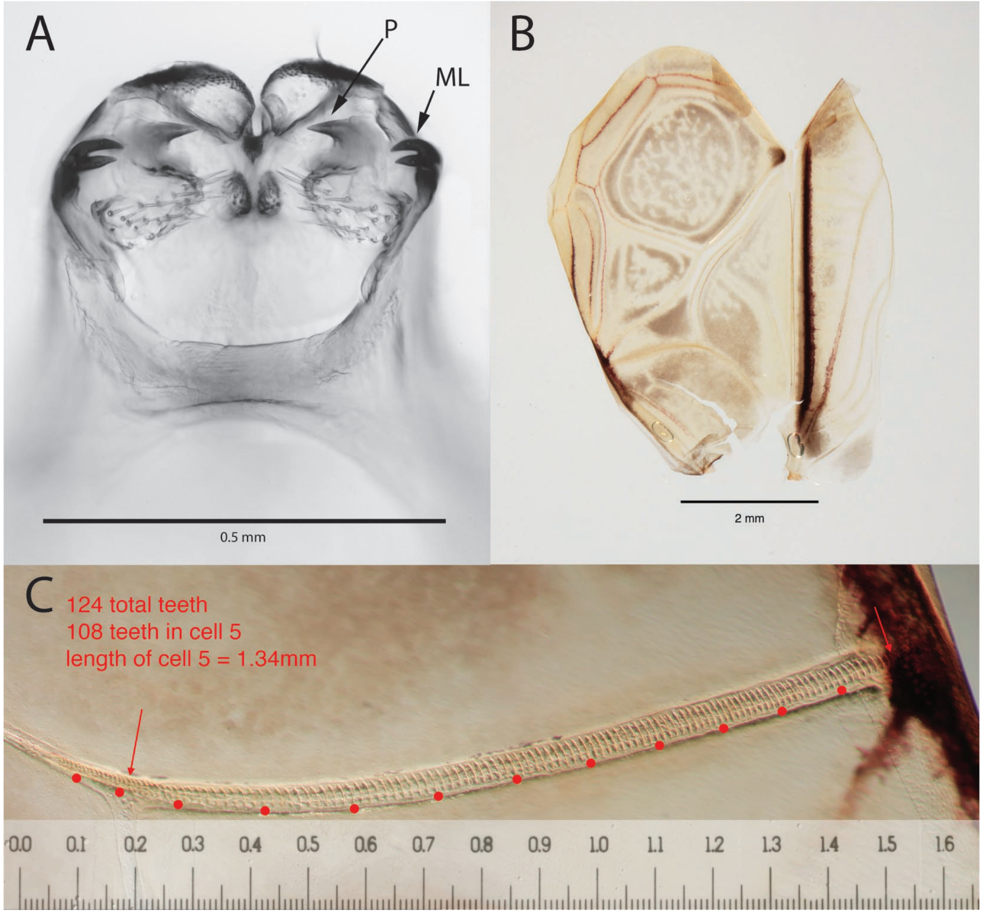


Fig. 2. A. Paratype male genitalia, oblique posterodorsal view, P = paramere, ML = median lophus; **B.** Paratype male excised left tegmen (recording numbers 140811_01 and 140723_15), posterior edge of tegmen at top of image; **C.** Paratype male, stridulatory file, same male imaged in B.

basal segment of the hind tarsus is longer than segments 2 + 3 combined, a feature that is also found in *A. imitator* (Saussure), *A. calusa* Walker & Funk, and many Neotropical species. The male tegmina in *A. hyalicetra* are broader than in every other *Anaxipha* species (Fig. 1B, C), although many Neotropical species have broad tegmina. With 124 teeth in the stridulatory file (Fig. 2C), *A. hyalicetra* overlaps in file characteristics only with *A. exigua* (Say), which is a fall species with narrow tegmina found in eastern deciduous forests. The male genitalia (Fig. 2A) are unique: the median lophi are bifurcate and hook inward, each paramere has a hooked tooth at the anterolateral corner, and the parameres slope anterolaterally from the midline (rather than a posterolateral slope or perpendicular orientation, cf. plate 13 Walker and Funk 2014). The variable PTR in male songs (Table 1, Fig. 3C) is unique among North American *Anaxipha* (see *Acoustic behavior* below).

Etymology.—*l. hyalo* (glassy) + *cetra* (a small light shield), referring to the broad, transparent male tegmina.

Acoustic behavior.—PR in *A. hyalicetra* is 45.4 s^{-1} (Table 1, Fig. 3B), identical to that of *A. fultoni* Walker and Funk and close to that of *A. imitator*. Phrasing differs between these species. The calling song phrasing of *A. hyalicetra* is a series of PT of irregular length that may be termed a chirp (Fig. 3A, C). Phrasing in both *A. fultoni* and *A. imitator* is a broken trill rather than an irregular chirp. The calling song phrasing of the new species is qualitatively similar to that of *A. litarena* Fulton from the beaches of the southeastern United States, except that the latter produces more regular PTR and PTD. The carrier frequency is 6 kHz. A series of harmonics extend to 43 kHz at 6 kHz intervals (Fig. 3A).

The scree plot (Fig. 4) has a distinct inflection point at n = 4 components. The four components extracted by maximum likelihood factor analysis (Table 2) may be interpreted as follows. Factor 1 describes PTR (together with mathematically related characters PTI, PTP, and PTdc). Factor 2 describes PTD, which is determined by PN. Factor 3 describes PR (with mathematically related characters PD, PP, and PI) and PTCF. Factor 4 describes pulse characteristics Pdc, PD, and PI, which contribute to PTD. The factor analysis model was rejected as a perfect fit for the data ($P = 4.64 \times 10^{-18}$); the four factors explain cumulatively 91% of variation. PTCF is the least classifiable character (i.e. highest uniqueness at 0.46).

Songs were significantly different between the field and the laboratory (MANOVA, $P = 9.32 \times 10^{-3}$). Notably, males produced more rapid PTR ($P = 3.65 \times 10^{-3}$) due to shorter PTD ($P = 8.06 \times 10^{-4}$) in the laboratory (Table 1). PTCF also differed between field and laboratory ($P = 1.21 \times 10^{-3}$; Table 1). Song character differences opposed relationships predicted by temperature: PR and PTR were faster and PD and PTD were shorter in the laboratory than in the field, despite a lower mean laboratory recording temperature (Table 1).

Males sang in aggregations but did not settle into predictable chorus phase relationships, neither synchronous nor alternating

Table 1. Song character descriptive statistics. All means are reported ± standard deviation with coefficients of variation (CVs) below. The *P* row shows *P*-value results from a MANOVA test that compared recordings between field and laboratory conditions. Temperatures between these conditions were compared with a 2-sample *t*-test.

		Temp	PR	PD	PI	PP	Pdc	PN	PTR	PTD	PTI	PTP	PTdc	PTCF
Combined mean		24.7 ± 0.9	45.4 ± 4.6	14.3 ± 2.3	7.9 ± 3.2	22.3 ± 2.3	64.4 ± 9.0	5.7 ± 1.8	3.5 ± 1.2	117.2 ± 43.4	223.4 ± 184.9	340.6 ± 194.0	37.7 ± 10.8	6.0 ± 0.4
	CV	0.03	0.46	0.38	1.33	0.23	0.01	0.55	0.40	16.10	153.06	110.46	0.03	0.03
Field mean		25.1 ± 0.8	44.1 ± 3.9	15.2 ± 2.1	7.0 ± 3.0	22.8 ± 2.1	66.8 ± 8.5	6.2 ± 1.7	2.9 ± 1.1	138.9 ± 42.7	278.2 ± 227.8	417.0 ± 225.4	37.8 ± 12.3	5.7 ± 0.3
	CV	0.023	0.351	0.282	1.319	0.196	0.011	0.462	0.436	13.141	186.597	121.789	0.040	0.019
Lab mean		24.1 ± 0.7	47.5 ± 5.1	12.8 ± 2.0	9.5 ± 3.2	21.3 ± 2.4	60.2 ± 8.6	4.8 ± 1.6	4.3 ± 0.6	86.9 ± 20.8	146.7 ± 34.9	233.7 ± 31.8	37.5 ± 9.0	6.3 ± 0.3
	CV	0.018	0.544	0.306	1.073	0.261	0.012	0.520	0.078	5.002	8.282	4.318	0.021	0.018
P			NS	0.015	NS	NS	NS	NS	3.60×10^{-3}	8.06×10^{-4}	NS	0.010	NS	1.21×10^{-3}

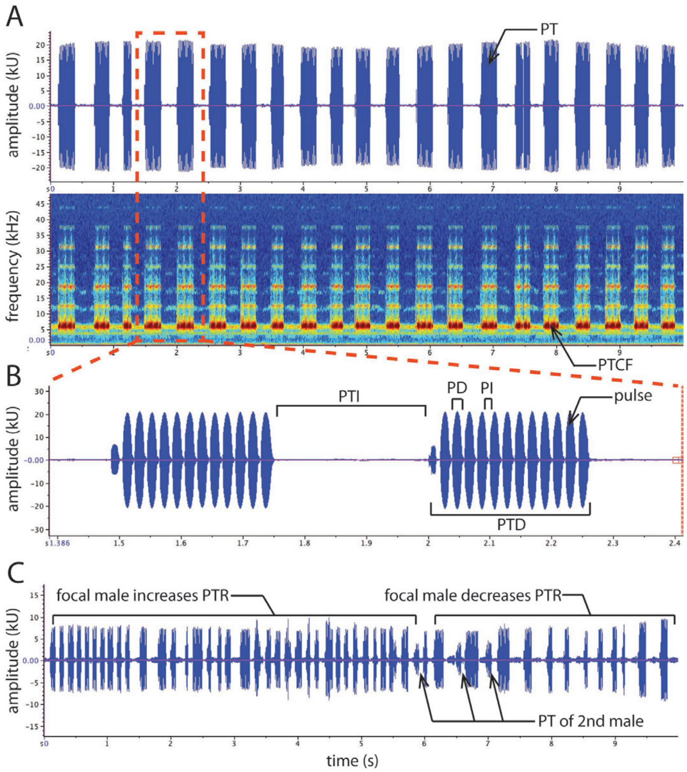


Fig. 3. A. Male calling song, field recording number 140723_11, oscillogram (above) and spectrogram (below), 10 s window, 25.4 °C. PTR = 2.2 s^{-1}, PTCF = 6.3 kHz; **B.** 1 s window of same recording as in A, expanded from region surrounded by red box, showing pulse structure; **C.** 10 s oscillogram of interaction between two males in the field, recording 140723_09, 23.9 °C. Changes in PTR of focal male are indicated.

(reviewed in Greenfield 2002). Males walked while singing, and, if on a stem, circled the stem (JAC pers. obs.). In the field, males were observed baffling by positioning themselves between twigs (JAC pers. obs.), a behavior that may improve broadcast by reducing destructive interference due to sound radiation to the rear of the insect (Forrest 1982, 1991, Greenfield 2002). When in close proximity in the field, one or both males may have increased their PTR by shortening their chirps (i.e. reducing PTD; Fig. 3C). To a human observer, the effect was a staccato chirp that reverted back to a lower PTR with longer PTD over time (e.g. Fig. 3A). PTdc remained unchanged during alteration of PTR.

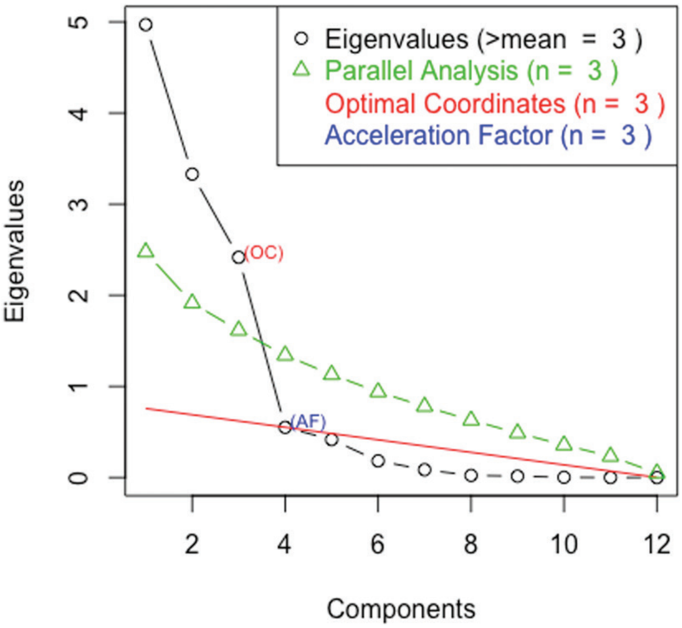


Fig. 4. Scree test results from the nFactors R package. The distinct inflection point of the eigenvalues plot at n = 4 components suggests extraction of that quantity of factors.

Table 2. Loadings of song characters onto four factors as returned by maximum likelihood factor analysis.

Character	Factor 1	Factor 2	Factor 3	Factor 4
PTR	-0.75	-0.48		
PTI	1.00			
PTP	0.98			
PTdc	-0.70	0.50		
PTD		0.91		0.37
PN	0.83			
PR		-0.99		
PP		0.99		
PD		0.47	0.53	0.70
PI		-0.47	0.46	0.63
Pdc		0.49		0.87
PTCF		-0.44	-0.50	

Discussion

A trickle of new species discoveries shows that there is still much to learn about the orthopteran fauna of Arizona, despite much historical systematic attention (Rehn 1908, Hebard 1935a, b, Ball 1942) and the popularity of the state as a destination for insect collectors and hobbyists. Mass collecting methods employed by general entomologists such as beating, sweeping, and light trapping are not comprehensive sampling strategies for orthopteran diversity and were not effective in collecting this new species. Macropterous *Anaxipha* are attracted to lights, especially in the tropics, but such sampling is not effective for micropterous species. Seasonality is also a consideration. Collectors generally sample Arizona after the onset of the monsoons in August, and thus may overlook species that are active early in the season such as the *Anaxipha* described here. Two southern Arizona katydids described in recent years: *Bucrates weissmani* Walker (Walker 2014) and *Microcentrum latifrons* Spooner (Spooner 1988), are also active as adults early in the season, the latter being sympatric with *A. hyalicetra*.

Collecting in the Atascosa and Pajarito Mountains in Santa Cruz County, Arizona, failed to find this cricket outside of the type locality. Collecting in adjacent Sonora, Mexico, may prove more fruitful. *Anaxipha hyalicetra* is evidently part of an incursion of Neotropical *Anaxipha* into North America. Once alpha diversity and higher level taxonomic relationships are better known, the species with long first hind tarsal segments may be transferred to a new genus. This set includes *A. hyalicetra*, *A. calusa*, and *A. imitator* among the North American fauna together with the majority of Neotropical species.

As we observed song character differences between field and laboratory conditions that oppose those predicted by temperature, the possibility that *A. hyalicetra* male behavior includes an aggressive chirp is worth investigating. Specialized aggressive songs in crickets are brief chirps that may be produced more frequently and at higher amplitude than calling song chirps (Alexander 1962, Brown et al. 2006). A staccato chirp characterized by fast PTR and short PTD (Table 1, Fig. 3C) was observed in field situations where two males were in close proximity. We have not performed controlled experiments to determine whether these song changes function in aggression, but it is possible that unintentional artificial crowding in the laboratory may have induced aggressive acoustic behavior, where these same changes to PTR and PTD were also observed. Aggressive songs signal competitive potential (Brown et al. 2006) should an encounter escalate to physical combat (Jang et al. 2008, Bertram et al. 2011, Bertram and Rook 2012), a behavior that is often observed in crickets that defend burrows or shelters (Jang et al. 2008, Bertram and Rook 2012). As *A. hyalicetra* is a vegetation-inhabiting cricket that has not been observed fighting, aggressive signaling behavior may function instead to regulate male spacing or increase male attractiveness (Mhatre and Balakrishnan 2006, Chamorro-R et al. 2007). An intriguing hypothesis worth testing in *A. hyalicetra* is that when aggregated, males may increase energy expenditure to appear more attractive to listening females (Jia et al. 2001, Mhatre and Balakrishnan 2006). PTR adjustments do not alter PTdc, which has among the lowest CV of any of the 12 measured song characters (2–4%; Table 1). PTdc may be a signal component that permits mate recognition (Mendelson and Shaw 2012) despite behavioral adjustment of PTR during intrasexual competition.

Acknowledgments

Thomas J. Walker contributed a valuable critique of an early version of the manuscript. The Orthopterists' Society supported the cost of publishing this work. The manuscript was improved by the suggestions of two anonymous reviewers.

References

Alexander RD (1962) Evolutionary change in cricket acoustical communication. Evolution 16: 443–467. https://doi.org/10.1111/j.1558-5646.1962.tb03236.x

Ball ER (1942) The Grasshoppers and Other Orthoptera of Arizona. University of Arizona Publications, Tucson.

Bertram SM, Rook V (2012) Relationship between condition, aggression, signaling, courtship, and egg laying in the field cricket, *Gryllus assimilis*. Ethology 118: 360–372. https://doi.org/10.1111/j.1439-0310.2011.02019.x

Bertram SM, Rook VLM, Fitzsimmons JM, Fitzsimmons LP (2011) Fine- and broad-scale approaches to understanding the evolution of aggression in crickets: aggression in Jamaican and spring field crickets. Ethology 117: 1067–1080. https://doi.org/10.1111/j.1439-0310.2011.01970.x

Brown WD, Smith AT, Moskalik B, Gabriel J (2006) Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. Animal Behaviour 72: 225–233. https://doi.org/10.1016/j.anbehav.2006.01.012

Chamorro-R J, Montealegre-Z F, González-O R (2007) Determinants of male spacing behaviour in *Panacanthus pallicornis* (Orthoptera: Tettigoniidae). Ethology 113: 1158–1172. https://doi.org/10.1111/j.1439-0310.2007.01428.x

Cigliano MM, Braun H, Eades DC, Otte D (2018) Orthoptera Species File Online v. 5.0/5.0.

Forrest TG (1982) Acoustic communication and the baffling behaviors of crickets. Florida Entomologist 65: 33–44. https://doi.org/10.2307/3494144

Forrest TG (1991) Power output and efficiency of sound production by crickets. Behavioral Ecology 2: 327–338. https://doi.org/10.1093/beheco/2.4.327

Greenfield MD (2002) Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication. Oxford University Press, New York.

Hebard M (1935a) Studies in the Orthoptera of Arizona. Part I. New genera, species and geographical races. Transactions of the American Entomological Society 61: 111–153.

Hebard M (1935b) Studies in the Orthoptera of Arizona. Part II. A list of the Dermaptera and Orthoptera of Arizona with new records and corrections of the literature subsequent to 1900. Transactions of the American Entomological Society 61: 269–316.

Jang Y, Gerhardt HC, Choe JC (2008) A comparative study of aggressiveness in eastern North American field cricket species (genus *Gryllus*). Behavioral Ecology and Sociobiology 62: 1397–1407. https://doi.org/10.1007/s00265-008-0568-6

Jia F-Y, Greenfield MD, Collins RD (2001) Ultrasonic signal competition among wax moths. Journal of Insect Behavior 14: 19–33. https://doi.org/10.1023/A:1007893411662

Mendelson TC, Shaw KL (2012) The (mis)concept of species recognition. Trends in Ecology and Evolution 27: 421–427. https://doi.org/10.1016/j.tree.2012.04.001

Mhatre N, Balakrishnan R (2006) Male spacing behaviour and acoustic interactions in a field cricket: implications for female mate choice. Animal Behaviour 72: 1045–1058. https://doi.org/10.1016/j.anbehav.2006.02.022

Otte D (1994) The Crickets of Hawaii: Origin, Systematics and Evolution. Orthopterists' Society, Philadelphia.

Otte D (2006) Eighty-four new cricket species (Orthoptera: Grylloidea) from La Selva, Costa Rica. Transactions of the American Entomological Society 132: 299–418. https://doi.org/10.3157/0002-8320(2006)132[299:ENCSOG]2.0.CO;2

Otte D, Perez-Gelabert D (2009) Caribbean Crickets. The Orthopterists' Society.

Pettersson Elektronik AB (2001) Bat Sound Pro. Pettersson Elektronik AB, Uppsala.

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Raiche G, Magis D (2015) Parallel Analysis and Non Graphical Solutions to the Cattell Scree Test. Universite du Quebec a Montreal, Montreal.

Rehn JAG (1908) An orthopterological reconnoissance of the southwestern United States. Part I: Arizona. Proceedings of the Academy of Natural Sciences of Philadelphia 60: 365–402.

Spooner JD (1988) *Microcentrum latifrons*, a new species of anguar-winged katydid from southwestern United States (Orthoptera, Tettigoniidae, Phaneropterinae). Transactions of the American Entomological Society 114: 311–317.

Tan MK (2012) Orthoptera in the Bukit Timah and Central Catchment Nature Reserves (Part 2): Suborder Ensifera. University of Singapore, Singapore.

Walker TJ (2014) A new North American species of *Bucrates* (Orthoptera: Tettigoniidae: Conocephalinae: Copiphorini). Journal of Orthoptera Research 23: 69–73. https://doi.org/10.1665/034.023.0101

Walker TJ, Funk DH (2014) Systematics and acoustics of North American *Anaxipha* (Gryllidae: Trigonidiinae). Journal of Orthoptera Research 23: 1–38. https://doi.org/10.1665/034.023.0102

Supplementary material 1

Authors: Jeffrey A. Cole, David H. Funk
Data type: WAV file
Explanation note: Male calling song supplementary file.

Link: https://doi.org/10.3897/jor.28.30143.suppl1

Epigenetic and genetic variation between two behaviorally isolated species of *Neoconocephalus* (Orthoptera: Tettigonioidea)

Gideon Ney[1], Johannes Schul[1]

1 Division of Biological Sciences, University of Missouri, 207 Tucker Hall, Columbia, Missouri, USA.

Corresponding author: *Gideon Ney* (gideon.ney@gmail.com)

Academic editor: *Alina Avanesyan* | Received 23 August 2018 | Accepted 31 January 2019 | Published 17 May 2019

http://zoobank.org/AD0139D9-3350-4863-95B5-E19ED5D3F6B2

Citation: Ney G , Schul J (2019) Epigenetic and genetic variation between two behaviorally isolated species of *Neoconocephalus* (Orthoptera: Tettigonioidea). Journal of Orthoptera Research 28(1): 11–19. https://doi.org/10.3897/jor.28.28888

Abstract

Epigenetic variation allows for rapid changes in phenotypes without alterations to nucleotide sequences. These epigenetic signatures may diverge over time among isolated populations. Epigenetic incompatibility following secondary contact between these populations could result in the evolution of reproductive isolating mechanisms. If epigenetic incompatibility drove the evolution of species isolating mechanisms, we expect to see significant epigenetic differentiation between these species. Alternatively, epigenetic variation could be the result of predominantly environmental variables and not align along species boundaries. A methylation sensitive amplified fragment length polymorphism analysis was performed on individuals of the closely related katydid species *Neoconocephalus robustus* and *N. bivocatus*. We observed significant variation in total methylation levels between species. However, genetic differentiation remained larger than epigenetic differentiation between species groups. We measured a significant correlation between the epigenetic and genetic distance between individuals. Epigenetic differentiation is therefore likely the result of an interaction between genetic and epigenetic loci and not a mechanism for species differentiation. We therefore did not find evidence to support our hypothesis of an epigenetically mediated mechanism for speciation between *N. robustus* and *N. bivocatus*.

Key words

genetic differentiation, methylation, MSAP, *Neoconocephalus*, population genetics

Introduction

Epigenetic variation can lead to changes in phenotypic expression without any change to the nucleic acid sequence (Berger et al. 2009). Unlike genetic variation, epigenetic changes can produce reversible, heritable phenotypic changes within a lineage (Jablonka and Lamb 1998). Epigenetically controlled phenotypic plasticity may therefore play an important role in rapid, adaptive changes (Ledón-Rettig et al. 2012, Burggren and Crews 2014). DNA methylation, the most commonly studied form of epigenetic modification, involves the addition of methyl groups, usually to CpG dinucleotides that regulate gene expression (Boyes and Bird 1991). Methylation regulated phenotypic plasticity has been documented across multiple taxonomic groups (Braam and Davis 1990, Rapp and Wendel 2005, Varriale and Bernardi 2006, Elango et al. 2009, Herrera and Bazaga 2010). Until recently, epigenetically dependent variation has been largely overlooked as an evolutionary mechanism contributing to speciation (Smith et al. 2016). Facultative phenotypes can be maintained in a population as adaptive alternatives to divergent environmental conditions. These alternative phenotypes may ultimately become fixed in a population by way of genetic assimilation (Pál and Miklós 1999, West-Eberhard 2005).

Phenotypic variation can also evolve in response to epigenetic incompatibility (= hybrid incompatibility caused by epialleles; Bente and Scheid 2017, Blevins et al. 2017) between groups. Following the epigenetic diversification of groups in isolation, intermediate forms may show reduced fitness following secondary contact (Jablonka and Lamb 1999). Aphids moved to a new host plant and allowed to reproduce asexually quickly developed a preference for the new host and produced morphological characteristics similar to conspecifics utilizing this host. Backcrossing to the parental line resulted in the production of non-viable offspring (Shaposhnikov 1966). Heritable phenotypic variation in aphids has been correlated with changes in methylation (Field et al. 1989, Walsh et al. 2010). Methylation dependent incompatibility could be reinforced by reproductive isolation (Pál and Miklós 1999).

In many animals, behavioral isolation plays a significant role in maintaining species boundaries. Acoustic communication has been studied as a mechanism for reproductive isolation in both vertebrate and invertebrate groups (Gerhardt and Huber 2002). *Neoconocephalus*, a New World genus of katydids, possesses a diverse range of habitat preferences (Walker et al. 1973, Frederick 2013) and call phenotypes (Schul and Patterson 2003, Beckers and Schul 2008, Deily and Schul 2009). Females utilize these calls in mate recognition and in phonotaxis, the directional movement towards a calling male (Greenfield 1990, Triblehorn and Schul 2009, Beckers and Schul 2010). The acoustic communication system of *Neoconocephalus* allows for reproductive isolation among the multiple species that may be found in sympatry (Schul et al. 2014).

The sibling species (Snyder et al. 2009) *N. robustus* (Scudder, 1862) and *N. bivocatus* Walker, Whitesell, & Alexander, 1973 differ both in their habitat preferences and call types. *Neoconocephalus robustus* is a grassland generalist and utilizes grasslands with a wide range of flora and environmental conditions. *Neoconocephalus bivocatus,* on the other hand, is a prairie obligate preferring drier habitats composed primarily of tall prairie grasses (Walker et al. 1973). Both species co-occur in some areas, e.g. at the edges of prairie remnants or along creeks within prairies. This species pair is largely morphologically cryptic but maintains divergent call characters and call preferences (Deily and Schul 2004, 2006). While the two species can be distinguished using genetic markers (e.g. mitochondrial haplotypes or AFLP markers (Snyder et al. 2009, Ney and Schul 2017)), genetic differentiation is weak and evidence for hybridization (e.g. intermediate calls) occur frequently. Population-level genetic variation was shown to be very low, with almost no geographically associated genetic variation between sites as distant as 448 km apart (Ney and Schul 2017). This suggests that these two species diverged very recently, most likely during the current glacial cycle (Frederick 2013).

A likely scenario of this divergence event includes an ancestral population living in both habitat ranges. In each habitat, different epigenetic patterns would be expressed, which then became fixed within each subpopulation, resulting in decreased hybrid fitness. Genetic differences leading to the differences in male calls and female preferences evolved later, in part driven by reproductive reinforcement (Deily and Schul 2004). Thus we hypothesize here that epigenetic differentiation, driven by the different environmental conditions experienced in their core habitats, drove divergence of the species. The lack of substantial genetic differentiation between *N. robustus* and *N. bivocatus* could point to an underlying epigenetic incompatibility driving species differentiation. This hypothesis predicts that the epigenetic differentiation between the species would be larger and more stereotyped than the genetic differences.

DNA methylation has been described in many insect groups including multiple orthopteran species (Sarkar et al. 1992, Robinson et al. 2011). Methylation sensitive amplified fragment length polymorphism (MS-AFLP) analysis is one of the few techniques that allows for the quantification of genome-wide patterns of cytosine methylation without any previous knowledge of genome sequences (Xiong et al. 1999). The MS-AFLP technique uses two isoschizomer restriction enzymes (MspI and HpaII) that recognize the same restriction site, cutting in the same location (5′-C^CGG-3′), but have different sensitivities to the presence of cytosine methylation. By comparing the presence/absence of fragments produced by both enzymes, the methylation status at each restriction site can be evaluated. In addition, genetic polymorphisms can be evaluated between individuals that lack the restriction site in both digestions as an indication of a change in nucleotide sequence.

To distinguish whether divergence of these two species was initiated by epigenetic, rather than genetic variation, we addressed two questions using a MS-AFLP technique. First, we asked to what extent epigenetic and/or genetic differentiation predicted species assignment. Second, we analyzed whether the patterns of genome-wide DNA methylation were correlated with genetic variation.

Materials and methods

Specimen collection.—We utilized a total of 94 males collected in the summers of 2006, 2013, and 2014 from eight grassland sites around the state of Missouri (Suppl. material 1: Table S1). We used males' calls to localize individuals in the field and collected them by hand after sunset. We identified males in the field as belonging to members of the target group through their call and morphological features, including cone pigmentation and body size, prior to collection (Walker et al. 1973). As the two species are morphologically cryptic, we identified individuals as either *N. bivocatus* or *N. robustus* based on their divergent call characteristics as described below. Individuals were collected from among eight grassland sites within Missouri and from within three different years (Suppl. material 1: Table S1). Thus, a range of epigenetic patterns, expressed within variable environmental conditions, was included in each species sample. Fixed differences observed between the two species are therefore likely to be species specific rather than the result of differences in environmentally mediated methylation patterns.

Call recordings.—We recorded male calls in 2006 and 2013 within three days of collection using an Audiotechnica ATR 55 microphone and a Marantz PMD-671 solid-state recorder (16 bit, 48 kHz sampling rate). Recordings were made outdoors with males placed in individual mesh cages (approximately 10×20×10 cm) spaced at least 3 m apart. In 2014, we recorded male calls in the field immediately preceding collection using a Tascam DR-40 linear PCM recorder (16 bit, 48 kHz sampling rate). Ambient temperatures ranged from 22–28 °C.

Temporal call analysis.—Call temporal patterns were analyzed and species assignments made as described in Ney and Schul (2017). In short, we marked each sound pulse produced during a single closing movement of the wings (Walker 1975) using custom software. The recordings were rectified and the envelope extracted with a temporal resolution of 0.125 ms. Pulses were detected automatically using a threshold-based algorithm and manually checked before saving the data to text-files. We analyzed about 2 s of each male's call containing 150–250 pulses. Further analyses were conducted on the text files in MS Excel.

Male calls of *N. robustus* have a single pulse rate of about 200/s, equivalent to a pulse period of about 5 ms (Walker 1975). Females recognize this pattern by the absence of silent gaps longer than about 2 ms (Deily and Schul 2004). In contrast, male calls of *N. bivocatus* have two alternating pulse periods of about 4.5 ms and 7 ms (Deily and Schul 2004), resulting in a 'galloping rhythm' or 'pulse pairs'. Female *N. bivocatus* recognize this pattern by the rate of the pulse pairs: pulse pair rates around 87/s are attractive and attractiveness decreases towards faster and slower rates. For the pulse pairs to be detectable, the two alternating pulse periods must differ sufficiently (J. Schul, unpublished work).

We quantified the ratio of the means of the alternating pulse periods (longer pp / shorter pp). For the single pulse calls of *N. robustus*, this should result in values close to one, while in *N. bivocatus* significantly larger values result (Bush and Schul 2010). Among the calls of 94 males analyzed, there were two distinct groups of values, one between 1 and 1.18 and a second group with ratios >1.38. A natural break occurred in the data between 1.18 and 1.38. We classified ratios <1.18 as '*N. robustus*', and >1.38 as '*N. bivocatus*' in call type.

Spectral call analysis.—Call spectra were analyzed and species assignments made as described in Ney and Schul (2017). In short, we analyzed the amplitude spectrum of male calls using a fast Fourier transformation (FFT, Hamming window, frame length 256) in Audacity v.1.3 (Audacity Team 2008). Spectra were averaged over 2 s of the call. The main energy in the spectrum of *Neoconocephalus* calls is concentrated in a narrow band between 7 and 15 kHz with the peak frequency differing among species (Schul and Patterson 2003). We measured the center frequency of this low frequency band as the geometric mean of the upper and lower cut-off frequencies at -3 dB from the peak amplitude.

In *N. bivocatus*, the center frequencies of this band have a mean of about 10 kHz among individuals, ranging from 7 to 15 kHz. Females have little spectral selectivity in this frequency range (Deily and Schul 2006). The center frequencies of calls with a pulse period ratio of >1.38 that also fell into this range of center frequencies were classified as *N. bivocatus*. One individual had a pulse period ratio greater than 1.38 and a center frequency lower than 7 kHz; this male was classified as an intermediate caller, as its call characteristics differed from that of both species.

In *N. robustus*, the low frequency band is narrower than in *N. bivocatus* and is typically limited to 10 kHz and below (Schul and Patterson 2003). Indeed, frequencies well above 10 kHz have an inhibitory effect on female phonotaxis (Deily and Schul 2006). Of the individuals with pulse period ratios <1.18, center frequencies of all but five individuals clustered between 6 and 9 kHz. The five remaining individuals had center frequencies ranging from 9.7 to 11.1 kHz, which would be less attractive for *N. robustus* females. These individuals were classified as possessing an intermediate call type. All intermediate callers were removed from the analysis of epigenetic and genetic differentiation.

Molecular analysis.—We aim here to analyze the differences of trans-generational methylation patterns between two species. Therefore, we selected tissue that is likely to have little tissue-specific methylation differences between the two species. We collected tissue from hind femurs (mostly muscle and cuticle) that should be under similar selection in both species and thus little differential tissue-specific methylation. Using leg tissue also avoids the risk of contamination from GI tract microbiota.

We removed the hind femurs of collected males and placed them in 95% EtOH for DNA preservation. We later extracted DNA from the hind femurs using the DNeasy Blood & Tissue Kit (Qiagen Inc., Valencia, CA, USA). DNA quantification was performed on each sample by spectrophotometry (NanoDrop 1000, Thermo Scientific, Wilmington, DE). Genomic DNA was stored at -80°C prior to molecular analysis.

We used a MS-AFLP assay modified from Xu et al. (2000). DNA (55 ng) from each sample was digested in two separate double digest reactions (EcoRI/HpaII and EcoRI/MspI). EcoRI selectively cuts the sequence 5′-GAATTC-3′. HpaII and MspI are isoschizomers, meaning they selectively cut at the sequence (5′-CCGG-3′), but differ in their sensitivity to cytosine methylation at those sites. HpaII will only cut if the external cytosine is hemimethylated. MspI cuts when the internal cytosine is either hemi or fully methylated. Both enzymes will cut if the target site is completely unmethylated. Using this method, we evaluated the CpG methylation of restriction sites by comparing the fragments produced by both digests.

Digestion and ligation were carried out together to prevent regeneration of restriction sites. Synthetic double stranded DNA adaptors (Xu et al. 2000) were ligated to the cleaved ends of restriction sites. The EcoRI/HpaII and EcoRI/MspI digestion/ligation reaction (11 ul final volume) is comprised of 1.1 μL 10X CutSmart™ buffer (New England Biolabs, USA), 0.55 μg/μL of Bovine Serum Albumin (BSA) (New England Biolabs), 0.3 μL water, 5 U of EcoRI HF, 1 U of either HpaII or MspI, 1 U T4 ligase (New England Biolabs), 1 μL ATP (10 μM), EcoRI adaptors (5 μM), either HpaII or MspI adaptors (50 μM), and 5.5 μL genomic DNA (10 ng/ μL). The reaction was incubated at 37°C for 2 hours. Preselective PCR was conducted with 1:10 dilute digestion/ligation products, the Eco+A (5′-GACTGCGTACCAATTCA-3′), and the HpaII/MspI+A (5′-GATGAGTCTAGAACGGA-3′) primers using thermocycler settings as described in Snyder et al. (2009). We performed selective PCR independently with three primer pairs (Table 1) and 1:100 dilute preselective PCR products from both the HpaII and MspI reactions. Fluorescently labeled Eco primers (Eco+AAC (6FAM), Eco+AGC (PET)) were used in selective PCR (as described in Snyder et al. 2009) and the products multiplexed and diluted to produce a 1:10 final dilution of each product. Fragments were separated in an ABI 3730 genetic analyzer at the DNA Core Facility, University of Missouri. We called MS-AFLP bands using GeneMarker v.1.6 (Hulce et al. 2011) using an automated peak-calling scheme (as described in Holland et al. 2008) and called alleles between 75–500 bp with a minimum peak intensity of 50.

Table 1. Loci produced by selective primer combinations used in the MS-AFLP analysis. Shown are the primer pair combinations, the number of scored bands per primer pair, and the number of those bands classified as polymorphic methylation sensitive loci (MSL), and polymorphic genetic loci.

*Eco*RI	*Msp*I/*Hpa*II	Bands	MSL	Genetic loci
-AAC	-ATC	277	183	265
-AGC	-AAT	227	49	102
-AGC	-ATC	318	170	301
	Total	822	402	668

Data analysis.—We obtained presence/absence fragment data for both EcoRI/HpaII and EcoRI/MspI datasets from GeneMarker (Hulce et al. 2011). Presence of a fragment in both the EcoRI/HpaII and EcoRI/MspI digestions (1/1) was described as unmethylated. The presence of a fragment in one digestion but not the other (0/1 or 1/0) was defined as methylated (either hemimethylated or internal cytosine methylated, respectively). If fragments were absent in both digestions (0/0) the loci were considered uninformative as this state could be due to either full methylation at the target site (methylation of both the inner and outer cytosine) or the absence of the fragment due to variation in the nucleotide sequence between individuals (Schulz et al. 2013, Fulneček and Kovařík 2014).

The methylation sensitivity of each locus was identified using the MSAP Package (Pérez-Figueroa 2013) in R v.3.1.2 (R Core Team 2015). Loci were classified as methylation sensitive loci (MSL) if there was evidence of methylation in at least 5% of the sampled individuals at that locus. Genetic markers were extracted from the MS-AFLP loci. Fragments that were present in one or both MspI and HpaII analyses were scored as present. Fragments that were absent in both reactions were scored as absent. This method of using MS-AFLP loci to estimate genetic parameters has been found to produce similar results to standard AFLP markers (Smith et al. 2016). Only polymorphic MSL and genetic loci that differed among sampled individuals were used in further analyses. We evaluated variation for each epigenetic (MSL) and genetic locus individually then calculated the mean diversity of MSL and genetic loci using Shannon's diversity index (I). We compared the relative frequency of total methylation (internal cytosine methylated and hemimethylated fragments) and unmethylated MSL between species. Significant variation between species was tested using a Mann-Whitney U test.

We tested for differences in MSL and genetic differentiation using two-way analyses of molecular variance (AMOVA; Excoffier et al. 1992) that grouped individuals again by species. Significance of the test statistic's (Φ_{ST}) deviation from zero was estimated based on 1000 permutations of individuals among groups. Principal coordinate analyses (PCoA) of both epigenetic and genetic loci were performed using the R stats package v.3.1.2 (cmdscale; R Core Team 2015) to visualize the Euclidean distance between species. A population structure analysis was implemented for all individuals using the program STRUCTURE v.2.3.3 (Pritchard et al. 2010). The admixture model was used, allele frequencies correlated, with a run length of 100,000 (Burnin = 10,000) for 10 replicates each of K = 1–10 (genetic clusters). The estimate of the most well supported K was calculated as described in Evanno et al. (2005) and implemented in Structure Harvester v.0.6.94 (Earl 2012). The program Clumpp v.1.1.2 (Jakobsson and Rosenberg 2007) was used to align the 10 repetitions of the most well supported number of clusters.

If similar signals exist for the MSL and genetic structure then epigenetic and genetic distance may be significantly correlated. We estimated the Euclidean distance between individuals for both epigenetic and genetic datasets using the R stats package v.3.1.2 (R Core Team 2015) and compared the distance matrices using a Mantel test (Mantel 1967; ade4 package v.1.7.2; Dray et al. 2007). We utilized 10,000 permutations of the design matrix to determine the significance of the correlation coefficient.

Results

Genome-wide variation in methylation.—We included 94 males in our analysis. We determined the males' species assignments based on the temporal and spectral frequency call preferences of *N. robustus* and *N. bivocatus*. The call analysis classified the 94 males as 31 *N. bivocatus*, 57 *N. robustus*, and 6 having an intermediate call type; five of the intermediates had the *N. robustus* temporal pattern and one the *N. bivocatus* pattern, with frequency spectra that fell outside of these respective species' specific pattern (Fig. 1). Individuals possessing intermediate call phenotypes were removed from further analyses. The MS-AFLP analysis yielded 227, 277, and 318 fragments in each of three selective PCR reactions (Table 1). Of these fragments, a total of 364 were polymorphic for their methylation status among sampled individuals and were classified as MSL. A loci-calling scheme, utilizing the MS-AFLP dataset, allowed for the inference of the genetic state of fragments among individuals, similar to a traditional AFLP analysis. In total, 668 polymorphic genetic loci were produced from 822 MS-AFLP fragments.

We compared whether species differed significantly in their proportion of genome-wide methylated sites. The relative frequency of genome-wide methylation (combined hemimethylation and internal cytosine methylation) showed low (Fig. 2; *N. robustus* = 0.272; *N. bivocatus* = 0.240) but significant variation between species (Mann-Whitney U, W = 587, p = 0.001243).

Epigenetic and genetic structure.—We examined epigenetic and genetic diversity as they relate to species assignment. The within-species epigenetic Shannon diversity index was 5.0616 ± 0.2054 and 5.0094 ± 0.2087, within *N. robustus* and *N. bivocatus,* respectively. *N. robustus* and *N. bivocatus'* genetic Shannon diversity indexes were 5.2802 ± 0.2242 and 5.2179 ± 0.1943, respectively. Diversity in the genetic loci, as measured in this study, was significantly greater than that of the MSL (epigenetic) diversity measured in both species (Wilcoxon rank sum test; *N. robustus*, W = 2760, p < 0.0001; *N. bivocatus*, W = 779, p = 0.0001).

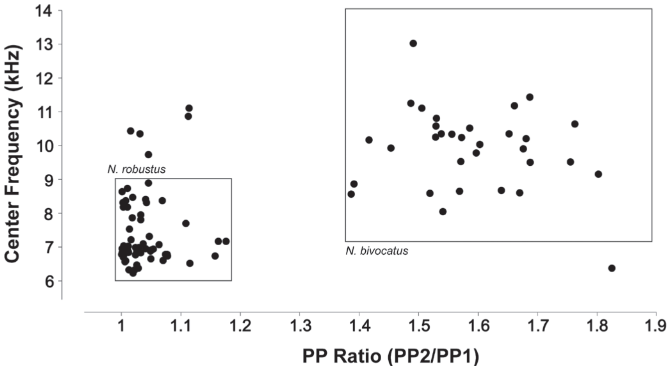


Fig. 1. Species assignment based on call pulse period ratio and center frequency. Labeled boxes indicate the calls classified as *N. robustus* and *N. bivocatus*. Individuals that fall outside of species classifications were removed from further epigenetic and genetic analyses (as described in Ney and Schul 2017).

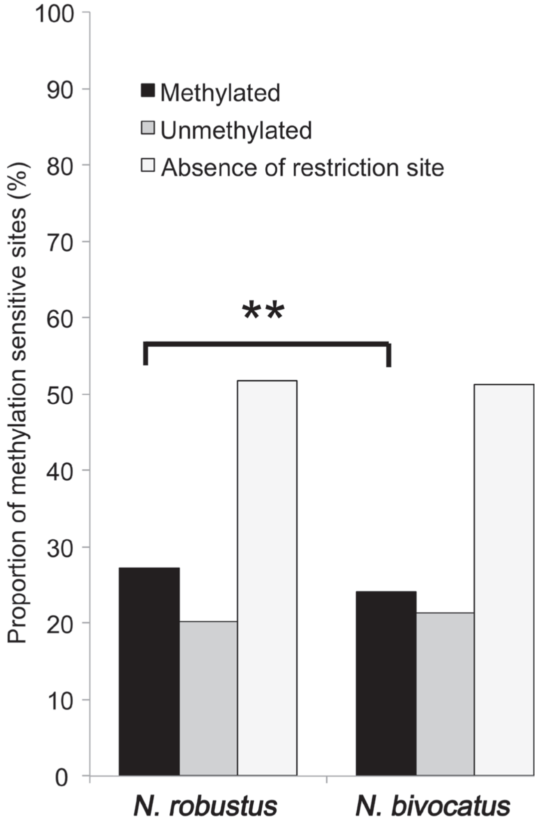


Fig. 2. Comparison of genome-wide methylation levels between species. Mann-Whitney U test; p<0.005 (**). Between-species significant variation is in total methylation (internal cytosine methylated and hemimethylated fragments).

Epigenetic and genetic structure was evaluated using a two-level AMOVA. The between-species epigenetic divergence was Φ_{ST} = 0.0504 (P < 0.0001). This is slightly less than one-third of the genetic divergence observed between species, Φ_{ST} = 0.1591 (P < 0.0001). Greater genetic variation between species would suggest that genetic mechanisms are underlying species differentiation (Table 2).

Table 2. Two-level AMOVA of MSL or genetic loci produced from MS-AFLP markers among populations grouped by species assignment. Included are genetic and epigenetic variance between groups, Φ_{ST}, and the corresponding p value.

	Between group variance	Within group variance	Φ_{ST}	p value
MSL (epigenetic)	3.429 (5.04%)	64.54 (94.96%)	0.0504	<0.0001
Genetic loci	15.38 (15.91%)	81.28 (84.09%)	0.1591	<0.0001

The principal coordinate analyses (PCoA), calculated using MSL and genetic profiles, showed that genetic variance was smaller than epigenetic variance within species (Fig. 3). The epigenetic PCoA between species elucidated little meaningful differentiation among groups, with ellipses (95% confidence intervals) overlapping almost entirely. The PCoA of genetic data between species explained 17.7% of the genetic variance in the first two coordinates (Fig. 3A) and showed moderate variation between individuals based on call phenotype, with species showing divergence in Euclidean space. Three *N. robustus* individuals clearly fell into the *N. bivocatus* cluster within the genetic PCoA (Fig. 3A), indicating a possible mismatch between phenotypic and genotypic assignments.

The Bayesian analysis of genetic structure revealed the best-supported number of genetic clusters to be K = 2, based on ΔK values (Fig. 4B; Evanno et al. 2005). These two genetic clusters aligned closely to species boundaries (Fig. 4A). As in the PCoA,

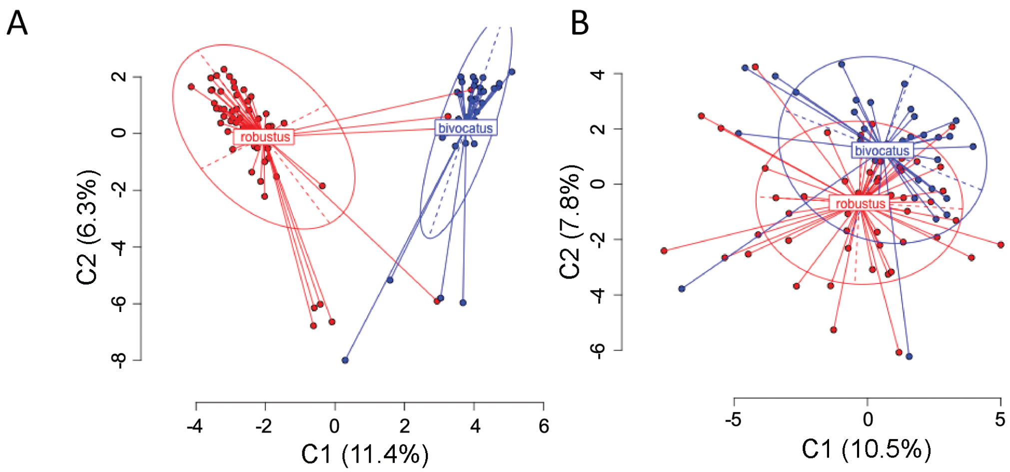


Fig. 3. PCoA of *N. robustus* and *N. bivocatus* utilizing genetic (A) and epigenetic (B) data. Plotted are the two most informative principal components calculated for the genetic and epigenetic loci datasets, as derived from the MS-AFLP fragment analysis. **A.** Genetic Euclidean distance with individuals grouped by species assignment. **B.** Epigenetic Euclidean distance with individuals grouped by species assignment. Group labels show the centroid of the points for each group. The long axis of the ellipse represents the direction of maximum dispersion and the short axis the direction of minimum dispersion.

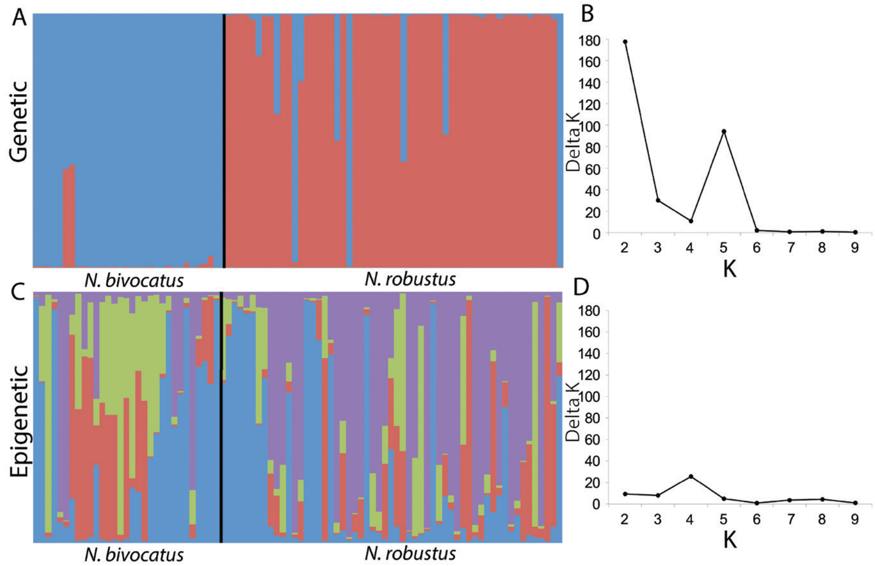


Fig. 4. Consensus shared ancestry population structure for epigenetic and genetic loci. **A.** and **C.** Bar plots using MS-AFLP loci to estimate genetic (A) and epigenetic (C) structure among *N. robustus* and *N. bivocatus* using the software package STRUCTURE. **B.** and **D.** Delta K graphs for K = 1–10 genetic clusters showing moderate support for K = 2 genetic clusters (B) and low support for K = 4 epigenetic clusters (D).

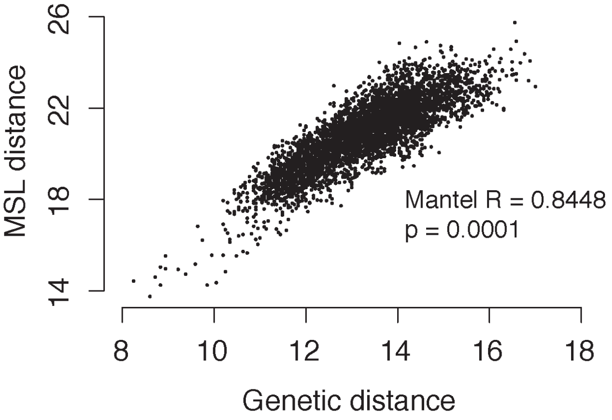


Fig. 5. Scatterplot of between-individual Euclidean genetic and epigenetic distance showing significant positive correlation between genetic and epigenetic differentiation. The correlation was tested using a Mantel test and 10,000 permutations of the design matrix to determine significance.

the same three individuals identified as *N. robustus* were assigned primarily to the *N. bivocatus* genetic cluster, indicating that they possess the *N. robustus* call type but a *N. bivocatus* genotype. As in the PCoA, the epigenetic structure analysis did not show support for significant epigenetic (MSL) structure between species groups. ΔK values did not rise above 30 for any permutation in the number of clusters (Fig. 4D), an indication of low support for epigenetic structure. In addition, the best supported number of clusters, K = 4, showed no grouping of epigenetic clusters by species assignment (Fig. 4C).

While significant epigenetic variation was observed between species, significant genetic variation was also detected. We investigated the correlation between inter-individual genetic and epigenetic Euclidean distance. Between-individual epigenetic and genetic distance showed a strong positive correlation (Fig. 5, Mantel R = 0.8448, p = 0.0001).

Discussion

We found significant differentiation among species in both epigenetic and genetic markers. Genetic differentiation, however, was larger than epigenetic differentiation between species. The AMOVA and PCoA analyses indicated that methylation patterns varied among individuals but showed little differentiation between species. Epigenetic distance among individuals correlated with inter-individual genetic differentiation, suggesting that the low levels of epigenetic differentiation between species have been pulled along by genetic differentiation.

Genetic differentiation.—Genetic differentiation between species was low but significant, as would be expected between two closely related taxa (Snyder et al. 2009, Ney and Schul 2017). Genetic structure aligned with species boundaries, with the exception of the three phenotypically *N. robustus* individuals that showed a majority assignment to the primarily *N. bivocatus* genotypic cluster. These mismatch genotype/phenotype assignments were confirmed for these three individuals in both the genetic structure analysis (Fig. 4A) as well as the genetic PCoA (Fig. 3A). Similar occurrences of mismatched genotype/phenotype individuals have been found between *N. robustus* and *N. bivocatus* previously (Frederick 2013, Ney and Schul 2017). These mismatched genotype/phenotype individuals are likely the result of recent hybridization events. A severe drought during the sampling period (Ney and Schul 2017) led locally to sharp population declines of one or both species. Both reductions in population sizes and environmental disturbances can increase rates of hybridization between closely related species (Lamont et al. 2003, Seehausen 2006).

Epigenetic variation.—*N. robustus* showed a significantly higher level of genome wide methylation than *N. bivocatus* (Fig. 2). This may be due to variation in the species' habitat preference. Variable environmental conditions can cause shifts in epigenetics, observed between diverging natural habitats as well as between natural and altered habitat types (Gao et al. 2010). *N. robustus*, unlike *N. bivocatus*, is a grassland generalist and may show epigenetic patterns resulting from exposure to a more variable set of environmental conditions during a lifetime and across generations. Because of this, *N. robustus* may possess a larger repertoire of adaptive genes for the varied environmental conditions it may utilize. The higher level of methylation found in *N. robustus* may therefore be the result of higher levels of methylation required to silence the large repertoire of adaptive genes when not in use.

While epigenetic differentiation between species was significant, it remained lower than genetic differentiation. This study did not show support for the epigenetic regulation of species-specific phenotypes; however, this does not eliminate a possible epigenetic mechanism underlying phenotypic differentiation. While the MS-AFLP technique has many benefits, there are also some inherent limitations to its application. For example, MS-AFLPs can underestimate genome-wide levels of methylation (Fulneček and Kovařík 2014). As a genome-wide scanning method MS-AFLP only detects methylation at 5′-CCGG-3′ sites. In addition, it is unable to discriminate between full methylation states (hypermethylation of both cytosines) and sequence variation at or near the restriction site (Xiong et al. 1999). Phenotypic variation controlled by a smaller number of methylated sites is unlikely to be detected. A similar investigation into genome-wide methylation found no significant differentiation in methylation between the solitarious and gregarious phases of *Locusta migratoria* (Robinson et al. 2011), despite divergent phenotypes and the identification of differentially expressed genes between morphs (Kang et al. 2004). Thus, this technique is most valuable as a first step in investigating genome-wide methylation patterns.

Correlation between epigenetic and genetic diversity.—MS-AFLP variation often shows correlations with genetic variation (Liu et al. 2012). In our study, individuals showing greater genetic variation on average showed greater epigenetic variation as well (Fig. 5). Changes in DNA methylation over time are correlated with genetic relatedness and suggest that DNA methylation maintenance may be under genetic control (Bjornsson et al. 2008). In addition, genetic variation in retrotransposons (i.e. their presence/absence) could affect the methylation state of retroelements, requiring more methylation if more repetitive elements are present (Michaud et al. 1994). Repetitive elements have been estimated to make up thirty percent of the genome of the orthopteran *L. migratoria* (Wilmore and Brown 1975). In addition, the retrotransposon SINE is differentially methylated between the solitarious and gregarious phases of the species (Guo et al. 2010).

Mechanisms of neutral evolution could also account for the correlation between epigenetic and genetic variation. In the event of substantial gene flow between species, strong divergent selection would be needed to maintain divergent epigenetic variation between species. Gene flow between groups would reduce differentiation accumulated via drift. Evidence from this study, however, suggests that genetic differentiation between species is significant and gene flow therefore relatively low (Table 2). Stochastic processes of drift then could allow epigenetic patterns to diverge between species in parallel, resulting in correlations between epigenetic and genetic variation without a causal link (Richards et al. 2010).

Conclusions

We hypothesized that the phenotypic variation observed between *N. robustus* and *N. bivocatus* was the result of an epigenetic-mediated mechanism of species differentiation that led to genetic isolation. While we found clear evidence of genomic methylation in *Neoconocephalus*, our findings did not support a role for methylation in species isolation. Both the lower level of epigenetic differentiations and the correlation between inter-individual epigenetic and genetic diversity support the alternative hypothesis, i.e. that differences in methylation patterns between species evolved in response to genetic variation. Epigenetics may still play a key role in phenotypic differentiation within *Neoconocephalus* katydids through the differential regulation of a relatively small number of genes of large effect; a mechanism not detectable with the methods used here. Further work identifying differentially expressed genes between call types could allow for the targeted analysis of methylation patterns at these sites.

Acknowledgements

We thank Katy Frederick and Nathan Harness for assistance with specimen collection and recording males. We thank Kim Hunter, Katy Frederick, and Megan Murphy for valuable feedback on the manuscript.

References

Audacity Team A (2008) Audacity (version 1.3) [computer program]. https://old.audacityteam.org/

Beckers OM, Schul J (2008) Developmental plasticity of mating calls enables acoustic communication in diverse environments. Proceedings of the Royal Society B: Biological Sciences 275: 1243–1248. https://doi.org/10.1098/rspb.2007.1765

Beckers OM, Schul J (2010) Female adaptation to developmental plasticity in male calling behavior. Behavioral Ecology and Sociobiology 64: 1279–1290. https://doi.org/10.1007/s00265-010-0942-z

Bente H, Scheid OM (2017) Epigenetic contribution to diversification. Proceedings of the National Academy of Sciences 114: 3558–3560. https://doi.org/10.1073/pnas.1702748114

Berger SL, Kouzarides T, Shiekhattar R, Shilatifard A (2009) An operational definition of epigenetics. Genes & Development 23: 781–783. https://doi.org/10.1101/gad.1787609

Bjornsson HT, Sigurdsson MI, Fallin MD, Irizarry RA, Aspelund T, Cui H, Yu W, Rongione MA, Ekström TJ, Harris TB, Launer LJ, Eiriksdottir G, Leppert MF, Sapienza C, Gudnason V, Feinberg AP (2008) Intra-individual change over time in DNA methylation with familial clustering. JAMA 299: 2877–2883. https://doi.org/10.1001/jama.299.24.2877

Blevins T, Wang J, Pflieger D, Pontvianne F, Pikaard CS (2017) Hybrid incompatibility caused by an epiallele. Proceedings of the National Academy of Sciences 114: 3702–3707. https://doi.org/10.1073/pnas.1700368114

Boyes J, Bird A (1991) DNA methylation inhibits transcription indirectly via a methyl-CpG binding protein. Cell 64: 1123–1134. https://doi.org/10.1016/0092-8674(91)90267-3

Braam J, Davis RW (1990) Rain-, wind-, and touch-induced expression of calmodulin and calmodulin-related genes in *Arabidopsis*. Cell 60: 357–364. https://doi.org/10.1016/0092-8674(90)90587-5

Burggren WW, Crews D (2014) Epigenetics in comparative biology: Why we should pay attention. Integrative and Comparative Biology 54: 7–20. https://doi.org/10.1093/icb/icu013

Bush SL, Schul J (2010) Evolution of novel signal traits in the absence of female preferences in *Neoconocephalus* katydids (Orthoptera, Tettigoniidae). PLoS ONE 5: e12457. https://doi.org/10.1371/journal.pone.0012457

Deily JA, Schul J (2004) Recognition of calls with exceptionally fast pulse rates: female phonotaxis in the genus *Neoconocephalus* (Orthoptera: Tettigoniidae). Journal of Experimental Biology 207: 3523–3529. https://doi.org/10.1242/jeb.01179

Deily JA, Schul J (2006) Spectral selectivity during phonotaxis: a comparative study in *Neoconocephalus* (Orthoptera: Tettigoniidae). Journal of Experimental Biology 209: 1757–1764. https://doi.org/10.1242/jeb.02189

Deily JA, Schul J (2009) Selective phonotaxis in *Neoconocephalus nebrascensis* (Orthoptera: Tettigoniidae): call recognition at two temporal scales. Journal of Comparative Physiology A 195: 31–37. https://doi.org/10.1007/s00359-008-0379-2

Dray S, Dufour AB, Chessel D (2007) The ade4 package-II: Two-table and K-table methods. R News 7: 47–52. https://pbil.univ-lyon1.fr/ade4/article/rnews2/rnews2.pdf

Earl DA (2012) Structure harvester: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources 4: 359–361. https://doi.org/10.1007/s12686-011-9548-7

Elango N, Hunt BG, Goodisman MA, Soojin VY (2009) DNA methylation is widespread and associated with differential gene expression in castes of the honeybee, *Apis mellifera*. Proceedings of the National Academy of Sciences 106: 11206–11211. https://doi.org/10.1073/pnas.0900301106

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. Molecular Ecology 14: 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131: 479–491. http://www.genetics.org/content/131/2/479.short

Field LM, Devonshire AL, Ffrench-Constant RH, Forde BG (1989) Changes in DNA methylation are associated with loss of insecticide resistance in the peach-potato aphid *Myzus persicae* (Sulz.). FEBS Letters 243: 323–327. https://doi.org/10.1016/0014-5793(89)80154-1

Frederick FH (2013) Investigating an adaptive radiation in temperate *Neoconocephalus* (Orthoptera: Tettigoniidae). PhD Thesis, Columbia, Missouri: University of Missouri. https://mospace.umsystem.edu/xmlui/handle/10355/44039

Fulneček J, Kovařík A (2014) How to interpret Methylation Sensitive Amplified Polymorphism (MSAP) profiles? BMC Genetics 15: 2. https://doi.org/10.1186/1471-2156-15-2

Gao L, Geng Y, Li BO, Chen J, Yang JI (2010) Genome-wide DNA methylation alterations of *Alternanthera philoxeroides* in natural and manipulated habitats: implications for epigenetic regulation of rapid responses to environmental fluctuation and phenotypic variation. Plant, Cell & Environment 33: 1820–1827. https://doi.org/10.1111/j.1365-3040.2010.02186.x

Gerhardt HC, Huber F (2002) Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions. University of Chicago Press.

Greenfield MD (1990) Evolution of acoustic communication in the genus *Neoconocephalus*. In: Bailey WJ, Rentz DCF (Eds) The Tettigoniidae: Biology, Systematics and Evolution. Srpinger-Verlag, Berlin, 71–97. https://doi.org/10.1007/978-3-662-02592-5_5

Guo W, Wang XH, Zhao DJ, Yang PC, Kang L (2010) Molecular cloning and temporal-spatial expression of I element in gregarious and solitary locusts. Journal of Insect Physiology 56: 943–948. https://doi.org/10.1016/j.jinsphys.2010.05.007

Herrera CM, Bazaga P (2010) Epigenetic differentiation and relationship to adaptive genetic divergence in discrete populations of the violet *Viola cazorlensis*. New Phytologist 187: 867–876. https://doi.org/10.1111/j.1469-8137.2010.03298.x

Holland BR, Clarke AC, Meudt HM (2008) Optimizing automated AFLP scoring parameters to improve phylogenetic resolution. Systematic Biology 57: 347–366. https://doi.org/10.1080/10635150802044037

Hulce D, Li X, Snyder-Leiby T, Johathan Liu CS (2011) GeneMarker genotyping software: Tools to increase the statistical power of DNA fragment analysis. Journal of Biomolecular Techniques 22: S35-S36. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3186482/

Jablonka E, Lamb MJ (1998) Epigenetic inheritance in evolution. Journal of Evolutionary Biology 11: 159. https://doi.org/10.1007/s000360050073

Jablonka E, Lamb MJ (1999) Epigenetic Inheritance and Evolution: The Lamarckian Dimension. Oxford University Press on Demand.

Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23: 1801–1806. https://doi.org/10.1093/bioinformatics/btm233

Kang L, Chen X, Zhou Y, Liu B, Zheng W, Li R, Wang J, Yu J (2004) The analysis of large-scale gene expression correlated to the phase changes of the migratory locust. Proceedings of the National Academy of Sciences 101: 17611–17615. https://doi.org/10.1073/pnas.0407753101

Lamont BB, He T, Enright NJ, Krauss SL, Miller BP (2003) Anthropogenic disturbance promotes hybridization between *Banksia* species by altering their biology. Journal of Evolutionary Biology 16: 551–557. https://doi.org/10.1046/j.1420-9101.2003.00548.x

Ledón-Rettig CC, Richards CL, Martin LB (2012) Epigenetics for behavioral ecologists. Behavioral Ecology 24: 311–324. https://doi.org/10.1093/beheco/ars145

Liu S, Sun K, Jiang T, Ho JP, Liu B, Feng J (2012) Natural epigenetic variation in the female great roundleaf bat (*Hipposideros armiger*) populations. Molecular Genetics and Genomics 287: 643–650. https://doi.org/10.1007/s00438-012-0704-x

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209–220. https://www.ncbi.nlm.nih.gov/pubmed/6018555

Michaud EJ, Van Vugt MJ, Bultman SJ, Sweet HO, Davisson MT, Woychik RP (1994) Differential expression of a new dominant agouti allele (Aiapy) is correlated with methylation state and is influenced by parental lineage. Genes & Development 8: 1463–1472. https://doi.org/10.1101/gad.8.12.1463

Ney G, Schul J (2017) Low genetic differentiation between populations of an endemic prairie katydid despite habitat loss and fragmentation. Conservation Genetics 18: 1389–1401. https://doi.org/10.1007/s10592-017-0987-x

Pál C, Miklós I (1999) Epigenetic inheritance, genetic assimilation and speciation. Journal of Theoretical Biology 200: 19–37. https://doi.org/10.1006/jtbi.1999.0974

Pérez-Figueroa A (2013) MSAP: a tool for the statistical analysis of methylation-sensitive amplified polymorphism data. Molecular Ecology Resources 13: 522–527. https://doi.org/10.1111/1755-0998.12064

Pritchard JK, Wen X, Falush D (2010) Documentation for STRUCTURE software, version 2.3. University of Chicago, Chicago, IL. http://burfordreiskind.com/wp-content/uploads/Structure_Manual_doc.pdf

R Core Team (2015) R: A Language and Environment for Statistical Computing (Version 3.1. 2): R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org

Rapp RA, Wendel JF (2005) Epigenetics and plant evolution. New Phytologist 168: 81–91. https://doi.org/10.1111/j.1469-8137.2005.01491.x

Richards CL, Bossdorf O, Verhoeven KJ (2010) Understanding natural epigenetic variation. New Phytologist 187: 562–564. https://doi.org/10.1111/j.1469-8137.2010.03369.x

Robinson KL, Tohidi-Esfahani D, Lo N, Simpson SJ, Sword GA (2011) Evidence for widespread genomic methylation in the migratory locust, *Locusta migratoria* (Orthoptera: Acrididae). PLoS ONE 6: e28167. https://doi.org/10.1371/journal.pone.0028167

Sarkar S, Rao SR, Gupta VS, Hendre RR (1992) 5-Methylcytosine content in *Gryllotalpa fossor* (Orthoptera). Genome 35: 163–166. https://doi.org/10.1139/g92-026

Schul J, Bush SL, Frederick KH (2014) Evolution of call patterns and pattern recognition mechanisms in *Neoconocephalus* katydids. In: Hedwig B (Ed.) Insect Hearing and Acoustic Communication. Springer-Verlag, Berlin, 167–183. https://doi.org/10.1007/978-3-642-40462-7_10

Schul J, Patterson AC (2003) What determines the tuning of hearing organs and the frequency of calls? A comparative study in the katydid genus *Neoconocephalus* (Orthoptera, Tettigoniidae). Journal of Experimental Biology 206: 141–152. https://doi.org/10.1242/jeb.00070

Schulz B, Eckstein RL, Durka W (2013) Scoring and analysis of methylation-sensitive amplification polymorphisms for epigenetic population studies. Molecular Ecology Resources 13: 642–653. https://doi.org/10.1111/1755-0998.12100

Seehausen O (2006) Conservation: Losing biodiversity by reverse speciation. Current Biology 16: R334–R337. https://doi.org/10.1016/j.cub.2006.03.080

Shaposhnikov GK (1966) Origin and breakdown of reproductive isolation and the criterion of the species. Entomological Review 45: 1–18.

Smith TA, Martin MD, Nguyen M, Mendelson TC (2016) Epigenetic divergence as a potential first step in darter speciation. Molecular Ecology 25: 1883–1894. https://doi.org/10.1111/mec.13561

Snyder RL, Frederick-Hudson KH, Schul J (2009) Molecular phylogenetics of the genus *Neoconocephalus* (Orthoptera, Tettigoniidae) and the evolution of temperate life histories. PLoS ONE 4: e7203. https://doi.org/10.1371/journal.pone.0007203

Triblehorn JD, Schul J (2009) Sensory-encoding differences contribute to species-specific call recognition mechanisms. Journal of Neurophysiology 102: 1348–1357. https://doi.org/10.1152/jn.91276.2008

Varriale A, Bernardi G (2006) DNA methylation in reptiles. Gene 385: 122–127. https://doi.org/10.1016/j.gene.2006.05.034

Walker TJ (1975) Stridulatory movements in eight species of *Neoconocephalus* (Tettigoniidae). Journal of Insect Physiology 21: 595–603. https://doi.org/10.1016/0022-1910(75)90163-8

Walker TJ, Whitesell JJ, Alexander RD (1973) The robust conehead: two widespread sibling species (Orthoptera: Tettigoniidae: *Neoconocephalus* "*robustus*"). Ohio Journal of Science 73: 321–30. http://hdl.handle.net/1811/22182

Walsh TK, Brisson JA, Robertson HM, Gordon K, Jaubert-Possamai S, Tagu D, Edwards OR (2010) A functional DNA methylation system in the pea aphid, *Acyrthosiphon pisum*. Insect Molecular Biology 19: 215–228. https://doi.org/10.1111/j.1365-2583.2009.00974.x

West-Eberhard MJ (2005) Developmental plasticity and the origin of species differences. Proceedings of the National Academy of Sciences 102 (Supplement 1): 6543–6549. https://doi.org/10.1073/pnas.0501844102

Wilmore PJ, Brown AK (1975) Molecular properties of orthopteran DNA. Chromosoma 51: 337–345. https://doi.org/10.1007/BF00326320

Xiong LZ, Xu CG, Saghai Maroof MA, Zhang Q (1999) Patterns of cytosine methylation in an elite rice hybrid and its parental lines, detected by a methylation-sensitive amplification polymorphism technique. Molecular and General Genetics 261: 439–446. https://doi.org/10.1007/s004380050986

Xu M, Li X, Korban SS (2000) AFLP-based detection of DNA methylation. Plant Molecular Biology Reporter 18: 361–368. https://doi.org/10.1007/BF02825064

Supplementary material 1

Author: Gideon Ney, Johannes Schul

Data type: PDF file

Explanation note: Table S1: Sample collection localities, locality coordinates, and number of each species sampled in each year (*N. robustus* / *N. bivocatus*).

Link: https://doi.org/10.3897/jor.28.28888.suppl1

Supplementary material 2

Author: Gideon Ney, Johannes Schul

Data type: CSV file

Explanation note: Matrix of MS-AFLP called fragments for all individuals.

Link: https://doi.org/10.3897/jor.28.28888.suppl2

The floriphilic katydid, *Phaneroptera brevis*, is a frequent flower visitor of non-native, flowering forbs

Ming Kai Tan[1], Hui Lee[1], Hugh Tiang Wah Tan[1]

1 Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore.

Corresponding author: *Ming Kai Tan* (orthoptera.mingkai@gmail.com)

Academic editor: *Michel Lecoq* | Received 13 January 2019 | Accepted 20 February 2019 | Published 17 May 2019

http://zoobank.org/986AA1EA-24FE-4B30-9865-7960FCB7871F

Citation: Tan MK, Lee H, Tan HTW (2019) The floriphilic katydid, *Phaneroptera brevis*, is a frequent flower visitor of non-native, flowering forbs. Journal of Orthoptera Research 28(1): 21–26. https://doi.org/10.3897/jor.28.33063

Abstract

Distribution of consumers in a patch of vegetation can be predicted by resource availability and explained by the resource-concentration and optimal-foraging hypotheses. These hypotheses have not been explored for flower-visiting Orthoptera because they are deemed less economically or ecologically important. Some flower-visiting orthopterans can provide pollination services, which warrants more attention. We studied a Singaporean, floriphilic katydid, *Phaneroptera brevis*, to investigate the following questions: 1) how frequently does *P. brevis* visit flowers compared to other flower visitors and 2) what factors predict the abundance of *P. brevis*? We collected abundance data for *P. brevis* and other flower-visiting arthropods and quantified seven environmental parameters, including flower abundance and host-plant species richness. We found that *P. brevis* frequents flowers significantly more often than some common and expected flower visitors such as hoverflies. In line with the prediction of the resource-concentration hypothesis, the abundance of *P. brevis* was positively correlated with a higher flower abundance. Owing to the limited information on unexpected wild flower visitors and pollinators, especially from the understudied tropics of Southeast Asia, we propose that *P. brevis* can be a model organism for future studies to answer fundamental questions on flower visitation.

Key words

florivores, flower visitor, optimal foraging, Orthoptera, resource concentration

Introduction

Resource availability (such as that of a floral resource) can help to predict how consumers (including pollinators and florivores) are distributed in a patch of vegetation, and this consumer-resource relationship has been studied extensively under various theoretical frameworks (e.g. resource-concentration hypothesis) to examine the interactions between insects and plants (e.g. Otway et al. 2005, Andersson et al. 2013). The resource-concentration hypothesis (Root 1973) was one of the earliest hypotheses proposed to explain insect-plant interactions, particularly of insect pests on monocultures and polycultures of agricultural crops (Andow 1991, Rhainds and English-Loeb 2003). It predicts that an insect occurs at a higher density when its host-plant species occurs at a greater density or patch size (Kareiva 1983, Rhainds and English-Loeb 2003). A mechanism to explain such a relationship is the optimal-foraging hypothesis, which predicts that the insect can forage more optimally or efficiently in a patch with a greater density of host plant species since the insect is more likely to find and utilize its host plant, for example for feeding and as a reproduction substrate, while spending less time and energy on travelling and exposing itself to predation while travelling (e.g. Pyke 1984, Sowig 1989).

The resource-concentration and optimal-foraging hypotheses have been tested extensively on various flower-visiting insects, particularly mutualistic pollinators such as bees (e.g. Real 1981, Sowig 1989, Goulson 2000, Westphal et al. 2003, Vrdoljak et al. 2016), probably owing to the importance of these insects in fruit farming. However, not all flower-visiting insects are equally well-studied, especially those deemed to be less economically or ecologically important. Examples of these understudied flower-visiting insects include the orthopterans. Although orthopterans are probably more diverse flower-visitors than previously thought (Tan et al. 2017a), they are rarely considered as important flower visitors in ecological studies. This is partly because there are few studies on how their abundances can be predicted by floral resources or other biotic and abiotic factors.

Phaneroptera brevis (Serville, 1838) (Fig. 1) is a tropical floriphilic katydid from Southeast Asia which has been observed to visit and feed on the flowers of many host-plant species (Tan et al. 2017a). Although Tan and Tan (2018a) recently also observed that the gentle foraging behavior can help with pollination in an insectary setting, we are unaware of how abundant these flower-visiting katydids are in their natural environment, how frequently they visit flowers, and why. Without these data, it is not possible to assess the importance of these flower-visiting katydids in flowering communities and their pollinating efficiency.

In this study, we aim to investigate the following two research questions: 1) how frequently does *P. brevis* visit flowers compared to other flower visitors and 2) what factors predict the abundance of *P. brevis*? We counted the types of flower-visiting arthropods (including *P. brevis*) and measured environmental and resource parameters in a wasteland site in Singapore that is representative of the habitat of *P. brevis*. We predicted that *P. brevis* is a frequent flower visitor and that its abundance can be predicted by resource abundance in accordance to the prediction of the resource-concentration hypothesis.

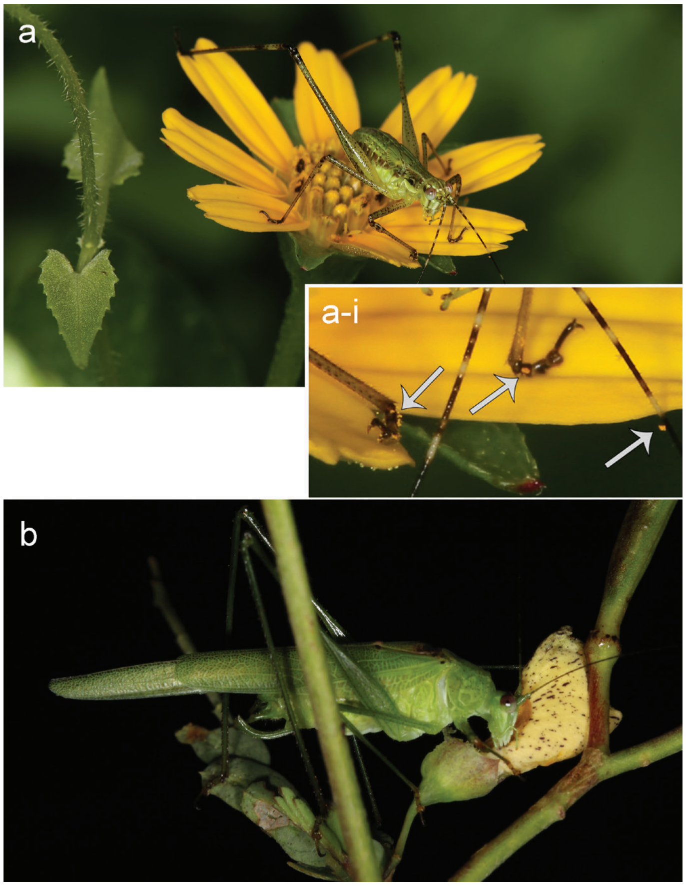


Fig. 1. A. Immature and **B.** Adult male individuals of *Phaneroptera brevis* visiting a capitulum of *Sphagneticola trilobata* (A) and an inflorescence of *Sesbania sesban* (B) at the study site in Singapore in the day (A) and at night (B). The arrows in the inset (a–i) indicate pollen grains attached to the body of the individual.

Materials and methods

Study subject.—*Phaneroptera brevis* belongs to the subfamily Phaneropterinae which is a group of katydids known to visit flowers. Native to Southeast Asia, *P. brevis* has been observed to visit and feed on the flowers of at least 13 species (Tan et al. 2017a). In Singapore, it is relatively common in open grasslands and forest edges that contain many flowering forbs, particularly on sites which contain *Bidens pilosa* L. (Asteraceae), *Sphagneticola trilobata* (L.) Pruski (Asteraceae), and *Neptunia plena* (L.) Benth. (Fabaceae) (Tan et al. 2017a). Although little is known about the life history of this katydid, several studies have examined the foraging behavior of *P. brevis* (e.g. Tan and Tan 2017, Tan et al. 2017b) and showed that this katydid prefers flowers to leaves (Tan and Tan 2017) and that its foraging performance can be influenced by flower abundance (Tan et al. 2017b).

Study locations and sampling.—Sampling for flower-visiting arthropods was conducted in a wasteland site of about 2,390 m^2 in Lorong Lada Hitam, off Mandai Road, Singapore (N1.41846°, E103.79164°). This site is dominated by non-native, naturalized weedy plants including *Bidens pilosa* and *Neptunia plena*. Surveys were conducted about once a week on non-rainy days at three broad time periods: in the morning (10 am–12 pm), afternoon (3–5 pm), and evening (7–9 pm). The surveys were conducted between August and September 2018. The same surveyor was involved in observing and recording the data throughout the surveys.

Data collection.—To minimize sampling bias, we first generated randomized points within the 2,390 m^2 wasteland site using QGIS software version 2.18.7 (QGIS Development Team 2019). A circular PVC hoop (i.e. hula hoop) of 70 cm interior diameter was used to delineate sampling quadrats, with the center of the hoop placed over the location of the GPS coordinates of the randomized points. We used a circular quadrat (area 0.385 m^2) because it has a lower perimeter-to-edge ratio than a square quadrat. For each survey, six quadrats were sampled. The hoop was gently placed over the vegetation with minimal disturbance. The hoop was then left for at least 20 min for the insects to acclimatize to the hoop before sampling began. Two methods were then employed (in the following order) to ensure a comprehensive survey of the flower-visiting insects:

1) Snapshot method (Garbuzov and Ratnieks 2014). For 30 s we counted and visually identified flower-visiting insects within each hoop. Earlier trials suggested that 30 s provided more than sufficient time for a snapshot survey of the flower-visiting insects for the size of the hoop used. This method allowed for a comprehensive sampling of the most prominent but fleeting flower-visiting insects such as Lepidoptera (butterflies and moths), Aculeata (bees and wasps), and Diptera (including hoverflies).
2) Timed interval method. While the snapshot method allowed a comprehensive sampling of Lepidoptera and Aculeata, less-fleeting and more well-camouflaged flower visitors (e.g. *P. brevis* and crab spiders) may be overlooked. To compensate for this, for the next 5 min we did a more thorough search for more cryptic insects, which included *P. brevis*, within the hoop. As it was impracticable to count the number of ants within the hoop, we only recorded the absence or presence of ants.

To obtain the total number and species of flower-visiting insects within each sampling point, data from both methods were pooled together. Only active flower-visiting insects, defined as any insect that intentionally moved in or on an inflorescence thereby touching the reproductive organs of the flower (Knop et al. 2018), were included. The total number of *P. brevis* adults and immatures inside the hoop was counted and we took note of whether the katydid was on a flower or on the leaves.

We grouped the flower-visiting arthropods into broad flower visitors:

1. Crickets and other katydids (suborder Ensifera, order Orthoptera);
2. Grasshoppers (suborder Caelifera, order Orthoptera);
3. Bees and wasps (subclade Aculeata, suborder Apocrita, order Hymenoptera, but not including the ants);
4. Ants (family Formicidae, suborder Apocrita, order Hymenoptera);
5. Floriphilic hoverflies (family Syrphidae, order Diptera);
6. All other flies (order Diptera);
7. Butterflies and moths (order Lepidoptera);
8. Cockroaches (order Blattodea);
9. Beetles (order Coleoptera);
10. True bugs (order Hemiptera);
11. Flower-visiting crab spiders (family Thomisidae, order Araneae).

The vegetation was also sampled within the hoop. Specifically, the number of plant species was recorded. For flowering species, the number of flowers was also counted for each species. For Asteraceae and Fabaceae species, inflorescences were counted instead of individual florets or flowers, respectively. We excluded the data for the Poaceae (grasses) owing to the vastly different floral morphology. Poaceae from the site are also mostly wind-pollinated so do not usually attract insect visitors (Culley et al. 2002). Environmental variables, including the brightness and temperature, were recorded using a HOBO pendant temperature/light 64K data logger. In total, 36 quadrats were sampled for altogether 107 times (over three time periods). One quadrat did not have complete data over the three time periods because of the presence of aggressive territorial dogs in the evening.

Data analysis.—To examine how frequently *P. brevis* visited flowers in comparison with other flower-visiting insects, we compared the frequency of visits to flowers for each type of flower-visiting insect. This was done by fitting a generalized linear mixed-effects model (GLMM) with the Poisson error via the log-link function using the glmer function from the R package lme4 (Bates et al. 2014). The flower visitor group was used as a fixed effect. The plot number was used as a random effect since each plot was sampled three times over the three time periods. We compared the least-square means of the frequency of visits to flowers between *P. brevis* and the different flower visitors using the emmeans function of the R package emmeans (Lenth 2018).

To investigate which factors predict the abundance of *P. brevis*, we performed a model selection via the information-theoretic approach (see Suppl. material 1 for more details). We first proposed a total of 39 candidate models with the abundance of *P. brevis* as the response (see Suppl. material 1 for the details and explanation of each proposed model). Each model contained a different combination of the following predictors: 1) abundance of all flower-visiting insects, 2) abundance of ambush predator crab spiders, 3) abundance of main competitors (bees, see Lindström et al. 2016), 4) presence or absence of ants, 5) time period of sampling (see Knop et al. 2018), 6) total flower abundance, and 7) plant species richness. We ensured that all models were biologically meaningful and not overfitted. We then ranked the models using the small sample size-corrected version using the Akaike information criterion (AICc) and the Akaike weights using the R package MuMIn (Barton and Barton 2015) (see Suppl. material 1 for how they were used to compare the models).

All statistical analyses were conducted using R software v.3.5.1 (R Core Team 2018).

Results

We observed that *P. brevis* frequents flowers significantly more often than some common and expected flower visitors such as hoverflies (Fig. 2); only bees and crab spiders visited flowers more frequently. *P. brevis* also frequents flowers more than lepidopterans, although this difference is not significant (Fig. 2). We did not observe any flower-visiting grasshoppers, beetles, and true bugs. Ants were encountered in 23 of 107 samples.

The best performing model for explaining the abundance of *P. brevis* (among 39 proposed models) contained flower abundance and the presence or absence of ants as important variables ($R^2_{GLMM(m)} = 0.06$, $R^2_{GLMM(c)} = 0.22$) (Table 1). Specifically, a high abundance of *P. brevis* was found to be associated with high flower abundance (estimate = 0.07, p-value = 0.011, 95% CI [0.02, 0.13], n = 107, Fig. 3). There was, however, no evidence of the effect of presence or absence of ants on the abundance of *P. brevis* (estimate = 0.17, p-value = 0.632, 95% CI [−0.55, 0.86], n = 107).

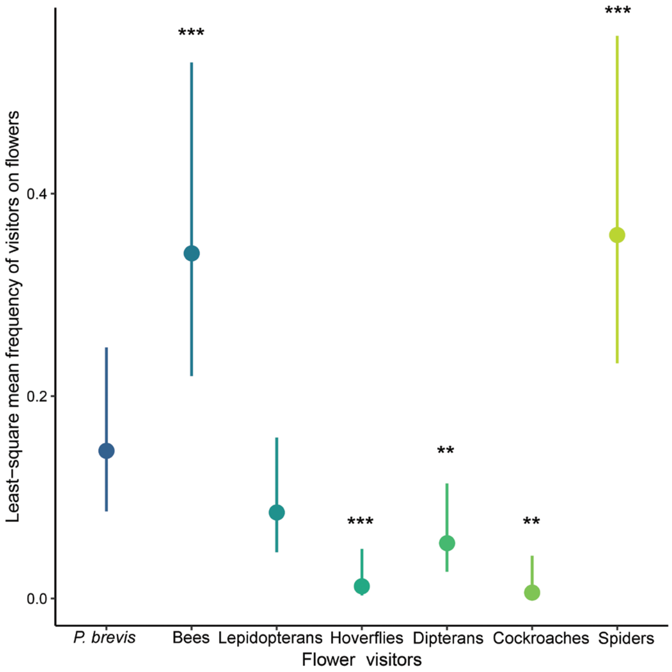


Fig. 2. Comparison of the least-square means of the frequency of visitors on flowers between *P. brevis* and other flower visitors. A generalized linear mixed-effects model with Poisson errors was fitted with different flower visitor as the fixed effect and the replicate number as the random effect. The significance between *P. brevis* and each flower visitor group is denoted as follows: **$P<0.01$; ***$P<0.001$.

Table 1. Summary of the top 10 models (out of 39 models) predicting the abundance of *P. brevis*. Generalized linear mixed-effects models with Poisson errors were fitted with replicate number as the random effect.

Models	df	AICc	Delta	Weight
~ total flower abundance + presence or absence of ants	4	177.4	0.0	0.50
~ total flower abundance × presence or absence of ants	5	179.6	2.2	0.17
~ total flower abundance + total flower abundance^2	4	181.2	3.8	0.08
~ total flower abundance + abundance of crab spiders	4	181.5	4.0	0.07
~ total flower abundance	3	182.2	4.8	0.05
~ plant species richness + presence or absence of ants	4	183.3	5.9	0.03
~ total flower abundance + time	5	183.5	6.1	0.02
~ total flower abundance × abundance of crab spiders	5	183.6	6.2	0.02
~ total flower abundance + abundance of all flower-visiting insects	4	184.2	6.8	0.02
~ plant species richness × presence or absence of ants	5	184.6	7.2	0.01

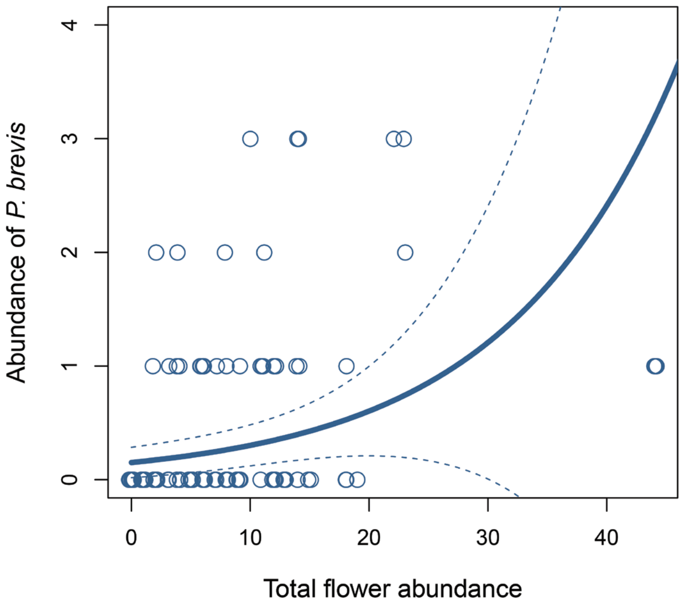


Fig. 3. High flower abundance was associated with high abundance of *P. brevis* (estimate = 0.07, p-value = 0.011, 95% CI [0.02, 0.13], $R^2_{GLMM(m)} = 0.06$, $R^2_{GLMM(c)} = 0.22$, n = 107). Generalized linear mixed-effects models with Poisson errors were fitted with the replicate number as the random effect.

Discussion

The major finding of our study is that *P. brevis* can be a considerably frequent flower visitor. This suggests that floriphilic orthopterans can play important roles in flowering communities both as florivores and potential pollinators, contrary to the generalization that orthopterans are unimportant flower visitors (Wardhaugh 2015, Ollerton 2017).

As a frequent flower visitor of non-native and potentially invasive species, *P. brevis* can help to reduce the spread of these weeds by feeding on the flowers. Florivory can directly and indirectly reduce reproductive success by causing damage to the reproductive parts and reducing attractiveness of the flowers to pollinators (McCall and Irwin 2006, Tan and Tan 2018b). Owing to *P. brevis* visiting flowers more frequently than other florivores (i.e. cockroaches, beetles, and true bugs), the katydid can be more efficient at weed control compared to other florivores. This, however, requires further validation given that the feeding efficiency of *P. brevis* can be variable (e.g. Tan and Tan 2017, Tan et al. 2017b) and the feeding efficiency of other florivores has not been measured and compared.

On the other hand, Tan and Tan (2018a) had previously demonstrated that *P. brevis* can forage gently on pollen grains without causing extensive damage to the reproductive parts. This may suggest that even though *P. brevis* visits flowers frequently, each individual may not be that efficient in damaging the reproductive parts and controlling weeds. Tan and Tan (2018a) also postulated that such behavior can help with pollination, but there is hitherto no direct evidence on how *P. brevis* can improve reproductive success of non-native weeds. Since *P. brevis* feeds mainly on non-native species, it is also unlikely that *P. brevis* has adapted to pollinating them and that any transfer of pollen is probably an artefact of its opportunistic feeding strategy. Therefore, in addition to the insectary experiment (Tan and Tan 2018a) and our observational study, controlled nursery or greenhouse experiments will also be needed to investigate more explicitly and quantify the feeding and pollination efficiencies of *P. brevis* to better understand their roles as flower visitors.

That high flower abundance is associated with higher *P. brevis* abundance is consistent with the predictions of the resource-concentration hypothesis and the optimal-foraging theory. A patch with a large quantity of floral resource may indicate a more favorable habitat for *P. brevis*, thus attracting the fully-winged adults to feed and lay eggs so that the nymphs can subsequently feed on the flowers. Although the juveniles are unlikely to disperse far, the adults of *P. brevis* can travel to and forage in vegetation patches with more resources. According to the prediction of the optimal-foraging theory, the adults should prefer to forage in patches of high flower abundance having travelled a great distance (Cresswell et al. 2000).

That more flowers attract more *P. brevis* individuals is not surprising since such a pattern has been observed in other flower visitors. Given that 1) there is a lack of descriptive studies on the relationships between the distribution of floral resources and the visitation activity of wild insects at the local scale and that 2) the existing literature tends to focus on monocultures and agricultural insect pests rather than natural communities (Otway et al. 2005, Scheper et al. 2015; but see Vrdoljak et al. 2016), our observations extend these hypotheses to include overlooked wild flower-visiting insect responses in relation to variation in floral resource density within vegetation patches. Furthermore, owing to the fact that *P. brevis* (and possibly other floriphilic katydids) were observed to be active and visit flowers day and night (although many other katydids are more nocturnal) (Tan et al. 2017a), its overall importance as a flower visitor may have been underestimated and overlooked in many studies which focused only on diurnal species (e.g. Garbuzov and Ratnieks 2014).

A limitation of our study is that sampling was conducted at only one site. Nonetheless, the site was selected because it is representative of the natural habitats of *P. brevis* and of forest edges in Singapore, thus providing a microcosm to answer our research questions on flower-visiting insect responses in relation to variation in floral-resource density within vegetation patches. Moreover, we restricted our study to one population of *P. brevis* because a concurrent study showed that individuals from different populations can exhibit consistent inter-population differences in behavior across time and/or contexts, which can in turn influence how they forage and respond to floral resources (Tan and Tan 2019). Since we did not also quantify population-level traits of *P. brevis* in this study, future investigations incorporating the traits of these different *P. brevis* populations can provide more insight into how different populations can respond differently to their environments (Tan and Tan 2019).

Our observations on understudied wild flower visitors from the tropics can also inspire unanswered ecological and evolutionary questions. First, the importance of floral resources, biotic interactions (e.g. predators and competitors), and abiotic predictors (e.g. time period) is likely to vary among flower visitors and in different systems (Hegland and Boeke 2006, Vrdoljak et al. 2016). There is currently insufficient ecological and behavioral data on the neglected flower visitors (including the orthopterans), especially in the tropics, to allow the explicit testing of many ecological hypotheses and to have a more generalizable understanding of flower visitors and their responses to floral resources in the tropics. We propose *P. brevis* as a model organism for studies on overlooked wild flower visitors and pollinators, especially in the understudied tropical habitats of Southeast Asia, to answer fundamental questions on flower visitation.

Acknowledgements

Permission for the study was granted by the National Parks Board of Singapore and the Singapore Land Authority (permit no. NP/RP18-123). The work of HL was part of her Undergraduate Research Opportunities Programme in Science (UROPS) module funded by the Department of Biological Sciences, National University of Singapore (NUS). The work of MKT was supported by the Lady Yuen Peng McNeice Graduate Fellowship of the NUS. The authors also thank Klaus-Gerhard Heller, Holger Braun, and an anonymous reviewer for providing constructive feedbacks to improve the manuscript. MKT conceived the study. HL collected the data. HL and MKT analyzed the data; all authors contributed to the writing. There is no conflict of interests among the authors.

References

Andersson P, Löfstedt C, Hambäck PA (2013) Insect density–plant density relationships: a modified view of insect responses to resource concentrations. Oecologia 173: 1333–1344. https://doi.org/10.1007/s00442-013-2737-1

Andow DA (1991) Vegetation diversity and arthropod population response. Annual Review of Entomology 36: 561–586. https://doi.org/10.1007/s00442-013-2737-1

Barton K, Barton MK (2015) Package 'MuMIn' Version 1. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H Dai D (2014) lme4: Linear mixed-effects models using Eigen and S4 (Version 1.1-7). https://cran.r-project.org/web/packages/lme4/lme4.pdf

Cresswell JE, Osborne JL, Goulson D (2000) An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. Ecological Entomology 25: 249–255. https://doi.org/10.1046/j.1365-2311.2000.00264.x

Culley TM, Weller SG, Sakai AK (2002) The evolution of wind pollination in angiosperms. Trends in Ecology & Evolution 17: 361–369. https://doi.org/10.1016/S0169-5347(02)02540-5

Garbuzov M, Ratnieks FL (2014) Quantifying variation among garden plants in attractiveness to bees and other flower visiting insects. Functional Ecology 28: 364–374. https://doi.org/10.1111/1365-2435.12178

Goulson D (2000) Why do pollinators visit proportionally fewer flowers in large patches? Oikos 91: 485–492. https://doi.org/10.1034/j.1600-0706.2000.910309.x

Hegland SJ, Boeke L (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. Ecological Entomology 31: 532–538. https://doi.org/10.1111/j.1365-2311.2006.00812.x

Kareiva P (1983) Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. In: Denno RF, McClure MS (Eds) Variable Plants and Herbivores in Natural and Managed Systems Academic Press, New York, 259–289. https://doi.org/10.1016/B978-0-12-209160-5.50015-5

Knop E, Gerpe C, Ryser R, Hofmann F, Menz MH, Trösch S, Ursenbacher S, Zoller L, Fontaine C (2018) Rush hours in flower visitors over a day–night cycle. Insect Conservation and Diversity 11: 267–275. https://doi.org/10.1111/icad.12277

Lenth R (2018) Emmeans: Estimated marginal means, aka least-squares means. Version 1.3.4. https://cran.r-project.org/package=emmeans

Lindström SA, Herbertsson L, Rundlöf M, Bommarco R, Smith HG (2016) Experimental evidence that honeybees depress wild insect densities in a flowering crop. Proceedings of the Royal Society B 283: 20161641. https://doi.org/10.1098/rspb.2016.1641

McCall AC, Irwin RW (2006) Florivory: the intersection of pollination and herbivory. Ecology Letters 9: 1351–1365. https://doi.org/10.1111/j.1461-0248.2006.00975.x

Ollerton J (2017) Pollinator diversity: distribution, ecological function, and conservation. Annual Review of Ecology, Evolution, and Systematics 48: 353–376. https://doi.org/10.1146/annurev-ecolsys-110316-022919

Otway SJ, Hector A, Lawton JH (2005) Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. Journal of Animal Ecology 74: 234–240. https://doi.org/10.1111/j.1365-2656.2005.00913.x

Pyke GH (1984) Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15: 523–575. https://doi.org/10.1146/annurev.es.15.110184.002515

QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Real LA (1981) Uncertainty and pollinator plant interactions: The foraging behavior of bees and wasps on artificial flowers. Ecology 62: 20–26. https://doi.org/10.2307/1936663

Rhainds M, English-Loeb G (2003) Testing the resource concentration hypothesis with tarnished plant bug on strawberry: density of hosts and patch size influence the interaction between abundance of nymphs and incidence of damage. Ecological Entomology 28: 348–358. https://doi.org/10.1046/j.1365-2311.2003.00508.x

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs 43: 95–124. https://doi.org/10.2307/1942161

Scheper J, Bommarco R, Holzschuh A, Potts SG, Riedinger V, Roberts SP, Rundlöf M, Smith HG, Steffan-Dewenter L, Wickens JB, Wickens VJ, Kleijin D (2015) Local and landscape level floral resources explain effects of wildflower strips on wild bees across four European countries. Journal of Applied Ecology 52: 1165–1175. https://doi.org/10.1111/1365-2664.12479

Sowig P (1989) Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia 78: 550–558. https://doi.org/10.1007/BF00378747

Tan MK, Artchawakom T, Wahab RA, Lee CY, Belabut DM, Tan HTW (2017a) Overlooked flower visiting Orthoptera in Southeast Asia. Journal of Orthoptera Research 26: 143–153. https://doi.org/10.3897/jor.26.15021

Tan MK, Leem CJM, Tan HTW (2017b) High floral resource density leads to neural constraint in the generalist, floriphilic katydid, *Phaneroptera brevis* (Orthoptera: Phaneropterinae). Ecological Entomology 42: 535–544. https://doi.org/10.1111/een.12414

Tan MK, Tan HTW (2017) Between florivory and herbivory: Inefficacy of decision-making by generalist floriphilic katydids. Ecological Entomology 42: 137–144. https://doi.org/10.1111/een.12369

Tan MK, Tan HTW (2018a) A gentle floriphilic katydid *Phaneroptera brevis* can help with the pollination of *Bidens pilosa*. Ecology 99: 2125–2127. https://doi.org/10.1002/ecy.2369

Tan MK, Tan HTW (2018b) Asterid ray floret traits predict the likelihood of florivory by the polyphagous katydid, *Phaneroptera brevis* (Orthoptera: Phaneropterinae). Journal of Economic Entomology 111: 2172–2181. https://doi.org/10.1093/jee/toy211

Tan MK, Tan HTW (2019) Individual- and population-level personalities in a floriphilic katydid. Ethology 125: 114–121. https://doi.org/10.1111/eth.12834

Vrdoljak SM, Samways MJ, Simaika JP (2016) Pollinator conservation at the local scale: flower density, diversity and community structure increase flower visiting insect activity to mixed floral stands. Journal of Insect Conservation 20: 711–721. https://doi.org/10.1007/s10841-016-9904-8

Wardhaugh CW (2015) How many species of arthropods visit flowers? Arthropod–Plant Interactions 9: 547–565. https://doi.org/10.1007/s11829-015-9398-4

Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecology Letters 6: 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Supplementary material 1

Authors: Ming Kai Tan, Hui Lee, Hugh Tiang Wah Tan
Data type: DOCX file
Explanation note: Supplementary Information on Statistical Analysis.

Link: https://doi.org/10.3897/jor.28.33063.suppl1

Review Article Journal of Orthoptera Research 2019, 28(1): 27-35

Big in Japan: The importance of riparian corridors for Orthoptera

Tim Gardiner[1], Nobuo Kuramoto[2], Misako Matsuba[3]

1 Environment Agency, Iceni House, Cobham Road, Ipswich, Suffolk, IP3 9JD, UK.

2 Faculty of Agriculture, Meiji University, Higashimita, Tama-ku, Kawasaki, Kanagawa 214-8571, Japan.

3 Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Kanagawa, 237-0061, Japan.

Corresponding author: *Tim Gardiner* (tim.gardiner@environment-agency.gov.uk)

Academic editor: *Alina Avanesyan* | Received 5 November 2018 | Accepted 20 February 2019 | Published 4 June 2019

http://zoobank.org/89A36FF7-F253-455A-A37A-4DC39B133513

Citation: Gardiner T, Kuramoto N, Matsuba M (2019) Big in Japan: The importance of riparian corridors for Orthoptera. Journal of Orthoptera Research 28(1): 27–35. https://doi.org/10.3897/jor.28.31380

Abstract

There are few studies on the Orthoptera of the floodplains, paddy fields, and levee embankments of Japan's riparian corridors. The research which has been undertaken indicates a relatively rich fauna (33% of Japan's grasshopper species recorded) with endangered species (e.g. *Eusphingonotus japonicus*) found on gravel floodplains, although diversity is restricted by forest cover and unfavorable land uses (e.g. agriculture). Management should focus on the alteration of levee mowing regimes to benefit orthopterans, and the control of invasive plant species and successional processes along river corridors, which appears to be important for grasshoppers of gravel substrates. Integrated Green Grey Infrastructure (IGGI) measures (levee terraces of Asteraceae plants) may enhance populations of Orthoptera and conserve declining plants such as *Aster tripolium* in Tokyo. More research is required throughout Japan to accurately determine the orthopteran fauna and appropriate conservation measures, particularly along super levees and in paddy fields.

Key words

conservation, ecosystem services, flood defense, floodplain, levee, paddy field, river

Introduction

A recent paper on the ecological niches of Korean Orthoptera in a meadow (Jung et al. 2018) highlights the dearth of research on conservation management techniques in temperate Asia. Linear corridors, such as riparian floodplains and associated levees, are of high importance for Orthoptera in Europe (Gardiner et al. 2015, Fargeaud and Gardiner 2018), but no assessment exists in Japan where an extensive network of flood defense levees are present in urban areas such as Tokyo (157 km of riparian levees; Tian 2014). The value of urban habitats with green corridors is illustrated by the banks and gardens of the Tokyo Imperial Palace where 45 species of Orthoptera (11% of Japan's estimated 390 species; Tojo et al. 2017) have been recorded (Biology Study Group 2001). Studies in the Tokyo area found a relationship between the distribution of green coverage and Orthoptera (Fukada 2002), with distance from existing habitats a key factor for determining species occurrence (Itagawa et al. 2012). Fifty species were collected in the Satoyama landscape (buffer zone between foothills and arable land) in Kanazawa (ElEla et al. 2012), while along the Nakatsu River the locally endangered grasshopper *Eusphingonotus japonicus* has been found on gravel habitats (Takeuchi and Fujita 1998).

Natural flood barriers such as sand dune forests and pine-covered islands (e.g. in Matsushima Bay; Fig. 1) can complement concrete and earthen levee embankments during storm surges and tsunamis (Tanaka 2012, Renaud and Murti 2013). These natural features function as vital secondary defenses when embankments overtop, or waves break during tsunamis, providing important ecosystem services (Renaud and Murti 2013). Movement of butterflies between the Urato Islands in Matsushima Bay (up to 6 km) is frequent, with wetlands, paddy fields, and linear levees contributing to host plant abundance (Yamamoto et al. 2007). However, green corridors, particularly in urban areas, may not be managed for the optimization of wildlife populations due to their human usage (Matsuba et al. 2016).

There are significant opportunities when rebuilding, repairing, and managing artificial and natural flood defenses to increase the abundance and diversity of wildlife (Cousins et al. 2017, Naylor et al. 2017, 2018). Mowing regimes can be altered to enhance populations of pollinators (Gardiner and Fargeaud 2018) such as endangered butterflies (Zhang and Miyashita 2017, Ohwaki et al. 2018), but could also be used to benefit orthopteran assemblages (Fargeaud and Gardiner 2018). Integrated Green Grey Infrastructure (IGGI) measures have been developed to provide engineers with a suite of options when it comes to the management of riparian embankments and floodplains (Naylor et al. 2017, 2018). Manipulation of floodplain vegetation to encourage Orthoptera (Yoshioka et al. 2010a) could benefit plant species such as the endangered *Aster kantoensis* (Takenaka et al. 1996, Kuramoto et al. 2005).

It is the aim of this review to highlight the current state of knowledge about the Orthoptera of riparian corridors in Japan and to ascertain which conservation management measures may be appropriate for further research and implementation.

Fig 1. Grassland buffering the shoreline on Fukuura Island in Matsushima Bay, acting as a natural flood defense. Grasshoppers (*Oxya* spp.) were numerous in this coastal corridor. Photo by T. Gardiner.

The overlooked Orthoptera

Japan is a global biodiversity hotspot with approximately 390 species of Orthoptera (Tojo et al. 2017). The native orthopteran fauna of the mainland (Honshu: 175 species) is species-poor compared to the islands (Bonin Islands: 0.07 spp./km^2, Honshu: 0.0008 spp./km^2; data from Yamanaka et al. 2015 and Cigliano et al. 2018), which in part reflects the extensive mainland development which has dramatically altered ecosystems (Nakamura et al. 2006). Suitable habitats for Orthoptera are becoming rarer; 61% of Japanese wetlands (current area 850 km^2; Natuhara 2013) have been lost in the last 100 years (Fujioka et al. 2010), concomitant with a steep decline in paddy field area since 1970 (Ichinose 2007, Katayama et al. 2015) to the current level of approximately 25,000 km^2 (6.6% of Japan's land area; Natuhara 2013). Riparian forest cover has been reduced due to the development of pasture (Table 1), which has led to riverbanks covered by native and alien plant species (Nakamura and Yamada 2005). The forest cover that remains is unlikely to be a favorable habitat for Orthoptera of open ground, restricting endemic species such as *E. japonicus* to pockets of gravel floodplain not encroached upon by trees. Unmanaged succession of riparian habitats to forest cover may be a critical threat to the persistence of this species (Takeuchi and Fujita 1998).

Where riparian wetlands have been converted to paddy fields (Table 1), they form a vital role in maintaining landscape heterogeneity through their network of levee banks (Fukamachi et al. 2005, Katayama et al. 2015, Normile 2016) and are an effective substitute for natural ecosystems (Natuhara 2013). Many paddy fields have been abandoned (Ichinose 2007, Yamada et al. 2013, Normile 2016) or converted to dry arable land, and those that remain are typically smaller than 1 ha (Fujioka et al. 2010) and intensively managed with chemical pesticides (Ichihara et al. 2014b, Katayama et al. 2015). The usage of pesticides has been linked to a decline in the abundance of harvestable grasshoppers for consumption (*Oxya* spp.) since the 1980s (Payne 2014). The proportion of modern riparian paddy fields with undeveloped land (e.g. levee banks 1–3 m high) has been reduced due to agricultural intensification and rationalization of the field network (Natuhara 2013). Where levees exist, natural vegetation cover has often been replaced with concrete to reduce mowing labor and improve slope stability (Fukamachi et al. 2005); this, however, removes suitable habitats for Orthoptera.

What is clear is that Orthoptera form an important part of grassland ecosystems (Gardiner 2018), consuming between 0.3–8% of net primary production (Köhler et al. 1987), although they are particularly wasteful feeders (e.g. *Chorthippus parallelus* consumes 2% of net primary production, but wastes 8%; Ingrisch and Köhler 1998). Orthoptera are also a vital constituent of food chains (Latchininsky et al. 2011). In a Japanese forest-stream ecosystem (Sato et al. 2011), orthopterans infected by nematomorph parasites (*Gordonius* spp.) were 20 times more likely to enter the watercourse, where they were a significant source of food (60% of their annual energy intake) for endangered Japanese trout (*Salvelinus leucomaenis japonicus*). In paddy fields and other riparian habitats in suburban areas (Kaneko et al. 2009), orthopterans were recorded in high abundance, consequently forming an important component (21.5% of food items) in the diet of the Japanese weasel *Mustela itatsi*. On open riverside plains, waterbirds feed on grasshoppers before and after the harvest in rice field wetlands (Fujioka et al. 2010), while on Sado Island, paddy field Orthoptera are essential in the diet of the endangered crested ibis *Nipponia nippon* (Yoshio et al. 2009; Table 2).

Despite their obvious role in sustaining food chains, studies on the Orthoptera of Japan in relation to riparian corridors are sparse. Yoshioka et al. (2010a) document species abundance on floodplain gravel and grassland along the Kinu River to the north of Tokyo (Table 2). The species list for gravel floodplain and buffer lands (Kinu grasslands) consisted of 12 recorded species, while 13 species were recorded in the Kitadan Valley wetland and surrounding habitats (ElEla et al. 2012). Three species were reported from the riverbed of the Nakatsu River (Takeuchi and Fujita 1998). In the coastal buffer lands of Tokyo, 10 species were recorded (Itagawa et al. 2012), although this may be a slight underestimate due to translation difficulties with the paper. A study of crickets on paddy field levees near Mount Fuji recorded seven species occurring on a levee and up to 15 m into the rice crop (Fig. 2).

The composition of the assemblages was markedly different between the six studies (due in part to three studies only focusing on one infraorder), with only two species each found in four studies (*Oxya yezoensis* and *Teleogryllus emma*) and one species found in three studies (*Atractomorpha lata*). Species such as *E. japonicus* are considered to be endemic to floodplain habitats and regionally rare (Takeuchi and Fujita 1998).

An interesting geographical influence can be noted from the comparison of two studies. The west coast study (Kitadan Valley) had the highest number of unique species (85% of 13 species), a difference reflected in the east coast samples (Tokyo) in which 70% of species were unique (Table 2). The east and west coast studies shared only two species in common (*O. yezoensis* and *T. emma*), which may in part be due to the artificial nature of the reclaimed coastal sites in Tokyo and the more natural wetland habi-

Table 1. Area of land use and vegetation types in Japanese riparian areas (after Miyawaki and Washitani 2004).

Land use	Estimated area (ha)	%	Value for Orthoptera
Native vegetation	71091	46	High
Pastures	18545	12	Medium*
Agricultural fields (incl. paddy fields)	17000	11	Medium*
Alien vegetation	12364	8	Low
Forestry	3091	2	Low
Others (urban etc.)	32455	21	–
Total	154545	100	

*value depends on the intensity of management (e.g. whether pesticides are used).

Table 2. Species of Orthoptera recorded in riparian corridors in Japan (X = recorded). Some studies only recorded one infraorder (Kinu, Nakatsu, and Fuji). The number of prefecture Red Data Lists a species is included in is also noted, and Japanese endemic species are in bold.

Infraorder, species	Kinu River[1]	Nakatsu River[2]	Fuji Paddy[3]	Sado Paddy[4]	Kitadan Valley[5]	Tokyo Coastal[6]	Prefect. Red List
Honshu location	Central	North	East coast	Sea of Japan	West coast	East coast	
Acrididea (grasshoppers)							
Acrida cinerea	X						
Atractomorpha lata	X			X		X	
Chorthippus biguttulus						X	
Eusphingonotus japonicus	**X**	**X**					**28**
Gastrimargus marmoratus	X						5
Glyptobothrus maritimus	X						2
Gonista bicolor	X						14
Locusta migratoria	X	X					1
Mongolotettix japonicus	X						2
Oedaleus infernalis	X	X					
Oxya yezoensis	**X**			**X**	**X**	**X**	
Parapodisma mikado					**X**		
Patanga japonica	X					X	
Shirakiacris shirakii	X						17
Stethophyma magister					X		4
Tetrix japonica					X		
Tettigoniidea (bush-crickets)							
Chizuella bonneti					X		1
Conocephalus maculatus				X		X	
Eobiana engelhardti subtropica					X		
Eobiana gladiella					**X**		
Euconocephalus varius						X	2
Gampsocleis buergeri					**X**		**3**
Mecopoda niponensis					X		18
Phaneroptera falcata						X	
Ruspolia lineosa				X		X	
Gryllidea (crickets)							
Dianemobius fasciatus			X				
Loxoblemmus arietuius			X				1
Mitius minor			X				5
Ornebius kanetataki						X	
Polionemobius taprobanensis			X				
Pteronemobius ohmachii			X				1
Teleogryllus emma			X	X	X	X	
Teleogryllus occipitalis					X		
Velarifictorus aspersus					X		
Velarifictorus micado			X		X		
No. species	12	3	7	5	13	10	15

[1] Yoshioka et al. (2010a); [2] Takeuchi and Fujita (1998); [3] Ichihara et al. (2014b); [4] Yoshio et al. (2009); [5] ElEla et al. (2012); [6] translated from Itagawa et al. (2012).

tats of the Kitadan Valley, but also because of differing sampling methods/biases (Gardiner et al. 2005) and differences in climate (the Sea of Japan coast is wetter than the Pacific coast) and isolation by mountainous terrain (Tojo et al. 2017).

When prescribing management techniques for different geographical regions of the Japanese archipelago, careful consideration should be given to their diverse orthopteran assemblages. Five studies in Table 2 are from Honshu Island (Japanese mainland), with much variation in the Orthoptera of Japan's 6852 islands which extend over 3000 km along the Pacific 'Ring of Fire' (Tojo et al. 2017). Genetic diversity is hugely varied throughout the archipelago for *Locusta migratoria* (Tokuda et al. 2010), *Podisma sapporensis* (Kowalczyk et al. 2008), and Tetrigidae (Ichikawa 1994). The life cycle of widely distributed species such as *L. migratoria* is markedly different across the islands, diapause being influenced by latitude (Tanaka 1994).

Further targeted research into the species present from a range of islands and latitudes will yield a longer list of Orthoptera in riparian areas. Only 35 species are listed in Table 2, a relatively small proportion of the Japanese Orthoptera (c. 390 species). Five (14%) of these are endemic to Japan (*Eobiana gladiella*, *E. japonicus*, *Gampsocleis buergeri*, *O. yezoensis*, and *Parapodisma mikado*). Fifteen species (43%) (including two of the endemics) are included in regional prefecture Red Data Lists (NPO Wildlife Research Association 2007) while the remaining 17 species are widespread (Cigliano et al. 2018). This indicates that riparian habitats may not be especially vital to the conservation of endemic species, which may be present in other ecosystems, but could be regionally important due to the high percentage of species listed in prefectural Red Data Lists. In floodplain habitats, seven regional Red Data List species have been recorded, compared to just three in riparian paddy fields (Table 2). This hints at the possible importance of semi-natural riverine environments for locally rare Orthoptera against those more intensively managed for rice production, which is a potential avenue for future research.

The absence of a national red data list of Japanese Orthoptera makes it harder still to form any definitive view on the value of riverine areas for endangered species. It's difficult to assess the importance of riparian environments without a much broader understanding of the species present. To fill this huge research deficit,

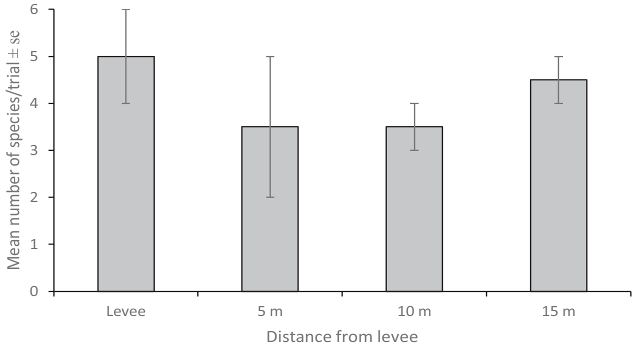


Fig. 2. The number of identified cricket (Gryllidae) species in a riparian paddy field near Mount Fuji at differing distances from a levee (after Ichihara et al. 2014b).

studies would need to focus on a wide geographical range, not just the main island of Honshu.

The differences in site preferences may also be due to the differing niches of species, for example of *Acrida cinerea*, *A. lata*, and *Oedaleus infernalis* (grass, Asteraceae, and bare ground, respectively; Jung et al. 2018). Research should focus on the habitat requirements of Orthoptera in riparian corridors such as levees, buffer lands, and floodplains. No definite list of the species present on flood defense embankments yet exists, although *A. cinerea* and *T. emma* have been recorded on super levees (15 m high) along the Arakawa River in Tokyo since 2016 (T. Gardiner unpublished data).

Itagawa et al. (2012) discovered that in grasslands mown intensively, species with high mobility and good flying ability (e.g. *O. yezoensis*) were the most successful orthopterans. The fragmentation of ecosystems in Tokyo has an influence over the distribution of Orthoptera and the composition of species assemblages. This further highlights the need for research into the detailed autecological requirements of key invertebrates on flood defense levees that link parks together and may allow the dispersal of species between sites.

Paddy levees in riparian habitats (Ichihara et al. 2014a) allow several species of Orthoptera to disperse into fields after irrigation water has receded (Ichihara et al. 2014b; Fig. 2). Seed-eating crickets have a weed suppression role (of the non-native *Lolium multiflorum*) in Fuji paddy fields (Ichihara et al. 2014c). Some species which prefer dry habitats were found predominantly on paddy levees (*Loxoblemmus* spp.; levee 4.0–4.4 individuals/trap/day, field 0.3–0.7 individuals), whereas others, which are tolerant of both dry and wet conditions (e.g. *T. emma*), showed no preference for the embankment and were recorded up to 15 m into the field (Ichihara et al. 2014b).

If management enhances the abundance and diversity of invertebrates, landscape corridors along rivers could provide vital ecosystem services (supporting, provisioning, regulating, and cultural functions; Millennium Ecosystem Assessment 2005). Orthoptera, by their consumption of primary production, role in cycling nutrients up the food chain, weed suppression in paddy fields (particularly of *L. multiflorum*; Ichihara et al. 2014a), and even pollination (Negoro 2002, 2003, Micheneau et al. 2010), fulfil a supporting role in ecosystems (Gardiner 2018). They are also a traditional food source (Mitsuhashi 1997, Payne and Van Itterbeeck 2017). *O. yezoensis* is the most popular edible grasshopper, rich in proteins (Mitsuhashi 1997), and abundant throughout Japan (Table 2).

The ecological requirements of many species of Orthoptera in riparian corridors are poorly known. The habitat requirements of species from the genera *Conocephalus* and *Ruspolia*, which have been commonly found near water in Japan (Table 2), are not known. This makes it difficult to assess the important niches which they inhabit and how to undertake effective conservation management. Research on the ecology of Asian Orthoptera is only beginning to emerge (Jung et al. 2018). Therefore, targeted studies on the riparian habitats of species linked to water are needed to fully assess the value of corridors for Orthoptera.

Greening the grey – measures to enhance riparian corridors for Orthoptera

Habitat preferences of Orthoptera may relate to choice of oviposition site (Choudhuri 1958), food preferences (Bernays and Chapman 1970a, b), vegetation height and biomass (Gardiner et al. 2002), and grassland management regimes (Clarke 1948). Vegetation structure is an important factor for grassland fauna (Duffey et al. 1974, Morris 2000, Gardiner 2009). Clarke (1948) and Gardiner and Hassall (2009) noted that vegetation height and density are the most important habitat factors for grasshoppers, particularly in respect to their influence on microclimate. Unfortunately, management of landscape corridors can often be detrimental to the needs of species due to human pressures on land use (Matsuba et al. 2016). In Tokyo, measures are already being undertaken along the Arakawa River super levees to improve the mowing regimes for invertebrates (Fig. 3). Outside of unmown areas, recreational land uses pose a threat to Orthoptera, particularly the establishment of baseball and football fields with their required short grass turf (<10 cm height), which is generally unfavorable for grasshoppers (Gardiner et al. 2002).

The Arakawa levee grasslands are cut at different heights for invertebrates, management which may be highly beneficial to orthopterans such as *A. cinerea* and *O. infernalis* which have differing ecological niches (Jung et al. 2018). The latter species prefers habitats with bare ground which are present on the trampled paths of levees, whereas *A. cinerea* has been most commonly recorded on grasses. Species such as *A. lata*, observed on the east and west coast (Table 2), have been found mainly on Asteraceae plants (Jung et al. 2018). In south-east Asia, six species of Orthoptera (including *Acrida* sp., *Atractomorpha* sp., and *Conocephalus maculatus*) have been observed visiting Asteraceae plants, feeding on the flowers (Tan et al. 2017a, b, Tan and Tan 2018a, b). Given the conservation measures being put in place for *Aster tripolium*, such as terraces on the riverside slope of flood defenses in Tokyo, it is likely that *A. lata* will have plenty of favorable habitat, although further experimental research is required to investigate the connection between grasshopper and plant. The creation of shorter grassland areas (but not uniformly <10 cm) through mowing should benefit *A. cinerea*, a species of Poaceae (Jung et al. 2018), and hotter swards (Gardiner and Hassall 2009).

The management of paddy field levees on floodplains could incorporate rotational mowing regimes (Fujioka et al. 2010) and a reduction in the frequency of cutting to conserve Orthoptera populations (Yoshio et al. 2009) and those of endangered butterflies (Ohwaki et al. 2018). Herbicide usage is the most damaging option for paddy levees; mowing and no management are better measures for conserving Orthoptera (Yoshio et al. 2009, Giuliano et al. 2018). In a study of paddy levee crickets at the foot of Mount Fuji, seed-eating crickets were in high abundance on plants such as *Phlox subulata* (Polemoniaceae), compared to weedy levees or those with *Zoysia japonica* (Poaceae), which were the least preferred (Ichihara et al. 2014a). It is suggested that the sowing of levee banks with plants favorable for crickets may assist them in their role of weed suppression (*L. multiflorum*) in paddy field ecosystems (Table 3).

Grazing can have benefits for Orthoptera (Gardiner and Haines 2008, Bazelet and Gardiner 2018) and might be ideal for conserving orthopterans on levees and floodplain grasslands. Grazing is an issue which needs careful consideration before the introduction of livestock so that populations of rare plants and grasshoppers are not endangered. Research should focus on the ecological requirements of key orthopteran species in riparian environments, relating abundance and assemblage diversity to sward height, microclimate, and botanical characteristics. The type of animal used for grazing could be a focus for future work in grazed riparian habitats. The maintenance of levees and floodplains in an early successional state by grazing livestock may be desirable for species such as *E. japonicus* and *O. infernalis* which are threatened by unmanaged development of woody vegetation.

In closed grassland swards, the creation and maintenance of bare earth is essential for the persistence of disturbance-dependent orthopterans (Gardiner et al. 2015) and may benefit early successional species such as *O. infernalis* in Japan. Trampling of levee vegetation may also occur due to grazing livestock and the action of walkers' feet on paths in Satoumi landscapes such as those in Matsushima Bay where *O. infernalis* is found on well-walked tracks (T. Gardiner unpublished data). The creation of scrapes on the flat berms of super levees in Tokyo could create suitable bare-ground niches for grasshoppers (Table 3). Trials on artificial soil disturbance in riparian grassland could run alongside studies on microclimate and vegetation cover. We advise against soil disturbance on the slopes of levee embankments due to the potential for destabilization and possible problems with soil erosion during breaching or overtopping in a flood. A summary of the most appropriate sward management techniques on flood defense and paddy levees is found in Table 3.

The selection of IGGI measures developed by Naylor et al. (2017) may provide benefits for Orthoptera. Options likely to be highly favorable for orthopterans include altered mowing regimes on levees and large-scale development incorporating enhanced habitat features, although it should be acknowledged that trials should be undertaken before any major changes are made to riparian habitats. Terraces of *A. tripolium* on the riverside slope of flood defenses in coastal areas may be of some value for grasshoppers, particularly *A. lata*, which could benefit from the increased provision of Asteraceae plants (Fig. 4), although a direct link between the two species would need to be determined before widespread implementation. The concrete levees of modern paddy fields offer very little habitat for Orthoptera (Fig. 5); greening of these structures could be investigated in future trials. Removal of concrete walls and replacement with grassy embankments might aid restoration of traditional paddy field systems.

Table 3. Sward management techniques for conserving populations of Orthoptera on flood defense and paddy levees in Japan (X indicates a suitable measure).

Technique	Flood levee	Paddy levee
Different cutting heights (10–20 cm)	X	X
Reduced number of cuts (<4 cuts)	X	X
Rotational mowing	X	X
Uncut refuges	X	X
Soil disturbance (scrapes, ruts etc.)*	X	
Reseeding with appropriate vegetation		X
Grazing livestock*	X	
Avoidance of herbicide application		X

*on flat berms only to avoid destabilizing embankment slopes.

The management of floodplains poses a different set of problems (Fig. 6). A detailed understanding of the geomorphology of the river system is essential (Washitani 2001, Nakamura et al. 2002). Japanese rivers are typically short and steep owing to the mountainous nature of the main island of Honshu (Yasuda et al. 2016). The seasonally high levels of rain and snow mean that rivers can flow rapidly, shifting sediments quickly (Nakamura et al.

Fig. 3. Arakawa super levee in Tokyo. Grassland is left uncut to produce a mosaic of habitats for Orthoptera. Photo by T. Gardiner.

Fig. 4. Flat terrace on the riverside slope of a flood defense embankment at Kasai Rinkai Park at the mouth of the Edogawa River in Tokyo Bay. The terrace is accumulating vegetation, including *Aster tripolium*, a rare and declining species in the Bay. Photo by T. Gardiner.

Fig. 5. Concrete paddy levee and field along the Tama River (Fussa) providing minimal habitat for Orthoptera. Photo by T. Gardiner.

2006). Such dynamic systems can be vulnerable to rapid changes in their geomorphology, increasing rainfall due to climate change and typhoons (Yasuda et al. 2016).

Invasive plants such as *Eragrostis curvula* present a threat to grasshopper populations on gravelly floodplains (Yoshioka et al. 2010a, b). Twelve species of grasshopper were negatively affected by the abundance of *E. curvula*; habitat specialists such as *E. japonicus* experienced significant declines in abundance with increasing *E. curvula* coverage (Yoshioka et al. 2010a). The reduction in open gravel habitat due to the spread of alien plants may also be a threat to other species such as the endemic *A. kantoensis* (Kuramoto et al. 1992, 2005).

Climate change will affect riverine ecosystems, making any habitat modifications susceptible to increasing pressures from, for example, typhoons (Hoshino et al. 2012, Yasuda et al. 2016). Riparian paddy fields fulfil a vital role in flood storage, preventing flooding downstream (Natuhara 2013). Riparian rehabilitation and natural flood management is well advanced in Japan, with over 23,000 river restoration schemes completed since 1991 (Nakamura et al. 2006). The combined threat from alien plants and climate change complicate the IGGI measures suitable for rivers and floodplains (Roca et al. 2017). River engineering measures could have potential benefits for Orthoptera in riparian ecosystems (Table 4), although this remains unproven due to the dearth of research throughout the world. Removing river levees may lead to a larger, more natural floodplain suitable for orthopterans such as *E. japonicus*. Alteration of riverbed levels creates a diversity of gravel substrates suitable for Orthoptera of early successional habitats (Nakamura et al. 2006), although modification of the geomorphology must be carefully undertaken in consultation with specialists (Nakamura et al. 2002).

Fig. 6. Gravel floodplain along the Tama River, early successional habitat for the endangered *Eusphingonotus japonicus* grasshopper and *Aster kantoensis*. Photo by T. Gardiner.

Table 4. Integrated Green Grey Infrastructure (IGGI) measures and their potential benefits for Orthoptera along rivers in Japan.

Aim of IGGI measure	Potential benefit for Orthoptera habitat
River embankment (levee) removal	Creation of larger floodplain habitat
Lowering/removal of weirs/culverts	More natural floodplain
Meander restoration of channel	More natural floodplain
Changing bed level of channel	Variation in gravel substrates
Regrading of river embankments (levees)	Shallower bank habitat
Narrowing river channels	Creation of larger floodplain habitat

Recommendations for further research and management

It is clear from this review that despite the Japanese Orthoptera being described in detail (Ichikawa et al. 2006, Murai et al. 2011), there is a large research deficit when it comes to the conservation management of habitats, particularly those of riparian areas. Despite this, a hypothetical relationship can be inferred from existing research (Table 1, Fig. 7) and subjected to further studies of orthopteran species composition throughout Japan. The natural floodplains with native vegetation can have a high diversity of Orthoptera including endemic and regionally endangered species (Yoshioka et al. 2010a); whereas with greater anthropogenic modification of riparian areas (flood defense levees and arable/paddy fields), diversity can decrease (Itagawa et al. 2012). This is often due to intensive management regimes, such as regular mowing on levees and chemical pesticide usage in paddy fields, creating an unsuitable environment for the persistence of Orthoptera (Ichihara et al. 2014b, Payne 2014). The traditional Satoyama landscape of paddy fields and terraces can have value for grasshoppers (e.g. Sado Isand; Yoshio et al. 2009) and crickets (e.g. near Mount Fuji; Ichihara et al. 2014b) but increasing abandonment of this way of farming will probably lead to a decrease in the diversity of Orthoptera (Natuhara 2013).

In the modified riparian landscape of paddy fields and terraces, levees could form corridors which allow the dispersal of Orthoptera in a similar way to sea wall flood defenses in Europe (Fargeaud and Gardiner 2018). Climate change may be behind the expansion in range of species such as *Phaneroptera nana* which has been found on a sea wall along the River Thames (Gardiner and Couch 2019 in press). Phaneropterinae have been recorded in Tokyo (Itagawa et al. 2012) and may utilize flood defenses for dispersal in Japan. Further research should aim to determine the importance of levee embankments for the dispersal of Orthoptera through unfavorable landscapes (intensively managed paddy fields and urban areas) in relation to climate change.

Given the importance of flood defense in Japan due to climate change and typhoons (Hoshino et al. 2012), green measures can be implemented during the maintenance and rebuilding of levees to enhance populations of common and scarce Orthoptera species. Such measures include alteration of mowing regimes and the design of vegetated terraces on riverside flood defenses. The presence of orthopterans such as *A. cinerea*, *A. lata*, and *O. infernalis*, which are common across a range of habitats, is a good indication of the success of management techniques.

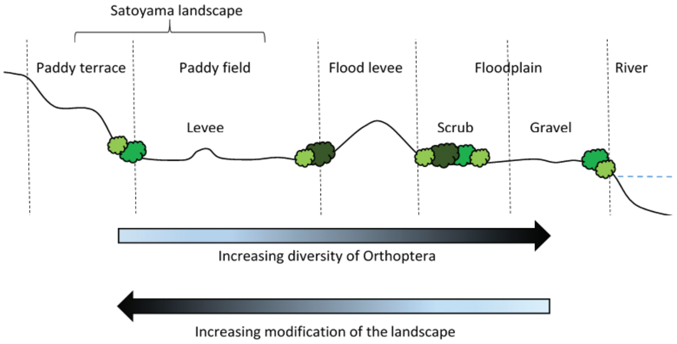


Fig. 7. Cross section of a floodplain ecosystem in relation to diversity of Orthoptera and anthropogenic modification of the landscape.

Acknowledgements

The authors would like to thank Rasuna Mishima (Meiji University) for assistance with surveys and field trips in Tokyo. The first author also acknowledges the support of Meiji University for funding visits to Japan to undertake research and lecture on green engineering of flood defenses. Dr. Hisako Okada assisted with field visits to record *A. kantoensis* on floodplains along the Tama River. We are also grateful to Klaus-Gerhard Heller for a thorough and helpful review of the paper.

References

Bazelet CS, Gardiner T (2018) Orthoptera response to grazing: An introduction to the special issue. Journal of Orthoptera Research 27: 1–2. https://doi.org/10.3897/jor.27.27213

Bernays EA, Chapman RF (1970a) Experiments to determine the basis of food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae) in the field. Journal of Animal Ecology 39: 761–776. https://doi.org/10.2307/2866

Bernays EA, Chapman RF (1970b) Food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae) in the field. Journal of Animal Ecology 39: 383–394. https://doi.org/10.2307/2977

Biology Study Group (2001) Biota of Imperial Palace Fukiage Garden. Sekai Bunkasha.

Choudhuri JCB (1958) Experimental studies on the choice of oviposition sites by two species of *Chorthippus* (Orthoptera: Acrididae). Journal of Animal Ecology 27: 201–215. https://doi.org/10.2307/2239

Cigliano MM, Braun H, Eades DC, Otte D (2018) Orthoptera Species File. Version 5.0/5.0. http://Orthoptera.SpeciesFile.org

Clarke EJ (1948) Studies in the ecology of British grasshoppers. Transactions of the Royal Entomological Society of London 99: 173–222. https://doi.org/10.1111/j.1365-2311.1948.tb01235.x

Cousins LJ, Cousins MS, Gardiner T, Underwood GJC (2017) Factors influencing the initial establishment of salt marsh vegetation on engineered sea wall terraces in SE England. Ocean and Coastal Management 143: 96–104. https://doi.org/10.1016/j.ocecoaman.2016.11.010

Duffey E, Morris MG, Sheail J, Ward LK, Wells DA, Wells TCE (1974) Grassland Ecology and Wildlife Management. Chapman and Hall, London.

ElEla SA, ElSayed W, Nakamura K (2012) Incidence of orthopteran species (Insecta: Orthoptera) among different sampling sites within Satoyama area, Japan. Journal of Threatened Taxa 4: 2476–2480. https://doi.org/10.11609/JoTT.o2775.2476-80

Fargeaud K, Gardiner T (2018) The response of Orthoptera to grazing on flood defense embankments in Europe. Journal of Orthoptera Research 27: 53–61. https://doi.org/10.3897/jor.27.25183

Fujioka M, Lee DS, Kurechi M, Yoshida H (2010) Bird use of rice fields in Korea and Japan. Waterbirds 33: 8–29. https://doi.org/10.1675/063.033.s102

Fukada S (2002) Correlation between number of the Orthoptera species and indices of local landscape diversity – a case study at Tsurimi River basin. Hiyoshi Review of Natural Science 32: 55–65.

Fukamachi K, Oku H, Miyake A (2005) The relationships between the structure of paddy levees and the plant species diversity in cultural landscapes on the west side of Lake Biwa, Shiga, Japan. Landscape and Ecological Engineering 1: 191–199. https://doi.org/10.1007/s11355-005-0019-8

Gardiner T (2009) Hopping Back to Happiness? Conserving Grasshoppers on Farmland. VDM Verlag, Saarbrücken.

Gardiner T (2018) Grazing and Orthoptera: A review. Journal of Orthoptera Research 27: 3–11. https://doi.org/10.3897/jor.27.26327

Gardiner T, Couch Y (2019 in press) Brexit backstop: Southern sickle-bearing bush-cricket (*Phaneroptera nana*) new to Essex. Essex Naturalist.

Gardiner T, Fargeaud K (2018) The effect of late cutting on bumblebees (*Bombus* spp.) in sea wall grassland. Aspects of Applied Biology 139: 43–50.

Gardiner T, Haines K (2008) Intensive grazing by horses detrimentally affects orthopteran assemblages in floodplain grassland along the Mardyke River Valley, Essex, England. Conservation Evidence 5: 38–44. https://www.conservationevidence.com/individual-study/2277

Gardiner T, Hassall M (2009) Does microclimate affect grasshopper populations after cutting of hay in improved grassland? Journal of Insect Conservation 13: 97–102. https://doi.org/10.1007/s10841-007-9129-y

Gardiner T, Hill J, Chesmore D (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. Journal of Insect Conservation 9: 151–173. https://doi.org/10.1007/s10841-005-2854-1

Gardiner T, Pilcher R, Wade M (2015) Sea Wall Biodiversity Handbook. RPS, 264 pp. http://www.essexfieldclub.org.uk/portal/p/Sea+Wall+Biodiversity+Handbook

Gardiner T, Pye M, Field R, Hill J (2002) The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippus* species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. Journal of Orthoptera Research 11: 207–213. https://doi.org/10.1665/1082-6467(2002)011[0207:TIOSHA]2.0.CO;2

Giuliano D, Cardarelli E, Bogliana G (2018) Grass management intensity affects butterfly and orthopteran diversity on rice field banks. Agriculture, Ecosystems & Environment 267: 147–155. https://doi.org/10.1016/j.agee.2018.08.019

Hoshino S, Esteban M, Mikami T, Takabatake T, Shibayama T (2012) Climate change and coastal defenses in Tokyo Bay. Coastal Engineering Proceedings 1: 1–15. https://doi.org/10.9753/icce.v33.management.19

Ichihara M, Inagaki H, Matsuno K, Saiki C, Mizumoto S, Yamaguchi S, Yamashita M, Sawada H (2014b) Postdispersal weed seed predation by crickets in a rice paddy field after irrigation water recedes. Japan Agricultural Research Quarterly 48: 63–69. https://doi.org/10.6090/jarq.48.63

Ichihara M, Matsuno K, Inagaki H, Saiki C, Mizumoto S, Yamaguchi S, Yamashita M, Sawada H (2014a) Creation of paddy levees to enhance the ecosystem service of weed seed predation by crickets. Landscape and Ecological Engineering 11: 227–233. https://doi.org/10.1007/s11355-014-0254-y

Ichihara M, Uchida S, Fujii S, Yamashita M, Sawada H, Inagaki H (2014c) Weed seedling herbivory by field cricket *Teleogryllus emma* (Orthoptera: Gryllidae) in relation to the depth of seedling emergence. Weed Biology and Management 14: 99–105. https://doi.org/10.1111/wbm.12035

Ichikawa A (1994) A revision of the family Tetrigidae (Orthoptera) of the Ryukyu Islands, southern Japan, with descriptions of new species and subspecies. (Part 1). Japanese Journal of Entomology 62: 457–474.

Ichikawa A, Kano Y, Kawai Y, Kawai M, Tominago O, Murai T (2006) Orthoptera of the Japanese Archipelago in Color – 2nd Edition. Hokkaido University Press, 687 pp.

Ichinose T (2007) Restoration and conservation of aquatic habitats in agricultural landscapes of Japan. Global Environmental Research 11: 153–160.

Ingrisch S, Köhler G (1998) Die Heuschrecken Mitteleuropas. Westarp Wissenschaften, Magdeburg.

Itagawa S, Ichinose T, Katagiri Y, Osawa S, Ishikawa M (2012) The relationship between green coverage distribution and inhabitation of Orthoptera on the reclaimed land in Tokyo Bay Area. Journal of the Japanese Institute of Landscape Architecture 75: 621–624. https://doi.org/10.5632/jila.75.621

Jung Y, Baek M, Lee S, Jablonski PG (2018) Microhabitat segregation among three co-existing species of grasshoppers on a rural meadow near Seoul, Korea. Journal of Orthoptera Research 27: 173–175. https://doi.org/10.3897/jor.27.28402

Kaneko Y, Shibuya M, Yamaguchi N, Fujii K, Okumura T, Matsubayashi K, Hioki Y (2009) Diet of Japanese weasels (*Mustela itatsi*) in a sub-urban landscape: Implications for year-round persistence of local populations. Mammal Study 34: 97–105. https://doi.org/10.3106/041.034.0205

Katayama N, Baba YG, Kusumoto Y, Tanaka K (2015) A review of post-war changes in rice farming and biodiversity in Japan. Agricultural Systems 132: 73–84. https://doi.org/10.1016/j.agsy.2014.09.001

Köhler G, Brodhun H-P, Schäller G (1987) Ecological energetics of Central European grasshoppers (Orthoptera: Acrididae). Oecologia 74: 112–121. https://doi.org/10.1007/BF00377354

Kowalczyk M, Tatsuta H, Grzywacz B, Warchałowska-Śliwa E (2008) Relationship between chromosomal races/subraces in the brachypterous grasshopper *Podisma sapporensis* (Orthoptera: Acrididae) inferred from mitochondrial ND2 and CO1 gene sequences. Annals of the Entomological Society of America 101: 837–844. https://doi.org/10.1093/aesa/101.5.837

Kuramoto N, Kobayashi M, Sugiyama S, Nomura Y, Sonoda Y, Ashizawa K, Hosogi D (2005) Studies on seed dispersal of restored *Aster kantoensis* populations on Tama River Floodplain. Journal of the Japanese Society of Revegetation Technology 31: 63–68. https://doi.org/10.7211/jjsrt.31.63

Kuramoto N, Takenaka A, Washitani I, Inoue K (1992) A conservation biology of *Aster kantoensis* growing along the Tama River. Journal of the Japanese Institute of Landscape Architecture 55: 199–204. https://doi.org/10.5632/jila1934.55.5_199

Latchininsky A, Sword GA, Sergeev M, Cigliano MM, Lecoq M (2011) Locusts and grasshoppers: Behavior, ecology and biogeography. Psyche 2011: 1–4. https://doi.org/10.1155/2011/578327

Matsuba M, Nishijima S, Katoh K (2016) Effectiveness of corridor vegetation depends on urbanization tolerance of forest birds in central Tokyo, Japan. Urban Forestry & Urban Greening 18: 173–181. https://doi.org/10.1016/j.ufug.2016.05.011

Micheneau C, Fournel J, Warren BH, Hugel S, Gauvin-Bialecki A, Pailler T, Strasberg D, Chase MW (2010) Orthoptera, a new order of pollinator. Annals of Botany 105: 355–364. https://doi.org/10.1093/aob/mcp299

Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-Being: Synthesis. Island Press, 155 pp.

Mitsuhashi J (1997) Insects as traditional foods in Japan. Ecology of Food and Nutrition 36: 187–199. https://doi.org/10.1080/03670244.1997.9991514

Miyawaki S, Washitani I (2004) Invasive alien plant species in riparian areas of Japan: The contribution of agricultural weeds, revegetation species and aquacultural species. Global Environmental Research 8: 89–101.

Morris MG (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biological Conservation 95: 129–142. https://doi.org/10.1016/S0006-3207(00)00028-8

Murai T, Ito F, Gakkai NC (2011) A Field Guide to the Orthoptera of Japan. Hokkaido University Press, 449 pp.

Nakamura F, Jitsu M, Kameyama S, Mizugaki S (2002) Changes in riparian forests in the Kushiro Mire, Japan, associated with stream channelization. River Research and Applications 18: 65–79. https://doi.org/10.1002/rra.621

Nakamura F, Yamada H (2005) Effects of pasture development on the ecological functions of riparian forests in Hokkaido in northern Japan. Ecological Engineering 24: 539–550. https://doi.org/10.1016/j.ecoleng.2005.01.010

Nakamura K, Tockner K, Amano K (2006) River and wetland restoration: Lessons from Japan. BioScience 56: 419–429. https://doi.org/10.1641/0006-3568(2006)056[0419:RAWRLF]2.0.CO;2

Natuhara Y (2013) Ecosystem services by paddy fields as substitutes of natural wetlands in Japan. Ecological Engineering 56: 97–106. https://doi.org/10.1016/j.ecoleng.2012.04.026

Naylor L, Coombes M, Kippen H, Horton B, Gardiner T, Cordell MR, Simm J, Underwood, GJC (2018) Developing a business case for greening hard coastal and estuarine infrastructure: Preliminary results. In K. Burgess (Ed.) Coasts, Marine Structures and Breakwaters 2017: Realising the Potential, 801–811. https://www.icevirtuallibrary.com/doi/full/10.1680/cmsb.63174.0801

Naylor LA, Kippen H, Coombes MA, Horton B, MacArthur M, Jackson N (2017) Greening the Grey: A Framework for Integrated Green Grey Infrastructure (IGGI). University of Glasgow, 160 pp. http://eprints.gla.ac.uk/150672/

Negoro H (2002) A survey of flower-visiting insects at Murodo-daira in the alpine zone of Mt. Tateyama, Toyama Prefecture, Hokuriku, Japan. Bulletin of the Toyama Science Museum 2002: 23–39.

Negoro H (2003) Addition to the survey of flower-visiting insects in the alpine zone of Mt. Tateyama, Toyama Prefecture, Hokuriku, Japan. Bulletin of the Toyama Science Museum 26: 73–101.

Normile D (2016) Nature from nurture. Science 351: 908–910. https://doi.org/10.1126/science.351.6276.908

NPO Wildlife Research Association (2007) Search system of Japanese red data. http://jpnrdb.com/index.html [accessed 8th January 2018]

Ohwaki A, Hayami S, Kitahara M, Yasuda T (2018) The role of linear mown firebreaks in conserving butterfly diversity: Effects of adjacent vegetation and management. Entomological Science 21: 112–123. https://doi.org/10.1111/ens.12289

Payne CLR (2014) Wild harvesting declines as pesticides and imports rise: The collection and consumption of insects in contemporary rural Japan. Journal of Insects as Food and Feed: 57–65. https://doi.org/10.3920/JIFF2014.0004

Payne CLR, Van Itterbeeck J (2017) Ecosystem services from edible insects in agricultural systems: A review. Insects 8: 24. https://doi.org/10.3390/insects8010024

Renaud F, Murti R (2013) Ecosystems and disaster risk reduction in the context of the Great East Japan Earthquake and Tsunami – A Scoping Study. IUCN, 56 pp.

Roca M, Escarameia M, Gimeno O, de Vilder L, Simm JD, Horton B, Thorne C (2017) Green Approaches in River Engineering – Supporting Implementation of Green Infrastructure. HR Wallingford, 84 pp. http://eprints.hrwallingford.co.uk/1400/

Sato T, Watanabe K, Kanaiwa M, Niizuma Y, Harada Y, Lafferty K (2011) Nematomorph parasites drive energy flow through a riparian ecosystem. Ecology 92: 201–207. https://doi.org/10.1890/09-1565.1

Takenaka A, Washitani I, Kuramoto N, Inoue K (1996) Life history and demographic features of *Aster kantoensis*, an endangered local endemic of floodplains. Biological Conservation 78: 345–352. https://doi.org/10.1016/S0006-3207(96)00036-5

Takeuchi M, Fujita H (1998) Habitat status of the grasshopper, *Eusphingonotus japonicus* (Saussure), in Kanagawa Prefecture, Japan. Japanese Journal of Applied Entomology and Zoology 42: 197–200. https://doi.org/10.1303/jjaez.42.197

Tan MK, Artchwakom T, Abdul Wahab RH, Lee C-Y, Belabut DM, Wah Tan HT (2017b) Overlooked flower-visiting Orthoptera in Southeast Asia. Journal of Orthoptera Research 26: 143–153. https://doi.org/10.3897/jor.26.15021

Tan MK, Leem CJ, Tan HT (2017a) High floral resource density leads to neural constraint in the generalist, floriphilic katydid, *Phaneroptera brevis* (Orthoptera: Phaneropterinae). Ecological Entomology 42: 535–544. https://doi.org/10.1111/een.12414

Tan MK, Tan HTW (2018a) A gentle floriphilic katydid *Phaneroptera brevis* can help with the pollination of *Bidens pilosa*. Ecology 99: 2125–2127. https://doi.org/10.1002/ecy.2369

Tan MK, Tan HTW (2018b) Asterid ray floret traits predict the likelihood of florivory by the polyphagous katydid, *Phaneroptera brevis* (Orthoptera: Phaneropterinae). Journal of Economic Entomology 111: 2172–2181. https://doi.org/10.1093/jee/toy211

Tanaka N (2012) Effectiveness and limitations of coastal forest in large tsunami: Conditions of Japanese pine trees on coastal sand dunes in tsunami caused by great east Japan earthquake. Journal of Japan Society of Civil Engineers, Ser. B1 (Hydraulic Engineering) 68: 7–15. https://doi.org/10.2208/jscejhe.68.II_7

Tanaka S (1994) Diapause as a pivotal factor for latitudinal and seasonal adaptation in *Locusta migratoria* in Japan. In: Danks HV (Ed.) Insect Life-Cycle Polymorphism. Series Entomologica 52. Springer, 173–190. https://doi.org/10.1007/978-94-017-1888-2_8

Tian K (2014) Tokyo Bay storm surge barrier: A conceptual design of the moveable barrier. Unpublished Master's thesis, Delft University of Technology.

Tojo K, Sekine K, Takenaka M, Isaka Y, Komaki S, Suzuki T, Schoville SD (2017) Species diversity of insects in Japan: Their origins and diversification processes. Entomological Science 20: 357–381. https://doi.org/10.1111/ens.12261

Tokuda M, Tanaka S, Zhu DH (2010) Multiple origins of *Locusta migratoria* (Orthoptera: Acrididae) in the Japanese Archipelago and the presence of two major clades in the world: Evidence from a molecular approach. Biological Journal of the Linnean Society 99: 570–581. https://doi.org/10.1111/j.1095-8312.2010.01386.x

Washitani I (2001) Plant conservation ecology for management and restoration of riparian habitats of lowland Japan. Population Ecology 43: 189–195. https://doi.org/10.1007/s10144-001-8182-8

Yamada S, Kitagawa Y, Okubo S (2013) A comparative study of the seed banks of abandoned paddy fields along a chronosequence in Japan. Agriculture, Ecosystems & Environment 176: 70–78. https://doi.org/10.1016/j.agee.2013.05.021

Yamamoto N, Yokoyama J, Kawata M (2007) Relative resource abundance explains butterfly biodiversity in island communities. Proceedings of the National Academy of Sciences 104: 10524–10529. https://doi.org/10.1073/pnas.0701583104

Yamanaka T, Morimoto N, Nishida GM, Kiritani K, Moriya S, Liebhold AM (2015) Comparison of insect invasions in North America, Japan and their Islands. Biological Invasions 17: 3049–3061. https://doi.org/10.1007/s10530-015-0935-y

Yasuda S, Shimizu Y, Deguchi K (2016) Investigation of the mechanism of the 2015 failure of a dike on Kinu River. Soils and Foundations 56: 581–592. https://doi.org/10.1016/j.sandf.2016.07.001

Yoshio M, Kato N, Miyashita T (2009) Landscape and local scale effects on the orthopteran assemblages in the paddy agro-ecosystems on the Sado Island, Japan with implications for the habitat management for the crested ibis. Ecology and Civil Engineering 12: 99–107. https://doi.org/10.3825/ece.12.99

Yoshioka A, Kadoya T, Suda SI, Washitani I (2010a) Impacts of weeping lovegrass (*Eragrostis curvula*) invasion on native grasshoppers: Responses of habitat generalist and specialist species. Biological Invasions 12: 531–539. https://doi.org/10.1007/s10530-009-9456-x

Yoshioka A, Kadoya T, Suda S, Washitani I (2010b) Invasion of weeping lovegrass reduces native food and habitat resource of *Eusphingonotus japonicus* (Saussure). Biological Invasions 12: 2789–2796. https://doi.org/10.1007/s10530-009-9684-0

Zhang X, Miyashita T (2017) Effects of local and landscape factors on the abundance of an endangered multivoltine butterfly at riverbanks. Entomological Science 21: 133–141. https://doi.org/10.1111/ens.12291

Research Article Journal of Orthoptera Research 2019, 28(1): 37–105

A review of the Acridinae *s. str.* (Orthoptera: Acridoidea: Acrididae) of eastern Africa with taxonomic changes and description of new taxa

George B. Popov[1†], Lincoln D. C. Fishpool[2], C. Hugh F. Rowell[3]

1 Agricultural Resources Management Department, Natural Resources Institute, University of Greenwich, Central Avenue, Chatham Maritime, Kent ME4 4TB, United Kingdom. (†Deceased 22nd December 1998)
2 12 Mountain Street, Chilham, Canterbury, Kent, United Kingdom.
3 Zoologisches Institut der Universität Basel, Switzerland.

Corresponding author: *C.H.F. Rowell* (hugh.rowell@gmail.com)

Academic editor: *Corinna S. Bazelet* | Received 26 August 2018 | Accepted 31 December 2018 | Published 18 June 2019

http://zoobank.org/A7E7FE9F-FB53-4C5A-9AAD-D9EF42792A8E

Citation: Popov GB, Fishpool LDC, Rowell CHF (2019) A review of the Acridinae *s. str.* (Orthoptera: Acridoidea: Acrididae) of eastern Africa with taxonomic changes and description of new taxa. Journal of Orthoptera Research 28(1): 37–105. https://doi.org/10.3897/jor.28.29312

Abstract

The Acridinae of eastern Africa are reviewed and recognized as comprising 42 core genera, belonging to five different tribes, together with *Xerophlaeoba* and *Dorsthippus*, which are unclassified but appear to be related to some extra-limital genera. Keys are given to tribes and genus groups as well as to genera and, where necessary, species within each genus.

The following new taxa are described: *Anacteana* **gen. n.**: *A. hollisi* **sp. n.** and *A. neavei burtti* **subsp. n.**; *Brachybothrus* **gen. n.**: *B. phyllopterus* **sp. n.** and *B. hola* **sp. n.**; *Coryphosima stenoptera colorata* **subsp. n.**; *Duronia chloronota phippsi* **subsp. n.**; *Oxyduronia* **gen. n.**: *O. anablepioides* **sp. n.**; *Sumba exilis* **sp. n.**

Nine new synonyms are recognized: *Sumba longicornis* Ramme, 1929 = *S. roseipennis* I. Bolívar, 1912, **syn. n.**; *Orthochirista variegata* Sjöstedt, 1931 = *Gymnobothrus linea alba* I. Bolívar, 1889, **syn. n.**; *Orthochirista elgonensis* Sjöstedt, 1931 = *Gymnobothrus linea alba* I. Bolívar, 1889, **syn. n.**; *Gymnobothrus gracilis* (Ramme, 1931) = *Gymnobothrus anchietae* I. Bolívar, 1889, **syn. n.**; *Gymnobothrus subcarinatus* (I. Bolívar, 1922) = *Gymnobothrus flexuosus* (Schulthess, 1898), **syn. n.**; *Gymnobothroides montanus* Kevan, 1950 = *Gymnobothrus levipes levipes* (Karsch, 1896), **syn. n.**; *Gymnobothroides keniensis* Johnston, 1937 = *Gymnobothrus levipes abbreviatus* (Chopard, 1921), **syn. n.**; *Gymnobothroides* Karny, 1915 = *Gymnobothrus* I. Bolívar, 1889, **syn. n.**; *Phloeochopardia* Dirsh, 1958 = *Gymnobothrus* I. Bolívar, 1889, **syn. n.**

The following 24 new or restored combinations, or new or restored states, are erected for previously described taxa: *Chokwea backlundi* **res. comb.** (formerly *Chromochokwea backlundi* (Uvarov, 1953)); *Chokwea eucteana* **comb. n.** (formerly *Platyverticula eucteana* Jago, 1983); *Sumba callosa* **comb. n.** (formerly *Rhabdoplea callosa* Uvarov, 1953); *Anacteana neavei* **comb. n** (formerly *Acteana neavei* I. Bolívar, 1912); *Anacteana neavei neavei* **stat. n.**; *Duronia chloronota curta* Uvarov, 1953, **stat. n. et comb.** (formerly *Duronia curta* Uvarov, 1953); *Coryphosima abyssinica* (Uvarov, 1934), **res. stat.** (formerly synonymized with *C. elgonensis* by Dirsh, 1966 (though this was ignored by Otte 1995)); *Coryphosima amplificata* (Johnston, 1937), **res. stat. et comb. n.** (formerly *Rastafaria amplificata amplificata* (Johnston, 1937)); *Coryphosima morotoensis* (Jago, 1968), **stat. n. et comb. n.** (formerly *Rastafaria amplificata morotoensis* (Jago, 1968)); *Coryphosima triangularis* (Bouvy, 1982), **comb. n.** (formerly *Rastafaria triangularis* Bouvy, 1982); *Gymnobothrus longicornis longicornis* **stat. n.**; *Gymnobothrus longicornis ephippinotus* Jago, 1966, **stat. n. et comb. n.** (formerly *Gymnobothrus ephippinotus* Jago, 1966); *Gymnobothrus longicornis sellatus* Uvarov, 1953, **stat. n. et comb. n.** (formerly *Gymnobothrus sellatus* Uvarov, 1953); *Gymnobothrus anchietae anchietae* **stat. n.**; *Gymnobothrus anchietae bounites* Jago, 1970, **stat. n. et comb. n.** (formerly *Gymnobothrus bounites* Jago, 1970); *Gymnobothrus anchietae flaviventris* Uvarov, 1953, **stat. n. et comb. n.** (formerly *Gymnobothrus flaviventris* Uvarov, 1953). *Gymnobothrus anchietae inflexus* Uvarov, 1934, **stat. n. et comb. n.** (formerly *Gymnobothrus inflexus* Uvarov, 1934); *Gymnobothrus levipes* (Karsch, 1896), **comb. n.**; *Gymnobothrus levipes levipes* (Karsch, 1896), **stat. n. et comb. n.** (formerly *Gymnobothroides levipes* (Karsch, 1896)); *Gymnobothrus levipes abbreviatus* (Chopard, 1921), **stat. n. et comb. n.** (formerly *Phloeochopardia abbreviata* (Chopard, 1921)); *Gymnobothrus pullus* (Karny, 1915), **comb. n.**; *Gymnobothrus pullus pullus* (Karny, 1915), **stat. n. et comb. n.** (formerly *Gymnobothroides pullus* Karny, 1915); *Gymnobothrus pullus minutus* (Ramme, 1929), **stat. n. et comb. n.**, **nom. res.** (formerly *Gymnobothroides minutus* Ramme, 1929); *Gymnobothrus pullus hemipterus* (Miller, 1932), **stat. n. et comb. n.** (formerly *Gymnobothroides hemipterus* Miller, 1932).

Key words

bionomics, brachypterous, diagnostic features, genus groups, macropterous, micropterous, new genera, new species, tribes

Preface

The following article was written in 1995 and first accepted for publication, subject to an extensive revision, in 1997, at a time when the first author's health was beginning to deteriorate. Unfortunately, the manuscript's revision was delayed, and death prevented George Popov from seeing this major taxonomic paper into its final form. Corrections and numerous minor changes were subsequently made by his colleagues, Drs N.D. Jago and S.V. Green, then at the Natural Resources Institute (NRI), University of Greenwich, Chatham Maritime, Kent ME4 4TB, UK.

The NRI discontinued acridology in the late 1990s and its acridological staff dispersed. The revised Popov manuscript was consequently not resubmitted for publication but copies of it circulated among interested acridologists. The third author (Rowell) is engaged in editing the Handbook to the Grasshoppers of East Africa

(Rowell and Hemp 2015, 2017, 2018), a project that had originally inspired much of the NRI's acridological work but which had been halted by the death in 2005 of Dr. N.D. Jago, the prime mover. In preparing the treatment of the Acridinae for the Handbook, it became obvious that the incorporation of Popov's revisionary work needed its formal publication. Dr. A. Hochkirch and Mrs. Margaret Jago kindly supplied Rowell with annotated PDFs of the original manuscript and these have served as the basis of the present paper. Dr. L.D.C. Fishpool, who had worked extensively with Popov, undertook much proofreading and editorial activity. Minor updates have been made to Popov's original text, including the incorporation of a few recently described species and synonyms and of some new distributional records, especially of Sahelian species from northern Uganda; also, edits were made to fit the manuscript to the requirements of the current journal and to include the usage of current African geopolitical names (e.g. D.R. Congo for the former Zaire, and to acknowledge the emergence of South Sudan). However, all taxonomic decisions and treatment, the illustrations, the opinions expressed, and almost the entire text are solely the work of Popov. In a few places some editorial comment on taxonomic matters has, however, been necessary and is marked as such.

The new taxa erected in this paper are therefore to be understood as authored by Popov alone, as the other authors' contributions have been exclusively editorial and not acridological.

Since this text was originally drafted, the NRI's grasshopper collection has been transferred to the Natural History Museum, London (NHMUK). All material referred to in the text as originating from the NRI now forms part of that museum's entomological collection.

Table of contents

Introduction

The subfamily Acridinae of the family Acrididae is a polyphyletic assemblage of taxa (Jago 1983a, b). It is closely similar to the subfamily Oedipodinae. The latter differs from the Acridinae in possessing a sound-producing mechanism of the femoroalary type consisting of a sharp ridge on the inner face of the hind femur and a corresponding serrated intercalary vein in the medial area of the tegmen (although there are some rare exceptions, such as *Sphingonotus* (*Parasphingonotus*) or *Sphingonotus* (*Neosphingonotus*), in which other tegminal veins are used)—a character absent in Acridinae. In some oedipodine taxa, however, this mechanism is only partially or weakly expressed and is thought incapable of sound production, so that there is no unanimity among acridologists on whether these two subfamilies should be kept separate or united.

This review is one of several taxonomic revisions required to provide the basis for a handbook and keys to the grasshoppers and locusts of eastern Africa, in preparation by the Natural Resources Institute, University of Greenwich, Chatham, U.K. (The handbook is currently appearing as Rowell and Hemp (Eds) (2015, 2017, 2018)). It is intended that, for this purpose, the two subfamilies

Acridinae and Oedipodinae will be treated as separate, in line with Uvarov (1966) and Otte (1981, 1984, 1995).

The following paper focuses upon the genera and species of Acridinae represented in eastern Africa, but in some cases taxa from other areas may be described in key form or given brief diagnostic definition in order to put the East African species into context.

Otte (1995), in his Orthoptera Species File (OSF), divided the subfamilies of the Acrididae into tribes. This had previously been standard only for the Pyrgomorphidae. Amongst the Acridinae, more than half of the species and genera listed in Otte's publication are classed as Tribe 'uncertain'. (Editorial comment: the OSF on-line (Cigliano et al. 2018) continues this tradition). In the present paper the taxa belonging to the Acridinae are newly grouped into tribes, which, where appropriate, are further divided into genus groups. The latter are intentionally chosen as units without formal nomenclatural status.

The principal characters used are as follows: external and internal genital structures of both sexes (primary importance); form and size; sculpturing of integument; structure of antennae, frons, and apex of head (including presence/absence of temporal foveolae); pronotal morphology; form of the organs of flight and sound-producing structures; shape of knee lobes of the hind femur, and, as appropriate, coloration.

The male epiphallus is particularly diagnostic and its structure is regarded as the principal character in the classification and grouping of the Acridinae (Jago 1983b). In females, however, the structure of the spermathecal duct provides characters for the separation of the two subfamilies. These facies have been little used hitherto. In the majority of Acridinae the duct is similar to that shown in Figs 1–3, having a characteristic 'proximal loop' (Slifer 1939), while the remainder of the duct is usually coiled in the form of a watch-spring positioned horizontally within the body cavity. In contrast, the duct of most Oedipodinae forms an untidy tangle, lacking the proximal loop, as seen (Fig. 4) in *Aiolopus thalassinus* (from Hollis 1968).

Previous authors have sometimes produced contentious solutions for the classification of certain acridine genera. Thus, Dirsh (1975) erected the Phlaeobinae as a separate subfamily within the Acrididae and the Pargainae as a subfamily within the Catantopidae. This was contested by Jago (1983b) who reduced both subfamilies to genus groups within the Acridinae.

1. Diagnosis of tribes and genus groups in the Acridinae and list of the sections of this paper

Tribe Truxalini

Type genus.—Truxalis Fabricius, 1775; priority for family-group names based on *Truxalis* dates from Truxalides Serville, 1838. First use as Truxalini by Thomas (1872). Until 1996, this taxon was often ranked as a separate subfamily (first use as Truxalinae by McNeill (1897)). Truxalines possess a stridulatory mechanism consisting of a serrated ridge on inner side of hind femur and sharp, raised radial and medial veins of tegmina. The strongly elongate body shape of the Truxalini is very similar to that of the *Acrida* genus group (tribe Acridini), and while the similarity of body form has been attributed to convergent evolution (Dirsh 1975), the striking fact that the genital structures of both sexes in the two groups are also remarkably similar cannot be explained as easily. Investigations by Jago (1996) confirmed that the two groups are in fact closely related, with the 'Truxalinae' representing a tribe of the Acridinae. The former taxon was consequently reduced again to the rank of tribe (Truxalini) within this subfamily. Epiphallus illustrated in Figs 5–7.

Editorial note.—Included genera: since the downgrading of the Truxalinae, no formal listing of the genera included in the "new" Truxalini has been published. Dirsh (1975) listed 6 genera within the Truxalinae: *Truxalis* Fabricius, 1775, *Truxaloides* Dirsh, 1951, *Acridarachnea* I. Bolívar, 1908b, *Chromotruxalis* Dirsh, 1951, *Xenotruxalis* Dirsh, 1951, and *Oxytruxalis* Dirsh, 1951, and this grouping was accepted by Jago (1996). The OSF (Cigliano et al. 2018) currently lists only *Truxalis*; it is not clear on what authority the other genera have been dropped; some are currently given as *incerta sedis* within the Acridinae. Popov, however, in his original manuscript, listed only three genera: *Chromotruxalis, Truxalis,* and *Truxaloides.* He probably excluded the other three genera only because they do not occur in East Africa, the focus of his revisionary work.

Discussion.—No changes are proposed at the species and generic levels. This tribe is not considered further in this paper.

Tribe Acridini

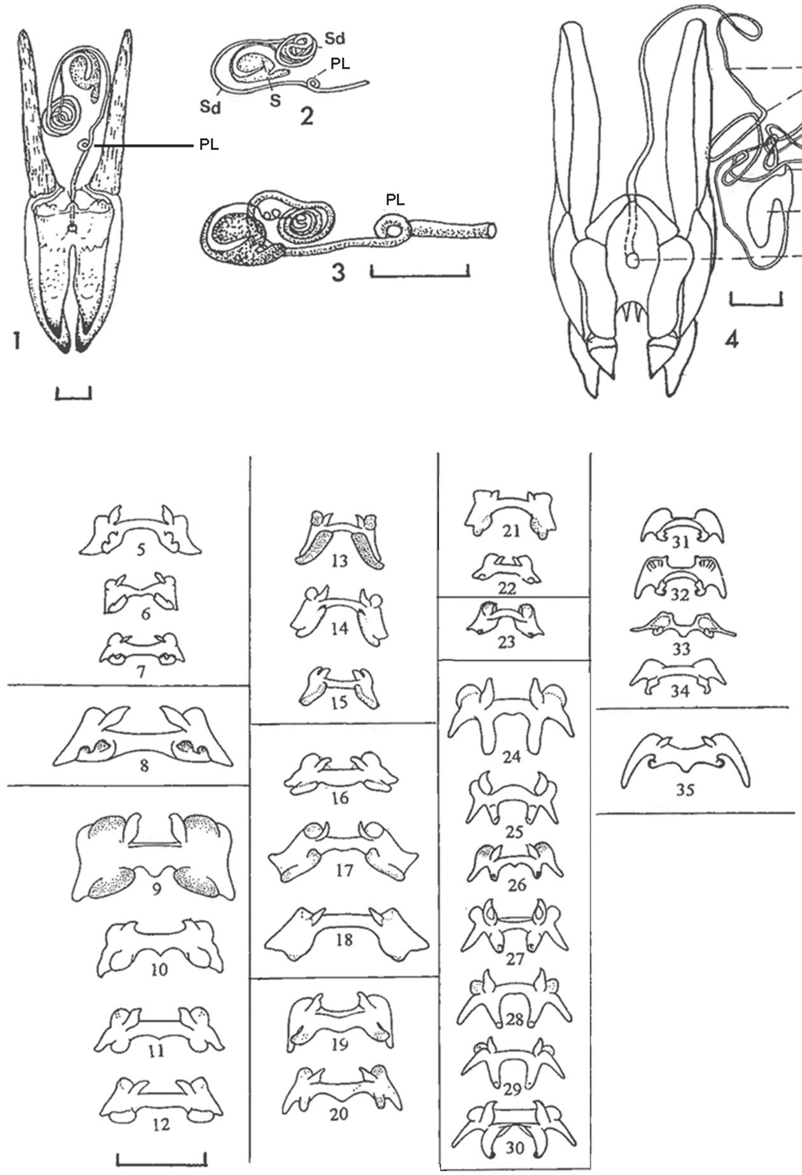
Type genus.—Acrida Linnaeus, 1758; priority for family-group names based on *Acrida* dates from Acridina MacLeay, 1821. First use as Acridini by Thomas (1872). The OSF (Cigliano et al. 2018) lists 10 genera in this tribe, most of which are Australian; only *Acrida* and *Acridarachnea* (the latter normally considered Truxaline) are African. In eastern Africa the tribe is represented only by the widespread genus *Acrida*. It shares its peculiar shape of body and head with the Truxalini, but differs in its mode of sound production, which consists of rubbing the hind wings against the tegmina in flight (crepitation), the wing having a wide, lustrous speculum in its medial area. This mechanism is not unique to *Acrida*, as it is also found in some other unrelated acridine genera and species, notably *Odontomelus scalata.* Epiphallus as in Fig. 8.

Discussion.—No changes are proposed at species or generic levels. This tribe is not considered further in this paper.

Tribe Phlaeobini and its genus groups

Type species.—Gomphocerus rusticus Stål, 1861 (= *Phlaeoba fumosa* Serville, 1838), by original monotypy. The first family-group name based on this genus is Phlaeobae Brunner von Wattenwyl, 1893. This group was also recognized by Johnston (1956). First use as Phlaeobini by Shumakov (1963). The taxon was briefly elevated to subfamily level (Phlaeobinae) by Dirsh (1975); Jago (1983b) subsequently reduced it back to a genus group within the Acridinae.

The tribe is defined by the following combination of characters: of small to medium size, body mostly elongate, cylindrical; antennae ensiform to narrowly ensiform, specialized or not; fastigium of vertex moderately elongate, its apex mostly parabolic-obtuse-angular, temporal foveolae weak or absent; pronotum mostly tectiform; tegmina and wings fully developed to strongly shortened, stridulatory mechanism not found; epiphallus bridge-shaped, bridge narrow, ancorae short, pointed, articulated with bridge, lophi monolobate, of variable width and depth, sometimes inflated, lateral plates moderately narrow with subacute or obtuse posterior projections (Figs 9–23); spermathecal duct with proximal loop and watch-spring medial coil of



Figs 1–35. Figs 1–4. Female spermathecal ducts. **1, 2.** In *Orthochtha-Euprepoptera-Lobopoma* genus group (after Popov and Fishpool 1992): **1.** Spermathecal duct in situ in relation to ovipositor valves; **2.** Spermathecal duct isolated (s, sd, PL); **3.** As Fig. 2, but in *Duronia* genus group. **4.** Female genital ducts of the Oedipodinae, represented by *Aiolopus thalassinus thalassinus* (Fabr.) (after Hollis 1968). Abbreviations applying to Figs 1–4: PL – proximal loop of spermathecal duct, characteristic of most Acridinae, to contrast with its absence in Fig. 4, which is characteristic of Oedipodinae; Sd – spermathecal duct; Sa – spermathecal aperture; S – spermatheca; Ad, Pd – apical and preapical diverticula of spermatheca. **Figs 5–39**. Male epiphalli representing tribes and genus-groups of the Acridinae *s. str.* (after Dirsh 1956). **Figs 5–7.** Tribe Truxalini: **5.** *Truxalis nasutus* (L.,1758); **6.** *Chromotruxalis cockerelli* (Uvarov, 1932); **7.** *Truxaloides serratus* (Thunberg, 1815). **Fig. 8.** Tribe Acridini: *Acrida turrita* (L.,1758). **Figs 9–23.** Tribe Phlaeobini: **Figs 9–12.** *Orthochtha-Euprepoptera-Lobopoma* genus group: **9.** *O. venosa* (Ramme, 1929); **10.** *O. g. dasycnemis* (Gerstaecker, 1869); **11.** *Euprepoptera polychroma* Uvarov, 1953; **12.** *Lobopoma ambages* Karsch, 1896. **Figs 13–15.** *Cannula-Glyphoclonus-Culmulus* genus group: **13.** *Cannula linearis* (Saussure, 1861); **14.** *Glyphoclonus miripennis* Karsch, 1896; **15.** *Culmulus stramineus* Uvarov, 1953. **Figs 16–18.** *Afrophlaeoba genus group*: **16.** *Paralobopoma gracilis* (Ramme, 1929); **17.** *Afrophlaeoba usambarica* (Ramme, 1929); **18.** *Chokwea burri* Uvarov, 1953. **Figs 19, 20.** *Duronia* genus group: **19.** *Duronia chloronota* (Stål, 1876); **20.** *Duroniella laticornis* (Krauss, 1909). **Figs 21, 22.** *Sumba-Rhabdoplea-Panzia* genus group: **21.** *Rhabdoplea munda* Karsch, 1893; **22.** *Sumba roseipennis* I. Bolívar, 1912. **Fig. 23.** *Ocnocerus-Anacteana* genus group: **23.** *Ocnocerus diabolicus* Karsch, 1893. **Figs 24–30.** Tribe Gymnobothrini: **24.** *Zacompsa festa* Karsch, 1893; **25.** *Coryphosima stenoptera* (Schaum, 1853); **26.** *Chirista compta* (Walker, 1870); **27.** *Comacris semicarinatus* (Gerstaecker, 1869); **28.** *Gymnobothrus pullus* (Karny, 1915); **29.** *Gymnobothrus lineaalba* I. Bolívar, 1889; **30.** *Malcolmburria angolensis* Uvarov, 1953. **Figs 31–34.** Tribe Pargaini: **31.** *Acteana alazonica* Karsch, 1896; **32.** *Odontomelus scalatus* (Karsch, 1896); **33.** *Machaeridia bilineata* Stål, 1873; **34.** *Parga cyanoptera* Uvarov, 1926. **Fig. 35.** Unclassified genera: **35.** *Xerophlaeoba deserticola* (Krauss). All scale-lines represent 1 mm: that under Fig. 1 applies to Figs 1 and 2; that under Fig. 3 applies to Fig. 3; that under Fig. 4 applies to Fig. 4; that under Fig. 12 applies to Figs 5–39.

variable length, occasionally with supplementary reservoir, spermatheca unspecialized.

This is the largest and the most widespread tribe of Acridinae, and can be readily subdivided into several distinct genus groups as follows:

***Orthochtha-Euprepoptera-Lobopoma* genus group**

Of medium size, slender, integument smooth. Antenna ensiform. Pronotum weakly tectiform to weakly sellate. Mostly fully winged, but some *Lobopoma* species micropterous. Epiphallus (Figs 9–12) with elongate ancorae; lophi wide, of varying depth. Female seminal duct of varying length and number of coils, sometimes (in *O. nigricornis* species group) with a supplementary seminal vesicle (Popov and Fishpool 1992: fig. 15).

Discussion.—No changes are proposed following the revision of all three genera in the genus group by Popov and Fishpool (1992). This genus group is not further considered in this paper.

***Cannula-Glyphoclonus-Culmulus* genus group**

Differing from the *Orthochtha-Euprepoptera-Lobopoma* genus group in the following respects: body elongate, very slender, sometimes straw-like. Antennae long, broadly ensiform. External upper knee-lobe more or less elongate. Wings full length or somewhat abridged. Epiphallus as in Figs 13–15. Included East African genera are *Cannula*, *Glyphoclonus*, and *Culmulus*; extralimital genera include *Cohembia* Uvarov, 1953, *Oxyolena* Karsch, 1893, *Gelastorhinus* Brunner, 1893, and *Gonista* I. Bolívar, 1898.

Discussion.—Taxonomic changes and redefinition of genera and species are given below, where necessary.

***Afrophlaeoba* genus group**

Closely related micropterous phlaeobine genera, mostly of restricted East African distribution. Included genera: *Afrophlaeoba*, *Brachyphlaeobella*, *Chokwea*, *Chromochokwea*, *Paralobopoma*, *Parodontomelus*, *Platyverticula*, and the Madagascan *Chlorophlaeobella* Jago, 1983. Below medium size, of medium to robust build and of predominantly cryptic coloration but occasionally (some *Chokwea*, *Chromochokwea*, and *Paralobopoma*) brightly colored. Similar in their general appearance to genus *Odontomelus* (Pargaini) but with female genital structures as in Fig. 3, except in *Platyverticula* which has a strongly retracted ovipositor. Epiphallus as in Figs 16–18.

Discussion.—Taxonomic changes to the genera *Chokwea* and *Platyverticula* are given later in this paper, coupled with redescription and redefinition of taxa where necessary.

***Ocnocerus* genus group**

This is divided into two related sub-groups:

(i) *Sumba-Rhabdoplea-Panzia* genus sub-group. Small, slender, mostly graminicolous taxa; integument rugose, callose, sometimes longitudinally ridged. Antennae ensiform to narrowly ensiform. Fully winged to micropterous. Epiphallus with short, round, somewhat globular lophi (Fig. 21, *Rhabdoplea munda* Karsch, 1893; Fig. 22, *Sumba roseipennis* I. Bolívar, 1912) which form broad lobate structures, and posterior lateral lobes of epiphallus which are produced into short, rounded or obtuse-angulate processes.

Discussion.—Taxonomic changes to the genera are given later in this paper, coupled with redescription and redefinition of taxa where necessary.

(ii) *Ocnocerus-Hyperocnocerus-Anacteana* (gen. n.) genus sub-group. Closely related to preceding, differing principally in having more terricolous habits. Size small, robust, integument coriaceous, sometimes ridged. Antennae specialized into basal, medial, and apical parts. Micropterous. Epiphallus as in Fig. 23.

Discussion.—This sub-group has undergone considerable internal rearrangement and descriptions of new taxa have been necessary for this paper.

***Duronia* genus group**

Included genera: *Duronia*, *Duroniella*, *Leopardia*, *Oxyduronia* (**gen. n**.).

In build, similar to *Orthochtha-Euprepoptera-Lobopoma* genus group, but all taxa fully winged. Differ primarily in genital structures, with epiphallic lophi intermediate in their shape between digitiform and lobiform, forming elongate, narrow, flattened lobes; posterior processes are elongate and pointed (Figs 19, 20). The genital structures in females are similarly distinctive. In particular, the spermathecal duct in its proximal half is relatively thick, of a large diameter; beyond the middle fold, the distal half is very thin, in the nature of a fine capillary (Fig. 98E). The females in this respect are transitional between Phlaeobini and Gymnobothrini, but closer to the former. This tribe is thus intermediate between two large generic clusters: the *Sumba-Rhabdoplea-Panzia* genus sub-group of the Tribe Phlaeobini and the Tribe Gymnobothrini.

Discussion.—Some redefinition of genera has been made and keys are provided to assist in identification to species level.

Tribe Gymnobothrini

Type genus.—*Gymnobothrus* I. Bolívar, 1889. Johnston (1968) recognized a group Gymnobothri. This large and distinctive tribe was designated by Dirsh (1975) as subfamily Gymnobothrinae, but this usage has not found favor. It contains 11 East African genera and several others from elsewhere. Most taxa are of similar appearance, of small to medium size, and medium sub-cylindrical build. Most are fully winged, but some are brachypterous or micropterous. Antennae narrowly ensiform to filiform. Temporal foveolae usually present, but often weak. Male genitalia provide the principal diagnostic features of the group, though not of the individual genera; epiphallus with narrow bridge, ancorae strong, long, with acute apices; lophi long, finger-shaped, almost perpendicular to the bridge, with hooked apices; lateral plates narrow, elongate, with sub-acute, slender, elongate posterior projections (Figs 24–30). Ancorae are large and articulate, which separates them from the Pargaini in which they are vestigial or absent.

Included East African genera: *Chirista*, *Comacris*, *Coryphosima*, *Roduniella*, *Gymnobothrus* (incorporating *Gymnobothroides* and *Phloeochopardia* as **n. syns.**), *Brachybothrus* (**gen. n.**) *Guichardippus*, *Malcolmburria*, *Rastafaria*, *Tenuihippus*, and *Zacompsa*.

Discussion.—Considerable revision within this tribe has required an extensive taxonomic treatment, which is presented below.

Tribe Pargaini

Type genus.—*Parga* Walker, 1870. Dirsh (1975) erected a subfamily Pargainae within his family Catantopidae, including 7 genera. This action was contested by Jago (1994), who returned them to the Acridinae.

Included genera: *Parga*, *Phryganomelus*, *Acteana*, *Machaeridia*, *Odontomelus* (including its synonyms (Jago 1994) *Amphicremna*, *Parga*, *Pargaella*).

This is another distinctive tribe. With the exception of *Acteana*, which is terri-graminicole and externally similar to the *Ocnocerus-Hyperocnocerus-Anacteana* **(gen. n.)** genus sub-group, its taxa are graminicoles of small to medium size, elongate, slender build with, in some cases, an integument which is longitudinally ridged and striated. Broadly ensiform antennae. Knee lobes are elongate. Organs of flight of variable shape and length. The epiphallus is the principal diagnostic feature of the group: bridge relatively narrow; ancorae absent or vestigial; lophi short, usually bilobate, narrowly rounded apically; lateral plates well developed (Figs 31–34).

Discussion.—The distinction between this tribe and the Phlaeobini is detailed below (p. 44, Table 2).

Unclassified genera

Only one East African acridine genus, *Xerophlaeoba*, cannot be assigned to the tribes listed above and so is placed in this cluster, but there are several others outside Africa and the group needs further study. Externally, *Xerophlaeoba* is very similar to the *Orthochtha-Euprepoptera-Lobopoma* genus group, but its genital structures (Fig. 35) are unlike those of any other group, and its systematic position is therefore ambiguous. (Otte (1995) listed it under Phlaeobini.)

Transitional genera

Editorial note.—Popov included in this group the genera *Paracinema*, *Jasomenia*, *Aiolopus*, *Uganda*, and *Dorsthippus*; epiphalli shown in Figs 36–39. He wrote "In some respects these genera bridge the gap between Acridinae and Oedipodinae. They are predominantly graminicoles" (as are most acridines) "and similar in general appearance to members of the *Duronia* genus group and the Gymnobothrini. The first three genera are alate with well-developed and, to some extent, serrated intercalary veins in the medial field of tegmina, but are said to be incapable of sound production. *Uganda* is a brachypterous/micropterous genus that could be related to *Paracinema*. The female genital structures are typically oedipodine rather than acridine". In the present editors' opinion, these genera are more usefully classified as oedipodines, as indeed they (other than *Uganda*) already are in the OSF (Cigliano et al. 2018). All morphological characters align them with this subfamily, and the alleged inability to stridulate is a negative character, logically difficult to substantiate, and possibly behaviorally determined. We have therefore omitted these "Transitional Genera" from the remaining text of this paper. Popov proposed no taxonomic changes within any of them.

Popov further wrote "*Dorsthippus* is an aberrant genus, apparently without close relation to other Acridinae. In general appearance it is reminiscent of some Palaearctic Gomphocerinae, but the absence of a stridulatory file on the inner face of hind femur and its genital structures suggest rather an affinity with the Acridinae". Logically, *Dorsthippus* could equally well be included in group 6, the "Unclassified Genera".

2. Detailed treatment of selected tribes and genus groups

2.1. The tribe Phlaeobini and its genus groups

Genus group diagnosis

The *Cannula-Glyphoclonus-Cumulus* genus group

Description.—Elongate, slender build and broadly ensiform antennae; sometimes extended genicular lobes (outer genicular lobes longer than inner, unlike Pargaini). Epiphallus with its large articulated ancorae and broad lobiform lophi (Figs 13–15), clearly indicates that this genus group is part of Tribe Phlaeobini and close to *Orthochtha* (Figs 9–12).

Discussion.—Strongly graminicolous habitat has led to convergent evolution in their morphology with the similarly adapted members of the Tribe Pargaini. Only the three genera with known East African distributions are included here, while others, some of them common elsewhere, such as *Cohembia* Uvarov, 1953 (Angola), *Oxyolena* Karsch, 1893 (a rare endemic from Togo), *Gelastorhinus* Brunner, 1893, and *Gonista* I. Bolívar, 1898 (disjunct distribution in western Africa and southern Asia), are omitted. *Gonista*, represented in D.R. Congo and Zambia by *G. longicercata* Bouvy, 1982, may eventually be collected in adjacent parts of Tanzania, and is therefore included in the key below.

Key to genera in the genus group *Cannula-Glyphoclonus-Culmulus*

1 Upper outer lobe of hind knee enlarged more than the inner 2
– Knee lobes not enlarged 3
2 Mesosternal interspace closed. Head more than twice as long as pronotum. Body extremely elongate, straw-like *Cannula* I. Bolívar, 1906
– Mesosternal interspace open. Head not more than half as long again as pronotum. Body slender, elongate, but not straw-like......... *Glyphoclonus* Karsch, 1896
3 Frontal ridge above antennal sockets lamelliformly compressed forming single carinula (Fig. 41). Apex of male abdomen as in Fig. 44......... *Culmulus* Uvarov, 1953
– Frontal ridge narrow, but not lamelliform, forming single carinula. Apex of male abdomen as in Figs 45, 46 .... *Gonista* I. Bolívar, 1898

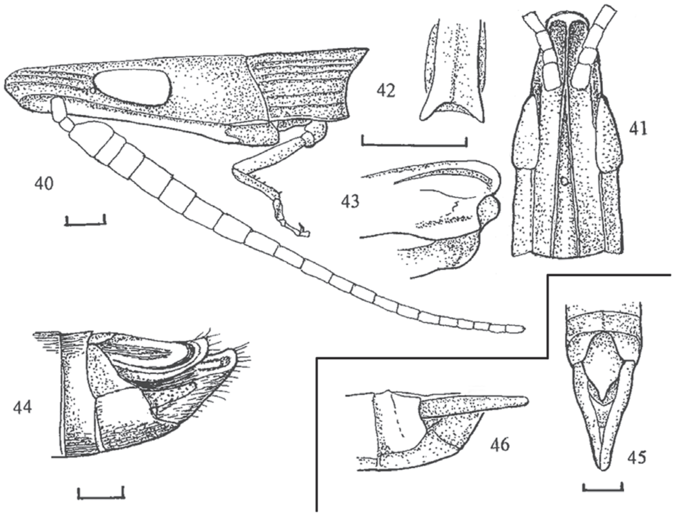
Generic diagnosis

Cannula I. Bolívar, 1906

Cannula I. Bolívar, 1906: 394. Nom. nov. for *Calamus* Saussure, 1861.

Type species.—*Calamus linearis* Saussure, 1861 by original designation.

Description.—As in key to genera. Size variable from medium to large, sexual dimorphism marked. Body very elongate, slender, straw-like. Antenna ensiform, strongly compressed, shorter than head and pronotum together. Head very elongate, narrow, conical. Fastigium of vertex more than twice length of basal part of head, with parabolic apex. Frontal ridge in upper half strongly, lamelliformly compressed, gradually widening in lower half. Pronotum short with well-developed medial carina and straight, parallel, lateral carinae with strong longitudinal ridges between them. Two sulci crossing dorsum; metazona shorter than prozona with roundly



Figs 40–46. *Cannula-Glyphoclonus-Cumulus* genus group. **Figs 40–44.** Male *Culmulus stramineus* Uvarov, 1953. **40.** Lateral aspect head and pronotum from left side; **41.** Anatomy of frons and frontal ridge; **42.** Left posterior femoral apex from above; **43.** Same as 42, from the side; **44.** Abdominal apex, oblique view from left side. **Figs 45, 46.** Male *Gonista longicercata* (Bouvy, 1982): **45.** Abdominal apex from above; **46.** Abdominal apex from left side.

excurved posterior margin. Mesosternal interspace closed. Tegmina well developed with dense venation and reticulation; wings shorter, sometimes much shorter. Hind femur very narrow, not reaching end of abdomen; external upper lobe of hind knee strongly elongate; lower lobes moderately elongate, of equal length. Male supra-anal and subgenital plates elongate, acutely angular; cerci short, conical. Epiphallus with narrow bridge, moderately large ancorae and very large lobiform lophi (Fig. 13). Ovipositor unspecialized.

Discussion.—The systematics of this genus are in a confused state. Numerous species have been described, but the majority was subsequently synonymized under the senior synonym *Cannula gracilis* (Burmeister, 1838). Roy (2003) described a new West African species from Mt. Nimba (*Cannula vestigialis* Roy, 2003). The only species recorded in East Africa is *Cannula gracilis*. This differs from the other common species, *C. karschi* (Kirby, 1910), not to date recorded in East Africa, in its slenderer build and in having shortened hind-wings.

Species notes

Cannula gracilis (Burmeister, 1838)

Fig. 13

Mesops gracilis Burmeister, 1838: 610.
Calamus linearis Saussure, 1861 (Dirsh 1966)
Full synonymy given in Dirsh (1970: 415, 416).

Material.—Holotype female: SOUTH AFRICA, Cape of Good Hope (MfN). Also: ETHIOPIA: L. Haradaka; L. Zwai; Mulu, above Mugor valley; nr. Adama, Bakuru Bridge, Didessa R. rd. UGANDA: Entebbe; Kawanda; Adachal; Kapeka; Bugwere; Mubende; Tororo; Teso; West Nile; Adjumani; Acholi; Karamoja. TANZANIA: Lotanguru; Tukuyu; Tabora; Old Shinyanga; Morogoro; Itymbya, 30 mi. W. Kahama; Ushirombo rd. 22 mi. W. Kahama; Mkwemi; Lake Rukwa. KENYA: Thika; Thiala hills; Lake Rudolf; Nairobi.

Description.—As for the genus. Whole insect figured in Dirsh (1965): 413, fig. 328. Coloration variable, mostly in shades of stramineous and light brown, but also greyish, with fire-melanic forms common. Black spot on hind wing appears and intensifies with maturation.

Distribution.—Widespread in Africa south of the Sahara.

Biology.—A strict graminicole, largely confined to savanna grasslands.

Editorial note.—Popov's original manuscript did not treat *Glyphoclonus* further, but it seems appropriate to include a brief description here:

Generic diagnosis

Glyphoclonus Karsch, 1896

Glyphoclonus Karsch 1896: 249.

Type species.—*Glyphoclonus miripennis* Karsch, 1896, by original monotypy.

Type locality.—MALAWI, Milanji.

Description.—(From Dirsh 1965). Of medium size, with very elongate body. Integument strongly carinate. Antenna ensiform, strongly compressed, slightly shorter than head and pronotum together. Head elongate, acutely conical, strongly carinate above; fastigium of vertex longer than longest diameter of eye, with broadly parabolic apex; fastigial foveolae absent; frons straight, frontal ridge in upper half strongly compressed, plate-like, in lower half slightly widening, sulcate in whole length, with high lateral carinulae. Eyes small, slightly flattened. Prosternum without process. Mesosternal interspace open, strongly constricted in middle. Elytra and wing fully developed; elytra narrow, with dense, rough venation; intercalary vein of medial area present. Wings brightly colored. Hind femur moderately narrow; external apical lobe of hind knee enlarged, slightly projecting downwards, inner one not specialized; external lower lobe slightly elongate-angular, shorter than upper; inner one of normal shape. Arolium large. Male supra-anal plate elongate-angular. Cercus slightly compressed, with obtuse apex. Subgenital plate elongate, acutely conical. Epiphallus (Fig. 14) with narrow bridge, moderately large ancorae and large, lobiform lophi. Ovipositor short, robust, with slightly curved valves; lower valve with relatively large external lateral projection.

Discussion.—The genus is monotypic, with only one known species. No changes in status are recommended.

Species notes

Glyphoclonus miripennis Karsch, 1896

Fig. 14

Glyphoclonus miripennis Karsch 1896: 250.

Description.—The generic description applies. Bases of hind wings in mature adult dark red, yellow, or orange. Abdominal tergites banded in dark blue.

Distribution.—Found principally in the African Sahel region, from SENEGAL to CHAD, but also occurs in D.R. CONGO, MALAWI, and UGANDA: Adjumani and W. Busoga.

Biology.—Fishpool and Popov (1984) record the species in MALI as being gramnivorous and mesophilous. In Uganda it occurs in dry grass savanna.

Generic diagnosis

Culmulus Uvarov, 1953

Culmulus Uvarov, 1953: 163.

Type species.—*Culmulus stramineus* Uvarov, 1953, by original designation.

Description.—As in key to genera. Small, body elongate, slender, straw-like. Integument ridged. Antenna ensiform, broad at base, as long as, or longer than, head and pronotum. Head elongate, narrowly pointed. Fastigium longer than longest diameter of eye, with parabolic vertex and medial carinula. Foveolae absent. Frontal ridge with margins lamelliformly compressed above antennal sockets, divergent below. Pronotum short, narrow with sharp parallel carinae. Dorsum crossed by two sulci. Metazona shorter than prozona, its hind margin obtuse-angular. Mesosternal interspace strongly constricted, open. Tegmina and wings fully developed, acutely pointed apically; venation and reticulation dense. Hind femur narrow, slender, not reaching tip of abdomen. Lobes of hind knee of equal length. Apex of male abdomen (Fig. 44). Epiphallus (Fig. 15).

Measurements.—See Table 1.

Discussion.—The genus contains two described species: *stramineus* Uvarov, 1953 and *crassior* Uvarov, l953, both described from Angola, but only the former reaches eastern Africa.

Species notes

Culmulus stramineus Uvarov, 1953

Figs 15, 40–44

Culmulus stramineus Uvarov, 1953: 164, figs 213–220.

Material.—Holotype male: ANGOLA: Moxico distr., Villa Luso (NHMUK).

Description.—As for the genus. General coloration light stramineous, somewhat darker dorsally; hind wing with base black.

Discussion.—Superficially this species is very similar to *Parga* spp., but differs in the following respects: antennae of simple unmodified ensiform structure, longer than head and pronotum; integument not as deeply ridged as in *Parga*; frontal ridge lamelliformly compressed in its upper third; lobes of hind knee are not enlarged; male epiphallic structures are as in Fig. 15, quite distinct from those in *Parga* (Fig. 34).

Measurements.—See Table 1.

Distribution.—ANGOLA, TANZANIA: S. of Uvinza, ZAMBIA: Mweru wa Ntipa. Adults VII–IX.

Table 1. Body dimensions of *Culmulus stramineus*.

	M (mm)	F (mm)
Pronotal length	3.5	4
Tegminal length	16	19
Hind femur length	9	10
Length of body	21.0–22.5	24.2–26.0

Genus group diagnosis

The *Afrophlaeoba* genus group

Description.—The differential diagnosis between the flightless Phlaeobini (the *Afrophlaeoba* genus group) and the morphologically convergent Pargaini is given in tabular form, using *Odontomelus kwidschwianus* (Pargaini) (Figs 47–51) and *Paralobopoma viridifrons* (Phlaeobini) (Figs 52–56) to represent the two taxonomic clusters (Table 2). Note that in the Phlaeobini, the apical valves of penis, albeit covered by a membrane, often protrude through the opening even in repose.

Discussion.—The flightless members of tribe Phlaeobini include eight genera; seven from eastern Africa (see p. 41) and one from Madagascar (*Chlorophlaeobella* Jago, 1983). They show remarkable convergent evolution with flightless groups of the Pargaini, particularly *Odontomelus* I. Bolívar and its allies. The taxonomic confusion that this caused was studied by Jago (1983b, 1994).

Table 2. Differentiation between Phlaeobini and Pargaini.

	Pargaini	Phlaeobini
Temporal foveolae	small but distinct	absent
Raised longitudinal ridge dorsally on anterior and mid-femora	present (Fig. 48)	absent (Fig. 53)
Lower lobes of hind knee	acute (Fig. 49)	rounded (Fig. 54)
Male sub-genital plate	elongate, acutely pointed (Fig. 50)	blunt, spoon-shaped (Fig. 55)
Epiphallus	(Fig. 51)	(Fig. 56)

Key to genera in the flightless *Afrophlaeoba* genus group

The genus group is predominantly East African. Only the East African taxa are considered here:

1 Fastigium of vertex nearly as wide as long; arcuate transverse sulcus of fastigium submarginal; as seen from above, interocular space nearly as wide as compound eye. 2

– Fastigium of vertex longer than wide; transverse arcuate sulcus of fastigium roughly in mid position, in line with front edge of compound eyes 3

2 Lateral pronotal carinae straight in male, weakly outflexed in female; width of prozona nearly equal to its length. Tegmina less than half as wide as long. Size small; male under 15 mm long. Integument very smooth and shiny. S.W. TANZANIA (Ufipa).. .... *Chromochokwea* Jago, 1983

– Lateral pronotal carinae straight to more or less inflexed in prozona, divergent posteriorly in metazona; prozona distinctly longer than wide. Width of tegmen more than half its length. Size larger; male over 15 mm long. Integument less shiny, often pilose. S.W. TANZANIA, N. MALAWI, N. ZAMBIA, S.E. D.R. CONGO, ANGOLA, BOTSWANA.......................…………………... *Chokwea* Uvarov, 1953

3 Very small dark species; length of female about 20 mm (male not known). Vertex, occiput, pronotal disc and thorax wrinkled and rugose. Lateral pronotal carinae straight and weakly divergent backwards; length of prozona less than 15 times its greatest width. A rare endemic (male unknown). S.W. UGANDA............. *Brachyphlaeobella* Jago, 1983

– Not with above combination of characters..4

4 Lateral pronotal carinae regularly and strongly incurved in prozona and flared outwards in metazona. Supra-anal plate in male nearly as wide as long; in female abdominal apex specialized, ovipositor valves truncated and retractile, cercus minute. N. SOMALIA............. .... *Platyverticula* Jago, 1983

– Lateral pronotal carinae not, or only gently, incurved; male supra-anal plate longer than wide; apex of abdomen of female not modified..5

5 Lateral pronotal carinae straight or gently bowed inwards in male and outwards in female. Disc of pronotum 3x longer than wide with, in male, prozona more than twice as long as wide. Medial dorsal carinula of vertex strong. In male, tips of cerci level with tip of supra-anal plate and sub-genital plate projecting only a little further. Coloration of both sexes in dull shades of brown and greyish. E. TANZANIA..... .... *Afrophlaeoba* Jago, 1983

– Lateral pronotal carinae weak but entire and straight, diverging towards the rear. Pronotal prozona as long as wide. Medial dorsal carinula of vertex weak or absent. Apices of cerci extending beyond tip of supra-anal plate; subgenital plate projecting strongly beyond tip of supra-anal plate. Males brightly colored..6

6 Transverse arcuate groove of vertex weak; fastigium in front of it rugose with at least traces of medial carinula. In male, fastigium half width of pronotal prozona. Colorful species; medial dorsal band on head, thorax and abdomen maroon or green; in females, legs with some green pigmentation. UGANDA, D.R. CONGO, RWANDA .... *Paralobopoma* Rehn, 1914

– Transverse arcuate groove of vertex level with compound eyes (Figs 62, 63). Fastigium of vertex concave, narrow. In males, length of pronotal prozona more than twice its narrowest width. Both sexes in shades of brown and black. Tegmina brown, or light and dark brown, never brightly colored. E. TANZANIA: Zanzibar. SOMALIA .. .. *Parodontomelus* Ramme, 1929

Generic diagnosis

Brachyphlaeobella **Jago, 1983**

Brachyphlaeobella Jago, 1983b: 122.

Type species.—Brachyphlaeobella achilles Jago, 1983b, by original designation.

Description.—As in key to genera (pp. 44, 45). Known only from the female types. Superficially most like *Afrophlaeoba* Jago but smaller. Antennae short and robust, weakly dilated basally. Fastigium of vertex about as wide as long; medial carinula weak, interrupted by transverse arcuate sulcus positioned slightly ahead of edge of compound eyes. Frontal ridge with lateral margins rounded and gradually fading below level of antennal sockets (sharp and entire down to clypeal suture in *Afrophlaeoba*). Pronotal prozona about 1.5x as long as greatest width of pronotal disc (proportionately longer in *Afrophlaeoba*). Lateral carinae weakly excurved; rear margin of metazona medially emarginate. Tegmina strap-like, slender and small, 6x longer than wide, barely extending half-way across first abdominal tergite. Tympanic membrane reduced, less than half width of first tergite and not covered by tegmen. Genital structures and hind knee-lobes unspecialized.

Discussion.—The genus is rare and, being small, is easily overlooked and could be mistaken for nymphs of other genera such as *Paralobopoma* and *Odontomelus*.

Species notes

Brachyphlaeobella achilles **Jago, 1983**

Brachyphlaeobella achilles Jago, 1983b: 124, fig. 64.

Material.—Holotype female and paratype female: UGANDA: Kigezi, Impenetrable Forest Res. 29°42'E, 01°00'S; Kigezi, 13 miles Kabale-Kisoro rd.; IX. (NHMUK).

Description.—Females. As for the genus. Vertex, occiput, pronotal disc and thorax wrinkled and rugose. Coloration light to dull brown, with lighter brown lateral carinae. One specimen with dark brown sides and a pale ochre dorsal stripe.

Distribution.—S.W. UGANDA.

Generic diagnosis

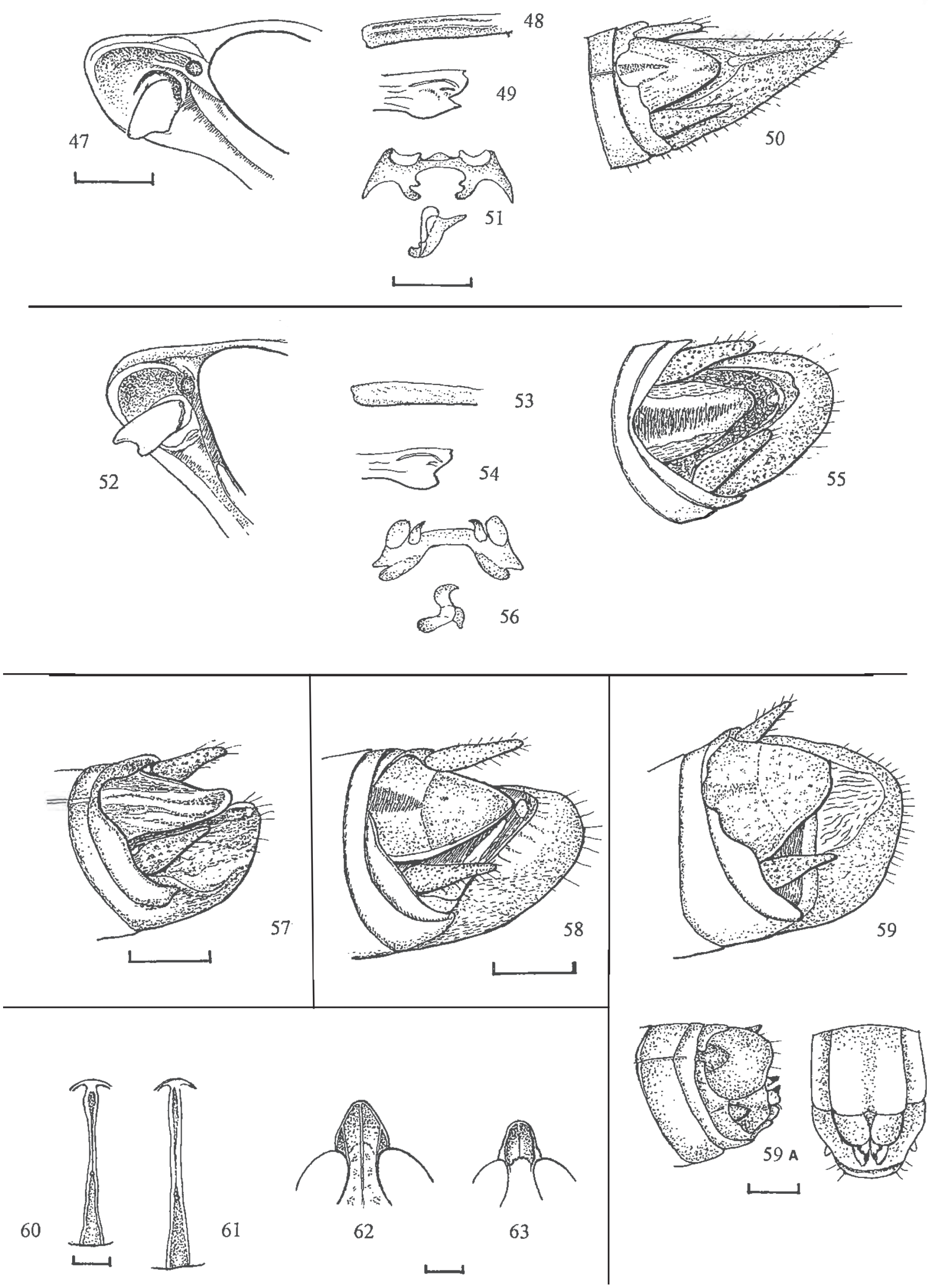
Platyverticula **Jago, 1983**

Platyverticula Jago, 1983: 116–121.

Type species.—Platyverticula ritchiei Jago, 1983b, by original designation.

Description.—As in the key to genera (pp. 44, 45). Of medium size, rather robust, superficially similar to *Chokwea*. Antennae thick, in male about 1.5x length of head and pronotum, in female slightly shorter; basal 3–4 segments of flagellum weakly flattened and broadened. Head acute in profile with frontal ridge straight, its margins wavy and irregular, constricted above ocellus, markedly divergent below it, but not constricted at junction with fastigium. Fastigium of vertex longer than broad in male, as broad as long in female. Arcuate transverse sulcus in forward position, but markedly less so than in *Chokwea* spp. Pronotal prozona lightly inflated in profile; posterior transverse sulcus forwardly arched, more so in female. Lateral carinae regularly incurved in prozona, flared outwards in metazona; hind margin of latter obtusely angularly emarginate. Tegmina symmetrically ovoid, their apices roughly level with hind margin of first abdominal tergite. Tympanum moderately developed, barely covered by tegmina. Hind femora moderately heavy, stockier than those of *Chokwea*; lobes of hind knee rounded. External and internal genital structures in male of characteristic shape (Fig. 59). In female, genital structures are even more characteristic (Fig. 59A), especially in the truncated retractile ovipositor valves and tiny triangular vestigial cerci.

Discussion.—A remarkable monotypic genus known only from Somalia. The specialized genital structures, particularly of the female, are unlike those of any other genus in this group, and indeed among the Acridinae as a whole. According to Jago (1983b: 120), the retractile ovipositor of *Platyverticula* resembles that of the



Figs 47–63. Figs 47–56. *Afrophlaeoba* genus group; comparison with Tribe Pargaini. **Figs 47–51.** Tribe Pargaini, male *Odontomelus kwidschwianus*: **47.** Lateral aspect head from left side showing foveolus; **48.** Dorsal aspect anterior left femur; **49.** Lateral aspect left hind knee (outer side); **50.** Oblique aspect of abdominal apex; **51.** Dorsal and lateral aspect (from left side) epiphallus. **Figs 52–56.** Tribe Phlaeobini, *Afrophlaeoba* genus group, *Paralobopoma viridifrons* male: **52.** Lateral aspect head from left side showing absence of lateral foveolus; **53.** Dorsal aspect anterior left femur; **54.** Lateral aspect left hind knee (outer side); **55.** Oblique aspect of abdominal apex; **56.** Dorsal and lateral aspect (from left side) epiphallus. **Figs 57–59.** *Afrophlaeoba* genus group, male abdominal apices: **57.** *Afrophlaeoba usambarica*; **58.** *Chokwea eucteana* **comb. n.**; **59.** *Platyverticula ritchiei*. **59A**. *P. ritchiei* female abdominal apices obliquely from above and from below. **Figs 60–61.** Male frontal ridge: **60.** *Parodontomelus brachypterus*; **61.** *Parodontomelus mazumbaiensis*. **Figs 62–63.** Male fastigium verticis from above: **62.** *Parodontomelus stoltzei* **comb. n.**; **63.** *Parodontomelus verticulus*. All scale lines represent l mm: that under Fig. 47 applies to Figs 48–50, 52 and 55; that under Fig. 51 applies to Fig. 56; that under Fig. 57 applies to 58 and 59; that under Figs 60 to 61 also; that under Fig. 59A to both figs; that under Fig. 62 to Fig. 63.

North American gomphocerine *Chloealtis* spp., which are known to oviposit in rotten wood and even animal dung, suggesting a similar highly specialized egg-laying behavior in *Platyverticula*.

The original description included a second species, *P. eucteana* Jago, 1983 from northern Zambia, which is here transferred to the genus *Chokwea* (pp. 49). The cerci are unmodified in *P. eucteana* and similar in structure to those in *Chokwea* spp.

Species notes

Platyverticula ritchiei Jago, 1983b

Fig. 59, 59A

Material.—Holotype male and allotype female: SOMALIA, Kismayu, littoral dune slack in and around grounds of Wamu Hotel, 28.vii.1981, J.M. Ritchie (NHMUK).

Description.—As for the genus. Figured in Jago (1983b): 118, figs 52–56. Distinctive species with unique pronotal disc and genital structures in both sexes. Coloration in shades of dark and lighter browns, without any traces of brighter pigmentation.

Distribution.—Known only from the type locality in SOMALIA. According to the collector (cited in Jago l983b), the species occurs under *Cordia* sp. bushes, which are approximately 1 m high x 2 m in diameter, growing within 500 m of the high tide line; this zone integrates with trees and bushes some 18 m high, forming a woodland. The bushes on the dunes are separated by bare sand.

Generic diagnosis

Afrophlaeoba Jago, 1983

Afrophlaeoba Jago, 1983b: 94.

Type species.—*Odontomelus usambaricus* Ramme, 1929: 260, by original designation.

Description.—As in the key to genera (pp. 44, 45). Of medium size, slender, superficially fairly similar to *Odontomelus*, but systematically nearest to *Parodontomelus* and *Paralobopoma*. Antennae narrowly ensiform, slender; in male somewhat longer than combined length of head and pronotum, in female always shorter. Frontal ridge very narrow with strong raised linear margins, more or less narrowed at medial ocellus, moderately divergent below. Pronotal disc rather broad, in females slightly inflated and about twice as long as wide; rear margin broadly emarginate. Lateral carinae strong, parallel or slightly divergent, in females sometimes slightly outcurved, only typical (hindmost) transverse sulcus strong, others weak or absent. Tegmina narrow, 4–5x as long as wide. Subgenital plate of male bluntly pointed, its dorsal tip enclosed by dorsal fusion of its cuticular tip (Fig. 57). Knees of hind femora unmodified, lobes rounded. Epiphallus (Fig. 17) closely similar to that in *Paralobopoma* (Fig. 16) and *Parodontomelus*. Coloration rather dull and uniform, predominantly in shades of brown.

Discussion.—Jago (1983b) illustrates the genus and gives keys to all four species.

Species notes.—No taxonomic changes are proposed, redefinition of the East African species is not attempted.

Generic diagnosis

Parodontomelus Ramme, 1929

Figs 60–63

Parodontomelus Ramme, 1929: 261.

Type species.—*Acteana brachyptera* Karny, 1915: 132, by subsequent designation.

Description.—As in key to genera (pp. 44, 45); figured in Jago (1983b): 105–106, figs 29–36. Superficially fairly similar to *Afrophlaeoba* but pronotal disc much narrower in prozona, and lateral carinae strongly divergent in metazona. Tegmina of similar length, but markedly broader than in *Afrophlaeoba*. Distinctive features are as follows: Antennae slightly flattened and broadened basally and evenly narrowing distally; in males always much longer than head and pronotum, in females sometimes shorter. Fastigium of vertex narrow and elongate; medial carinula strong, but transverse sulcus weak or absent, level with front margin of compound eyes. Disc of pronotum: length-width ratio of prozona 2.5–3.0. Tegmina short and broad; length-width ratio 2.0–2.9. Hindwing rudimentary much shorter than tegmen. Hind femora deep at base and very slender towards knee; length-depth ratio 4.2–5.1. Hind knee unmodified. Genital structures as in *Afrophlaeoba*.

Editorial comment.—Johnsen (1990) transferred *Chokwea stoltzei* Johnsen, 1983 to *Parodontomelus*. Further, since Popov's orginal draft, two new East African species have been added to the genus: *Parodontomelus microptilu*s Baccetti, 1997 from SOMALIA, and *Parodontomelus luci* Hochkirch, 1998 from the Udzungwa Mts. of TANZANIA. Hochkirch (1998) also restored *Parodontomelus arachniformis* Jago, 1983 from synonymy. Hochkirch (1998) gives a revised key to the species; a modified version of this is presented below instead of Popov's original, as that included only three species.

Key to species in the genus *Parodontomelus* (males)

Modified from Hochkirch (1998).

1 Tegmina minute (0.8 mm), scarcely reaching posterior margin of the mesonotum. Posterior margin of metazona deeply indented. SOMALIA: Basso Giuba.......... *microptilus* Baccetti, 1997

– Tegmina small but reaching at least the first abdominal tergite. Posterior margin of metazona not concavely indented.......... 2

2 Tegmina dark brown throughout.......... 3

– Tegmina light brown in anal area.......... 4

3 Male frontal ridge as in Fig. 60; length/depth ratio of hind femur 4.3. TANZANIA: E. coastal forests.......... *brachypterus* (Karny, 1915)

– Frontal ridge as in Fig. 61; length/depth ratio of hind femur 4.7. TANZANIA: W. Usambara Mts.......... *mazumbaiensis* Jago, 1983

4 Smaller species, total length <20mm, hind femur <11 mm. Fastigium of vertex as in Fig. 63. Tegminal apices fall short of hind margin of abdominal tergite 1. TANZANIA: Pugu Hills...... *verticulus* Jago, 1983

– Large species, length of hind femur >11 mm. Median carinula of vertex continuous, sometimes lowered on occiput but never obsolete 5

5 Subgenital plate not carinulate but ending in a point. Anal area of tegmen only slightly lighter brown than pre-anal area. Hind margin of epiphallic lophi straight. TANZANIA: Udzungwa Mts.......... *luci* Hochkirch, 1998

– Subgenital plate carinulate medially on dorsal surface, posterior to supra-anal plate. Anal area of tegmina light brown, distinctly lighter than pre-anal areas. Hind margin of epiphallic lophi concave 6

6 Hind femora broader (3.1 mm), length to depth ratio 4.6; upper (hind) margin of tegmina convex; tegmina longer (3.5 mm) and broader (1.55 mm) reaching midway between abdominal segments I and II; eyes longer (2.76 mm) and broader (1.73 mm) in lateral view. Inner margin of epiphallic lophi straight. TANZANIA: Uluguru Mts. ....*stoltzei* (Johnsen, 1983)

– Hind femora less broad (<3.0 mm) length to depth ratio >4.8; upper (hind) margin of tegmina straight; tegmina shorter (<3.0 mm) and not as narrow (<1.3 mm) reaching or only slightly exceeding rear margin of first abdominal segment; eyes shorter (2.61 mm) and narrower (<1.64 mm) in lateral view. Inner margin of epiphallic lophi concave. TANZANIA: E. Usambara Mts., Zanzibar, and Mafia Island; KENYA: Shimba Hills, Mrima Hill, Jilore Forest, and Gogoni Forest. ....*arachniformis* Jago, 1983

Species notes

Parodontomelus stoltzei (Johnsen, 1983)

Fig. 62

Chokwea stoltzei Johnsen, 1983: 53–55, figs 5, 6a-l.
Parodontomelus stoltzei (Johnsen, 1990).

Material.—Holotype male *stoltzei*: TANZANIA: Uluguru mts., Kimboza forest, 18.VII.1981 Stoltze and Scharff (ZMUC).

Description.—As in key above. Other diagnostic features include the following: antennae brownish to brownish black; exceptionally long. General coloration striking and variable; predominantly buff-pale brownish, with a contrasting dark lateral band extending from antennal sockets across genae to upper edge of lateral pronotal lobe, sometimes invading hind part of metazona of disc, then upper part of pleura and to lower side of tegmen and tapering along side of abdominal tergites. Hind knee and most of hind tibia black, hind tarsus pale brownish. Upper area of tegmen and external and internal lower areas of hind femur sometimes reddish. Large size distinctive (see measurements in Johnsen 1983).

Distribution.—E. TANZANIA: Uluguru Mts.

Parodontomelus brachypterus (Karny, 1915)

Fig. 60

Acteana brachyptera Karny, 1915: 132, by subsequent designation, Ramme, 1929: 262, 275.

Material.—Holotype female: TANZANIA: nr. Dar es Salaam (NHMV).

Description.—As in key above. Differs from the other members of genus in its combination of uniformly brown tegmina and robust hind femora and, in male, by hind femur length/depth ratio of 4.3. General coloration in dull shades of brown.

Distribution.—Known only from the type locality, but probably occurs in other local forest relicts in the coastal area.

Parodontomelus mazumbaiensis Jago, 1983

Fig. 61

Parodontomelus mazumbaiensis Jago, 1983b: 111, figs 29, 33, 43, 44.

Material.—Holotype male: TANZANIA: W. Usambara Mts., Mazumbai Forest Res., VI. 1967 (NHMUK).

Description.—As in key above. Known only from the unique male type. Similar to *P. brachypterus* in uniform brownish coloration of tegmina, but fastigium of vertex and pronotal disc narrower.

Distribution.—TANZANIA: Eastern end of W. Usambara Mountains, in relict forest.

Parodontomelus verticulus Jago, 1983

Fig. 63

Parodontomelus verticulus Jago, 1983b: 112, figs 29, 32, 35, 41, 42.

Material.—Holotype male: TANZANIA: Pugu Hills, S.W. of Dar es Salaam, II. III. 1967, N.D. Jago (NHMUK).

Description.—As in key above. Generally similar to *P. stoltzei*, but size smaller; apex of head and frontal ridge narrower, and tegmen shorter and deeper. Coloration similar to *stoltzei* but lacking light ochre facial markings.

Distribution.—TANZANIA: known only from Pugu Hills.

Editorial note.—Popov's original manuscript synonomized *P. arachniformis* Jago, 1983 under *P. stoltzei*. Although this was never actually published, Hochkirch (1998) contested the proposed synonomy and "prophylactically" restored *arachniformis*, mainly on the grounds of differences in the epiphallic lophi. We accept his arguments, and here list *arachniformis* and the subsequently described species *O. luci* and *O. microptilus* as valid species of the genus.

Parodontomelus arachniformis Jago, 1983

Parodontomelus arachniformis Jago, 1983b: 108.

Material.—Holotype male *arachniformis*: TANZANIA: E. Usambara Mts., Kwamkora For. Res., 7. IV. 1966, N.D. Jago (NHMUK).

Description.—As in key above. Jago (1983) writes of male "Colour distinctive. Antennae black. Area between lateral carinae of frons grey or ochre, a band from base of antennae across genae being light brown to cream (sometimes fading on genae). Body with light brown dorsal stripe. Laterally dark brown stripe on head, as deep as eye, extending across lateral lobe of pronotum and occupying about upper two thirds of that lobe, or reduced in depth across head and forming black band across upper fifth of pronotal lateral lobe. Hind femora light brown, olivaceous externally, orange below and with apical quarter black. Hind tibiae black with black spines". The female coloration is however variable. Hochkirch (1998) figures the epiphallic lophi of five species of the genus, showing differences in their outlines.

Distribution.—TANZANIA: E. Usambara Mts.; Zanzibar: Bububu; Coast region: Mafia district: Utende; KENYA: Shimba Hills, Jilore Forest, W. of Malindi; Mrima Hill Forest, S. of Kakoneni.

Parodontomelus luci Hochkirch, 1998

Description.—As in key above.

Distribution.—TANZANIA: Udzungwa Mts.

Parodontomelus microptilus Baccetti, 1997

Description.—As in key above. Differs from all other species of the genus in being micropterous rather than brachypterous.

Distribution.—SOMALIA: Basso Giuba, Belet Amin.

Generic diagnosis

Chokwea Uvarov, 1953

Fig. 18

Chokwea Uvarov, 1953: 153–54, figs 190, 191; 156.

Type species.—*Chokwea burri* Uvarov, 1953: 154, 78, by original designation.

Description.—As in the key to genera. Of medium size, slightly more robust and less elongate than *Afrophlaeoba* and *Parodontomelus,* with somewhat shorter and broader vertex and disc of pronotum. Arcuate transverse sulcus is always anterior to mid-point of fastigium, and often submarginal along to its front edge. Shape of pronotal disc variable in width and degree of flexure of lateral carinae but providing distinctive specific characters.

Discussion.—The most widespread taxon in this genus group, being recorded from Angola and Botswana to D.R. Congo, Zambia, and Malawi to southwestern Tanzania. *Chokwea,* as originally described by Uvarov (1953), contained four new species: *burri* (the type species for the genus) from Angola; *bredoi* from Zambia; and *backlundi* and *fitzgeraldi*, both from Tanzania. The last two were removed by Jago (1983b) to his new genus *Chromochokwea*, but *backlundi* is reinstated here as a *Chokwea* sp. *Chromochokwea* Jago thus becomes a monotypic genus with *fitzgeraldi* as type species. *Platyverticula eucteana* Jago, 1983b is newly transferred to *Chokwea* because its phallic structures are more typical of that genus. In addition, Jago (1983b) described a new species *C. malawii* from the Chikangwa area of Malawi, while more recently Johnsen (1991) added another new species, *C. forchhammeri,* from the Serowe area of Botswana. Of the six current species of *Chokwea* just two, *backlundi* and *eucteana* (both from the Ufipa area of Tanzania), are recorded from eastern Africa.

The nomen dubium *Chokwea testacea* Otte, 1995 is not treated here.

Key to species in the genus *Chokwea*

1 Fastigium of vertex with centrally placed transverse arcuate sulcus . 2
– Fastigium of vertex with transverse arcuate sulcus well ahead of mid position, or without one 3
2 Coloration in shades of buff and light brown, tegmina similarly light brown. BOTSWANA................................ *forchhammeri* Johnsen, 1991
– Coloration in shades of light and dark brown and black; tegmina in male black, in female light brown above, dark below; knees in both sexes black. MALAWI.. *malawii* Jago, 1983
3 General coloration including tegmina in sombre shades of brown and grey; lateral pronotal carinae strongly incurved. ZAMBIA; TANZANIA: Ufipa ....*eucteana* (Jago, 1983), **comb. n.**
– Coloration includes bright pigmentation, particularly strong in males; tegmina reddish, brownish, or purplish................................ 4
4 Lateral pronotal carinae moderately incurved, markedly divergent behind the typical sulcus 5
– Lateral pronotal carinae almost straight in male, slightly divergent in female. TANZANIA .... *backlundi* Uvarov, 1953, **comb. res.**
5 Hind knee reddish without any black. ANGOLA, D.R. CONGO ....*burri* Uvarov, 1953
– Hind knee black. ZAMBIA: Mbala.......................*bredoi* Uvarov, 1953

Only the two species with East African distribution are considered below.

Species notes

Chokwea backlundi Uvarov, 1953, res. comb.

Chokwea backlundi Uvarov, 1953: 155,156, figs 194, 195.
Chromochokwea backlundi (Uvarov) (Jago 1983b).

Description.—As in keys to genera and species. Rather robustly built, brightly colored species. Antennae very slightly compressed basally, reaching posterior edge of tegmina in male, markedly shorter in female. Pronotal disc particularly characteristic, with large shallow puncturation and with lateral carinae straight and parallel in prozona and weakly divergent in metazona, more markedly so in female. General coloration brownish with more or less olivaceous-green pigmentation; legs a brighter green; tegmina reddish.

Distribution.—TANZANIA: Ufipa plateau.

Chokwea eucteana (Jago, 1983), comb. n.

Fig. 58

Platyverticula eucteana Jago, 1983b: 120.

Description.—As in the keys to genera and species. Size large and build elongate for genus. Pronotal disc with strongly incurved lateral carinae. In pronotal morphology species resembles *Platyverticula ritchiei*, but its genital structures are typical of *Chokwea*. Coloration in subdued shades of brown and grey only.

Distribution.—ZAMBIA: Abercorn, Mbala; TANZANIA: Ufipa, Mpui.

Generic diagnosis

Paralobopoma Rehn, 1914

Figs 16, 52–56

Paralobopoma Rehn 1914: 73.

Type species.—*Paralobopoma bugoiensis* Rehn, 1914: 73, by original designation.

Description.—As in key to genera (pp. 45). Close to *Parodontomelus* and *Afrophlaeoba*, but of somewhat more robust build, with shorter head and broader disc of pronotum, less than twice as long as wide. Antennae narrowly ensiform longer than head and pronotum together. Frontal ridge shallowly sulcate with obtuse carinulae. Fastigium of vertex elongate-parabolic with weak carinula and transverse sulcus just ahead of anterior edge of compound eyes. Pronotum weakly tectiform, median carina distinct; lateral carinae weaker, straight, parallel or weakly divergent and largely obliterated in metazona. Metazona about 1/3 length of prozona, its hind margin broadly emarginate. Tegmina reduced to narrow strap-like scales, their tips about level with hind margin of second abdominal tergite. Ovipositor unspecialized; male subgenital plate as in *Parodontomelus*. Hind femora with rounded genicular lobes. Coloration as a rule includes some green pigmentation, brighter in male. Color green or brown with a yellow marginal pronotal band, and often with a broad dark lateral stripe along upper margin of lateral pronotal lobes.

Discussion.—In his revision of the genus, Jago (1983b) recognized four species. All species of the genus are found in or around the Western (Albertine) Rift Valley. *P. sjostedti* Ramme, 1931 was described from an unspecified locality in N.W. Tanzania, and is also known from extreme eastern D.R. Congo (Mt. Kabuzi, W. shore of Lake Kivu). *P. viridifrons* Jago, 1983 is widely distributed in W. Uganda. These are the only species of the genus known to occur in East Africa as it is politically defined. The other species are from eastern D.R. Congo or Rwanda. Jago (1983b) gives keys to all species. The genus is now in need of a further revision.

Species notes

As no taxonomic changes are proposed here, redefinition of the East African species is not attempted.

Genus group diagnosis

The *Ocnocerus* genus group

Description.—This genus group is part of tribe Phlaeobini. Its members share the following combination of characters. Size small, of medium fusiform build. Integument characteristically sculptured, pitted, ridged, and more or less rugose. Antennae of variable structure, greatly shortened, flattened and modified in *Hyperocnocerus*, less so in *Ocnocerus* and *Anacteana* (and even less in the remaining genera), being nearly filiform and greatly elongate in some species and subspecies of *Sumba*. Head short, moderately pointed, fastigial foveolae absent; fastigium of vertex parabolic to trapezoidal. Pronotum weakly tectiform, more or less convex; medial carina weak but distinct, with lateral carinae weaker and sometimes partly or completely obsolete. Pronotal metazona shorter than prozona, its hind angle incurved or straight (*Anacteana* spp., *Rhabdoplea angusticornis*), or obtuse-angular (the remaining taxa). Mesosternal interspace open, often tranverse; metasternal interspace closed or very narrow. Tegmina and wings fully developed, shortened or vestigial; micropterism may be general for a genus (*Anacteana*), or occur as a polymorphism within a species (*Rhabdoplea munda*). Wing venation and reticulation from sparse to dense when transverse veinlets become thickened and more serrated and membrane of tegmina opaquer (especially marked in *Panzia*). Hind femur moderately robust, knee lobes on both sides rounded and not expanded. External male genitalia simple, unspecialized, cerci conical. Supra-anal plate cordate; subgenital plate short, subconical. Phallic structures are of the phlaeobine type with well-developed ancorae and spatulate lophi of variable depth and width. They bear an outer and sometimes an inner small spherical lobe and relatively short anterior and posterior processes. Uniquely, the ectophallic membrane is somewhat thickened and, on each side, bears an area of appressed, fine, silky setae (Figs 64, 65). This feature was first noted by Descamps and Donskoff (1968) in their *Sumba rubripes*, but it is common to the whole genus group, although its development in some genera, e.g. *Anacteana* **gen. n.**, is less marked. Valves of ovipositor unspecialized; lower pair with an external lateral projection. Subgenital plate with a medial projection; spermathecal duct with basal loop, medial coil and spermatheca with apical and pre-apical diverticula of somewhat variable shape (Fig. 66).

Discussion.—The *Ocnocerus* genus group includes *Ocnocerus* I. Bolívar, 1884, *Hyperocnocerus* Uvarov, 1953, *Anacteana* **gen. n.**, *Sumba* I. Bolívar, 1909, *Panzia* Miller, 1929, and *Rhabdoplea* Karsch, 1893. No changes are made here in *Ocnocerus,* with its two species *bayaoi* I. Bolívar, 1889 and *diabolicus* Karsch, 1893, or in the monotypic genera *Hyperocnocerus* and *Panzia. Acteana alazonica* Karsch, 1896 and *Acteana neavei* I. Bolívar, 1912 are not congeneric, so a new genus *Anacteana* **gen. n**. is erected here with *neavei* as the type. *A. alazonica* Karsch, 1893 is transferred to the Pargaini as the type species of *Acteana* Karsch, 1893.

Rhabdoplea is now considered to contain only two species: *R. munda* Karsch, 1893 and *R. angusticornis* Uvarov, 1953, while *R. callosa* Uvarov, 1953 is transferred to *Sumba*. The following taxa are thus now placed in *Sumba: granulifera*, *punctata*, *semicarinata*, and *callosa* (all Uvarov, 1953), *roseipennis* I. Bolívar, 1912, *rubripes* Descamps & Donskoff, 1968, and *exilis* **sp. n.**

Key to genera in the *Ocnocerus* genus group

1 Micropterous, organs of flight reduced to lateral scales 2
– Fully winged... 3
2 Antenna simple, narrowly ensiform; lateral pronotal carinae linear, low but distinct throughout; dorsum of pronotum with callose, parallel, longitudinal ridges, especially in the metazona; hind margin broadly rounded........ *Rhabdoplea* Karsch, 1893 (micropterous form)
– Flagellum of antennae divided into a broadly ensiform basal part, a narrowly ensiform middle part, and a cylindrical, more or less filiform, tapering apical part (Figs 69–72); lateral pronotal carinae obsolete throughout, or at least in the metazona, sculpturing of dorsum of pronotum not in parallel ridges, hind margin of metazona straight, or emarginate .... *Anacteana* **gen. n.**
3 Antennae strongly reduced, their length equal to that of head and modified as in Fig. 73. Disc of pronotum strongly ridged and furrowed... *Hyperocnocerus* Uvarov, 1953.
– Antennae not strongly reduced and modified as above.................... 4
4 Antennae much shorter than combined length of head and pronotum; basal segments of flagellum flat and broad, their apical angles protruding; medial segments flat and narrow, but apical ones cylindrical and tapering (Fig. 74). Pronotal disc with strongly punctate cuticle, but not longitudinally ridge or furrowed .... *Ocnocerus* I. Bolívar, 1889.
– Antennae ensiform, basal segments of flagellum somewhat flattened and expanded (Fig. 75), but not modified as above, their length equal to, shorter than, or longer than combined length of head and pronotum.. 5

5 As under couplet 2 above but fully winged; venation sparse, intercalary vein distinct, membrane of tegmina transparent ....*Rhabdoplea* Karsch, 1893 (alate form)
– Venation and reticulation relatively dense, intercalary vein weak, indistinct or absent; membrane of tegmina more or less opaque. Hind margin of pronotum obtuse-angular, prozona/metazona ratio <1.2.......... 6
6 Reticulation in apical part of tegmina and wings regular, transverse veinlets thickened and dentate (Fig. 76)..............*Panzia* Miller, 1929
– Hind margin of pronotum broadly rounded, prozona/metazona ratio >1.2. Reticulation in apical part of wing and tegmen less regular, transverse veinlets not unduly thickened and dentate (Fig. 77)........ ....*Sumba* I. Bolívar, 1909

The *Ocnocerus* genus group can be divided into two genus subgroups: *Sumba-Rhabdoplea-Panzia* and *Ocnocerus-Hyperocnocerus-Anacteana* (gen. n.).

Genus sub-group diagnosis

Sumba-Rhabdoplea-Panzia genus sub-group

Description.—Separated from the *Ocnocerus-Hyperocnocerus-Anacteana* genus sub-group chiefly on the basis of their less modified antennal morphology.

Discussion.—These three genera have many similar morphological facies: genital structures; general habitus and sculpturing of the integument; structure of antennae, frons and fastigium; pronotum and sternum; wing shape, venation, and reticulation. Genital structures and coloration are rather unstable characters and subject to intra- and inter-specific variation. *Rhabdoplea* and *Panzia* are readily redefined, while the remaining species and subspecies are newly placed under *Sumba*.

Generic diagnosis

Sumba I. Bolívar, 1909

Sumba I. Bolívar, 1909: 288, 289.

Type species.—*Sumba roseipennis* I. Bolívar, 1912: 78, by subsequent designation (I. Bolívar 1912).

Description.—Diagnosis in key to genera above (p. 50).

Discussion.—While *Rhabdoplea* and *Panzia* can be defined on a suite of narrowly variable characters, *Sumba* is defined on characters subject to a wider range of variation. These include sculpturing of the integument which, in *Sumba*, varies from relatively fine (but always distinct) to very coarse and rugulose, although never showing the distinctive regular parallel ribbing of *Rhabdoplea*. Likewise, wing shape and venation show a wide range of variation from narrow with sparse reticulation (as in *S. roseipennis*, which is similar to *Rhabdoplea*), to broad with sparse reticulation (as in *S. granulifera*, which is similar to *Panzia*). Table 3 summarizes geographical variation in selected morphometric ratios.

The genus was first described by I. Bolívar (1909) in a key without any species included. In 1912 he described the first species, *Sumba roseipennis*. The present study reduces *S. longicornis* Ramme to a synonym of *S. roseipennis* and describes *Sumba exilis* **sp. n.** from the Ngaoundéré area of north central CAMEROON and western UGANDA.

Sumba species fall into two distinct clusters: first, the widespread *S. roseipennis* species group consisting of closely related taxa, which are also similar in appearance to *Rhabdoplea* (includes *S. rubripes* and *S. exilis* **sp. n.**), and second, three species in the *S. semicarinata* species group, also including *S. punctata* and *S. granulifera*, together with the fourth, *S. callosa* (transferred from *Rhabdoplea*), which are local, rather distinctive endemics, of which *S. granulifera* shows some similarity to *Panzia uvarovi*.

Table 3. Geographical variation in morphometric ratios amongst *Sumba*.

	rubripes (mm)	*exilis* (mm)	*roseipennis* (numbered by location) (mm)				
			1	2	3	4	5
Antennal length/ pronotal length (male)	1.7	1.25	1.5	1.4	1.1	1	0.8
Tegminal length/ tegminal width (male)	NA	8.2	7.5	7.8	7.5	7.3	7.4

Locality no.: 1. Uganda, Kepeka; 2. Zaire, Park Nat. de Garamba; 3. Tanzania, Katavi; 4. Namibia, Waterberg; 5. Swaziland, Mbabana.

Key to *Sumba* species (*semicarinata* species group) (Key 1)

1 Relatively slender, head pointed (Figs 78–81) sculpturing relatively smooth and shiny, not rugulose or granulose. Lateral pronotal carinae distinct, thick or linear, although weaker in the metazona. Tegmina and wings narrow (tegmen length/width ratio >6), venation and reticulation sparse 2
– More robust, head less acute, sculpturing coarse, with marked callosities and rugosities. Lateral pronotal carinae thick, callose and irregular in prozona, obsolete in metazona. Tegmina and wings broad, (tegmen length/width ratio <6), venation and reticulation dense... 3
2 Integument smooth and shiny, though coarsely punctured. Frontal ridge thick, not sulcate, fastigial and pronotal carinae thick and callose, hind wing hyaline ....*punctata* Uvarov, 1953
– Frontal ridge sulcate with well-defined margins. Fastigial and pronotal carinae linear. Hind wing colored, or infumate (but hyaline in *S. exilis*)...see *roseipennis* species group, Key 2
3 Head short, frons broadly concave; eye round, length/width ratio around 1.2. Fastigum of vertex very broad and short (Fig. 86) ....*callosa* (Uvarov, 1953), **comb. n.**
– Frons in profile only weakly convex or straight; eye elongate, length/width ratio>1.2. Fastigium of vertex not unduly broad and short (Figs 87, 88).. 4
4 Sculpturing coarsely rugose and callose all over head and most of thorax, but roughly aligned as longitudinal callosities in metazona of pronotum. Base of antenna narrowly ensiform. Frontal ridge not expanded between antennae. Reticulation of tegmina rather loose and very irregular. Hind wings yellow basally. ....*semicarinata* Uvarov, 1953
– Sculpturing on head and pronotum consisting of regularly scattered rounded tubercles; basal antennal segments broadly ensiform; frontal ridge distinctly expanded between antennae. Reticulation of tegmina exceptionally dense. Hind wings rose colored at base, lightly infumate apically.. *granulifera* Uvarov, 1953

Key to *Sumba* species (*roseipennis* species group) (Key 2)

1 Of slender elongate build; sculpturing on occiput as longitudinal dorso-lateral row of callose ridges separated by a deep furrow; face straight, or weakly concave in profile; fastigium triangular, elongate, pointed apically (Figs 82–83). Tegmina very narrow, tapering and down-curved apically; hind wing hyaline. CAMEROON, UGANDA . ... *exilis* **sp. n.**

– Of less slender and less elongate build; sculpturing fine but does not form a distinctive pattern. Face weakly convex in profile; fastigium parabolic, not distinctly pointed apically. Tegmina straight, not down-curved apically; hind wing colored, yellow, or pink basally and more or less infumate apically.. 2

2 Antennae exceptionally long and narrow, reaching base of hind legs in male and flattened but scarcely widened basally. Lower sulcus of hind femur and hind tibia red. D.R. CONGO.................................... .... *rubripes* Descamps & Donskoff, 1968

– Of variable build, from relatively slender to robust. Antennae of variable length: as long as, shorter than, or longer than the combined length of head and pronotum, but not exceptionally long and narrow as in *S. rubripes*. No red on hind legs. Grasslands of Africa south of the Sahara ....*roseipennis* I. Bolívar, 1912 *sensu lato*

Species notes

Sumba roseipennis I. Bolívar, 1912

Figs 65, 66, 78–81

Sumba roseipennis I. Bolívar, 1912: 78.
Sumba nigrescens Miller, 1929: 67, figs 17, 18 (syn. Dirsh 1966).
Sumba longicornis Ramme, 1929 **syn. n.**

Material.—Holotype female *roseipennis*: ZAMBIA (MRAC, Tervuren). Holotype male *nigrescens*: TANZANIA, Kalula (NHMUK). Paratype male *longicornis*: CENTRAL AFRICAN REPUBLIC, Ouham River, Bozoum (NHMUK).

Further material (NHMUK, unless stated otherwise): SOUTH AFRICA: Pretoria, IV. SWAZILAND (now ESWATINI): Mbabane. NAMIBIA: Waterberg (Nat. Mus. Nam., Windhoek). ANGOLA: Villa Luso; Quirimbo, 3 mi. N. of Santa Comba; Mt. Lubiri, 6 mi. N.W. Alto Hama. D.R. CONGO: Lubumbashi; Parc National de Garamba. ZIMBABWE: Mashonaland, Harare (as Salisbury). ZAMBIA: Mbala (Abercorn), Lake Chila; Mweru wa Ntipa; Chambosi River. TANZANIA: Plateau 5 mi. S.W. of Sumbawanga; 8 mi. S. of Chala Mission; Ushirombo Road, 16 mi. W. Kahama; 13 mi. S. Biharamulo; Katavi plains; 137 kms. Sumbawanga-Mpando. UGANDA: mile 60, Mubende-Masaka; mile 35, Mbarare-Masaka; Kampala; Mbarara; Koki; Koki-Lawanda; Kapeka; Masaka; Buhimba; Msaka-Lwango. CAMEROON: 27 km N.W. Banyo, Ngaoundéré.

Description.—As in the key. Coloration similar to that in *Rhabdoplea*, in shades of stramineous and brown, occasionally in shades of grey. Greenish hues, mostly in dull olivaceous shades, occur locally and apparently represent populations from particularly wet and green habitats. Fire melanism common and may predominate in some series. Hind wings pink or yellow at base; usually somewhat infumate apically. Wing color forms often sympatric. Shade and depth of pigmentation varies, probably in relation to maturation; immature adults' wings may be colorless.

Discussion.—Geographical variation in *S. roseipennis* parallels that of *Orthochtha dasycnemis* (Gerstaecker). Thus, the more slender, elongate individuals with narrower wings and fastigia are from D.R. Congo (Lubumbashi), and the stouter ones, with broader wings and shorter fastigia, from South Africa and Namibia; specimens from the intermediate areas and West Africa, are of an intermediate build. Antennal length and width are also variable; stouter, more robust specimens in southern Africa have shorter antennae, while more slender ones in West Africa (the original *S. longicornis*) have longer antennae. Local variability is also great in some areas (populations in some parts of Uganda and Tanzania) whose structural differences almost span the extremes of the geographical range of variation. Specimens from near Chala Mission in N.E. Tanzania are as robust as those from Swaziland (now eSwatini), while those from near Biharamulo in N.W. Tanzania are as slender as those from Lubumbashi. The phallic structures, however, exhibit no notable differences between these populations. Table 4 (p. 54) gives morphometric data on *roseipennis.*

Distribution.—A variable species of wide geographical distribution: TOGO to CENTRAL AFRICAN REPUBLIC, CAMEROON, D.R. CONGO, UGANDA, KENYA, TANZANIA, ZAMBIA, ZIMBABWE, ANGOLA, NAMIBIA, and SOUTH AFRICA.

Sumba rubripes Descamps & Donskoff, 1968

Sumba rubripes Descamps & Donskoff, 1968: 1225–8, figs 29–36.

Material.—Holotype male, allotype female: CONGO REP., Brazzaville (MNHN, Paris). Paratypes 3 males, 3 females, CONGO REP., Brazzaville; Odzala (MNHN, but donated to NHMUK).

Description.—As outlined in Key 2; differs from *S. roseipennis* in its longer and narrower antennae and different coloration. Males usually with a yellow medial dorsal band extending from fastigium to tip of tegmina; head and thorax greenish or brownish, underside yellow. Anterior and middle legs greenish, hind legs red, hind knee with some black; hind wings yellow, or rose at base, infumate apically. Some of the long paratype series are all black, presumably a result of fire melanism.

Females: coloration similar, but hind legs yellow. Table 4 gives morphometric data for *rubripes.*

Discussion.—Closely similar to *S. roseipennis*. Apparently restricted to the Congo Republic.

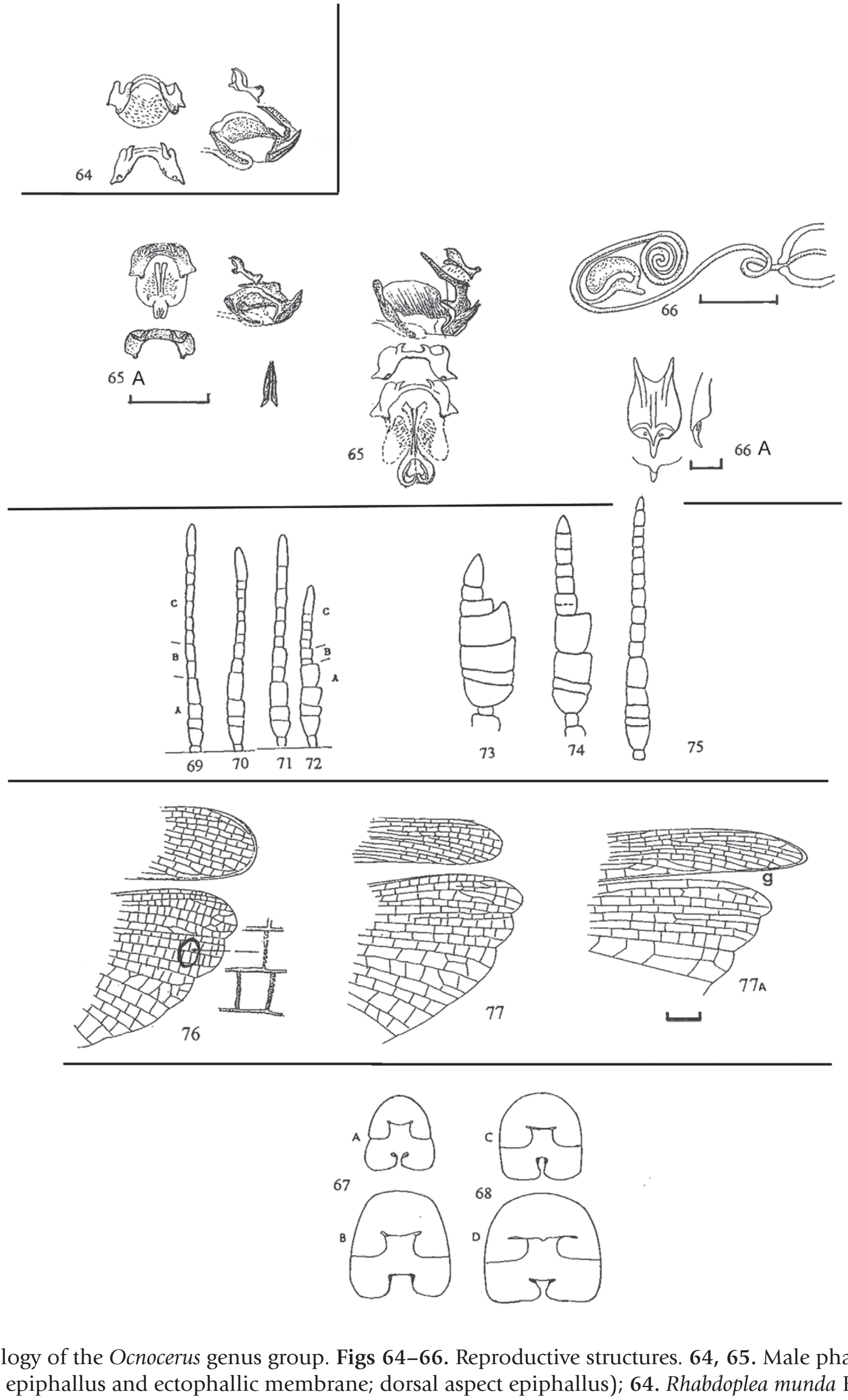
Distribution.—Known only from the original type material.

Sumba exilis sp. n.

http://zoobank.org/F8888FBE-32D8-4C83-A574-74555BDEA80B
Figs 65A, 77A, 82–85, 88A

Material.—Holotype male, CAMEROON: Scarp at Ngaoundéré, 23–27.XI.1980, Jago and Popov; 1 male, 1 female paratypes, same data. UGANDA: 1 female, Mbarara, 1.1934, Johnston (NHMUK).

Description.—Head and thorax coarsely sculptured in ridged shiny callosities and intervening furrows (Figs 82–83). Antennae moderately widened in basal third, cylindrical apically, in males slightly longer and in female shorter than combined length of head and pronotum. Head acute, face oblique, straight to weakly concave in profile; frontal ridge with well-defined margins, fas-



Figs 64–77. Morphology of the *Ocnocerus* genus group. **Figs 64–66.** Reproductive structures. **64, 65.** Male phallic complex (lateral aspect whole complex; epiphallus and ectophallic membrane; dorsal aspect epiphallus); **64.** *Rhabdoplea munda* Karsch, 1893; **65.** *Sumba roseipennis* I. Bolívar, 1912; **65A**. *S. exilis* **sp. n.; 66.** *S. roseipennis,* female genitalic complex - (**66.** Spermathecal duct; **66A.** Subgenital plate, entire from above, tip from ventral aspect and tip from lateral aspect, left side). **Figs 67–68.** Meso- and metasterna of: **67A.** *Acteana alazonica* Karsch, 1896 male, and **68B**. Same, female; **68C**. *Anacteana neavei neavei* I. Bolívar, 1912 male; **68D**. Same, female. (Note: *Acteana* is not a member of this genus group, it is a member of the Pargaini, but very similar to *Anacteana.* See Figs 331–340). **Figs 69–75**. Antennal morphology. **Figs 69–72.** Variation in antennae of *Anacteana n. neavei*. **69.** Male Tanzania, Ufipa; **70.** Female same locality; **71.** Male Zambia, Mweru wa Ntipa; **72.** Female, same locality. **Figs 73–75.** Antennal morphology, other genera. **73.** *Hyperocnocerus sulculatus;* **74.** *Ocnocerus diabolicus;* **75.** *Panzia uvarovi.* **Figs 76, 77, 77A.** Fore and hind-wing apices. **76.** *Panzia uvarovi* (including enlarged section showing thickened cross-veins); **77.** *Sumba callosa*; **77A.** *Sumba exilis* **n. sp.**, showing longer and more pointed tegmen. All scale lines represent l mm: that under Fig. 66 applies to Figs 64, 65 and 65A; that under Fig. 66A applies uniquely to it; that under Fig. 77A applies to Figs 76–77A.

Table 4. Measurements of *Sumba* species (mm).

	roseipennis		*rubripes*		*exilis*		*punctata*	*semicarinata*		*granulifera*		*callosa*	
	M	F	M	F	M	F	M	M	F	M	F	M	F
Antennal length	5.1–5.8	6.5–7.0	8.0–9.0	7.0–8.0	6.2	6.3–8.2	6.3	7.1	5.0–6.2	6.2	5 .6	6	6
Antennal width	?	?	0.3	0.25	?	?	0.42	0.42	0.5	?	0.55	0.2	0.2
Pronotal length	2.4–2.8	2.8–3.5	2.5–2.6	3.0–3.6	2.7	3.0–3.3	3	2.8	3.5	3.3	3.4	3	3.5
Prozona/metazona ratio	1.38	1.3	1.4	1.3	2.3	?	1.15	1.3	1.2	1.2	1.1	?	?
Tegminal length	12.5–13.5	13.2–15.5	11.2–12.9	12.3–14.3	14	13.0–15.0	13.7	12.0–12.8	12.8–14.5	16	16.0–17.0	13.8	14
Tegminal width	1.7	2.5	1.8	2.4	1.7	1.7–2.0	2	2.1	2.8	2.5	2.7	2	2
Length/width ratio tegmen	7.3–7.9	5.28–6.2	6.2–7.1	5.1–6.0	8.82	#	6.85	6.00	5.0	6.50	6.00	7.00	7.00
Hind femur length	8.2–10.0	10.0–12.0	9.6–10.7	10.4–11.9	9.8	9.2–10.0	8.6	8.5–9.0	10.5–11.0	11	12	9.3	11.2
Hind femur depth	1.6–1.7	1.8–1.9	1.7	1.9	1.9	2.0–2.2	1.8	2.3	2.6	2.5	2.8	2.3	2.6
Length/depth ratio hind femur	#	#	#	#	5.2	#	4.8	3.8	4.1	4.4	4.3	4	4.3
Total length	14.0–16.0	17.0–22.0	16.7–18.9	17.9–20.5	15.8	16.2–19.0	16	14.3–16.5	16.3–20.0	17 .5	19.0–22.5	14	18

? = missing data
= single ratio cannot be calculated

tigial constriction marked. Fastigium longer than wide in both sexes, margins and medial carinula linear and distinct, arcuate sulcus in mid position (Figs 82–83). Dorsum of pronotum regularly tectiform, hind angle broadly rounded, carinae low but distinct; only typical and second sulci distinct; metazona/prozona ratio 2:3. Mesosternal lobes in both sexes weakly transverse, interspace longer than broad; metasternal interspace closed. Tegmina narrow, tapering and down-curved apically; venation and reticulation sparse, intercalary vein absent (Fig. 77A). External genital structures unspecialized, as in *S. roseipennis*. Phallic structures exceptionally small. Coloration in shades of light brown and stramineous, paler dorsally. Hind wings hyaline. Hind legs color of body; tibial spines black tipped. Table 4 gives morphometric data for *exilis.*

Distribution.—Known to date only from CAMEROON and UGANDA. Quite possibly, the real distribution may be less disjunct than this suggests.

Discussion.—Similar in size to *S. roseipennis*, but more slender build, sculpturing of dorsum of pronotum and colorless wings.

Sumba punctata Uvarov, 1953

Sumba punctata Uvarov, 1953: 133, figs 145, 146.

Material.—Holotype male: ANGOLA: Moxico dist. (NHMUK).

Description.—As in Key 1. Of medium size, rather slender. Integument shiny, coarsely punctured. Antenna slightly longer than combined length of head and pronotum. Frontal ridge rather thick, not sulcate, expanded above medial ocellus. Fastigium parabolic, about as wide as long, medial carinula distinct, arcuate sulcus well behind middle. Pronotal carinae thick, callose, but lateral carinae obsolete in metazona; metazona slightly shorter than prozona, its hind angle narrowly rounded. Tegmina extend beyond hind knees, venation sparse. Coloration uniformly buff with some scattered brown dots, particularly on face; sides of head and thorax somewhat darker. Wings hyaline. Table 4 gives morphometric data for *punctata.*

Discussion.—A distinctive species only known from Angola and male holotype (females unknown).

Distribution.—Known only from locality of unique holotype. ANGOLA, Moxico distr., Upper Luena valley.

Sumba semicarinata Uvarov, 1953

Fig. 88

Sumba semicarinata Uvarov, 1953: 134, figs 147, 148.

Material.—Holotype male: D.R. CONGO: Tenke, 30.VII-9. VIII.1931 (NHMUK); 1 paratype male, same data as type series. Besides the type, material examined from the following localities: 1 female, Elisabethville, 11–17.IX.1931, J. Ogilvie; l F, Sakania, IX.1931, A.A. Mackie; 1 male, 1 female, Nasantoye, XI–XII.1927, M. Burr (NHMUK); 1 male, 1 female, Lubumbashi, Bouvy (NHMUK). TANZANIA: 13 mi. S. Biharamulo; 29 mi S. Kibondo; 20 mi. S. Uvinza; 34 mi. S. Uvinza; IX.1964, N.D. Jago (NHMUK).

Description.—As in Key 1. A distinctive species in its robust build, highly sculptured, rugose integument and broad tegmina and wings. Antennae rather narrow basally, in male slightly longer and in female shorter than combined length of head and pronotum. Frontal ridge rather broad with wavy margins; fastigial constriction weak. Fastigium parabolic, rather short, medial carinula distinct, arcuate sulcus behind middle (Fig. 88). Pronotal carinae thick, lateral irregularly wavy in prozona, obsolete in metazona; metazona slightly shorter than prozona. Tegmina extend beyond hind knee, broad, not tapering apically. Venation and reticulation very irregular. Coloration variable, ground pigment somewhat speckled in shades of brown and charcoal grey; hind femur and tibia brown, hind wings yellow basally, infumate apically. Table 4 gives morphometric data for *semicarinata.*

Distribution.—D.R. CONGO, TANZANIA, ANGOLA, ZAMBIA (Dirsh 1970).

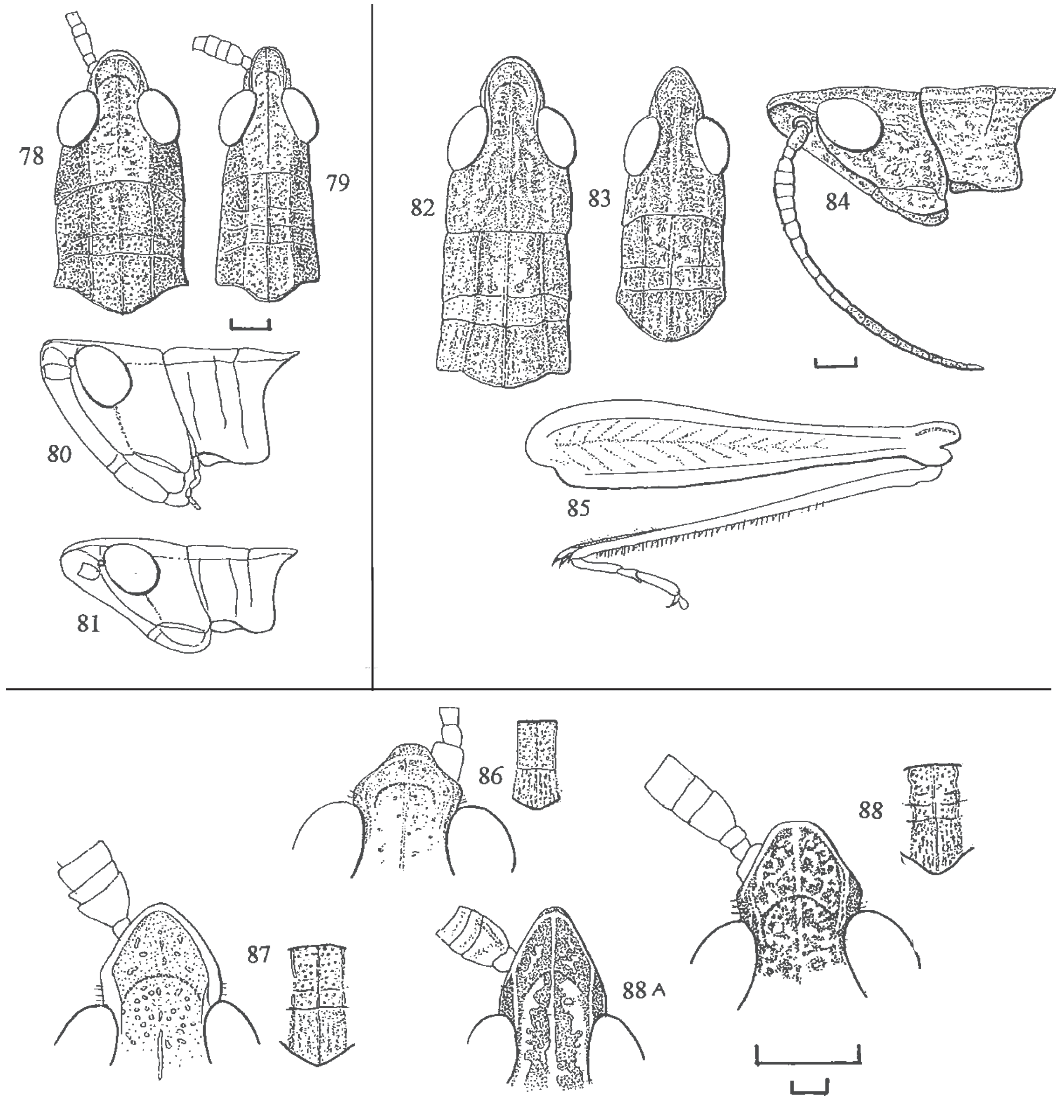
Sumba granulifera Uvarov, 1953

Fig. 87

Sumba granulifera Uvarov, 1953: 134–135, figs 149, 150.

Material.—Holotype male: ANGOLA: Villa Luso, Moxico dist. (NHMUK); 1 male, 2 females, same data as holotype; 5 females, Luchase dist.: river Lungue Bungu and river Quangu.

Description.—As in Key 1. Antennae rather wide at base and slightly shorter than combined length of head and pronotum in both sexes. Frontal ridge rather narrow, weakly expanded between antennae, fastigial constriction narrow. Fastigium as in Fig. 87, its medial carinula weak. Pronotum and head granulate, but meta-



Figs 78–88. Figs 78–85. Morphology of *Sumba* spp. **78–81.** *S. roseipennis* head and pronotum: **78.** Female holotype from above; **79.** Male topotype from above; **80.** Female holotype from left side; **81.** Male topotype from left side. **Figs 82–85.** *S. exilis*: **82.** Female paratype, head and pronotum from above; **83.** Male holotype, head and pronotum from above; **84.** Male holotype from left side; **85.** Left hind femur of male holotype. **Figs 86–88.** Morphology of fastigium verticis and pronotal disc in *Sumba* spp.: **86.** *S. callosa*; **87.** *S. granulifera*; **88.** *S. semicarinata*; **88A.** *S. exilis* (fastigium only, pronotal disc not shown). Scale lines represent 1 mm: that under Fig. 79 applies to Figs 78, 80–85 and to drawings of pronotal discs Figs 86–88; that under under Fig. 88 applies also to fastigium verticis depicted in Figs 86–88, 88A.

zona longitudinally rugulose. Medial carina sharp, lateral carinae irregular in prozona, obsolescent in metazona. Tegmina broad, with very dense reticulation. Wings broad, with three anterior sectors produced and rounded apically. Genital structures of typical *Sumba* type, without specialized features. General coloration reddish-ochraceous to brownish. Antennae blackish. In some female specimens abdominal tergites have alternating broad dark and narrow light bands. Wings bright rose (ANGOLA) to vermilion (D.R. CONGO: Katanga), lightly infumate apically. Some specimens from burnt areas are dark brown with brighter colored wings Table 4 gives morphometric data for *granulifera.*

Discussion.—Similar morphologically to *Panzia uvarovi* Miller but lacking specialized venation of latter. Generally larger and more robust than other *Sumba* species and distinctive in the peculiar granular sculpturing of its integument and the dense reticulation of the tegmina.

Distribution.—D.R. CONGO: Katanga, ANGOLA, ZAMBIA: Mbala, Kafue river at Chingola and Kabundi forest at Chingola. The habitat was given as grassland, some burnt, and *Brachystegia-Isoberlinia* woodland (Johnsen 1984).

Sumba callosa **(Uvarov, 1953), comb. n.**

Figs 77, 86

Rhabdoplea callosa Uvarov, 1953: 141–142, figs 169–171.

Material.—Holotype male: ANGOLA: Moxico dist. river Munhango. (NHMUK). Type series including holotype 2 males ANGOLA, Moxico district, Munhango river, VIII; 1 male, 4 females, Villa Luso, V; 1 female, middle Luena river, V; 1 male, Langiliko river, VI; 3 males, 4 females, Mu-Simoj river, IX–X; 3 males, 2 females, Bihe district, Cohemba, VIII; 9 males, 10 females, Luchase dist., Quangu river, 5000′ (1524m), X. 1 male, 1 female, D.R. CONGO: Katanga (as Shaba) province, river Lubudi, XI.

Description.—As in Key 1. A distinctive species recognizable by its very short fastigium (Fig. 86) and round, bulging eyes. Of medium size, integument rugose. Antennae slightly longer than head and pronotum together, weakly expanded and flattened at base. Frons convex in profile, practically parallel-sided with wavy margins; fastigial constriction very weak. Fastigium very broad and short. Eyes round, large, bulging. Pronotum weakly tectiform, its surface callose and rugose; medial carina smooth, lateral carinae callose and parallel in prozona, weaker and feebly divergent in metazona. Lateral lobes deeper than long, lower margin sinuate. Tegminal apices extend beyond hind knees of folded posterior femora. Venation fairly dense with incomplete false veins (Fig. 77). Coloration mottled reddish chocolate-brown and ivory-white with brown spots. Hind femur reddish-brown with blackish dots, knee blackish. Hind tibia dirty brown with black spines.

Wings infumate, sometimes rose at base. Table 4 gives morphometric data for *callosa.*

Discussion.—This species and *S. granulifera* Uvarov, 1953 form a bridge morphologically between *Sumba* and *Panzia*.

Distribution.—ANGOLA, D.R. CONGO.

Editorial comment.—Johnsen 1984: 307 suggested that *Rhabdoplea callosa* might be synonymous with *Sumba roseipennis*, thus foreshadowing Popov's transfer to the latter genus.

Generic diagnosis

Rhabdoplea Karsch, 1893

Rhabdoplea Karsch 1893: 54, 69.

Type species.—*Rhabdoplea munda* Karsch, 1893: 70, designated by Kirby, 1910: 147.

Description.—Rather wide frontal ridge, with well-defined margins and very weak fastigial constriction; parabolic fastigium with sharp margins and carinulae and arcuate sulcus behind middle. Pronotal sculpturing distinctive, including well-defined parallel lateral carinae and longitudinal callose striations. Micropterous and macropterous forms occur; latter with rather narrow tegmina and wings with loose venation and reticulation, plus presence of a distinct intercalary vein in medial field of tegmina. Epiphallus has rather short lophi, with elongate outer lobes (Fig. 64).

Discussion.—*Rhabdoplea s. str.* now contains only the widespread *R. munda* Karsch, 1893, and the closely related *R. angusticornis* Uvarov, 1953 (ANGOLA). They share the same characteristic structure and sculpturing of pronotum and tegminal morphology described above. The medial field of the tegmina has a more transparent membrane and a rather looser reticulation than is usually found in *Sumba* spp.

Species notes

Rhabdoplea munda Karsch, 1893

Figs 21, 64

Rhabdoplea munda Karsch, 1893.
Rhabdoplea angustula Karsch, 1893 (syn. Dirsh 1970).
Rhabdoplea elegans (Karny, 1907) (syn. Dirsh 1966).
Rhabdoplea klaptoczi (Karny, 1915) (syn. Descamps & Donskoff 1968).
Rhabdoplea mira Karsch, 1893 (syn. Descamps & Donskoff 1968).

Material.—Male and female types: TOGO: Bismarckburg, (MfN, Berlin). Other specimens (*including micropterous insects): ETHIOPIA: Lake Zwai. SOUTH SUDAN: nr. Juba. UGANDA: *Kepeka, *Bulumezi, *Nakasongola, *Buddu Kakuto, *Luwero, Lango; Bwamba; Karamoja; Bugoma Forest; Adachal; Dokolo; Hoima. TANZANIA: Morogoro; Rukwa valley; Kafukola; Old Shinyanga; 30 mi. N. of Kahama.

Description.—*R. munda*, by comparison with *R. angusticornis*, has antennae somewhat shorter and broader; proportionally longer pronotal metazona; prozona/metazona ratio in *R. munda* is 1.3 (*angusticornis* 1.8); hind margin of metazona convex (straight in *angusticornis*); is micropterous, or macropterous (*angusticornis* always micropterous). General coloration in shades of light brown to stramineous, with or without some darker speckling or striation. Narrow, pale, more or less distinct band present along lower side of genae and lateral pronotal lobes; dorsum and underside generally paler. Darker shades of brown may occur in micropterous form, with the dorsum light brown and sides dark brown; narrow lateral yellowish-white band is particularly contrasting, and hind femora are rusty-orange with dark knees. Table 5 gives morphometric data for *R. munda.*

Discussion.—*R. munda* Karsch, 1893 and *R. angusticornis* Uvarov, 1953 are very similar in appearance. *R. munda* in macropterous form has wings extending well beyond the tip of the abdomen and the hind knees; in the micropterous form the wings are dorso-lateral, well separated dorsally, varying in shape, being scale-like, or attenuate, but seldom extending beyond the middle of the abdomen.

Distribution.—*R. munda* is a widespread species, found in grasslands from western Africa to ETHIOPIA, eastern, central and southern Africa.

Rhabdoplea angusticornis Uvarov, 1953

Rhabdoplea angusticornis Uvarov, 1953: 139, figs 166–168.

Material.—Holotype female: ANGOLA: Moxico and Bihe distr., Upper Luena River (NHMUK).

Description.—Differs from *R. munda* in narrower, longer antennae and in shorter metazona of pronotum with a straighter hind margin (for further details see under *munda*). Coloration as in the brachypterous form of *munda*. Micropterous. Table 5 (p. 57) gives morphometric data for *R. angusticornis*.

Table 5. Measurements of *Rhabdoplea* spp.

	munda (mm)		*angusticornis* (mm)	
	M	F	M	F
Antennal length	6	6	8.2	7.0
Antennal width	0.2	0.2	0.2	0.2
Pronotal length	3	3.5	3	3.6–4.0
Tegminal length	13.8	14	Other measurements as in *R. munda* (macropterous form)	
Tegminal width	2	2		
Tegminal length/width ratio	7	7		
Hind femur length	9.3	11.2		
Hind femur depth	2.3	2.6		

Discussion.—Nothing published on its bionomics, but likely to be similar to *R. munda*.

Distribution.—ANGOLA, CONGO REP. (Descamps and Donskoff 1968), RWANDA (Dirsh 1970), ZAMBIA (Johnsen 1984).

Generic diagnosis

Panzia Miller, 1929

Panzia Miller, 1929: 68.

Type species.—*Panzia uvarovi* Miller, 1929: 68, by monotypy and original designation.

Material.—Holotype male: TANZANIA: Kalula (NHMUK).

Description.—As for genus. Tegmen with broad, rounded tip, opaque membrane and dense reticulation; wing broadly rounded, with sparse reticulation and regularly spaced, strongly serrated transverse veinlets of dark apical fascia (Fig. 76). Integument rugose and tuberculate. Antennae shorter than combined length of head and pronotum in both sexes (Fig. 75); moderately ensiform basally. Frontal ridge narrow, deeply sulcate, with well defined, irregularly wavy margins and very narrow fastigial constriction. Fastigium triangular, rounded apically, about as long as wide. Pronotum relatively narrow, median carina strong; lateral carinae weak and irregular in prozona, indistinct in metazona. Metazona subequal to prozona, its hind margin obtuse angular. Mesosternal lobes quadrate with rounded angles.

Discussion.—Genital structures in *Panzia* closely resemble those of *Sumba*.

Species notes

Panzia uvarovi Miller, 1929

Figs 75, 76

Panzia uvarovi Miller, 1929: 68, pl.5 f.2; pl.9 f.39, 40.

Material.—Holotype male: TANZANIA: Kalula, 60 km S. of Tabora (NHMUK).

Description.—As for the genus. Phallic structures as in *Sumba*. Coloration uniform pinkish-brown or brownish, without any notable markings, but occasionally with a narrow medial longitudinal dorsal stripe. Hind wings bright lemon-yellow to orange with a broad outer dark fascia. Measurements in Table 6.

Table 6. Morphometric measurements of *Panzia uvarovi*.

	M (mm)	F (mm)
Antennal length	6.5–7.2	7.5
Antennal max. width	0.7–0.8	0.7
Pronotal length	3.3	3.8
Prozona/metazona ratio	1.1	1.1
Tegminal length	16.5	17
Tegminal width	2.8	3
Tegminal length/width ratio	1.76	1.8
Hind femur length	10.5	11.6
Hind femur depth	2.5	2.6
Hind femur length to depth ratio	4.2	4.5
Total length	18.0–20.0	21.0–23.0

Distribution.—Apparently highly localized in central TANZANIA. Also in ZAMBIA (Kafue National Park).

Genus sub-group diagnosis

Ocnocerus-Hyperocnocerus-Anacteana (gen. n.) genus sub-group

Description.—Separated from the *Sumba-Rhabdoplea-Panzia* genus sub-group chiefly on the basis of antennal morphology. In *Ocnocerus* and *Hyperocnocerus* the antennae are strongly shortened, and clearly divided into basal, medial and terminal portions, each with differing morphology of the flagellar segments.

Generic diagnosis

Ocnocerus I. Bolívar, 1889

Ocnocerus I. Bolívar, 1889: 89.

Type species.—*Ocnocerus bayaoi* I. Bolívar, 1889: 99, pl. 1, f. 4, 4a, by original designation.

Description.—See key to *Ocnocerus* genus group, p. 50.

Discussion.—The genus includes two species, only one of which is East African. Details are given below.

Key to species of *Ocnocerus* I. Bolívar, 1889

1 Antennae much shorter than head and pronotum, the basal flagellar segments strongly widened. Fastigium short and rounded ....*diabolicus* Karsch, 1893

– Antennae about as long as head and pronotum together, and basal flagellar segments only slightly widened. Fastigium relatively long and angular .... *bayaoi* I. Bolívar, 1889

Species notes

Ocnocerus bayaoi I. Bolívar, 1889

Ocnocerus bayaoi I. Bolívar, 1889.
Ocnocerus burri Kevan, 1955 (syn. Dirsh 1966).

Material.—Holotype male *bayaoi*: ANGOLA: Duque de Bragança (original type lost); neotype chosen by Dirsh (1966). Holotype male *burri* Kevan, 1955: 74: ANGOLA: Villa Luso (NHMUK). Synonymized by Dirsh (1966): 378, who designated the neotype for the species.

Distribution.—ANGOLA: In addition to the type localities, also recorded from: Moxico Dist. and Bihe Dist. (Uvarov 1953); Dundo; Xa-Ua, R. Luita, Cuilo; Zovo, Mabete, Caungula; Roure Dondo Sombo; Alto Chicapa; Lunda; Kalakembe; Shukote (Dirsh 1966).

Ocnocerus diabolicus Karsch, 1893

Fig. 74

Ocnocerus diabolicus Karsch, 1893: 63, 64, fig. 5.

Material.—Holotype female: TOGO: Bismarckburg (MfN, Berlin).

Description.—Smaller, and comparatively more slender, than *O. bayaoi*, with shorter and wider antennae (Fig. 74).

Distribution.—West Africa: all countries from SENEGAL to NIGERIA, and Northern UGANDA (Arua, Adjumani, Acholi and Karamoja) in grassland savannas.

Generic diagnosis

Hyperocnocerus Uvarov, 1953

Type species.—*Ocnocerus sulculatus* Karsch, 1893, by original designation (Uvarov 1953:138).

Material.—Holotype male: TOGO: Bismarckburg.

Description.—See key to *Ocnocerus* genus group, p. 50. Similar to *Ocnocerus*, but antennae even shorter and more profoundly modified.

Species notes

Hyperocnocerus sulculatus (Karsch, 1893) (Uvarov 1953: 138)

Hyperocnocerus angolensis Uvarov, 1953: 139, figs 163–165.

Material.—Holotype male, ANGOLA: Moxico dist. Villa Luso (NHMUK), (synonymized by Dirsh 1970: 421).

Description.—Antennae illustrated (Fig. 73).

Discussion.—A rare but very distinctive species, with disjunct distribution. Found in clearings in wooded grassland habitats.

Distribution.—TOGO, GHANA, ZAMBIA, ANGOLA: Route Dundo-Sombo; Cassa; Lovua; Xa-Ua, R. Luita, Cuilo. D.R. CONGO: Kalemie (05°56′S, 29°12′ E), xii; Katanga (as Shaba): Mujiaie, vii; Lulua: Kapanga (06°37′S 170 20′E) viii; Kasai: Kamonia (06°52′S, 20°56′E); Parc National de Garamba. UGANDA: Zoka Forest, Adjumani.

Generic diagnosis

Anacteana gen. n.

http://zoobank.org/5E9B98C8-1965-4491-9B3F-39B392D6980C

Figs 89–96

Type species.—*Acteana neavei* I. Bolívar, 1912: 79, here designated (NHMUK).

Description.—Similar to *Acteana* in size and general appearance, but more robust. Integument as in *Acteana*. Antennae shorter than the combined length of head and pronotum. Pronotum straight, or weakly convex in profile; medial carina low, lateral carinae weak; hind margin broadly rounded with a small medial indentation. Mesosternal lobes as in *Acteana*, with broadly rounded angles, quadrate, or transverse in female. Metasternal interspace in both sexes narrow or closed. Tegmina lateral, scale-like, as in *Acteana*, but much broader, up to half the total length. Genital structures characteristic of *Ocnocerus* genus group: epiphallus with well developed ancorae (Figs 90, 91, 96).

Discussion.—On the basis of its genital structures the new genus *Anacteana* clearly belongs to the *Ocnocerus* genus group, while *Acteana*, despite its superficial resemblance, must be regarded as a member of the *Parga* genus group. The two genera may be differentiated as follows:

1 Tegmina narrow, about five times longer than wide. Metasternal interspace wide (Fig. 67); hind margin of pronotum shallowly excised; epiphallus without ancorae (Fig. 31) ....*Acteana* Karsch, 1893
– Tegmina broad, about twice as long as wide. Metasternal interspace narrow (Fig. 68); pronotum with only a small excision; epiphallus with well-developed ancorae (Figs 90, 91, 96) .... *Anacteana* **gen. n**.

A. neavei I. Bolívar, 1912, formerly attributed to *Acteana*, is now removed to the new genus *Anacteana*, erected here to accommodate the typical *neavei* recorded from its type locality in the Katanga province of D.R. Congo, to the Ufipa-Rukwa area of Tanzania and the adjacent Lungu area of Zambia, together with *A. neavei burtti* (**subsp. n.**) and *A. hollisi* (**sp. n.**) described here. *A. neavei burtti* occurs in a broad belt across central Tanzania from around Kilosa to Tabora and Kahama, whilst *A. hollisi* is recorded from the Gabela area of western Angola.

While in their size, rugosity, robust build and micropterism, the two species are superficially alike, they differ markedly in a number of structural features, as given in the keys and the diagnoses.

Key to species and subspecies in the genus *Anacteana*

1 Head and pronotum as in Fig. 89, genital structures as in Fig. 90. W. ANGOLA .... *A. hollisi* **sp. n.**
– Not as above 2
2 Smaller (male 13–15 mm, female 15–20 mm); antennae shorter and more dentate. Genital structures as in Fig. 91. C. TANZANIA: Kilosa-Singida-Tabora-Kahama-Shinyanga areas ....*A. neavei burtti* **subsp. n.**
– Larger (male 14–15.5 mm, female 16–21 mm), antennae longer and less dentate. Head and pronotum (M) in side view (Fig. 95). Genital structures as in Fig. 96. TANZANIA: Ufipa, Rukwa areas. ZAMBIA: Mweru. D.R. CONGO: Katanga... .... *A. neavei neavei* (I. Bolívar), **stat. n.**

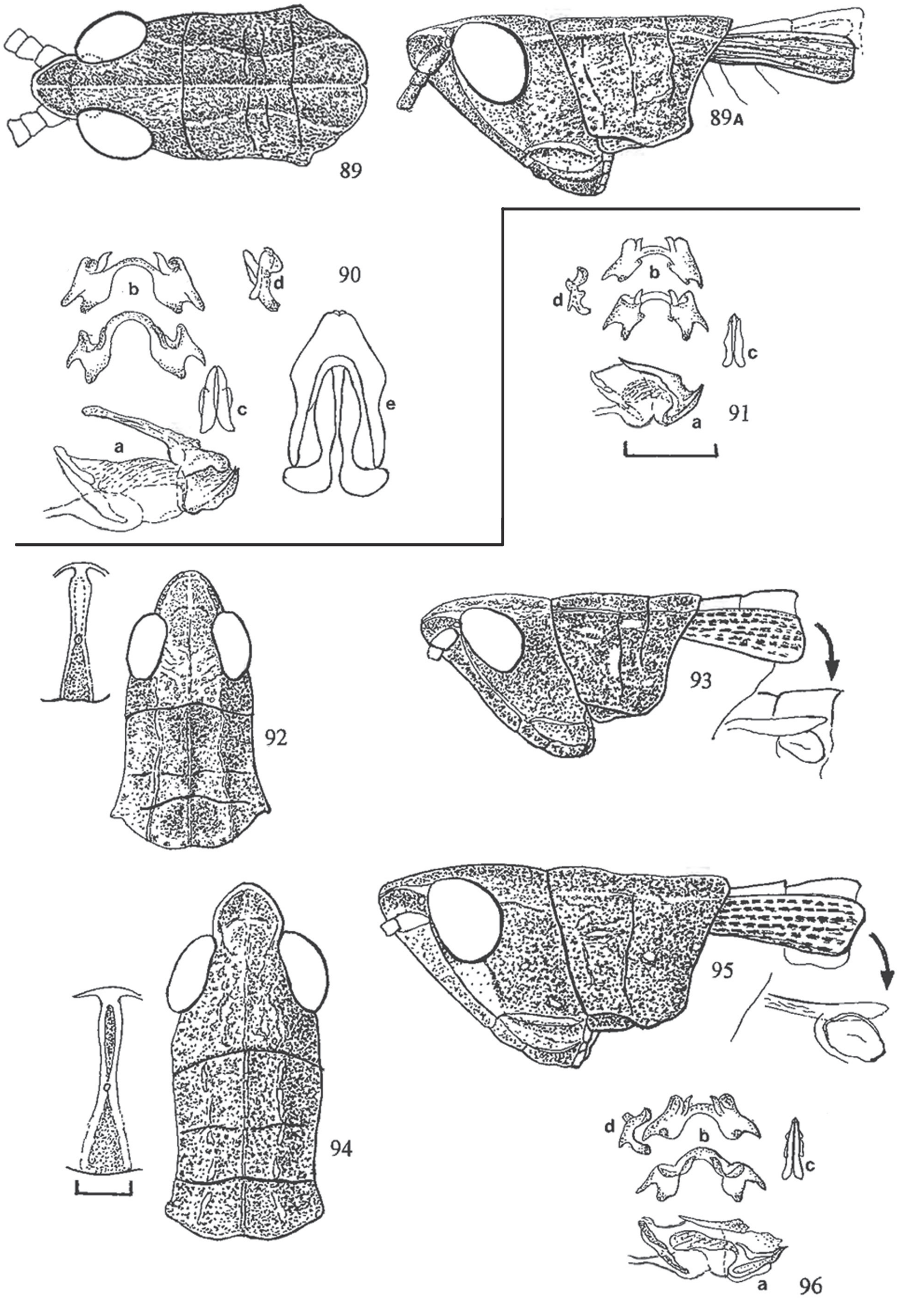
Species notes

Anacteana neavei (I. Bolívar, 1912), comb. n.

Type species.—*Acteana neavei* I. Bolívar, 1912 here designated.

Material.—Holotype female: D.R. CONGO (as Congo Belge): Bunkeya-Lukafu (MRAC, Tervuren).

Description.—See below, under nominate subspecies.



Figs 89–96. *Anacteana* spp. morphology. (See also Fig. 68). **Figs 89–90.** *A. hollisi:* **89.** Dorsal aspect head and pronotum; **89A.** Lateral aspect head and pronotum; **90.** Male phallic morphology: **A.** Phallic complex from left side, epiphallus removed; **B.** Epiphallus from two aspects (upper fig. from plane of lophi, lower fig. from vertical to lophi); **C.** Aedeagal valves from ventral aspect; **D.** Epiphallus from right side; **E.** Phallic complex from dorsal aspect, epiphallus removed; **Figs 91–93.** *A. neavei burtti*: **91.** Male phallic morphology (explanation for lettering A–E. as for Fig. 90); **92.** Dorsal aspect head and pronotum and frontal ridge; **93.** Lateral aspect left side, head and pronotum; **Figs 94–96.** *A. neavei neavei* **94.** Dorsal aspect head and pronotum and frontal ridge; **95.** Lateral aspect left side, head and pronotum; **96.** Phallic morphology. All scale lines represent 1 mm: scale under Fig. 91 applies to Figs 90, 91, 96; scale under Fig. 94 applies to Figs 89–95, including frontal ridge and tympanic membranes. Arrowed insets to right of Figs 93 and 95 show size of hindwings and tympana concealed by tegmina.

Discussion.—Synonymies and references are given in the key and under the subspecies. This is a widespread species recorded from many localities in an area extending from north-central Tanzania to northwestern Zambia and the Katanga province of D.R. Congo. As might be expected from its micropterism and limited vagility, there is considerable geographical variation. The smaller, more slender specimens with the shortest, most dentate antennae are from Shinyanga-Kahama, and the bulkiest, with the longer, smoother and more slender antennae, are from the Ufipa-Katanga areas. At their extremes of variation, the two are sufficiently distinct to be regarded as separate species, but given the occurrence of intermediate forms, it is preferable to regard them as subspecies of *neavei*, with the typical subspecies at the southwestern and *A. n. burtti* subsp. n., named after its collector the late Eric Burtt, at the northeastern end of the range. The southern highlands of Tanzania appear to form a barrier between them.

Anacteana neavei neavei (I. Bolívar, 1912), stat. n.

Figs 68, 69–72, 94–96

Acteana neavei I. Bolívar, 1912: 79; Dirsh (1966: 38, fig. 194); Dirsh (1970: 421–2); Johnsen (1984: 302–304, figs 266A, B).

Material.—Besides Holotype – D.R. CONGO (as CONGO Belge): Bunkeya-Lukafu, (Shelford Neave) (MRAC, Tervuren). TANZANIA: 1 male, 1 female Ufipa, 17–18.xi.1963, D. Vesey-Fitzgerald, (NHMUK); ZAMBIA: 3 females, Abercorn, 30.i.1962, D.V-Fitzgerald; Mporokose Dist, Mweru wa Ntipa, 3 males, 2 females, 8–13. vii.1952; 5 males, 3 females, 20.X.1957; l male, l female, shore of Lake Tanganyika 1942, E. Burtt (NHMUK); 1 male, 2 mi. E. of Abercorn, in dry Miombo woodland, 7.X.1964; 2 males, 1 female, env. of Kalambo falls, N. of Abercorn, Miombo woodland, 4.X.1964, N.D. Jago (NHMUK). ZAMBIA (cited by Johnsen (1984: 302–304)): Chingola, Kabundi forest, in grassland within *Brachystegia-Isoberlinia* woodland, adults: VI, X & XII 1952; 5 males, 3 females, 20. x.19S7; 1 male, 2 mi. E. of Mbala (as Abercorn), in dry Miombo woodland, 7.x. 1964; 2 males, 1 female, env. of Kalambo falls N. of Mbala (as Abercorn), Miombo woodland, 4.X.1964, N.D. Jago (NHMUK).

Description.—Comparatively stout, integument finely and uniformly rugulose. Antenna as in Figs 69–72. Head and pronotum as in Fig. 95; frons straight in profile. Pronotum weakly inflated in the middle; carinae low, thick and indistinct; prozona/metazona ratio 2.0–2.3 (Fig. 94); sternal plates as in Figs 68C, D. Tegmen parallel-sided with rounded apex, 1.5–2x as long as wide. Hind femur moderately robust. Genital structures as in Fig. 96, structure of epiphallus and spermatheca are particularly diagnostic. Coloration predominantly in shades of ochraceous; dorsum and sides of head and thorax, including tegmina and hind tibiae darker, and the underside and the lower sulcus of hind femur of a lighter hue; tibial spines tipped black. Otherwise no distinctive markings.

Females more uniformly colored than males.

Measurements.—In Table 7 (p. 61).

Distribution.—Cited by Johnsen (1984) (p. 302–304): ZAMBIA: Chingola, Kabundi forest, in grassland within *Brachystegia-Isoberlina* woodland, adults: V–IX & XII. In Katanga Province of D.R. CONGO, it differs somewhat from specimens in northern ZAMBIA and the adjacent parts of TANZANIA (ca. 8°10′ S, 31°33′ E) particularly in its smaller size (17.5 mm vs. 18–22 mm) and shorter and broader tegmina (length-width ratio 1.5 vs. 2.1). However, such differences are also found in the other subspecies and in the absence of adequate material, taxonomic distinction is not required.

Anacteana neavei burtti subsp. n.

Figs 91–93

Material.—Holotype male: TANZANIA: Shinyanga, 5.xii.1947, E. Burtt (NHMUK). Paratypes: 5 males, 6 females, same data as the type; 6 males, 5 females, Shinyanga district, Tinde, ii.1945; 4 males, 5 females, Old Shinyanga, 25.XI.1950; 4 males, 5 females, Old Shinyanga, 25.XI.1950; 1 male, ditto, 22.VIII.1953; 1 female, ditto, 3.I.1959; 1 female, ditto, Block XI, 9.xii.1949; 1 male, 17 females, Ushorombo Road, 15 and 22 mi. W. Kahama, X, XI & XII, II. 1946–1948; 3 females, Mshugha, 35 mi. S.E. of Singida, 17. XII.1936; 1 female, Singida, 14 mi. N. of Kahama, 10. VIII.1953; l male, l female, Mpwapwa Mt. Wilkins 5500′ [06°23′S, 36°38′E], 26.XI.1948; 1 male, 2 females, Mpwapwa, 29. XI.1948; l male, Kibariani, 3.XII.1948 (all E. Burtt); l male, Galata Station, 60 mi. W. of Amani [09°05′S, 38°36′E], 17.VII.1937; l female, Lake Rukwa, 1949, G. Burnett (Paratypes: NHMUK; MRAC Tervuren; MNHN Paris).

Description.—Differs from the nominate subspecies in more slender build and, in the Shinyanga populations in particular, in smaller size. Antennae generally shorter and more dentate. Pronotum less inflated, with sharper, more distinct carinae (Figs 92, 93). The sternal plates, tegmina and genital structures (Fig. 91) also exhibit some differences from those in *A. n. neavei*. Coloration variable in shades of ochraceous, grey and darker charcoal-grey. There is often a broad, pale ochraceous dorsal stripe, particularly in males; the females are generally more uniformly colored. The underside is pale brownish, or fawn, often with fine dark speckling; lower sulcus of hind femur yellowish, tibiae dark-brown, spines tipped blackish-brown.

Measurements.—In Table 7.

Distribution.—N., C., and W. TANZANIA.

Anacteana hollisi sp. n.

http://zoobank.org/28D22555-4D31-41C9-BF10-9573ABD96048

Figs 89, 89A, 90

Material.—Holotype male: ANGOLA: 7 mi. W. Gabela [11.00′S, 14.30′E], 16–18.iii.1972, South African Exp. BM 1972; 2 female paratypes, same data as the Type (NHMUK).

Description.—Similar in size, but more slender than *A. n. neavei* and closer in general appearance to the larger specimens *of A. n. burtti* from Singida and Mpwapwa. Sculpturing of integument as in *neavei*. Antennae proportionately longer and less dentate than in *neavei*, equal in male and subequal in female to the combined length of head and pronotum. Dorsum of pronotum relatively narrow (Fig. 89), carinae low and thick, but distinct, lateral ones somewhat inflexed in middle; three transverse sulci distinct, metazona more than half length of prozona, its hind margin broadly rounded, medial indentation very weak in male, indistinct in female. Tegmina as in Fig. 89A. Mesosternal interspace narrower than lobe in male, quadrate in female. Hind femur slightly slenderer than in *neavei*—length/width ratio 3.7 vs. 3.2. External and internal genital structures as in Fig. 90; shapes of epiphallus and spermatheca are particularly distinctive. Coloration cryptic in shades of grey and brownish, very similar to that of *A. n. burtti*. No distinctive markings. Measurements in Table 7.

Table 7. Measurements of *Anacteana* spp.

	n. neavi (mm)		*n. burtti* (mm)		*hollisi* (mm)	
	M	F	M	F	M	F
Antennal length	5.5–6.3	5.5–7.0	4.2–5.4	3.8–4.2	7.4	5.4
Pronotal length	3.6–3.8	4.2–4.4	2.8–3.0	3.5–4.2	3.7	4.4
Prozona/metazona ratio	2.1	2.1	2.08	2.07	1.47	1.6
Tegminal length	2.8	3.2–3.4	2.02	2.8–3.6	2.8	3.7
Tegminal width	1.3	1.5–1.6	1.1	1.3–1.5	1.1	1.7
Tegminal Length/ width ratio	2.15	2.13	3.12	2.3	2.5	2.2
Hind femur length	9.5–10.5	11.5–12.5	7.2–7.8	8.5–10.2	9.1	10.7
Hind femur depth	2.8–3.1	3.7–4.0	2.2–2.6	3.0–3.4	2.4	3.1
Hind femur length to depth ratio	#	#	3.1	2.9	3.7	3.4
Total length	15.0–16.5	17.5–22.0	13.0–15.0	16.0–20.0	15.5	22

= single ratio cannot be calculated

Genus group diagnosis

The *Duronia* genus group

Description.—Besides characteristics of male (Figs 19, 20, 97) and female (Fig. 98) genitalia, the included genera share the following characters: size medium or smaller; integument finely rugose; antennae narrowly ensiform, equal to shorter than length of head and pronotum; frontal ridge broad, sulcate, with thick margins, more or less constricted at junction with fastigium; apex of head conical, more or less pointed, fastigial foveolae absent; pronotum weakly tectiform, dorsum more or less flat, carinae strong, length of metazona equal or subequal to that of prozona, its hind angle obtuse-angular; tegmina and wings fully developed, reticulation dense, intercalary vein in medial area absent; hind femur of slender to medium build, knee lobes of equal length, outer rounded, inner acute; abdominal appendages simple, unspecialized in both sexes.

Discussion.—This group includes only four genera: *Duronia* Stål, 1876 (type species *chloronota* Stål, 1876); *Duroniella* I. Bolívar, 1908a (type species *fracta* Krauss, 1890); *Leopardia* Baccetti, 1985 (type species *bivittata* Baccetti, 1985); and *Oxyduronia* **gen. n.** (type sp. *anablepioides* **sp. n.** here described). Its position relative to other tribes and species groups is considered on p. 41. In their species composition and geographical distribution, the four genera vary considerably: *Duronia* contains just one variable widespread species recorded throughout Africa south of the Sahara, S.W. Arabia, and Madagascar; *Duroniella* contains over a dozen closely related species (some possibly synonyms), which occur in a wide belt across the southern Palaearctic and the adjacent part of Eremian zone from Mauritania and North Africa to the Near East, Central Asia to China; the two remaining genera are monotypic East African endemics of very limited distribution: *Leopardia* in southern Somalia and northern Kenya, and *Oxyduronia* **gen. n.** in S.W. Tanzania and N. Malawi.

Key to genera in the *Duronia* genus group

1 Larger; males >20mm, females >30mm .... *Duronia* Stål, 1876

– Smaller; males mostly <20mm, females <30mm 2

2 Lateral pronotal carinae straight or weakly excurved, parallel; arolia large 3

– Lateral carinae wavy in prozona, divergent in metazona, arolia very small (Fig. 113) .... *Duroniella* I. Bolívar, 1908a

3 Compound eye small, measured vertically smaller than sub-ocular distance. Fastigium acutely pointed (Figs 99, 100) frontal ridge at junction with fastigium strongly narrowed (Fig. 104); pronotal carinae acutely raised .... *Oxyduronia* gen. n.

– Compound eye larger, measured vertically equal to or larger than sub-ocular distance (Figs 101, 102). Fastigium parabolic; frontal ridge at junction with fastigium not strongly narrowed (Fig. 103); pronotal carinae not sharply raised.............. *Leopardia* Baccetti, 1985

Generic diagnosis

Duronia Stål, 1876

Duronia Stål, 1876: 21.

Type species.—Phlaeoba (Duronia) chloronota Stål, 1876: 48 by original designation. *Rodunia* I. Bolívar, 1908a: 99 (syn. Uvarov 1953). Type species: *Phlaeoba chloronota* Stål, 1876, by original designation I. Bolívar 1908a: 100, footnote.

Description.—See genus group diagnosis and key (this page).

Discussion.—Uvarov (1953) clarified much of the hitherto existing confusion and established the generic synonymy as above. He then listed eight currently valid species attributed to the genus. Of these, *D. sanguinolenta* (I. Bolívar, 1889) was dubious since the original type is lost. Six African species were keyed; one of them, *D. curta* Uvarov, 1953, was described as new. A later revision by Dirsh (1962) reduced the eight species to two (the type for the genus *Duronia chloronota* Stål, 1876, and *D. curta* Uvarov, 1953). The rest, including the Madagascan *D. faeta* (I. Bolívar, 1890), were reduced to synonyms of *D. chloronota*.

A study of genitalia of both the sexes in a large number of specimens broadly confirms Dirsh's conclusion that *Duronia* is represented throughout its vast distribution area (including much of Africa south of the Sahara, Madagascar, and S.W. Arabia), by one variable species, *D. chloronota* Stål. Even the Madagascan populations do not differ markedly. Only in southern Africa is there sufficient differentiation to suggest subspecific status (hitherto described as *D. curta* Uvarov). Likewise, specimens from Kasewe Forest Reserve in Sierra Leone comprise individuals of very large size, with expanded, somewhat inflated pronota and basally yellow hind wings with infumate apices. These are described here as *Duronia c. curta* and *D. c. phippsi* **subsp. n.**, respectively (the latter dedicated to its collector, the well-known entomologist-acridologist, the late John Phipps).

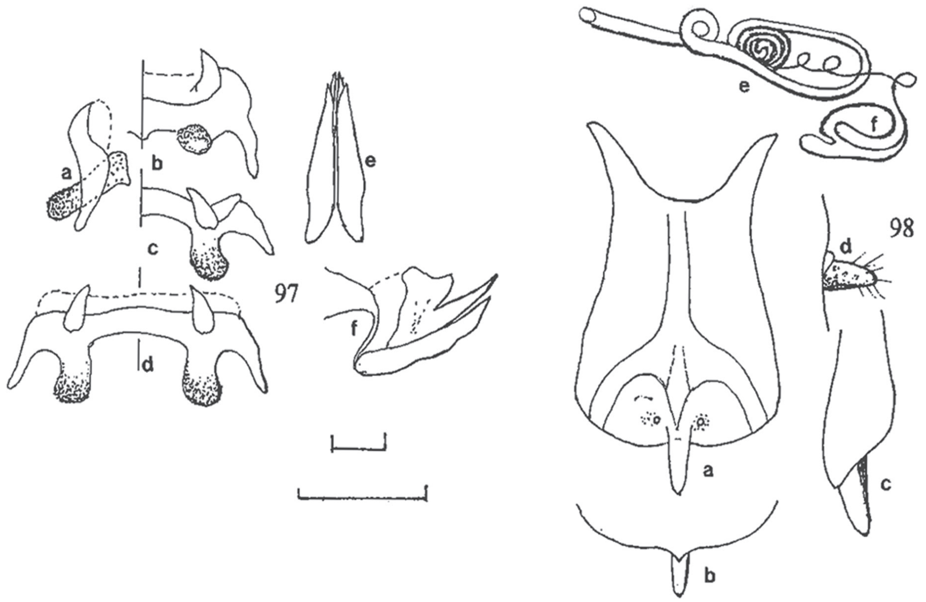
Species notes

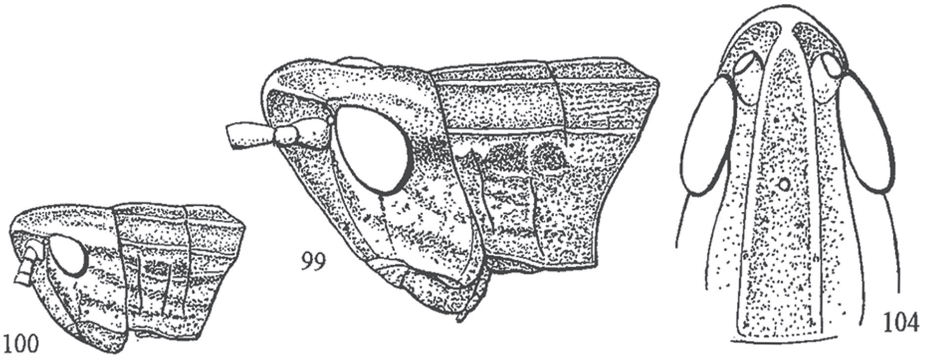
Duronia chloronota (Stål, 1876)

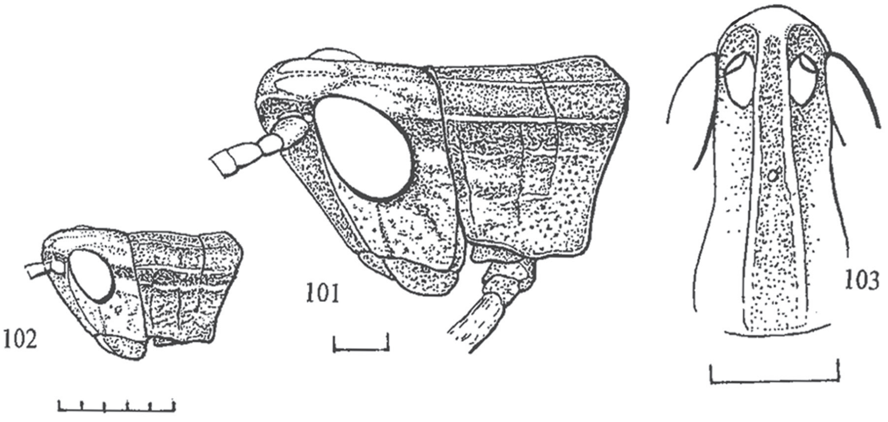
Phlaeoba (Duronia) chloronota Stål, 1876: 48.
Phlaeoba viridula var. liturata I. Bolívar, 1889 (syn. Dirsh 1962).
Phlaeoba laeta I. Bolívar, 1890 (syn. Dirsh 1963).
Phlaeoba tricolor Karny, 1907 (syn. Dirsh 1962).
Rodunia acuminata I. Bolívar, 1912 (syn. Dirsh 1962).
Duronia victoriana Rehn, 1914, (syn. Dirsh 1962).

Material.—Included are all the types studied by Dirsh, and also the abundant material in NHMUK collection acquired since that time.

Description.—For diagnosis see under nominate subspecies.







Figs 97–104. *Duronia* genus group. **Figs 97–98.** *Duronia chloronota phippsi* **n. subsp**.: **97.** Male genitalic structures: **A–D.** Epiphallus, **A.** Laterally, **B–D.** Dorsally and dorso-posteriorly (**B–C.** Right half only); **E–F.** Aedeagal valves ventrally and laterally from right side, respectively. **98.** Female genitalic structures: **A.** Subgenital plate dorsally; **B.** Apex of same ventrally; **C.** Idem, laterally from right side; **D.** Cercus; **E.** Spermathecal duct; and **F.** Spermatheca. **Figs 99, 100, 104.** *Oxyduronia anablepioides* **gen.n. et sp.n**. **99–100.** Oblique aspect of head and pronotum; **99.** Male from left side; **100.** Female from left side; **104.** Male frontal ridge. **Figs 101–103.** *Leopardia bivittata* Baccetti. **101, 102.** Oblique aspect of head and pronotum. **101.** Male from left side; **102.** Female from left side; **103.** Male frontal ridge. All scale lines under Figs 97, 101, and 103 represent 1 mm – lowermost scale applies to Figs 97 A–F, the uppermost to Figs 98 A–E; that below Fig. 101 applies also to Fig. 99; that below Fig. 103 also applies to Fig. 104. Scale under Fig. 102 represents 5 mm and applies also to Fig. 100.

Duronia chloronota chloronota (Stål, 1876)

Material.—Syntype and long series of material lodged at NHMUK, London.

Description.—Diagnosis as for genus group. Size (in mm): total length, male 20–30, female 28–44. Integument finely rugose. Antenna ensiform, somewhat shorter than combined length of head and pronotum. Head conical, face oblique, straight, or broadly convex; variable even in same locality. Fastigium parabolic with fine medial and lateral carinulae. Frontal ridge sulcate with high carinulae diverging downwards. Dorsum of pronotum flat, wide, with sharp strong carinae; lateral carinae straight, parallel, or slightly divergent backwards; only posterior sulcus crossing dorsum, metazona slightly shorter than prozona, its posterior margin obtuse-angular. Male genital structures as in Fig. 97 (*D. c. phippsi*). Coloration extremely variable in shades of dark to light-brown and stramineous, often with admixture of shades of green and presence of dark lateral fascia. Dorsum predominantly in shades of brown, but occasionally in other colors, including a vivid deep pink pigmentation; sides are frequently green.

Discussion.—There is no marked constancy in color patterns; sometimes a local population may exhibit a fairly homogeneous picture, while another elsewhere presents a wide range of variation. This could be a reflection of the ecological conditions of the habitat, but precise observations are lacking.

Distribution.—The typical subspecies is by far the most widespread and variable of the three. Occurs in whole Ethiopian region except for deserts; all East African countries including SOMALIA (omitted from COPR (1982) but cited in Johnsen and Schmidt (1982) and Baccetti and Abukar (1987)); in much of southern Africa replaced by *Duronia chloronota curta* (Uvarov 1953).

Duronia chloronota curta (Uvarov, 1953), stat. n. et comb. n.

Duronia curta Uvarov, 1953: 144–145, figs 174–175.

Material.—Type material and others in NHMUK, London.

Description.—Differs from nominate subspecies in its smaller size but proportionately more robust build, shorter rounded head, and thick, practically parallel lateral carinae of pronotum. Coloration as in nominate subspecies. Size (in mm); total length: males, 22–2; females, 32–37.

Discussion.—South African species are intermediate with nominate subspp.

Distribution.—SOUTH AFRICA (former Natal, Orange Free State, and Cape Province), ZIMBABWE.

Duronia chloronota phippsi subsp. n.

http://zoobank.org/9AA00DA8-1563-4DB2-8482-80C75DC3FAF8
Figs 97, 98, 105–107

Material.—Holotype male: SIERRA LEONE, Kasewe Forest Reserve, 22.Xl.1964 NHMUK. 20 male, 20 female paratypes, same data, NHMUK.

Description.—Differs from other subspecies in its more robust build and larger size. Proportionally longer and more expanded antennae; frontal ridge as in Fig. 107, markedly narrowed at junction with fastigium. Pronotum somewhat inflated, dorsum with strong, raised carinae; lateral carinae somewhat outflexed. Pronotal metazona length of prozona, its hind angle sharp, slightly attenuate (Figs 105, 106). Coloration deep green dorsally, brownish laterally with fine, sparse, dark speckling; hind wings hyaline to faintly yellowish basally, infumate apically. Size (in mm); total length: males, 22–25; females, 32–37.

Discussion.—Habitat is moist grassland in forest clearings.

Generic diagnosis

Durionella I. Bolívar, 1908a

Durionella I. Bolívar, 1908a: 100.

Type species.—*Duronia fracta* Krauss, 1890: 260 (I. Bolívar 1908a), by original designation; (but given as *Duroniella lucasii* (I. Bolívar, 1881) by subsequent designation in OSF (Cigliano et al. 2018)).

Description.—As in description of genus group and key to genera.

Discussion.—A widespread genus of a dozen or so closely related species, some of which are possibly synonyms. Genus in need of revision. Only species so far recorded in East Africa is *Duroniella acuta* Uvarov, 1952. The reduced arolia correlate with the marked geophilous tendencies of members of the genus.

Species notes

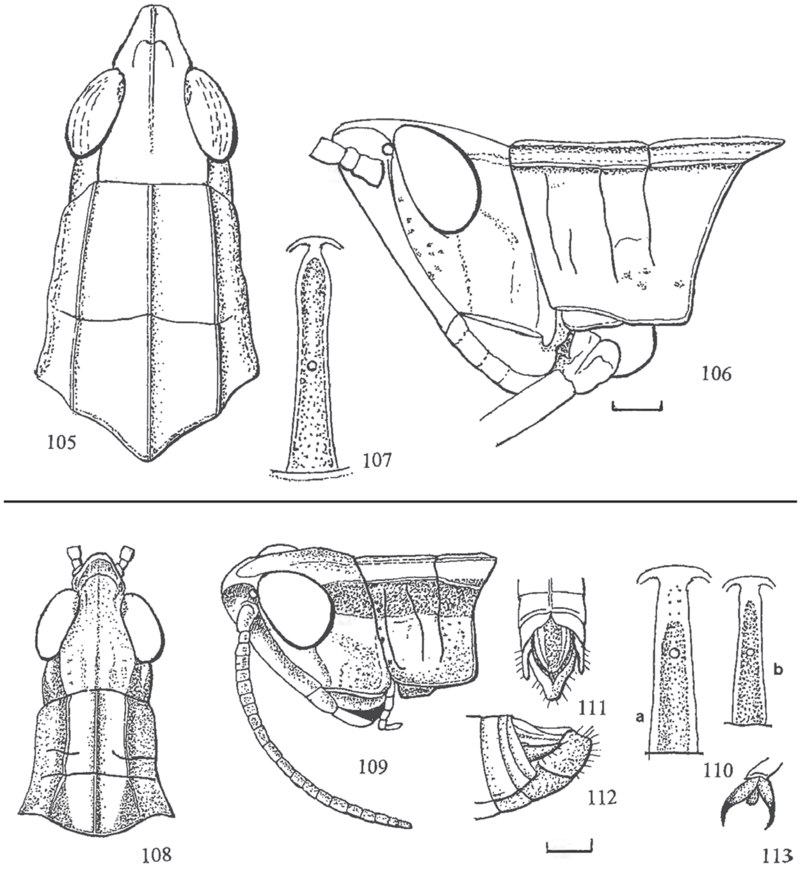
Duroniella acuta Uvarov, 1952

Figs 108–113

Duroniella acuta Uvarov, 1952: 42, 180.

Material.—ERITREA: Archico, X; Wakhiro, XI; Ghibdo valley 30 mi. W. of Assab. ETHIOPIA: Paradisso, IX. SOMALIA: Bihendulah, 25 mi. N.W. Berbera, X; Tug Hodna E. of Karin, III; Las Dureh plain, XII. (Also, Red Sea coast of Saudi Arabia and Yemen south of 20°N).

Description.—Slightly below medium size. Size (in mm): males 17.5–19.5, females 25.0–26.5. Head and pronotum as in Figs 108, 109. Integument matt to finely rugulose. Antennae narrowly ensiform; in male longer than, in female shorter than, head and pronotum. Frontal ridge moderately sulcate (Fig. 110), with thick, somewhat wavy margins, weakly divergent downwards. Fastigium of vertex moderately prominent, longer than broad; apex acutely parabolic. Pronotal disc weakly tectiform, smooth, carinae low, but distinct throughout; lateral carinae weakly inflexed in prozona, divergent in metazona. Pronotal metazona 0.8x length of prozona, its hind angle obtusely angulate. Tegmina extend beyond hind knees, membrane semitransparent; intercalary vein in medial area present. Hind femur slender; arolia very small (Fig. 113). External genital structures as illustrated in Figs 111–112. Coloration in buff and pale green variants; a faint dark fascia extends from antennal socket through genae and upper side of lateral pronotal lobes to medial area of tegmina, where it is bordered by a contrasting pale green stripe along costal area; hind wings hyaline; hind femur, including knee, a darker shade of brown than dorsum; hind tibiae pinkish brown. Green forms with pastel green sides are found predominantly among females.



Figs 105–113. *Duronia* genus group. **Figs 105–107.** *Duronia chloronota phippsi* **n. subsp**.: **105, 106.** Head and pronotum dorsally and from left side, respectively; **107.** Frontal ridge. **Figs 108–113.** *Duroniella acuta* Uvarov: **108, 109.** Male head and pronotum from above and oblique view, respectively; **110.** Frontal ridge **A.** Male; **B.** Female; **111.** Male abdominal apex from above; **112.** Male abdominal apex from oblique aspect, left side; **113.** Tip of hind tarsus showing small pulvillus. All scale lines represent 1 mm: of two scales under Fig. 112, only uppermost applies to Figs 105–112, while lowermost applies to Fig. 113.

Discussion.—Comparison of the East African material with the types of *D. acuta* from Saudi Arabia, the types of *D. cooperi* Uvarov, 1943 from Egypt, and *D. lucasii* (I. Bolívar, 1881) from North Africa, shows East African material to be conspecific with the Arabian *D. acuta* (only differing in minor details such as smaller size and paler coloration). This species is closely related to the Egyptian *D. cooperi,* but both are quite distinct from the North African *D. lucasii* on the basis of phallic morphology. Records of *D. lucasii* from Somalia (cited in Johnsen and Schmidt 1982) should be considered a misidentification.

Distribution.—ERITREA, ETHIOPIA, SOMALIA, SAUDI ARABIA, YEMEN.

Generic diagnosis

Leopardia Baccetti, 1985

Leopardia Baccetti, 1985: 299.

Type species.—Leopardia bivittata Baccetti, 1985: 305, by monotypy.

Description.—The diagnosis of the genus is as in the key to genera; for species see below.

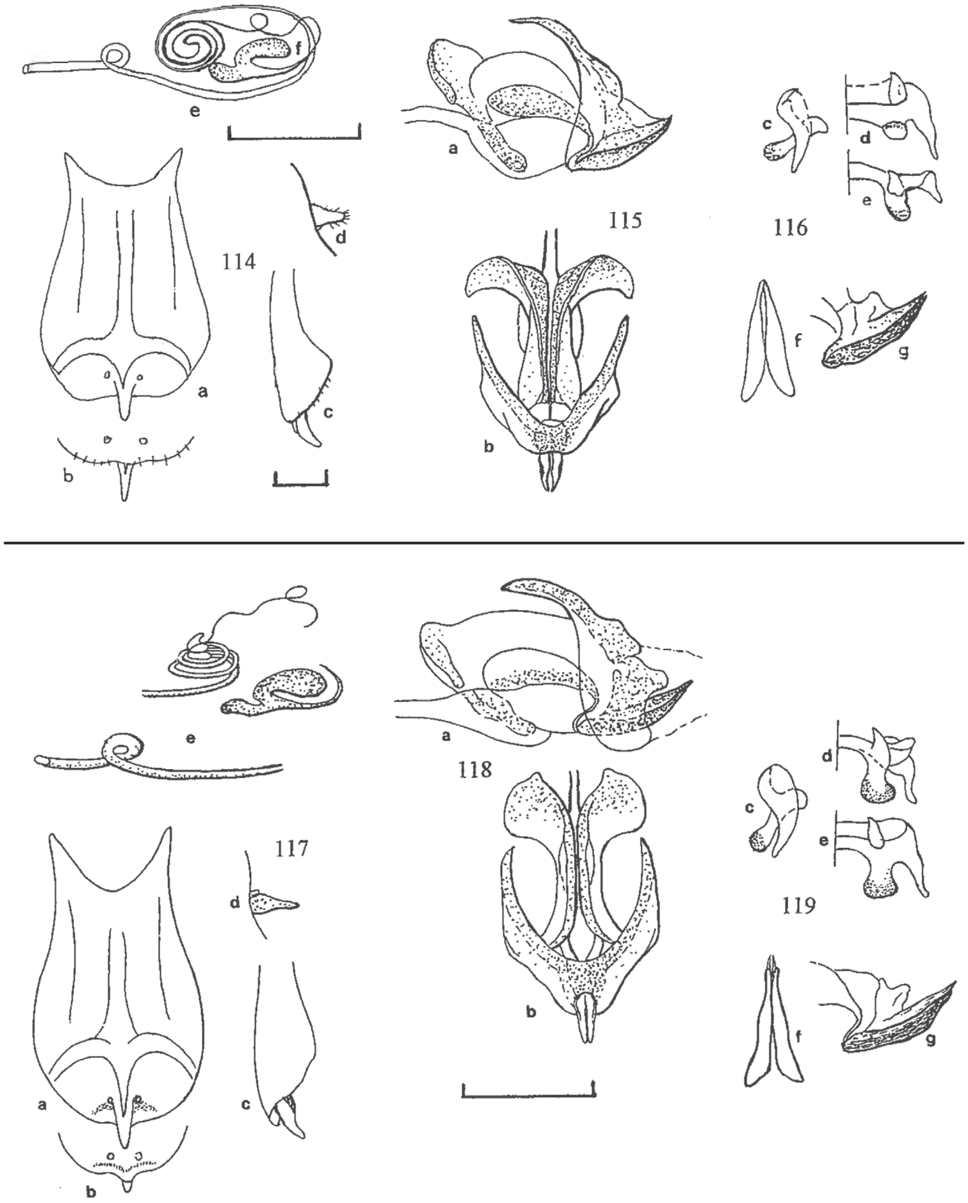
Species notes

Leopardia bivittata Baccetti, 1985

Figs 101–103, 114–116

Material.—SOMALIA: Giohar; Misciani (Genale) (Type localities); Nr. Afmadu; Mogadiscio. KENYA: 22 km N.W. of Witu along road to Garsen (02°18′S, 40°17′E) 65 m. Dry thicket with lush roadside grass; Hola (01°30′S, 40°00′E); Yasere, Moyale Dist. (03°30′N, 38°55′E). Grass and thorn bush, Adults: VI, XI, XII.

Description.—Below medium size. Size (in mm): total length males 17–20, females 25–33. Integument moderately shiny, finely pitted, somewhat pilose. Antennae narrowly ensiform, in male slightly longer, in female shorter, than combined length of head and pronotum. Head short, acutely pointed with oblique, straight, to weakly convex frons. Frontal ridge broad, margins thick, well-defined, weakly divergent downwards; fastigial constriction weak (Fig. 103). Fastigium of vertex parabolic, with well-defined medial and lateral carinulae and arcuate sulcus in forward position; surface of fastigium flat to weakly convex, meeting frons at an acute angle to form a sharp overhang above antennal fossae; lacking foveolae. Pronotum weakly tectiform, dorsum in metazona and anterior part of prozona finely pitted; front margin straight, hind



Figs 114–119. *Duronia* genus group. Genitalic structures: **Figs 114–116.** *Leopardia bivittata*: **114.** Female subgenital plate dorsally**; B.** Apex of same, ventrally; **C.** Idem laterally; **D.** Cercus; **E.** Spermatheca and duct; **115.** Phallic complex, epiphallus removed, **A.** Laterally, **B.** Dorsally; **116.** Male dissected phallic components, **C–E.** Epiphallus laterally, dorsally and dorso-posteriorly (right half), aedeagal valves, **F.** Ventrally and **G.** Idem, laterally. **Figs 117–119.** *Oxyduronia anablepioides* **n. gen. et sp. n.: 117.** Female, **A.** Subgenital plate dorsally; **B.** Apex of same ventrally; **C.** Idem laterally; **D.** Cercus; **E.** Spermathecal duct and spermatheca; **118.** Male, lateral and dorsal aspect phallic complex, epiphallus removed: **A.** Laterally, **B.** Dorsally; **119.** Dissected phallic components, **C–E.** Epiphallus laterally, dorsally and dorso-posteriorly (right half), **F.** Aedeagal valves ventrally, **G.** Idem, laterally. Scale lines all 1 mm: Scale under Fig. 114C refers to Figs 114A–D and 117A–D, scale under Fig. 114E refers to Figs 114E and 117E, and scale under Fig. 118B refers to Figs 115, 116, 118, and 119.

margin obtuse-angular; medial carina strong, lateral carinae weaker, but well defined throughout. Only hind sulcus distinct, interrupting all three carinae. Metazona distinctly shorter than prozona in both sexes; lateral pronotal lobes with sinuous, ascending lower margin and rounded posterior and anterior angles; a strong longitudinal callose ridge, parallel to, and somewhat below, the upper margin, with area between darkened, a character more pronounced in females (Figs 101, 102). Mesosternal lobes weakly transverse, interspace length/width ratio 3:2 in males, 1:1 in females. Tegmina narrow and tapering, with parabolically rounded apex, not quite reaching hind knees in either sex; membrane semitransparent, reticulation sparse, intercalary vein in medial area weak or absent. Hind wings distinctly shorter than tegmina. Hind knees with short, rounded outer and subacute inner lobes. Tibiae length of femora, spines moderately long, inner spurs twice length of outer. Male abdominal appendages as in Figs 111–112. Ovipositor with short, robust valves, curved at apices; lower valves without basal tooth. Internal genital structures as in Figs 114–116, rather similar to those in *Duronia*; hind margin of subgenital plate without marked medial projection. Coloration marbled and speckled in shades of brown and stramineous, with dorsum occasionally greenish (more often so in males). Lateral dark fascia varies in intensity, extending from antennal pits along upper margin of lateral pronotal lobes, sometimes filling much of the space between lateral pronotal carinae and ridge on lobe and thence to medial field of tegmina. Tip of abdomen in males yellowish of varying intensity, probably in response to sexual maturation. Hind femur brown, hind knee and base of tibia more or less dark, more intensely in males; hind tibiae brownish with spines tipped black.

Distribution.—SOMALIA, KENYA.

Generic diagnosis

Oxyduronia gen. n.

http://zoobank.org/B8114A7E-BB30-404D-B0F8-63F600040C6B

Type species.—Oxyduronia anablepioides **sp. n.**, here described and designated.

Description.—Below medium size, of medium build. Integument finely rugulose, matt, weakly pilose. Antennae relatively thick, narrowly ensiform, somewhat shorter than length of head and pronotum. Head short, apex sharply pointed; frons oblique, straight to weakly convex in profile. Frontal ridge broad, deeply sulcate with thick margins divergent downwards and narrowly constricted at junction with fastigium. Fastigium of vertex broad, acutely parabolic, its surface convex, meeting the frons at acute angle, forming a projecting sharp overhang above antennal fossae; temporal foveolae absent; carinulae low but distinct, positioned along margin; arcuate sulcus weak, well in front of the middle. Compound eye small, narrowly pointed apically; sub-ocular distance greater than longest diameter of eye in both sexes. Pronotum weakly tectiform; dorsum finely pitted and ridged especially in metazona and anterior part of prozona; anterior margin straight to weakly curved, hind margin obtuse angular with slightly produced rounded apex. Pronotal carinae sharp and raised; lateral carinae straight to outflexed, particularly in female; parallel to weakly divergent caudad, particularly in male. Only typical sulcus distinct on dorsum, interrupting all carinae; metazona subequal to prozona in both sexes. Lateral pronotal lobes flat to weakly concave with irregular ridges and callosities; a submarginal ridge is present below its upper margin but is less marked than in *Leopardia*; lower margin parallel to upper in its posterior part and ascending in its anterior half; lower hind angle sharp. Mesosternal lobes transverse with rounded angles, interspace wide. Tegmina narrow with parabolic, tapering and somewhat swept back apices; reticulation moderately dense; intercalary vein in medial area weak or absent. Hind wings narrow, pointed and distinctly shorter than tegmina. Hind femora moderately slender; hind knee with lower outer lobe short and rounded, inner subacute. Hind tibiae slender, slightly shorter than femora; inner spurs twice length of outer; arolia large. Abdominal appendages in male unspecialized, elongate and slender; concealed genital structures similar to those in *Duronia* and *Leopardia* (Figs 117–119). Epiphallic bridge (Fig. 119) moderately robust, arched and without median process; lophi digitiform, markedly widened and flattened but not upturned apically; posterior projections elongate and slender. Aedeagal valves as in Fig. 118. Ovipositor with short robust upturned valves; lower valves without basal tooth. Structure of spermathecal duct (Fig. 117) and spermatheca similar to that in *Duronia*; subgenital plate with rounded median projection.

Discussion.—Genus monotypic. In its general characteristics, and particularly its genital structures, it is like *Leopardia*, and is a fairly close relative of *Duronia*. However, the structure of head and pronotum in *Oxyduronia* is sufficiently distinctive to fully warrant generic recognition.

Species notes

***Oxyduronia anablepioides* sp. n.**

http://zoobank.org/47DD2570-EC4F-49FE-9D07-EC687A96D819

Figs 99, 100, 104, 117–119

Material.—Holotype male: S.W. TANZANIA: Ufipa plateau, 16 mi. N.N.W. of Sumbawanga, Mkundi Plantation, 16–27.V.1966, N.D. Jago (NHMUK). Paratypes: 3 males, 1 female, same data as holotype; l female, Ufipa, Malenja, 1.IV.1950, H. Backlund; l male, Ufipa, Nsangu, 7000′ (2134 m) 13.III.1959, Vesey-Fitzgerald. MALAWI: l male, N. Rukuru, Nyika Plateau, 18.III.1967, Whellan (NHMUK).

Description.—As for genus. Size (in mm): total length: males 18–20, females 32–34. Antennae in male subequal to equal, in female distinctly shorter than combined length of head and pronotum. Tegmina not quite reaching hind knee. Coloration both sexes in shades of green and brown; dorsally grass-green, sides marbled and spotted in varying shades of brown, except for green longitudinal stripes in upper part of lateral pronotal lobes and anal and precostal areas of tegmina. Membrane of tegmen thicker and brown basally, semi-transparent and pinkish apically; hind wing hyaline, faintly infumate apically. Hind femora including knee, brown; outer face with more or less pronounced greenish wash. Hind tibiae dirty brown, spines tipped blackish-brown. Underside brownish.

Distribution.—S.W. TANZANIA: Ufipa Plateau and N. MALAWI.

2.2 The tribe Gymnobothrini

Tribal diagnosis

Introduction.—Some taxa have been reviewed here based on literature descriptions only. This study is, therefore, preliminary and does not resolve all the taxonomic complexities of this group. The genus *Gymnobothrus*, in particular, will ultimately require a more thorough revision.

Description.—As defined on p. 41.

Discussion.—Included genera: *Brachybothrus* **gen. n.,** *Chirista* Karsch, 1893, *Comacris* I. Bolívar, 1890, *Coryphosima* Karsch, 1893, *Guichardippus* Dirsh, 1959, *Gymnobothrus* I. Bolívar, 1889, *Malcolmburria* Uvarov, 1953, *Oxybothrus* Uvarov, 1953 (as yet not recorded in eastern Africa), *Rastafaria* Ramme, 1931, *Roduniella* I. Bolívar, 1914, *Tenuihippus* Willemse, 1994, and *Zacompsa* Karsch, 1893.

This review presents the genera alphabetically. *Gymnobothroides* Karny, 1915 **syn. n**. and *Phloeochopardia* Dirsh, 1958 **syn. n.** are newly synonymized under *Gymnobothrus.* In the taxonomic treatments below, generic diagnosis of monotypic genera requires reference to the key (p. 67 below), while the fuller diagnostic description is given under the species.

These twelve genera have similar genital structures (Figs 24–30), notably a very distinctive epiphallus with elongate digitiform lophi, and are thus regarded as a closely related group, here given the rank of a tribe within Acridinae. Externally they resemble members of the *Sumba* genus group, but unlike them do not have specialized antennae or peculiar sculpturing of the integument. The single *Rastafaria* species is micropterous, *Brachybothrus* **gen. n.** and *Guichardippus* species are brachypterous, and *Coryphosima* and *Gymnobothrus* species exhibit all stages of wing development; the remaining genera are all fully winged. While most are terri-graminicoles, some are graminicoles, and the two *Brachybothru*s **gen. n.** species are geophilous and have reduced arolia. Most of the genera contain few species, each with a rather limited geographical distribution, with the exception of *Coryphosima* and *Gymnobothrus,* which are fairly large genera containing widespread species. Critical characters, such as the structure of the vertex of the head and the pronotum, are often highly variable both geographically and within a population. Species have often been erected erroneously and extensive synonymy is frequently necessary. Thus Dirsh (1965) listed 11 species of *Coryphosima*, but five years later he attributed 16 synonyms to *Coryphosima stenoptera* (Schaum, 1853) (Dirsh 1970), five of which he regarded as valid species in 1965. Jago (1970) also discussed such complexities. Species are best defined on a combination of characters. Detailed structure of head and pronotum is useful in this respect, but the genital structures much less so. As a whole, the genera within this tribe are very similar and rather difficult to distinguish without careful examination.

Coloration, as in many Acridinae, is variable and usually several variants occur sympatrically. However, in some cases, the coloration of the lower inner and outer face of the hind femur provides a stable diagnostic feature.

Key to East African genera in the tribe Gymnobothrini

1 Frontal ridge very narrow at junction with fastigium and broadly widened towards clypeus; medial pronotal carina lamellate, raised and deeply notched by typical transverse sulcus. D.R. CONGO, W. TANZANIA .... *Malcolmburria* Uvarov, 1953

– Margins of frontal ridge sub-parallel, or weakly divergent; fastigial constriction not unduly marked. Medial pronotal carina linear, not lamellate and raised 2

2 Antennae narrowly ensiform, widened and compressed basally, cylindrical apically. Fastigium of vertex pointed (Fig. 121; Figs 316–317). Pronotum weakly tectiform with almost straight well-developed lateral carinae reaching hind margin and weakly divergent caudad. Fully winged; of slender build (similar to *Sumba*) 3

– Not with above combination of characters; in particular, lateral carinae not straight and not reaching hind margin of pronotum 4

3 Size slightly larger, of average build (male 12–15 mm). Fastigial foveolae absent, metazona roughly the length of prozona. Fastigial foveolae absent, metazona roughly length of prozona. CAMEROON, UGANDA, KENYA, D.R. CONGO; locally common in wet habitats . ... *Roduniella* I. Bolívar, 1914

– Size very small (male 11–12 mm), of very slender build. Fastigial foveolae present, metazona 1.4x length of prozona (Figs 316–322). A rare ZAMBIAN endemic........................ *Tenuihippus* Willemse, 1994

4 Antennae shorter than combined length of head and pronotum, compressed in basal part and thickened in apical half; brachypterous. SOMALIA .... *Guichardippus* Dirsh, 1959

– Not as above; antennae of varying length and thickness, sometimes slightly compressed and widened basally, but not otherwise specialized 5

5 Rim of fastigium of vertex narrow and projecting, no trace of temporal foveolae. Fully winged 6

– Rim of fastigium of vertex thick, temporal foveolae present, though sometimes as little more than faint granular pits along or below the rim, or even obsolete (see Jago (1970) for an illustration) 7

6 Pronotal carinae in prozona straight, parallel, obliterate in metazona; costal and subcostal area of wing inflated at apex, medial and cubital area widened; lustrous with regular sparse transverse veinlets (Fig. 125). GUINEA, KENYA, TANZANIA, SOUTH AFRICA.............. ....*Comacris* I. Bolívar, 1890

– Lateral pronotal carinae distinct throughout, incurved in prozona, strongly divergent in metazona (Fig. 123); wing venation normal unspecialized. Widespread in W. Africa, also in CONGO REP., D.R. CONGO, and UGANDA ....*Chirista* Karsch, 1893

7 Tegmina and wings fully developed or shortened, but in dorsal position 8

– Tegmina lobiform, positioned laterally 11

8 Pronotum weakly sub-cylindrical; lateral carinae obliterate between first and second transverse sulci and almost so in metazona. Coloration usually as contrasting broad longitudinal dark and light bands (Fig. 323). W. Africa to ETHIOPIA, D.R. CONGO ....*Zacompsa* Karsch, 1893

– Pronotum more or less tectiform or saddle-shaped, compressed in middle; lateral carinae distinct in metazona 9

9 Pronotum shortened, strongly compressed in middle; metazona much shorter than prozona; lateral carinae callose, interrupted by sulci and obliterate between first and second sulcus; brachypterous; arolia small (Figs 297, 299). KENYA, SOMALIA ....*Brachybothrus* **gen. n.**

– Pronotum not strongly shortened and compressed; metazona as long as, slightly shorter than, or longer than prozona; arolia not unduly small 10

10 Fastigial foveolae weak, sometimes absent. Dorsum of pronotum flat; lateral carinae sharp and parallel to subparallel in prozona, more or less divergent, weak or obliterate in metazona; macropterous or brachypterous (but see also micropterous species under couplet 12). Widespread south of the Sahara..*Coryphosima* Karsch, 1893

– Fastigial foveolae concealed from above, but usually distinct, shallow and elongate. Pronotum somewhat constricted in middle; pronotal carinae well developed; lateral carinae straight, or slightly or strongly incurved; tegmina and wings fully developed or shortened. Widespread south of Sahara ....*Gymnobothrus* I. Bolívar, 1889

11 Lateral pronotal carinae strongly, almost angularly incurved............ ....*Gymnobothrus* (micropterous species)[1]

– Lateral pronotal carinae moderately or weakly incurved, or straight and parallel in prozona and divergent in metazona 12

12 Pronotum subcylindrical, lateral carinae moderately and broadly incurved. ETHIOPIA, KENYA, UGANDA.......... *Rastafaria* Ramme, 1931

– Pronotum weakly tectiform lateral carinae straight or only weakly incurved..................................... *Coryphosima* (micropterous species)[1]

---

[1] See couplet 10 for macropterous and brachypterous forms.

Generic diagnosis

Roduniella I. Bolívar, 1914

Roduniella I. Bolívar, 1914: 84.

Type species.—Duronia insipida Karsch, 1896: 84, by original designation.

Description.—In key to genera and Figs 120–122. Epiphallus Fig. 122.

Species notes

Roduniella insipida (Karsch, 1896)

Figs 120–122

Duronia insipida Karsch, 1896.
Duronia duria Karsch, 1896 (syn. Uvarov 1938).
Duronia ituriensis Rehn, 1914 (syn. Uvarov 1953).
Roduniella ugandae Miller, 1932 (syn. Uvarov 1938).

Material.—Holotype female (*D. insipida*): UGANDA: Sesse Islands (MfN).

Description.—Integument smooth, matt. Antennae narrowly ensiform, flattened basally, as long as, or slightly longer than, combined length of head and pronotum. Frontal ridge narrow with thick margins, slightly expanded between antennae, shallowly sulcate and weakly expanded below medial ocellus (Fig. 120). Fastigium concave, triangular, with rounded apex and straight strong margins. Medial carinula weak to obsolescent; arcuate sulcus well behind middle (Fig. 121). Pronotum weakly tectiform with carinae distinct; lateral carinae parallel in prozona, weakly divergent in metazona; metazona as along as or slightly longer than prozona, its hind margin obtuse-angular. Coloration in shades of green, predominantly grass green, with brownish and yellowish patches and stripes (note dark blackish-brown lateral stripe extending from antennal pit across upper margin of lateral pronotal lobe and thorax but leaving a clear oblique stripe in middle of latter, then crossing medial and cubital areas of tegmina). Hind femur and tibia fawn/brown.

Measurements.—(In mm). Size small; total length: male 12–15, female 18–22.

Discussion.—Hygrotypic to mesohygrotypic, frequenting marshes and lake shores, usually in grasslands liable to flooding. Adults recorded throughout the year, thus probably breeding without marked interruption.

Distribution.—CAMEROON, UGANDA, KENYA, D.R. CONGO. In UGANDA recorded from: Entebbe, Kampala, Kazinga channel, Bwamba, Bugoma forest, Kakamiro, but also at altitude from Ruwenzori, at 4,500′ (1370 m) and 8,000–9,000' (2438–2743 m), and Mount Elgon 5,000–7,000′ (1850–2134 m).

Generic diagnosis

Chirista Karsch, 1893

Chirista Karsch, 1893: 54, 75.

Type species.—Stenobothrus comptus Walker, 1870: 762 (Sierra Leone), by subsequent designation I. Bolívar, 1909, note.

Description.—Recognition as in the key to genera.

Species notes

Chirista compta (Walker, 1870)

Figs 123, 124

Gymnobothrus varians Karsch, 1891 (Barombi) (syn. I. Bolívar 1909).
Chirista varians Karsch, 1893:76 (syn. I. Bolívar 1909).
Duronia virgula I. Bolívar, 1890 (Ashanti) (syn. I. Bolívar 1909).
Duronia pegasus Rehn, 1914 (D.R. CONGO) (syn. Uvarov 1953).

Description.—Moderately slender. Size (in mm): total length: males 14.5–17.0, females 18.0–21.0. Integument finely rugose and dotted. Antennae filiform, in males about as long as combined length of head and pronotum; in females somewhat shorter. Frontal ridge weakly sulcate, margins slightly divergent downwards. Fastigium of vertex moderately concave, narrowly parabolic with sharp margins; foveolae absent. Pronotum weakly selliform, median carina linear; lateral carinae more obtuse, strongly incurved in prozona, divergent in metazona. Latter with obtuse-angular hind margin and as long as, or slightly longer than, prozona (Fig. 123). Tegmina and wings fully developed, tegmina relatively narrow, intercalary vein weak or absent. Epiphallus with rather short lophi (Fig. 124). General coloration variable, particularly in females, in shades of green and/or brown, paler dorsally and ventrally; in brown individuals usually a dark brownish lateral stripe of varying width extending backwards from antennal pits across upper half of lateral pronotal lobes, but interrupted by a conspicuous oblique clear stripe on mesothorax; in green variants this band is narrowly confined to upper edge of lateral pronotal lobes. Darker blackish-brown color forms could be fire-melanic. Hind wings hyaline, or slightly infumate.

Distribution.—Widespread from western Africa to D.R. CONGO and ANGOLA, to UGANDA (Bwamba, Jinja, Mabira forest, Kampala, Lake George, Buruli, Samburu falls) and ETHIOPIA (Dembi Forest – Felix and Massa 2016). In Uganda one of the most common forest-edge species.

Generic diagnosis

Comacris I. Bolívar, 1890

Comacris I. Bolívar, 1890: 312.

Type species.—Chrysochraon semicarinatus Gerstaecker, 1869: 218, by subsequent designation (I. Bolívar 1909).

Description.—Recognition as in the key to genera. Venation of hind wings very distinctive (key to genera and Fig. 125); complete absence of fastigial foveolae is also diagnostic.

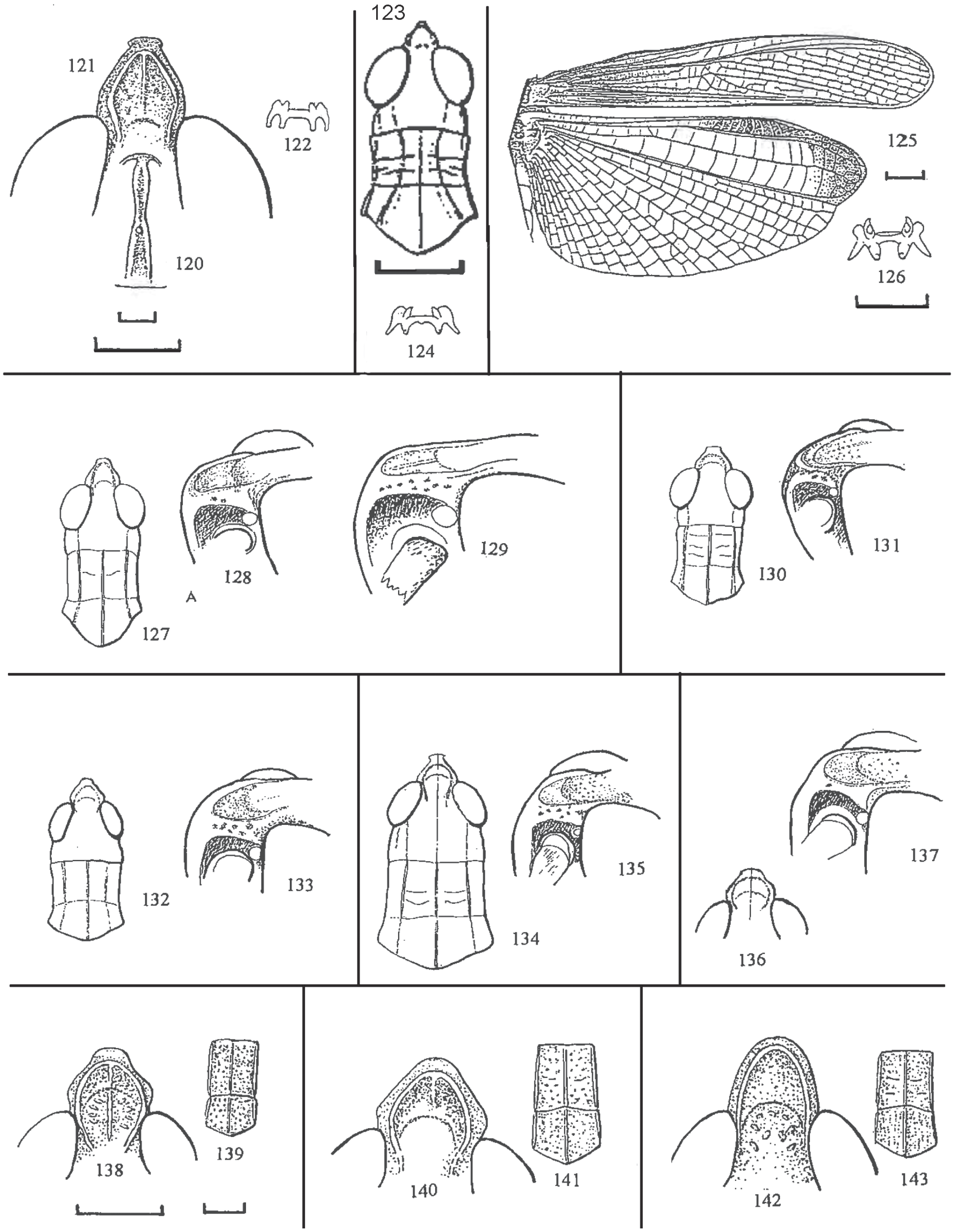
Species notes

Comacris semicarinatus (Gerstaecker, 1869)

Figs 125, 126

Chrysochraon semicarinatus Gerstaecker, 1869: 218.
Comacris sansibaricus I. Bolívar, 1890: 313 (syn. Karsch 1900: 275).

Material.—Holotype male (*semicarinatus*): KENYA: Wanga (material not available); Types male and female *sansibaricus*: Zanzibar.



Figs 120–143. Tribe Gymnobothrini. **Figs 120–122.** *Roduniella insipida* male: **120.** Frontal ridge; **121.** Vertex from above; **122.** Epiphallus. **Figs 123, 124.** *Chirista compta* male: **123.** Head and pronotum from above; **124.** Epiphallus (after Dirsh 1965). **Figs 125, 126.** *Comacris semicarinatus* male: **125.** Fore and hindwings, note hind wing speculum; **126.** Epiphallus. **Figs 127–143.** *Coryphosima* spp: **127–129.** *C. stenoptera*: **127.** Head and pronotum male from above; **128.** Oblique view of vertex and weak foveolar pits; **129.** Oblique view of vertex and stronger foveolar pits; **130–131.** *C. brevicornis*: **130.** Head and pronotum male from above; **131.** Oblique view of vertex. **132–133.** *C. stenoptera vicina*: **132.** Head and pronotum male from above; **133.** Oblique view of vertex. Note: now a synonym of *C. stenoptera stenoptera*. **134–135.** *C. bintumana*: **134.** Head and pronotum of male from above; **135.** Oblique view of vertex. **136–137.** *C. maliensis*: **136.** Male vertex from above; **137.** Oblique view of vertex. **138–139.** *C. cytidonotus*: **138.** Male vertex from above; **139.** Pronotal disc. **140–141.** *C. vumbaensis:* **140.** Male vertex from above; **141.** Pronotal disc. **142–143.** *C. abyssinica:* **142.** Male vertex from above; **143.** Pronotal disc. All scale lines represent 1 mm: that under Fig. 126 applies to Figs 122, 124 and 126; that under Fig. 125 applies to Fig. 120 (lower fig.) and Fig. 125; that under Fig. 138 applies to Figs 121, 128, 129, 131, 133, 135, 137, 138, 140, 142; that under Fig. 139 applies to Figs 127, 130, 132, 134, 136, 139, 141 and 143. That under Fig. 123 applies to Fig. 123 only.

Other series: TANZANIA: Zanzibar: Korogwe, Dar-es-Salaam, Tanga, Miombo, Mlingano, Ngomeri; SOUTH AFRICA: Durban.

Description.—Size (in mm): Small; total length: male 16–17, female 22–24. Integument finely rugose, matt. Antennae rather thick, basally slightly compressed, in males somewhat longer than combined length of head and pronotum. Frontal ridge weakly sulcate, margins low weakly divergent. Pronotum weakly tectiform, almost flat; lateral carinae strong, straight and slightly divergent in prozona, obliterate in metazona. Metazona equal in length to prozona, its hind margin obtuse-angular. Tegmina extending beyond hind knees, rather broad; intercalary vein in medial area weak. Hind-wing venation specialized, costal and subcostal areas inflated at apex, medial and cubital areas strongly expanded, lustrous with regular, sparse, transverse veinlets (Fig. 125). Epiphallus with relatively short incurving lophi (Fig. 126). General coloration uniformly brownish to greenish-brown, probably a somewhat brighter green in life. Some specimens with a darker dorsal medial stripe. Hind knee dark. Frons, gena and ventral part of pronotal lobe white or cream colored.

Discussion.—*C. semicarinatus* is predominantly East African where it is best known from coastal grasslands. However, the type locality (Wanga) is in Western Kenya. The only other species, *C. lamottei*, is known only from Guinea, Mt. Nimba. It differs from the type species in its smaller size and shorter wings. Biology little known, but habitat apparently predominantly short moist grasslands. Adults in IV and VIII–XII.

Distribution.—Predominantly East African, but also reaches Kwazulu-Natal in South Africa. KENYA; TANZANIA; SOUTH AFRICA. Given this distribution, presence in MOZAMBIQUE seems probable.

Generic diagnosis

Coryphosima Karsch, 1893

Coryphosima Karsch, 1893: 54, 72.

Type species.—*Coryphosima brevicornis* Karsch, 1893: 72 (type female, TOGO: Bismarckburg) by original designation.

Paracomacris Karsch, 1900: 276 (syn. Dirsh 1958).

Description.—Recognition as in the key to genera. Genital structures characteristic of *Gymnobothrus* genus group, show little variation and are of little taxonomic use. Epiphallus (Fig. 25).

Discussion.—A large genus showing considerable taxonomic variation and, like other genera in the *Gymnobothrus* group, individual variation may be large even at a single locality. Some recent synonymy, however, is thought unjustified. Consequently, carefully defined criteria have been established here, enabling definition of species and subspecies to be made on a consistent basis: geographically distinct populations are considered as valid species if there are no intermediate forms, but in the presence of clinal links they are considered to be subspecies.

In addition to the principal characters used previously to diagnose taxa, this study has found that wing length and structure are informative in dividing these taxa into three groups: macropterous, brachypterous, and micropterous. These are treated sequentially below.

1) Macropterous group: Folded wings reach or extend beyond the tip of abdomen; this group contains several closely related taxa, with *Coryphosima stenoptera* (Schaum, 1853) (Fig. 127) as the most important element. This group has been subjected to a number of revisions, as follows:

i) Uvarov (1953), in his preliminary review of the species and subspecies of *Paracomacris* Karsch, 1900, cited seven macropterous species and subspecies, with 12 synonyms. To size (i.e. body length, length of elytra, and hind femur) he added width of the costal and subcostal (scapular) area of the tegmen and the shape of the radial vein as of major diagnostic importance. These criteria divided his material into three species groups:
  a) Scapular area narrow, radial vein straight: *P. centralis centralis, P. centralis planicola,* and *P. acuta*.
  b) Scapular area broad, radial vein sinuous: *P. stenoptera stenoptera, P. st. montana, P. st. pharaonis.*
  c) Scapular area and radial vein of intermediate width and shape: *P. producta*.
ii) Dirsh (1966, 1970) stated that Uvarov's tegminal characters were, in his opinion, too variable to define species entities. He consequently published an extensive synonymy under *stenoptera,* as follows:

Coryphosima (=Paracomacris) stenoptera =
Chrysochraon stenopterus Schaum, 1853.
Stenobothrus productus Walker, 1870 (syn. Dirsh 1966).
Duronia tricarinata I. Bolívar, 1890 (syn. Uvarov 1953).
Coryphosima brevicornis Karsch, 1893 (syn. Dirsh 1966).
Paracomacris deceptor Karsch, 1900 (syn. Uvarov 1953).
Duronia pooensis I. Bolívar, 1905 (syn. Johnston 1956, Dirsh 1958).
Phlaeoba pharaonis Karny, 1907 (syn. Dirsh 1966).
Phlaeoba pharaonis var. *alterrima* Karny, 1907 (syn. Uvarov 1953).
Paracomacris stenoptera pharaonis (Karny, 1907) (syn. Uvarov 1953).
Paracomacris centralis Rehn, 1914 (syn. Dirsh 1966).
Rodunia pharaonis var. *virescens* Karny, 1915 (syn. Dirsh 1966).
Rodunia pharaonis var. *ferruginea* Karny, 1915 (syn. Dirsh 1966).
Duronia acuticeps I. Bolívar, 1915 (syn. Uvarov 1953).
Rodunia deceptor f. *kilimana* Sjöstedt, 1931 (syn. Uvarov 1953).
Paracomacris centralis planicola Uvarov, 1953 (syn. Dirsh 1966).
Paracomacris acuta Uvarov, 1953 (syn. Dirsh 1966).

iii) Johnsen (1984) synonomized *C. vicina* (Dirsh, 1956) with *C. stenoptera* (Schaum, 1853).
iv) Mestre (1988) rightly reinstated *Coryphosima brevicornis* Karsch, 1893 as a valid species.
v) The present paper. Popov wrote: "In view of transitional forms, this study makes *C. vicina* (Dirsh, 1956) (macropterous; South Africa) a subspecies of *C. stenoptera*, as *C. stenoptera vicina* (Dirsh, 1956)".

Editorial note.—Popov seems to have been unaware of Johnsen's (1984) synonomy, but both authors follow the same rationale. We accept Johnsen's synonomy, considering it to be corroborated by Popov's opinions.

The macropterous group also includes: *Coryphosima stenoptera montana* (Uvarov, 1953) and *Coryphosima stenoptera colorata* **subsp. n.**, both from Ethiopia.

There are now, therefore, two macropterous species (*stenoptera* and *brevicornis*), the first of which has three subspecies.

Key to macropterous species and subspecies of *Coryphosima* in western and eastern Africa

1 Size relatively small, total length male 12–15 mm, female 16–20 mm, but robust; tegmina barely reaching tip of abdomen.............. 2
– Larger and more slender, male 16–23 mm, female 20–28 mm, tegmina extending well beyond tip of abdomen 3
2 Fastigium of vertex very broad, transverse sulcus well forward (Fig. 131). Highlands of S.W. TOGO, S.E. GHANA, S. IVORY COAST, GUINEA: Mt. Nimba ....*brevicornis* Karsch, 1893
– Fastigium of vertex not unduly broad, arcuate sulcus behind the middle (as in Fig. 129). Highlands of ETHIOPIA ....*stenoptera montana* (Uvarov, 1953)
3 Coloration bright and contrasting, including shades of blue. ETHIOPIAN highlands .... *stenoptera colorata* **subsp. n.**
– Coloration in shades of brown and stramineous, dorsally often green. Widespread across western to eastern, central and southern Africa .... *stenoptera stenoptera* (Schaum, 1853)

2) Brachypterous group: Tegmina and wings strongly abbreviated; when folded, their apices falling well short of the tip of abdomen but overlapping dorsally. All brachypterous *Coryphosima* spp.—except one, the west African *C. maliensis* Descamps, 1965—are high altitude species, of limited vagility and localized distribution. The taxa are closely related and are probably the outcome of relatively recent speciation. Interspecific differences, although small, are fairly stable and are not indicators of trivial variability (*contra* Dirsh 1966).

The East African species are:
Coryphosima elgonensis (Uvarov, 1930)
= *Paracomacris loveni* Sjöstedt, 1933a (syn. Uvarov 1938).
Coryphosima (=*Paracomacris) abyssinica* Uvarov, 1934 (syn. Dirsh 1966, now **res. stat**.).
Coryphosima vumbaensis (Miller, 1949).
Coryphosima cytidonota Jago, 1970.
Coryphosima danieli Massa, 2016.

The West African species are:
Coryphosima maliensis Descamps, 1965.
Coryphosima nimbana Chopard, 1958 (GUINEA, Mt. Nimba); syn. with *elgonensis* by Dirsh 1966 but restored by Mestre and Chiffaud 2006.
Coryphosima bintumana Roy, 1964 (SIERRA LEONE, Bintumani Mts.); also syn. with *elgonensis* by Dirsh 1966, but restored by Mestre and Chiffaud 2006.

Key to the brachypterous species and subspecies of *Coryphosima* in eastern Africa

1 Lateral pronotal carinae straight, parallel to sub-parallel (Fig. 139). Fastigium of vertex as in Fig. 138, arcuate sulcus near middle. N.W. TANZANIA .... *cytidonota* Jago, 1970
– Lateral pronotal carinae more divergent, especially in metazona. Arcuate sulcus of fastigium well behind the middle............................ 2
2 Antennae thick and short, barely reaching hind margin of pronotum, or shorter; sculpturing coarse, metazona with parallel rugosities. UGANDA: Mt. Elgon ....*elgonensis* (Uvarov, 1930)
– Antennae longer and more slender, sculpturing finer....................... 3
3 Fastigium of vertex about as wide as long (Fig. 140). ZIMBABWE: Vumba Mts... *vumbaensis* (Miller, 1949)
– Fastigium of vertex distinctly longer than wide (Fig. 142) scapular field of tegmina narrow. ETHIOPIA: Jem-Jem and Chillalo; SOUTH SUDAN: Imatong Mts ....*abyssinica* (Uvarov, 1934)
4 Fastigium of vertex parabolic, prominent, 1.1 times longer than broad, its surface concave, margins smooth. Antennae nearly longer than head and pronotum together, the first 7–8 segments flattened, others rounded. Tegmina very short and wide (extending barely to 4th abdominal tergite). ETHIOPIA: Bale Mts ....*danieli* Massa, 2016

Key to the brachypterous species and subspecies of C*oryphosima* in western Africa

1 Of robust build, costal area of tegmina with a network of fine veinlets 2
– Of slender build, costal and subcostal area of tegmina with a network of thick, callose veinlets; lateral pronotal carinae weak (Fig. 134); foveolae of vertex as a row of fine dots (Fig. 135). SIERRA LEONE: Bintumani Mts ....*bintumana* Roy, 1964
2 Metazona and lateral lobes of pronotum strongly and callosely sculptured; size large (male 16 mm, female 25 mm). IVORY COAST, LIBERIA, GUINEA: Mt Nimba .... *nimbana* (Chopard, 1958)
– Sculpturing finer, temporal foveolae as in Fig. 137. S.W. MALI, Klela region to N. GHANA..................................*maliensis* Descamps, 1965

3) Micropterous group: Tegmina and wings reduced to barely the length of pronotum, in lateral position, not overlapping dorsally. The three species placed in this group: *C. amplificata* (Johnston, 1937), *C. morotoensis* (Jago, 1968), and *C. triangularis* (Bouvy, 1982) are here all transferred from *Rastafaria* Ramme, 1931, where they were placed by Bouvy (1982). They differ substantially from the type species *R. abessinica* Ramme, 1931 in the structure of the fastigium, pronotum, genitalia and the type of coloration, in all these respects being much closer to *Coryphosima* and differing from the remaining taxa in that genus principally in a further reduction of the length of the organs of flight. This wing reduction in *Coryphosima* does not merit generic separation.

Key to the micropterous species and subspecies of *Coryphosima* in eastern Africa

The three micropterous species share a similar distinctive coloration, comprising contrasting broad longitudinal blackish-brown stripes on an ivory-white to fawn ground, which varies in detail between the species.

1 Dorsum pale fawn to cream without a medial dark stripe (Figs 145, 146).. 2
– Dorsum with a black medial dorsal band extending from occiput to tip of abdomen. D.R. CONGO: Katanga Prov.; N.W. ZAMBIA........... ....*triangularis* (Bouvy, 1982)
2 Lateral pronotal carinae interrupted by typical sulcus only (Fig. 148) outer face of hind femora suffused with black. Mt. KENYA................ .... *amplificata* (Johnston, 1937)
– Lateral pronotal carinae interrupted by all three transverse sulci (Fig. 150); outer face of hind femur light brown, immaculate. UGANDA: Mt. Moroto..*morotoensis* (Jago, 1968)

Species notes

1. Macropterous species

Coryphosima stenoptera stenoptera (Schaum, 1853)

Figs 127–129

Synonyms as above under *C. stenoptera*.

Material.—SENEGAL: Ziguinchor, Dieberine, Oussouye, Dakar. SIERRA LEONE: Mt. Aureol, Freetown, Kent, Bo Sewa beach, Kavina, Regent, Lumley beach; Gola. IVORY COAST: Man-Danané Road. LIBERIA: Bewi hills, Monrovia. MALI: Dogo, Kara. GHANA: Northern, Western and Eastern regions, many localities. TOGO: Pagala. NIGERIA: western province, Lagos, Ibadan. CAMEROON: Bamenda. SOUTH SUDAN: Imatong Mts. ETHIOPIA: Dessie area, 8000′ (2440 m) (series provides a clinal link with *C. stenoptera montana*), Addis Ababa. SOMALIA: Tug Hodma E. of Karin, Bihendula, Nr. Berbern. UGANDA: Many localities including: Kampala, Entebbe, Bulemwezi, Lawero, Kapeka, Bugoma Forest, Kivuvu, Katangula, Butiaba, Kigezi, Acholi, W. Nile Dist., Tororo, Luwero, Bwamba, Mabira forest, Lango, Mbale, Bunioni-Kashenji, Terinyi, Katunguru. KENYA: Mt. KENYA (*Juniper*/*Podocarpus* forest), Aberdares 7000′ (2130 m) (clinal link with *C. s. montana*), Thika 4,500′ (1370 m), Kakamega forest, Narok, Masai Mara, Nyeri, Nairobi, Baringo, Turkana, Ngong, Kericho, Kapenguria, Kipleleo plain. ERITREA: Archico. TANZANIA: Tukuyu, Milepa plain, Malagarasi, Lake Rukwa, Kahama, Ngudu, Ngorongoro Rest House, Mkomasi Stn. 60 mi. W. Amani, Bugeno, Kakagwe, Mbulumbul, Muheza, Kilimanjaro, Victoria Nyanza, Ukerewe, Moyawosi, Namanyele. Old Shinyanga, 10 mi. N. Ussure, Msigiri Road, Singida dist. (types of *Paracomacris centralis planicola* Uvarov, 1953—exceptionally large size: M 18–21 mm, F 25–28 mm). RWANDA: Kisenye. D.R. CONGO: Lake Albert: mouth of Semliki River, Kawa, Gety, Bogoro-Gety, Mahagi port, Bunia, Aru, Ratchuru, grass plain near Lake, Bambesa, Djugu Huri forest, Lubumbashi, Katanga: river Lubudi, Mt. Ruwenzori 6000′ (1830m). ZAMBIA: Mwinilunga dist, Abercorn (Mbala), Mweru-wa-Ntipa, Konta plain, Musombwe, Lake Bangweulu, Kalungurishi, Lake Chila, Malagarasi. MOZAMBIQUE: Luabo, Beira, Salone forest, Zambesi: R. Sene Sugar Estate, Mucheve. ZIMBABWE: Salisbury distr. (Harare), Amandas, Silukut 4700′ (1430m), Zimbabwe R, 4800′ (1460m), Umtali Vumba, Umtali Xmas pass, Odzi dist. Mashonaland 5000′ (1525m). ANGOLA: Moxico dist. Luena river, Lumeje river, Munhango river; Villa Luso, river Lungue Bangu, 9 mi. N.W. Sa. de Bandeira, 10 mi. N.E. Cacula, Santa Comba, Lubizi S.W. Alto Hama, Salazar, 10 mi. E. Gabela, Luimbale, Moxico dist: upper Luena river, river Lumeje, valley of Lotombwe, Busaco; Bihe dist: Cohemba, Luchase dist: river Quangu (types of *Paracomacris acuta* Uvarov, 1953 with exceptionally narrow, acute apex of the head). BOTSWANA: Moremi Res., Gazaland, Chirinda forest. SWAZILAND (now ESWATINI): Mbabane. SOUTH AFRICA: Transvaal (Gauteng): Johannesburg, Tzaneen; Louis Trichardt; Nghelele Zutpansberg distr.; Kwa-Zulu Natal: Royal National Park, Tugela valley (transitional *stenoptera-vicina* forms). *C. vicina* material; Zululand: Eshowe, Umfolosi dist. Hagana Hluhluwe 2000′ (610 m), Mtubatuba; Pondoland, Ft. St John; Cape Prov. (Western and Eastern Cape): Eland Height, 15 mi. S.W. Mount Fletcher; Swellendam; Deepwalls Forest, Knysna dist. 1700′ (520 m); Grahamstown; Aberdeen-Somerset East; Ketberg; Wymberg Hili; LESOTHO: Mokhotlong.

Description.—As in key to genera and species. Size (in mm): Types of *Paracomacris centralis planicola* Uvarov, 1953 are of exceptionally large size, total length: males 18–21, females 25–28 - remaining material is in range: males 14–17, females 17–20. Antennae rather thick, cylindrical apically, slightly compressed but scarcely widened basally. Frontal ridge shallowly sulcate with obtuse lateral carinulae. Fastigium parabolic, shallowly concave, longer than wide, margins low and narrow, but distinct, medial carinula weak, or absent. Arcuate sulcus well behind middle (Figs 127, 128); fastigial rim thick, foveolae absent, or as weakly impressed small pits concealed from above (Fig. 129). Pronotal disc flat to weakly tectiform, median carina linear; lateral carinae straight and weakly divergent caudad, strong in prozona, weak and more or less obliterate in metazona; typical sulcus in mid position, interrupting medial and lateral carinae. First and second sulci weaker, not interrupting carinae (Fig. 127). Tegmina and wings fully developed, usually extending beyond hind knees; tegmina semi-transparent, rather narrow; intercalary vein of medial area present. Width of costal area and curvature of subcostal and radial veins variable. General coloration variable in shades of brown, from black/brown to stramineous, darker dorsally, paler ventrally; dorsum occasionally pigmented green especially in females. A dark blackish-brown lateral band is usually present, extending from post-ocular area across upper part of lateral pronotal lobes, to tegmina; a sulphurous stripe in basal part of radial veins is sometimes present. Wings hyaline to yellowish at base, infumate apically; hind knees dark brown-black, hind tibiae greyish-brown.

Discussion.—A fairly strict graminicole. Continuous reproduction with several annual generations.

Distribution.—Widespread in mesotypic and meso-hygrotypic savannas and grasslands from westem to eastern, central and southern Africa. Recorded in all East African countries, often common. The now synonomized *C. vicina* (Dirsh, 1956) (syn. Johnsen 1983) extends the range of this subspecies to SOUTH AFRICA and LESOTHO (Figs 132, 133).

Coryphosima stenoptera montana (Uvarov, 1953)

Paracomacris stenoptera montana Uvarov, 1953: 195.
Coryphosima stenoptera montana (Uvarov, 1953) (syn. Dirsh 1958).

Material.—ETHIOPIA: Djem-Djem forest, 2400–3000 m; Mount Chillalo, 2400 m; Wooroomon. Further material from Mt. Chillalo, moorland ca. 3000 m collected together with specimens of the brachypterous *C. abyssinica* Uvarov, 1934, but without any intermediate forms.

Description.—Differs from nominate subspecies in smaller size, but rather robust build and generally somewhat darker coloration. Fastigium of vertex elliptical. Pronotum short, rugulose; lateral carinae parallel. Subcostal area expanded with few widely spaced veinlets. Size (in mm): total length: males 13–15, females 18–21mm.

Distribution.—ETHIOPIA. Clinal links between subspecies *montana* and *stenoptera* are apparent at lower altitudes on the Ethiopian plateau.

Coryphosima stenoptera colorata subsp. n.

Figs 151–153

Material.—Holotype male: ETHIOPIA: West of Mendi-Alendi-Asosa road, 1400 m. 17–20.IX.1976, Jago. All paratypes—5 males, 1 female, same data as holotype; female, West of Nejo, 2200 m 16–19.IX.1976, Jago (NHMUK).

Description.—Size close to nominate subspecies from lowland and mid altitude areas, males l7 mm, females 20–23 mm. General build slightly more slender, integument smoother, fastigium of vertex narrower (Fig. 152) and antennae longer (Fig. 153)—9 mm instead of average of 7 mm in male, but most striking difference is in coloration (discolored in dry specimens): in male antennae black; upper half of body in shades of brown, dorsum paler and upper sides of thorax dark chocolate-brown (Fig. 151) (contrasting with broad white stripe below which extends from gena to base of hind femur); abdomen with pale blue below in life; red undersides to hind femur and tibia with a ferruginous orange tinge; hind knee and adjacent part of tibia brownish-black, without a sub-basal pale ring. Hind wings hyaline, somewhat infumate apically. Coloration in females more subdued.

Discussion.—Habitat among long grass in shade adjacent to riverine woodland in marshy valley at 4,600 ft (1,400 m). Accompanied by *Amesotropis* spp., with *Oxya hyla, Rastafaria abessinica,* and *Orthochtha* spp. in adjacent swamp hollow.

Distribution.—ETHIOPIAN highlands.

Coryphosima brevicornis Karsch, 1893

Figs 130, 131

Coryphosima brevicornis Karsch, 1893: 64, fig. 5.

Description.—Diagnosis as in key. Of more stocky build and smaller size than *stenoptera*. Wings relatively short, barely reaching tip of abdomen. Uniquely broad fastigium of vertex with arcuate transverse sulcus located well forward (Figs 130, 131). Coloration in brighter and more contrasting shades of brown than in *C. s. stenoptera*, with a distinctive broad dark lateral stripe; outer face of hind femur dark yellow, knee black. Size (in mm). Total length: males 12–15, females 16–20.

Distribution.—Highlands of S.W. TOGO, S.E. GHANA, S. IVORY COAST, GUINEA (Mt. Nimba).

2. Brachypterous species.

Coryphosima cytidonota Jago, 1970

Figs 138, 139

Material.—Known only from type series. TANZANIA: Kasulu region, 24 km W. of Kasulu, 1500–2000 m, IX (NHMUK, ANSP).

Description.—As in key to species. Size smallest for genus; total length: males 11–12, females 15–17 mm. Antennae slightly flattened basally; in males rather longer than combined length of head and pronotum. Fastigium of vertex as in Fig. 138, arcuate sulcus near middle; anterior area smooth, posterior area coarsely callose; margins and medial carinula weak but distinct. Temporal foveolae absent. Pronotal disc as in Fig. 139, lateral carinae straight, almost parallel and nearly complete in metazona. Metazona distinctly shorter than prozona, its hind margin obtuse angular. Tegmina vary in length from almost reaching supra-anal plate, to barely reaching posterior edge of fifth abdominal tergite; costal field surpassing middle of anterior border of tegmen. Hind femora relatively heavy. General coloration in shades of dark and lighter brown, with a contrasting black and creamy lateral stripe extending obliquely from base of antenna, across gena and lower part of lateral pronotal lobe. Dorsum of pronotum uniform brown, of light brown with medial carina narrowly edged with dark brown. Tegmina uniform brown. Hind femora pale brown, upper outer face and knee blackish; hind tibiae light brown, blackish towards extremities.

Distribution.—N.W. TANZANIA.

Coryphosima elgonensis (Uvarov, 1930)

Figs 154–157

Paracomacris elgonensis Uvarov, 1930: 249.
Paracomacris loveni Sjöstedt, 1933 (syn. Uvarov 1938).

Material.—KENYA: Aberdares N. face, Chebuswa 00°14′S, 34°36′E, 3300 m; grassy ridge between dense *Erica* bush; 0°15′S, 36°35′E, 3380 m; moorland and heath zone at base of inselberg. Mt. KENYA 00°0′S, 37°18′E. UGANDA: Mt Elgon, alpine and heath zones at altitudes of 3000–4000 m on both the Ugandan and Kenyan sides. Adults I–III.

Description.—As in the key. Size slightly larger than preceding species (Fig. 154). Size (in mm): total length: males 13–16, females 16–20. Antennae somewhat shorter and incrassate. Fastigium of vertex as in Fig. 155, broadly parabolic, its rim thick; temporal foveolae present as small indentations (Fig. 156), arcuate sulcus well behind middle. Dorsum of pronotum (Fig. 157), lateral carinae straight, slightly divergent and weak in metazona. Costal area of tegmen expanded and extending beyond middle of tegmen. General coloration mottled brown, often with admixture of green. Dark lateral and often a dark medial dorsal stripe (Figs 154, 157) characteristic.

Distribution.—KENYA and UGANDA: Mt. Elgon. KENYA: Aberdares.

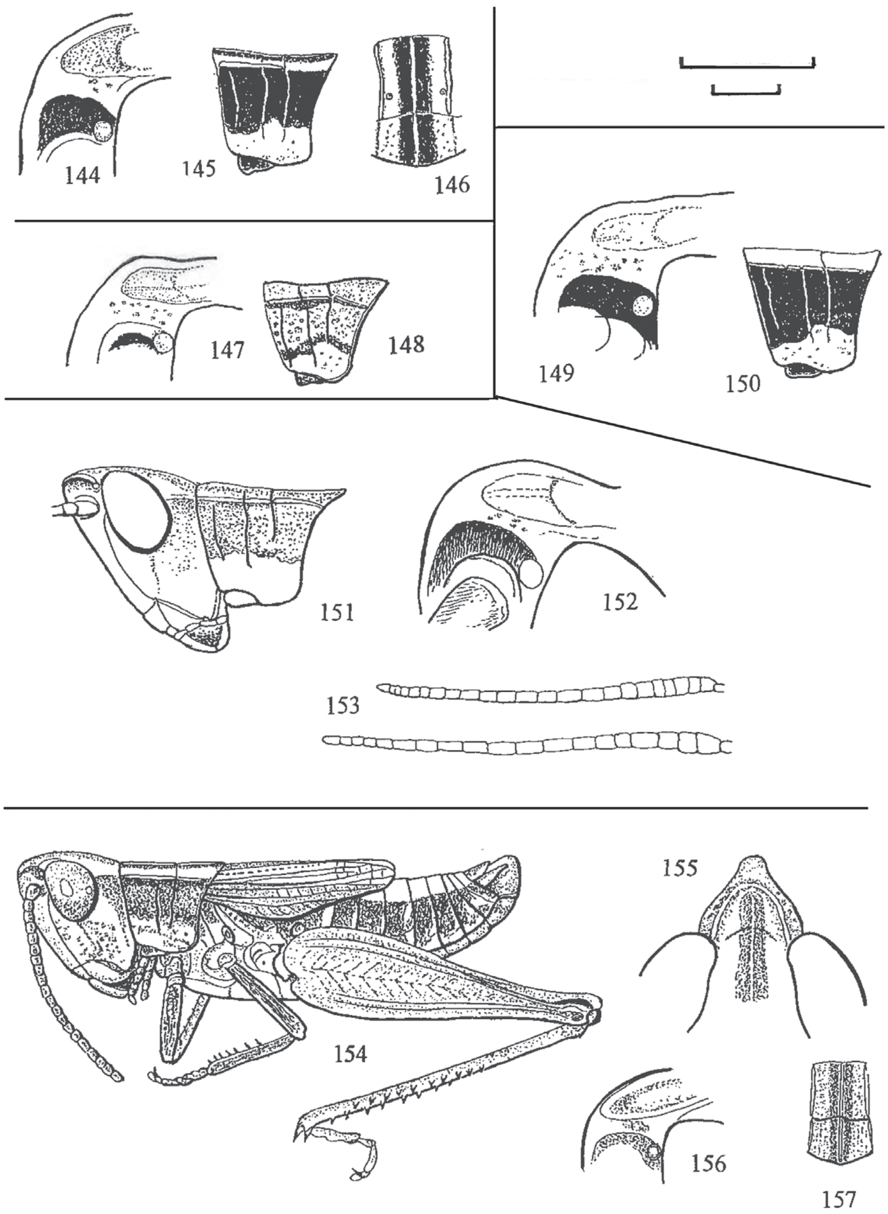
Coryphosima abyssinica (Uvarov, 1934), res. stat

Figs 142, 143

Paracomacris abyssinica Uvarov, 1934: 601.
Coryphosima abyssinica (Uvarov, 1934) (syn. Dirsh 1958).

Material.—ETHIOPIA: Wouramboulchi, near Djem Djem, ca. 3000 m Arusi/Bale Prov. Shashamene-Goba road, 2610 m short turf/bush heath. Chillalo, moorland 3000 m SOUTH SUDAN: Imatong Mts.

Description.—As in the key. In size similar to, or slightly larger than, *C. elgonensis* but more slender. Antennae slender, exceeding length of head and pronotum in male. Fastigium of vertex (Fig. 142), parabolic, distinctly longer than wide. Pronotal disc (Fig. l43); metazona subequal in length to prozona, but proportionately longer than in other brachypterous species. General coloration mottled in shades of predominantly darker browns without admixture of green pigmentation; dark lateral band occurs predominantly in males.



Figs 144–157. Tribe Gymnobothrini. *Coryphosima* spp. **Figs 144–146.** *C. triangularis*: **144.** Oblique view of vertex; **145.** Lateral aspect pronotum; **146.** Pronotal disc. **Figs 147, 148.** *C. amplificata*: **147.** Oblique view vertex; **148.** Lateral aspect pronotum; **Figs 149, 150.** *C. morotoensis*: **149.** Oblique view vertex; **150.** Lateral aspect pronotum. (see also Fig. 163). **Figs 151–153.** *C. stenoptera colorata* male: **151.** Lateral aspect head and pronotum; **152.** Oblique view of vertex; **153.** Comparison of antennae in subsp. *stenoptera* (upper) and *colorata* (below). **Figs 154–157.** *C. elgonensis* male: **154.** Lateral aspect whole insect; **155.** Dorsal aspect vertex; **156.** Oblique view of vertex; **157.** Pronotal disc. All scale lines represented by 1 mm: Upper scale line applies to Figs 144, 147, 149, 152, 155, 156; lower scale applies to Figs 145, 146, 148, 150, 151, 153, 154, 157.

Discussion.—South Sudan series are darker, with a more deeply sulcate frontal ridge, and a smoother surface of fastigium of vertex than Ethiopian material. Subspecific status is, however, not warranted. Dirsh (1966) synonymized *abyssinica* with *elgonensis*, but this has been widely ignored by subsequent authors (Johnston 1968, Otte 1995, Cigliano et al. 2018) and it is here formally restored from synonymy.

Distribution.—ETHIOPIA, SOUTH SUDAN. Montane species, probably terri-graminicole. Adults X, XI and II.

Coryphosima vumbaensis (Miller, 1949)

Figs 140, 141

Paracomacris vumbaensis Miller, 1949.

Material.—Known only from the type series. ZIMBABWE: Vumba Mts., 1520 m.

Description.—As in the key. Size and build similar to *C. abyssinica*. Fastigium of vertex broadly parabolic, as wide as long (Fig. 140).

Lateral pronotal carinae absolutely straight and evenly divergent caudad (Fig. 141); metazona subequal to prozona. Costal field of tegmen not surpassing middle of anterior border. Coloration in shades of brown, paler and less contrasting than in other species.

Distribution.—ZIMBABWE.

Coryphosima danieli Massa, 2016

Material.—Known only from the type series. ETHIOPIA: Bale Mts., 2380 m.

Description.—As in the key. A very small species, size (in mm): males 12.3–13.2, females 16.5–18.0. Antennae nearly longer than head and pronotum together, the first 7–8 segments flattened, others rounded. Foveolae absent. Face oblique, frontal ridge with parallel margins, except near the ocellus, where it is narrowed. Frontogenal carinae evident. Fastigium of vertex parabolic, prominent, 1.1x longer than broad, its surface concave, margins smooth. Pronotum disc slightly tectiform, with irregular longitudinal rugosities, central carina raised, interrupted only by typical sulcus, prozona just longer than metazona. Lateral carinae parallel, lower than central carina, broader and flattened in metazona. Anterior margin of pronotum nearly straight, posterior rounded. Lateral lobes as long as deep, their surface rugulose, lower margin little ascendant. Mesosternal space as long as wide, metasternal space much smaller, nearly square. Prozona slightly longer than metazona. For images, see Felix and Massa 2016, that is also the source of this description.

3. Micropterous species

Coryphosima amplificata (Johnston, 1937), res. stat. et comb. n.

Figs 147, 148

Paracomacris amplificata Johnston, 1937: 217–8, f. l.
Coryphosima amplificata (Johnston, 1937) (syn. Dirsh 1956).
Gymnobothroides amplificata amplificata Jago, 1968: 1, 3, 11.
Rastafaria amplificata amplificata Bouvy, 1982: 430, f. 68, 69, 87.

Material.—Known only from type series. KENYA: Mt. Kenya, V, *Juniper-Podocarpus* zone (NHMUK).

Description.—Size slightly smaller than other species in group. Size (in mm): males 12–13, females 17.5–22.0. Antennae about 1.5x the length of head and pronotum, basal segments slightly flattened and expanded. Frontal ridge broad, shallowly concave with thick, nearly parallel margins. Fastigium of vertex (Fig. 147), carinulae and margins distinct; foveolae represented by shallow pitting. Pronotum (Fig. 148) weakly tectiform, lateral carinae distinct, subparallel in prozona, weakly divergent and partly obsolescent in metazona, interrupted by typical sulcus only. General coloration contrasting chestnut-black and cream; dorsum of pronotum cream, without dark marking; the dark band along the lateral lobes is weaker than in other species and is usually confined to narrow fasciae along the upper margin and below the middle of the lobe, the intervening area clear or with faint dark speckling. Discoidal area of tegmina with a black band and sometimes, more often in females, with a yellowish speculum. Abdomen with broad black lateral band attenuating apically. Outer face of hind femora suffused with black; lower face reddish, knees black.

Distribution.—KENYA: Mt. Kenya.

Coryphosima morotoensis (Jago, 1968), stat. n. et comb. n.

Figs 149, 150, 163

Gymnobothroides amplificata morotoensis Jago, 1968.
Rastafaria amplificata morotoensis Bouvy, 1982.

Material.—Known only from type series. UGANDA: Mt. Moroto, 3000 m, VIII 1966 (NHMUK).

Description.—Differs from *C. amplificata* in larger size. Size (in mm): total length males 15–17, females 20–29. Antennae 1.7x length of head plus pronotum. Fastigium of vertex (Fig. 149) somewhat broader, with weaker carinula; foveolae as weak or weaker. Pronotum with inflexed and markedly divergent lateral carinae interrupted by all three transverse sulci (Fig. 150). Epiphallus as in Fig. 163—compare with *Rastafaria*, Fig. 162. Coloration generally light brown and black; dorsum of pronotum without black, but side band strong, covering 2/3 of lateral lobe of pronotum (Fig. 150). Abdominal side band more interrupted and fainter; tegmina shiny-black in anterior 3/5; posterior femora light brown, immaculate. Females generally similar to males but antennae shorter, about equal to length of head and pronotum. Area of tegmen between C and Sc with a creamy calloused speculum in many specimens, thus unlike males.

Distribution.—UGANDA: Moroto Mt.

Coryphosima triangularis Bouvy, 1982 comb. n.

Figs 144–146

Rastafaria triangularis Bouvy, 1982.

Material.—D.R. CONGO: Katanga (as Shaba) Prov., Likasi (type locality), 10 mi. S. Kapona, 1570 m; Lubumbashi. ZAMBIA: N.W. Prov. Kapushi; Kipundu; 16 mi. N. of Mwinilunga (NHMUK).

Description.—Main diagnostic character is the triangular shape of the pyriform vesicle of the tympanum (Bouvy 1982).

Discussion.—Size and structural details species closely resembles *morotoensis* (compare Figs 144 and 149); separated by presence of a dark dorso-medial band which extends from occiput to tip of abdomen (Figs 145, 146).

Distribution.—D.R. CONGO, ZAMBIA.

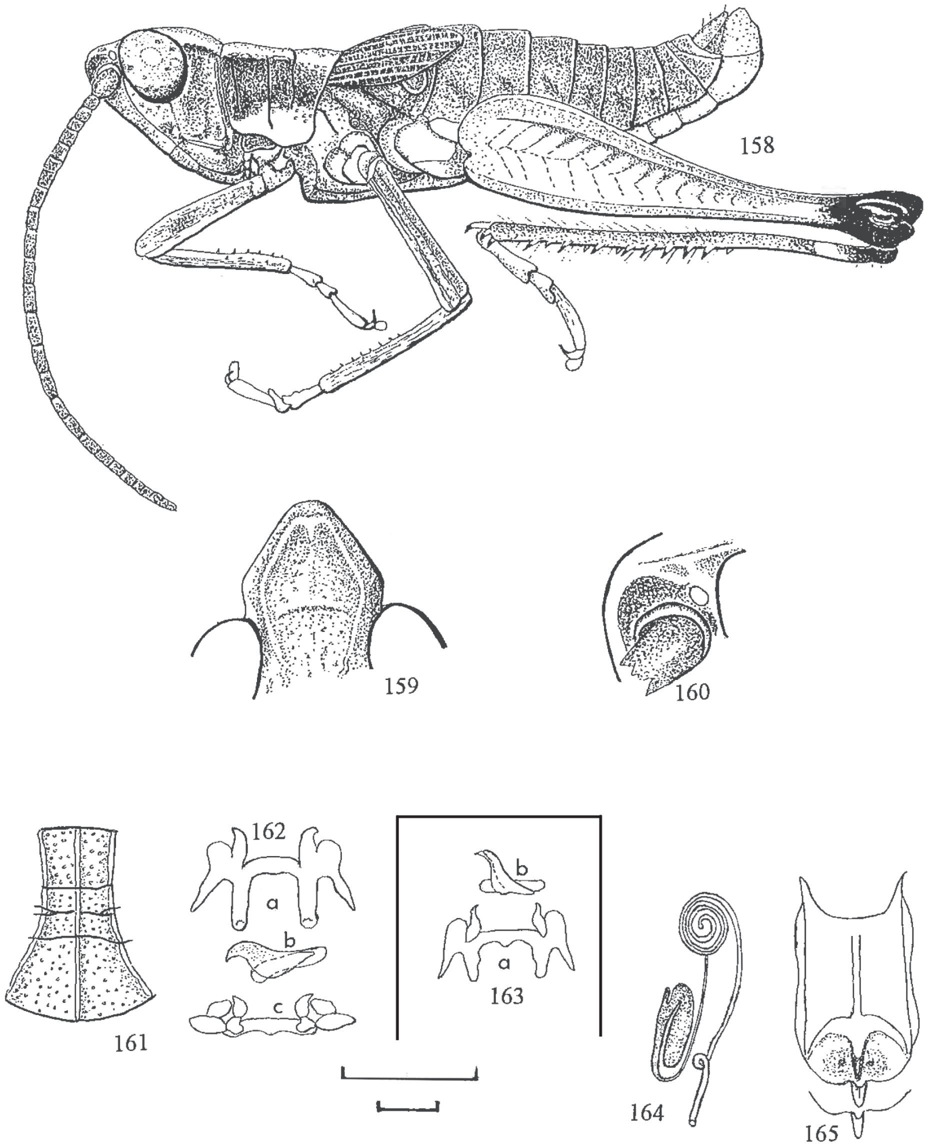
Generic diagnosis

Rastafaria Ramme, 1931

Rastafaria Ramme, 1931: 931, figs 8–18, pl. XI, fig. 9.

Type species.—*Rastafaria abessinica* Ramme, 1931: 932, by original designation.

Description.—As in the key to genera. Head pointed, somewhat inflated (Fig. 158); antennae almost twice combined length of head and pronotum in male, but only slightly longer in female. Frontal ridge rather thick, flat to weakly sulcate, markedly narrowed at junction with fastigium of vertex; latter excavate and elongate with arcuate sulcus well behind middle (Fig. 159). Pronotum sub-cylindrical, lateral carinae inflexed, weak to obsolete, but occasionally partly raised and callose, particularly in females; hind edge of pronotal disc



Figs 158–165. Tribe Gymnobothrini. **Figs 158–162, 164–165.** *Rastafaria abessinica*: **158**. Whole male insect lateral aspect; **159**. Dorsal aspect vertex; **160**. Oblique view vertex; **161**. Pronotal disc; **162**. Epiphallus; **164**. Female spermatheca; **165**. Female sub-genital plate from above and its apex from below. **Fig. 163.** Epiphallus of *C. morotoensis.* All scales represent 1 mm: (upper) applies to Figs 159, 160, 162, 163; (lower) applies to Figs 158, 161, 164, 165.

broadly rounded to slightly emarginate (Fig. 161). Tegmina varying from slightly shorter to slightly longer than pronotal disc. Hind femora relatively slender. Male cerci elongate, tapering, but with rounded apices; supra-anal plate with medial groove extending half way to tip. Epiphallic lophi more elongate and robust than in most other members of group (Fig. 162; compare with Fig. 163). Coloration extremely variable, but characteristically with green and olivaceous pigmentation much in evidence. Female anatomy as in Figs 164, 165. Measurements (in mm); total length males 12–16, females 15–22.

Discussion.—In re-establishing *Rastafaria*, Bouvy (1982) considered that it included *R. abessinica* and three other taxa*: amplificata amplificata* (Johnston, 1937) and *amplificata morotoensis* Jago, 1968, transferred from *Gymnobothroides*, and *Rastafaria triangularis* Bouvy, 1982, described as new. Here *Rastafaria* becomes a monotypic genus again.

Species notes

Rastafaria abessinica Ramme, 1931
Figs 158–162, 164–165

Rastafaria abessinica Ramme, 1931: 931–2, 5 figs.
Gymnobothroides hypsophilia Jago, 1968 (Bouvy 1982).

Material.—ETHIOPIA: Kefa prov. W. of Jimma (Bellela forest), 2075 m; 16 km N.E. of Jimma (Badabuna forest); Walaga prov. 4 km N.E. of Nkemte; 6.4 km W. of Ghimbi; between Bambesi and Asosa; between Mendi and Bambesi; 33.6 km W. of Mendi; Shewa prov. 13.4 km W. of Hager Hiwot; Guder-Nkemte rd. W. of Mendi. UGANDA: Bugisu, Mt. Elgon, above Bumasifwa, Bumagabula (34°27′E 01°09′N), 2400 m. KENYA: Kericho (NHMUK).

Description.—As in generic key and description. A distinctive species recognizable especially from structure of its head and pronotum and its striking coloration. Structural and color variation is considerable not only between samples from different localities, but also in material from same locality, notably in a very long series of *G. hypsophilia* from Mt. Elgon. Among these, the range of color variation is truly remarkable; in males general coloration is olivaceous green to green with black antennae with or without a lateral black stripe variously developed and coupled with fine dark speckling; underside of abdomen yellowish apically. Hind femora with knees black, remainder yellow and lower inner and outer areas more or less suffused with bright pink pigmentation. Hind tibiae dull greyish blue. Females exhibit an even greater range of color variation, some are even brighter green than males, with a rich suffusion of crimson on lower inner and outer areas of hind femur, while others are of predominantly brown pigmentation with a well-marked broad dark lateral stripe. Brown variants are more usual in Ethiopian populations, which also exhibit considerable differences from Ugandan ones, notably in shape of frontal ridge and pronotal disc. The single male specimen from Kericho, Kenya, is close to Ugandan series.

Distribution.—ETHIOPIA, UGANDA, and KENYA; habitats at medium to high altitude.

Generic diagnosis

Gymnobothrus I. Bolívar, 1889

Gymnobothrus I. Bolívar, 1889: 100.
Ogmothela Karsch, 1896 (syn. Uvarov 1953).
Pseudochirista I. Bolívar, 1909 (syn. Uvarov 1953).
Orthochirista Sjöstedt, 1933 (syn. Uvarov 1953).
Gymnobothroides Karny, 1915 **syn. n**.
Phloeochopardia Dirsh, 1958 **syn. n.**

Type species.—*Gymnobothrus linea alba* I. Bolívar 1889: 100, by original designation.

Description.—As in key to genera (p. 67). Size below medium, mostly small. Size (in mm); total length: males 11–20, females 16–30. Antennae filiform, occasionally incrassate, basal segments sometimes flattened, rarely weakly expanded; length variable from less than to sometimes considerably more than that of combined length of head and pronotum. Frons oblique, slightly excurved; frontal ridge mostly flat or weakly sulcate, fairly broad with obtuse lateral margins weakly diverging downwards; constriction at junction with fastigium of vertex mostly weak. Fastigium concave, parabolic or trapezoidal with well-developed carinulae and shallow, but usually distinct, transverse arcuate sulcus in varying positions. Fastigial rim thick, temporal foveolae narrow, shallow and rugose, concealed from above. Pronotum more or less constricted; medial carina strong; lateral carinae partly or completely developed and more or less incurved; of three transverse sulci crossing pronotal disc only posterior one interrupts medial carina, but the others may also cut lateral carinae; metazona as long as, longer than, or shorter than prozona, its hind margin obtuse-angular, broadly rounded and occasionally weakly emarginate. Tegmina and wings fully developed, shortened, or vestigial; reticulation of tegmina moderately dense, with intercalary vein of medial area usually present. Hind femora moderately slender; arolia moderately large. External and internal genital structures characteristic for group, but shape of epiphallus may additionally be diagnostic. Coloration variable, even in sympatric populations speckled, marbled or striped patterns of cryptic hues and shades of grey, brown, stramineous, with some dark maculation; green pigmentation very rare, but various degrees of fire melanism common. Bright coloration (red, orange, ferruginous or yellow) of lower outer and/or inner face of hind femur in some of the species diagnostic.

Discussion.—*Gymnobothrus* is closely related to the other large genus *Coryphosima*, from which it differs principally in a greater diversity of structural characters (see above). *Gymnobothrus* was reviewed by Uvarov (1953), who provided an annotated list citing 22 African species, two of them with subspecies. Further changes in species composition were made by Dirsh (1966, 1970) and Jago (1968, 1970). Bouvy (1982) focussed upon *Gymnobothroides*, a genus separated from *Gymnobothrus* only on the basis of tegminal reduction (cf. Uvarov 1953, Jago 1968). However, in line with reasoning pursued in reviewing *Coryphosima* (see above), the present author considers *Gymnobothroides* to be members of *Gymnobothrus* which have undergone extreme forms of wing reduction. They are predominantly species of restricted, disjunct distribution in highland habitats, and some show close affinities with species in adjacent lowlands. For instance, *Gymnobothroides pullus* and *Gymnobothrus rimulatus* are so close morphologically (cf. Figs 247–258) that they are certainly congeneric. Here 21 species are considered valid; of these, the two Madagascan species *G. madacassus* Bruner and *G. variabilis* Bruner, plus two others (*G. oberthuri* I. Bolívar and *G. romeri* Karny), are omitted from this review because of lack of information. Some taxa are based on local variants or are clearly synonymic with valid ones.

Distribution.—Whole of Africa south of the Sahara.

Diagnosis of species groups

Species groups are divided into **macropterous** (with species sub-groupings keyed below), **brachypterous** and **micropterous** genera.

Key to species groups and sub-groups within the genus *Gymnobothrus*

Macropterous group: Apices of folded wings and tegmina reach or surpass tip of abdomen.

1 Pronotal constriction weak, disc relatively flat, lateral carinae straight and weakly divergent caudad, or parallel, more or less slightly inflexed in prozona and more divergent in metazona. All pronotal carinae interrupted by posterior transverse sulcus and lateral carinae by one other; costal area of tegmen often with a distinct whitish stripe .... *lineaalba* sub-group
– Pronotum more or less constricted, lateral carinae more or less distinct, roundly or angularly inflexed, interrupted by all three transverse sulci 2
2 Lateral carinae angularly convergent in an X pattern onto first sulcus, strongly defined .... *cruciatus-longicornis* sub-group
– Lateral carinae more or less regularly, roundly incurved and strongly, or often weakly, defined 3

3 Antennae slender, much longer than head and pronotum together; metazona longer than prozona; lower outer area of hind femur reddish-ferruginous .... *temporalis* sub-group

– Antennae thick and shorter than, or barely longer than, head and pronotum together; lower outer area of hind femur yellowish .... *anchietae* sub-group

Brachypterous group: Tegmina and wings abbreviated, reaching only the middle of abdomen, or somewhat shorter, but in dorsal position. Includes *G. rimulatus* Karsch and *G. bounites* Jago which have close affinities with the *cruciatus* and *anchietae* species groups respectively.

Micropterous group: Tegmina and wings vestigial in lateral position (= the former genus *Gymnobothroides* Karny).

Macropterous group: **The *lineaalba* species sub-group**

Discussion.—Includes two species: *G. lineaalba* I. Bolívar, 1889 (widespread; savanna and woodland savanna belts Africa south of the Sahara) and *G. carinatus* Uvarov, 1941 (South Africa).

Key to species in *lineaalba* species sub-group

1 Strongly raised pronotal carinae; lateral pronotal carinae cut by both third and first sulcus (Fig.181). Epiphallus Fig. 182. SOUTH AFRICA .... *carinatus* Uvarov, 1941

– Pronotal carinae not strongly raised; lateral pronotal carinae cut by second and third sulcus (Figs 166, 168, 174). Epiphallus Figs 177, 178. Widespread south of Sahara................*lineaalba* I. Bolívar, 1889

Species notes

Gymnobothrus lineaalba I. Bolívar, 1889

Figs 166–180

Gymnobothrus linea alba I. Bolívar, 1889.
Chortoicetes subparallelus Rehn, 1914 (syn. Dirsh 1970).
Chortoicetes albomarginatus Karny, 1915 (syn. Uvarov 1953).
Pseudochirista houyi Ramme, 1931 (syn. Uvarov 1953).
Orthochirista variegata Sjöstedt, 1931. **syn. n.** (Fig. 166A).
Orthochirista elgonensis Sjöstedt, 1931, **syn. n.**

Material.—GUINEA: Mamou (type locality of *Chortoicetes albomarginatus* Karny). Central African Republic: Pama Quelle, (type locality of *Pseudochirista houyi* Ramme). UGANDA: Entebbe; Kakumiro; Mubende; Lake Rudolf (now KENYA); Buddu Kakuto; Lwango Buddu; Bugwere; Kapeka; Masaka Lwango; Kalisizo; Lango; Kabwe; Ankole; Lubale-Lwentobo; Ankole Lwasamaire, Koki; Lake George; Kazinga Channel; Kibale; Tororo; Chiawante Lango. KENYA: Donyo Sabuk; Thika; Mombasa; Baringo; Masai Mara; Witu Forest Res. Maralal; Emali range S. of Sultan Hamud; Emsu dist. 00˚41′S, 37˚28′E; Chyulu hills S.E. end, 77 kms from Makutano; Taita hills. ETHIOPIA: Addis Ababa; Lake Zwai; Sire; Harrar; Lake Bishoftu. ZAMBIA: Chyanga; Chingola, Mbala, Ndola. D.R. CONGO: Bunia upland 4500′; Gety; Kasenyi. ANGOLA: 3 mi. N. Sta. Comba. SOUTH AFRICA: Free State, Witzeishoek, 6100′ (1860 m); Kwa-Zulu Natal; Transvaal (Gauteng).

Description.—Relatively slender build; size medium to below medium for genus. Integument smooth, matte. Antennae thick, weakly flattened and dilated basally; as long as, to slightly longer than head and pronotum in male, somewhat shorter in female. Antennae with conspicuous white annuli in life. Frontal ridge broad with low thick margins weakly divergent towards clypeus; fastigial constriction weak (Fig. 167). Fastigium of vertex oblong, weakly concave with low margins, longer than wide in male (Fig. 176), shorter in female; temporal foveolae narrowly elongate (Fig. 175). Pronotal disc broad, weakly tectiform, somewhat variable in shape as in Figs 168–174; lateral carinae straight and weakly divergent caudad, or parallel, more or less slightly inflexed in prozona and more divergent in metazona. Lateral carinae vary from weak to strong and callose; first transverse sulcus weak, second strong, cutting lateral carinae (Fig. 166). Wings extend beyond hind knees and in some specimens (notably from Uganda) are exceptionally long. Genital structures as in Figs 179–180. Coloration variable in shades of brown, stramineous, and grey; dorsum usually paler than sides; face sometimes speckled, bearing an oblique ochraceous stripe below ocellus; pronotal disc uniformly colored, or sometimes with narrow dark brown stripes bordering contrastingly pale medial carina; lateral pronotal lobes often with a broad dark stripe and a large yellowish spot below (Fig. 166). Costal area of tegmina often with a contrasting white stripe and medial area with a chain of alternating dark and light spots. Wings hyaline, slightly infumate apically. Hind femur with dark knee and three more or less distinct oblique stripes across upper face; lower outer face greyish, inner ochraceous. Hind tibia greyish, with pale sub-basal ring. Measurements (in mm): total length males 12.0–16.5, female 17.0–24.0.

Discussion.—Our material exhibited considerable structural and color variation. Much of this occurs within sympatric populations. On this basis *G. variegatus* (Sjöstedt) and *G. elgonensis* (Sjöstedt), are variants *of G. lineaalba* and become **new synonyms** of it. (cf. Fig. 166A vs. Figs 168–174).

Distribution.—SIERRA LEONE, GUINEA, GHANA, IVORY COAST, CAMEROON, UGANDA, KENYA, SOUTH SUDAN, TANZANIA, ANGOLA, ZAMBIA, ZIMBABWE, MALAWI, ETHIOPIA, LESOTHO, NAMIBIA, SOUTH AFRICA.

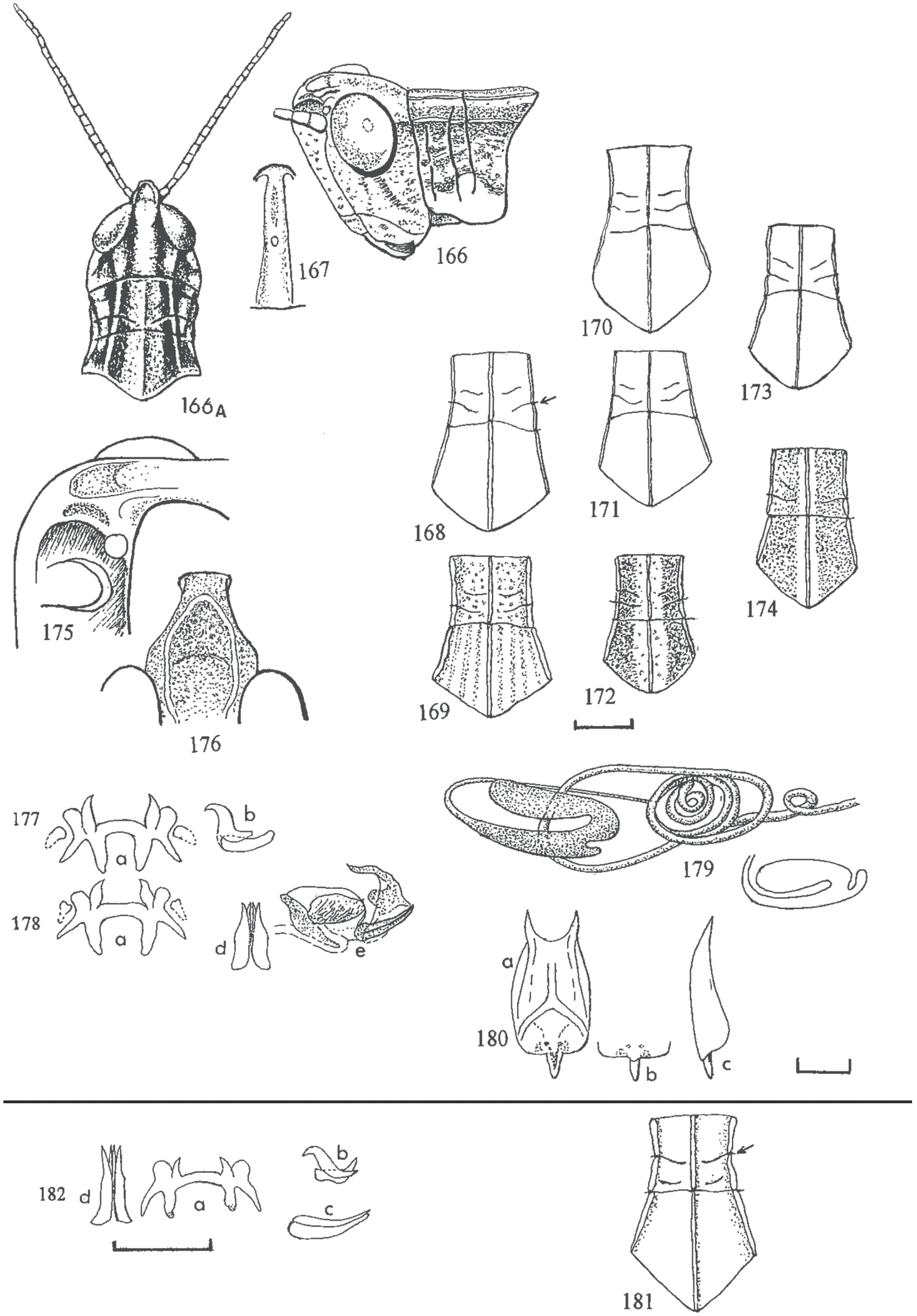
Gymnobothrus carinatus Uvarov, 1941

Figs 181,182

Gymnobothrus carinatus Uvarov, 1941: 50.

Material.—SOUTH AFRICA: Western Cape (as Cape Province): Cape peninsula, Groote Schuur, Kirstenbosch; Constantia Nek; (Orange) Free State: Zostron; Kwa-Zulu Natal: Drakensberg. LESOTHO: Mokhotlong.

Description.—Slightly smaller but more robust than preceding species. Size (in mm); total length: males 14–15, females 17–18. Sculpturing of integument somewhat coarser. Antennae barely the length of head and pronotum, somewhat incrassate and flattened basally. Frontal ridge thick, sulcate below medial ocellus. Fastigium of vertex parabolic, considerably longer than wide; temporal foveolae kidney-shaped, deep. Pronotal disc rugulose (Fig. 181), medial carina strongly raised, acute; metazona longer than prozona, its hind margin forming a right angle with the tip rounded; lateral carinae well developed, weakly inflexed in prozona and interrupted by the first and the main transverse sulci. Epiphallus as in Fig. 182. Coloration similar to *lineaalba* except for the unusual occurrence of females with dark-green dorsum, not known in other species of the genus. Upper face of hind femur immacu-



Figs 166–182. Tribe Gymnobothrini. **Figs 166–180**. *Gymnobothrus lineaalba*: **166A.** *Orthochirista variegata* Sjöstedt (**n. syn.** of *Gymnobothrus lineaalba)*, reproduced from Sjostedt (1931). **166.** Oblique view head and pronotum; **167.** Frontal ridge; **168–174.** Variation in pronotal disc; **175.** Oblique view vertex; **176.** Dorsal view vertex; **177, 178.** Variation in phallic structures; **179.** Female spermatheca; **180.** Female subgenital plate **A.** Dorsally and its apex **B.** Ventrally and **C.** Laterally. **Figs 181, 182.** *Gymnobothrus carinatus:* **181.** Male pronotal disc; **182.** Epiphallus and aedeagal valves. Scale lines all represent 1 mm: bottom left scale under Fig. 182 applies to Figs 175–179, 182; scale under Fig. 172 applies to all the rest.

late brown; lower outer face yellowish; inner face and tibia light brownish. Both light and fire melanic forms occur.

Distribution.—SOUTH AFRICA.

Macropterous group: The *cruciatus-longicornis* species sub-group

Description.—All possess a pronotal disc with a distinctive X pattern of more or less straight, angularly convergent lateral pronotal carinae.

Discussion.—Includes two species: *Gymnobothrus longicornis* (Ramme, 1931) and *Gymnobothrus cruciatus* I. Bolívar, 1889.

Key to species in *cruciatus-longicornis* species sub-group

1 Antennae slender and much longer than combined length of head and pronotum even in females; frontal ridge with a marked constriction at its junction with fastigium of vertex (Fig. 189). Lateral pronotal carinae mostly weak and obliterated between first and second transverse sulci; hind femur with distinctive dark pattern (Fig. 191). ....*Gymnobothrus longicornis* (Ramme, 1931)

– Antennae only slightly longer than or same length as head and pronotum; frontal ridge only weakly constricted at its junction with vertex (as in Fig. 190). Lateral pronotal carinae mostly strong and not obliterated between first and second sulci. Hind femur mostly immaculate or with a short blackish stripe in middle of upper external area (Fig. 192).........................*Gymnobothrus cruciatus* I. Bolívar, 1889

Species notes

Gymnobothrus longicornis (Ramme, 1931)

Figs 183–192

Pseudochirista longicornis Ramme, 1931: 921, 927, pl.11, fig. l.
(Transferred to *Gymnobothrus* by Uvarov 1953: 122).

Material.—Holotype male *longicornis*: CENTRAL AFRICAN REPUBLIC: Bosum, Sanga-Lobadje.

Description.—As defined in the key above.

Discussion.—The various subspecies in this complex include several closely related taxa which are distributed across western Africa to East Africa and south to ANGOLA. In view of their close similarity and occurrence of clinal links between these species, they are here reduced to the level of subspecies under *longicornis* Ramme. It is conceivable, however, that two other extant taxa, *oberthuri* I. Bolívar, 1890 and *romeri* (Karny, 1909), from Tabora and Amani in TANZANIA respectively (not reviewed here as no material was available), could also belong to this group and thus in due course take precedence as older synonyms of *longicornis*.

Gymnobothrus longicornis ephippinotus Jago, 1966, stat. n. et comb.

Gynmobothrus ephippinotus Jago, 1966: 1949–1951, figs 18–25.

Material.—GHANA: Northern Region, Masaka, Tamale rd; Bulkwere; Bole; Yeji; Cambogu Upper reg.: Han; Tamu; N. of Nakpanduri, Gambaga scarp; Volta reg: 2ml.W of Kpandu; Ashanti reg: Jema; Keti Krachi. BURKINA FASO: 2 mi. N.E. of Kantchari. NIGERIA: Bida; Oyo; Kanije; Shagunu; Onigbu; Akwanga; Matyoro Lakes, 25 mi. N. Gombe.

Description.—General coloration dark blackish and brown markings against lighter background, often with dorso-medial cream stripe. Lateral pronotal lobes lighter ventrally. Tegmina with a series of 5–6 dark spots in medial area. Male abdomen reddish ventrally at maturity. Coloration of hind femora: upper area with 3 dark blackish spots extending as paler broad diffuse markings onto outer area; lower outer area with brownish-black stripe; inner area yellowish to blackish. Hind tibiae bluish-grey with black pigment basally, distally and ventrally. Measurements in Table 8.

Discussion.—Similar to nominate subspecies from CAMEROON, differing from it principally in more concave fastigium of vertex and more intensive black pigmentation, particularly of hind femora.

Distribution.—Guinea savanna of GHANA, BURKINA FASO, NIGERIA, and probably adjacent countries of western Africa. Adults in II, III, IV, V, VII, XII.

Gymnobothrus longicornis longicornis (Ramme, 1931), stat. n.

Figs 183–192

Pseudochirista longicornis Ramme, 1931: 925, 927, pl. 11, fig. l.

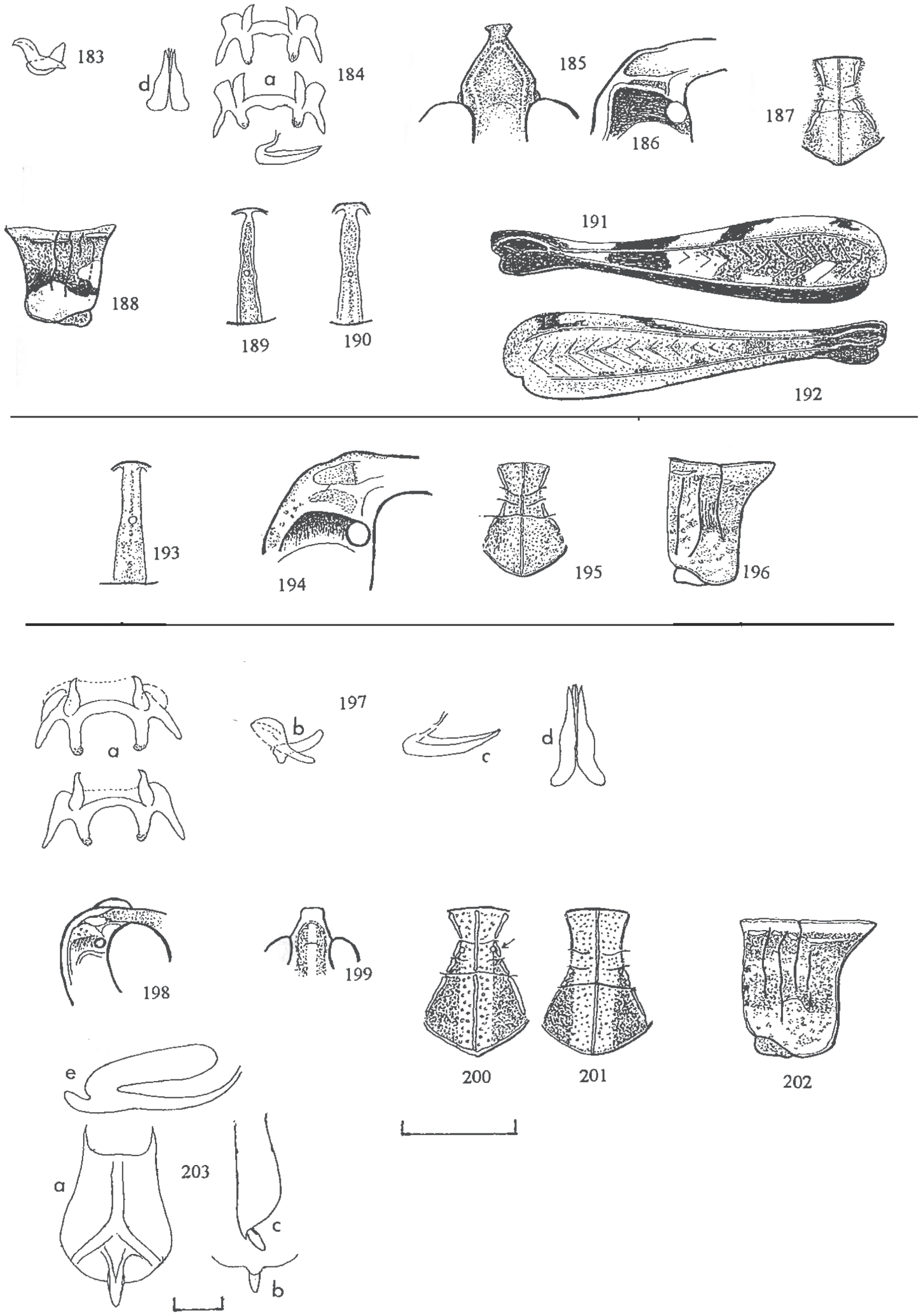
Material.—UGANDA: Koki; Lango district; Chiawanto; Adechal; Lake Albert, Butiaba; Fort Portal; Bundebugyo. TANZANIA: Mkwemi, 22 mi. W. of Kahama; Morogoro; Mpwapwa, Mt. Kibabiani; 28 mi. N. Biharamulo.

Description.—In size and general build similar to subsp. *ephippinotus*. Size (in mm): total length: males 14.0–19.0, females 16.5–22.0. Antenna about 1.5x length of head and pronotum, its medial segment about 3 times longer than wide. Frontal ridge (Figs 189, 190), with fairly sharp margins, narrowly constricted apically, its surface pitted and shallowly sulcate. Fastigium of vertex less elongate and concave than in *ephippinotus*; foveolae narrow and deeply sulcate. Pronotum as in *ephippinotus*, but lateral carinae slightly stronger. Coloration in lighter shades than in *ephippinotus*, more uniform and less speckled. Dorsum is generally paler than sides; abdomen and underside fawnish; dark pattern on lateral pronotal lobes (Fig. 188). Pattern on outer face of hind femur as in Fig.191; lower inner and outer face blackish brown.

Discussion.—The original paratype from Cameroon shows close similarity to the material from the Imatong area of South Sudan and from Uganda. In these, the fastigium of vertex is more broadly rounded, frontal ridge less sulcate, and lateral pronotal carinae stronger. Coloration of the Imatong specimens is also fairly simi-

Table 8. Morphometric measurements of *Gymnobothrus longicomis ephippinotus*.

	M (mm)	F (mm)
Antenna/length of head plus pronotum ratio	1.5	1.5
Tegminal length	16–19	17.5–21.5
Hind femur length	10–12	12–14
Total length	15–20	17–23



Figs 183–203. Tribe Gymnobothrini. **Figs 183–192.** *Gymnobothrus longicornis*: **183, 184.** Variation in epiphallus and aedeagal valves; **185.** Dorsal view male vertex; **186.** Oblique view male vertex; **187.** Male pronotal disc; **188.** Lateral view pronotum; **189.** Frontal ridge (C.A.R., Bosum); **190.** Frontal ridge (Tanzania, nr Kahama); **191.** Posterior femur, pattern on outer side (Cameroon); **192.** Ditto, Tanzania. **Figs 193–196.** *Gymnobothrus longicornis sellatus* male: **193.** Frontal ridge; **194.** Oblique view vertex; **195.** Pronotal disc; **196.** Lateral aspect pronotum. **Figs 197–203.** *Gymnobothrus cruciatus* male: **197.** Epiphallus and aedeagal valves; **198.** Oblique view vertex; **199.** Dorsal view vertex; **200.** Pronotal disc (Tanzania syntype *elongata)*; **201, 202.** Lateral aspect pronotum (Tanzania and Angola, Villa Luso holotype *cruciatus* s.str.); **203.** Female: **E.** Spermatheca and **A–C.** Aspects of subgenital plate. All scales 1 mm: that under Fig. 200 applies to Figs 183–186, 194, 197–199; that under Fig. 203 applies to Figs 187–193, 195, 196, 200–203.

lar: pronotal disc mostly pale, but occasionally edged with dark brown; lateral dark fascia is strong, covering upper 2/3 of pronotal lobes, but with a contrasting large cream spot along its anterior edge. Abdomen orange with a chain of intricate spots along tergites; series of spots on tegmina is faint and outer face of hind femur has a large pale spot, while upper face bears 3 alternating dark and pale spots; sub-basal pale spot is particularly vivid and contrasting in melanic forms. Lower outer face is brown and inner yellow. Hind tibia greyish brown with a broad pale sub-basal ring.

In Ugandan material antennae are equally long and slender, scarcely dilated basally; frontal ridge narrow, deeply sulcate at the ocellus, less so above and below; fastigium of vertex more parabolic; temporal foveolae narrow or broader, deeper below edge of rim, incompletely marginate below. Lateral pronotal carinae somewhat stronger and prozona subequal in length to metazona. Coloration in contrasting patterns of browns and pale cream; face a triangular mask of brown edged with cream; dark lateral fascia broad, paler in middle, its pattern on lateral pronotal lobes as in Fig. 188. Dark pattern on outer face of hind femur as oblique faint stripes, lower outer face dark brown, inner yellow.

In Tanzanian specimens (Mkwemi, Kahama) antennae are long, slender, and completely black; ratio to length of head and pronotum, 1.5 in male. Frontal ridge pitted and somewhat sulcate at ocellus, but fastigial constriction less marked (Fig. 190). Temporal foveolae consist of multiple shallow pits. Lateral pronotal carinae rather weak. Coloration is distinctive, predominantly in contrasting deep dark brown and cream; usually a pale dorso-medial stripe edged with dark brown present; face a mask of lighter brown triangle bordered with cream; pattern of lateral pronotal lobes brown, ochre and cream; abdomen is ferruginous with brown speckling; black pattern on hind femur confined to three spots on upper face and hind knee, but outer face slate-grey and brown, with lower outer face orange and inner face yellow (Fig. 192). Specimens from Morogoro are darker, have shorter antennae and a broader frontal ridge.

Distribution.—CAMEROON, CENTRAL AFRICAN REPUBLIC, SOUTH SUDAN, UGANDA, TANZANIA.

Gymnobothrus longicornis sellatus (Uvarov, 1953), stat. n. et comb. n.

Figs 193–196

Gymnobothrus sellatus Uvarov, 1953.

Material.—ANGOLA: Moxico dist. rivers Lumeje; Munhango, Lungue Bungu, Mu-Simoj; Bihe dist. Cohemba. Also, Tundavala; Bruco; 15 mi. N. Sa de Bandeira; River Langiliko.

Description.—Size (in mm): males 16–19, females 18–21. Similar to other subspp. in size, general appearance, and elongate antennae; differs in following respects: Frontal ridge broadly sulcate from above ocellus downwards, flat and punctured elsewhere, its fastigial constriction weak (Fig. 193). Fastigium of vertex strongly concave, pentagonal, about as long as broad; temporal foveolae fairly large, incompletely marginated below (Fig. 194). Pronotum markedly more constricted ('sellate') than in other subspecies; lateral carinae obliterated between first and second sulci and in posterior 2/3 of metazona, strongly callose elsewhere (Fig. 195). Lateral pronotal lobes much deeper than long, their surface very uneven (Fig. 196). Coloration brown, mottled with ivory-white, buff, and grey; lateral pronotal lobes with typical pattern brown above, ivory-white below. Tegmina grey with a series of brownish spots along discoidal field and beyond it. Abdomen reddish-brown below; upper face of hind femur with large brownish-black spots, outer face brown above, yellow below, while lower outer area brown. Hind tibia yellowish touched with black on inner and outer face.

Discussion.—The specimens from Bruco are less sellate and coriaceous and more like those from Tanzania.

Distribution.—ANGOLA. Adults recorded in VI, VIII, IX, X.

Gymnobothrus cruciatus I. Bolívar, 1889

Figs 197–203

Gymnobothrus cruciatus I. Bolívar, 1889: 101.
Chortoicetes fallax Karny, 1907 (syn. Dirsh 1966).
Pseudochirista fallax elongata Miller, 1925 (syn. Dirsh 1966).
Pseudochirista meruensis Sjöstedt, 1929 (syn. Uvarov 1953).

Material.—TANZANIA: Tukuyu vii.1923, N. C. E. Miller (Holotype male and 7 males, 11 female paratypes (some IX.1924) of *Pseudochirista fallax elongata* Miller); Morogoro; Mpwapwa, Mt. Wilkins 6000′ (1830 m); Mkwemi 22 mi. W. Kahama; 60 mi. W. Amani; 6 mi. W. Kibau; 8 mi. S. Chala Mission. UGANDA: Lake George; Kigezi, Kashonji 7000′ (2135 m). SOMALIA: Haud. D.R. CONGO: Lake Edward; Kasenyi. ANGOLA: Villa Luso 3000′ (915 m), 7.VI.1927, M. Burr (labelled by Uvarov as homotypic with cotype of *G. cruciatus* I. Bolívar). KENYA: Turkana. ZAMBIA: Kabundi forest at Chingola (Johnsen 1984).

Description.—Closely similar to *G. longicornis*; similar but of more variable size and of more robust build. Size (in mm): total length males 13–18, females 17–23. Antennae usually thin, barely longer than head and pronotum in male, shorter in female. Frontal ridge broad, narrowly sulcate at medial ocellus, flat or convex elsewhere; margins low and thick, only weakly divergent towards clypeus and constricted at junction with fastigium. Fastigium parabolic; arcuate sulcus near mid position (Fig. 199). Foveolae mostly weak, elongate and narrow, or as series of shallow pits (Fig. 198). Pronotum of rather variable structure; carinae straighter than in *longicornis* and mostly strong and callose throughout, even between first and second sulci, but becoming obsolete towards rear margin of metazona. Latter longer than prozona and more broadly expanded than in *longicornis* (Figs 200–202). Epiphallus as in Fig. 197; spermatheca as in Fig. 203.

General coloration brownish, mottled and striped; face often with several alternating horizontal dark and light stripes; occiput and pronotal disc with a pale dorso-medial stripe edged with dark-brown lateral stripes, contrasting with callose ivory-white lateral carinae. Lower posterior part of lateral pronotal lobes with large ochraceous spot; abdomen light brown; tegmina with series of blackish spots in medial area; hind femur uniformly brown, sometimes with a small blackish stripe in middle of upper external area; lower areas brownish or yellowish. Hind tibia brownish with a pale sub-basal ring.

Discussion.—There is considerable structural, size, and color variation, with some specimens, for instance those from Mt. Wilkins in Tanzania (NHMUK collection), being fairly distinct from others. Subspecies status for them does not, however, seem justified at present. The types of *Pseudochirista fallax elongata* Miller were examined and are considered conspecific with a specimen of *Chortoicetes fallax* Karny bearing that author's name label. A specimen of *G. cruciatus* I. Bolívar (det. Uvarov) is also a close match with neotype material of I. Bolívar; this confirms the synonymy proposed by Dirsh (1966, 1970), and which is therefore adopted here.

Distribution.—KENYA, TANZANIA, UGANDA, SOMALIA, D.R. CONGO, ANGOLA, ZAMBIA.

Macropterous group: The *temporalis* species sub-group

Discussion.—This group includes the two closely related species: *Gymnobothrus temporalis* (Stål, 1876) and *Gymnobothrus flexuosus* (Schulthess, 1898). The latter was established by Kevan (1950) as a subspecies of the former, but in view of the marked morphological and color differences and their broadly sympatric distribution, which is indicative of an ecological rather than geographical distinction, the two taxa are here re-established as distinct species.

Key to species in *temporalis* species sub-group (Figs 204–224)

1 Tegmina extend well beyond the hind knees. Pronotal metazona considerably longer than prozona (Figs 205, 209). Hind femur without distinct dark bands along upper face; lower faces in shades of ferruginous-reddish .... *G. temporalis* (Stål, 1876)

– Apices of folded tegmina only just reach hind knees of posterior femora. Pronotal metazona only slightly longer than prozona (Figs 213, 217, 221). Hind femur with distinct dark bands on upper face; lower faces in shades of yellow-ochraceous .... *G. flexuosus* (Schulthess, 1898)

Species notes

Gymnobothrus temporalis (Stål, 1876)[2]
Figs 204–212

Epacromia temporalis Stål, 1876: 49, type female, NAMIBIA: Ovambo (NR, Stockholm)
Chirista virgata Karsch, 1893 (syn. Uvarov 1926), type female, TOGO (MfN)
Chirista flavolineata Karsch, 1893 (syn. Uvarov 1926), type male (MfN)
Chirista manca Karsch, 1893, types male, female (MfN) (syn. Uvarov 1926)
Chirista interrupta Karsch, 1896, female, TANZANIA: Zanzibar (syn. Sjöstedt 1909)
Chirista lacustris Rehn, 1914, female, D.R. CONGO (MfN) (syn. Uvarov 1926)
Chirista emini Rehn, 1914, female, D.R. CONGO, L. Albert (MfN) (syn. Dirsh 1970)
Zacompsa temporalis Uvarov, 1926 (syn. Uvarov 1953)
Pseudochirista temporalis fasciata Sjöstedt, 1931, types male, female, CONGO: Musana (NRM Stockholm) (syn. Uvarov 1953)

Material.—Series examined from: SENEGAL, GUINEA BISSAU, MALI, GUINEA, LIBERIA, SIERRA LEONE, TOGO, BENIN, IVORY COAST, GHANA, NIGERIA, CHAD, CAMEROON, ETHIOPIA, SOMALIA, SOUTH SUDAN, UGANDA, KENYA, TANZANIA, CONGO, D.R. CONGO, RWANDA, MALAWI, ZAMBIA, ZIMBABWE, NAMIBIA, MOZAMBIQUE, BOTSWANA, SOUTH AFRICA (former Transvaal, Natal, Orange Free State, Cape Province).

Description.—Medium to larger size for genus; medium build. Size (in mm): total length males 15–19, females: 21–28. Integument finely rugulose and pitted. Antennae in male somewhat longer than, in female slightly shorter than head and pronotum. Frontal ridge broad, weakly sulcate at and below ocellus, flat to convex above with thick margins; only weakly constricted at junction with fastigium and divergent towards clypeus (Figs 208, 212). Fastigium elongate-parabolic (Figs 207, 211); its surface concave, sloping towards transverse sulcus. Latter roughly in mid-position. Foveolae distinct, kidney-shaped (Figs 206, 210). Pronotum somewhat compressed in middle. Medial carina distinct; lateral carinae often weak and little more than a chain of small callosities interrupted by all three transverse sulci, inflexed and convergent towards first sulcus, parallel between first and second, and broadly outflexed and divergent beyond. Metazona distinctly longer than prozona, its hind margin broadly rounded (Figs 205, 209). Genital structures are of little diagnostic value. Coloration variable; often dull in sombre shades of browns and greys with darker black and lighter stramineous and white speckling and mottling; fire melanism frequent. Distinctive pale patterns occur in less than a quarter of specimens, more often in males. These include a striking pale spot in lower part of lateral pronotal lobes and sub-basal part of upper face of hind femur, sometimes with two smaller, less distinctive spots further towards knee of hind femur (including a preapical ring before knee and a corresponding pale sub-basal ring on tibia). Hind knee black in male, paler brown in female. Dorsum generally paler, sometimes with a pale dorsal band of varying width; when narrow, usually bordered with dark blackish brown pigmentation. Sides often have a dark lateral band on genae and upper margin of lateral pronotal lobes. Underside of male abdomen towards its tip and lower outer (plus often inner faces of hind femur), ferruginous to reddish. Pale markings more striking in black melanic specimens and reddish tinge more intensive on maturation.

Discussion.—*G. temporalis* is the most common and widespread species in the genus. There is considerable clinal geographical variation in size, shape and coloration; subspecific taxonomic subdivisions are not warranted. Dirsh (1970) took the same view when synonymizing *G. emini* under *G. temporalis.* It appears to have a strategy of adult quiescence, 1–2 generations annually.

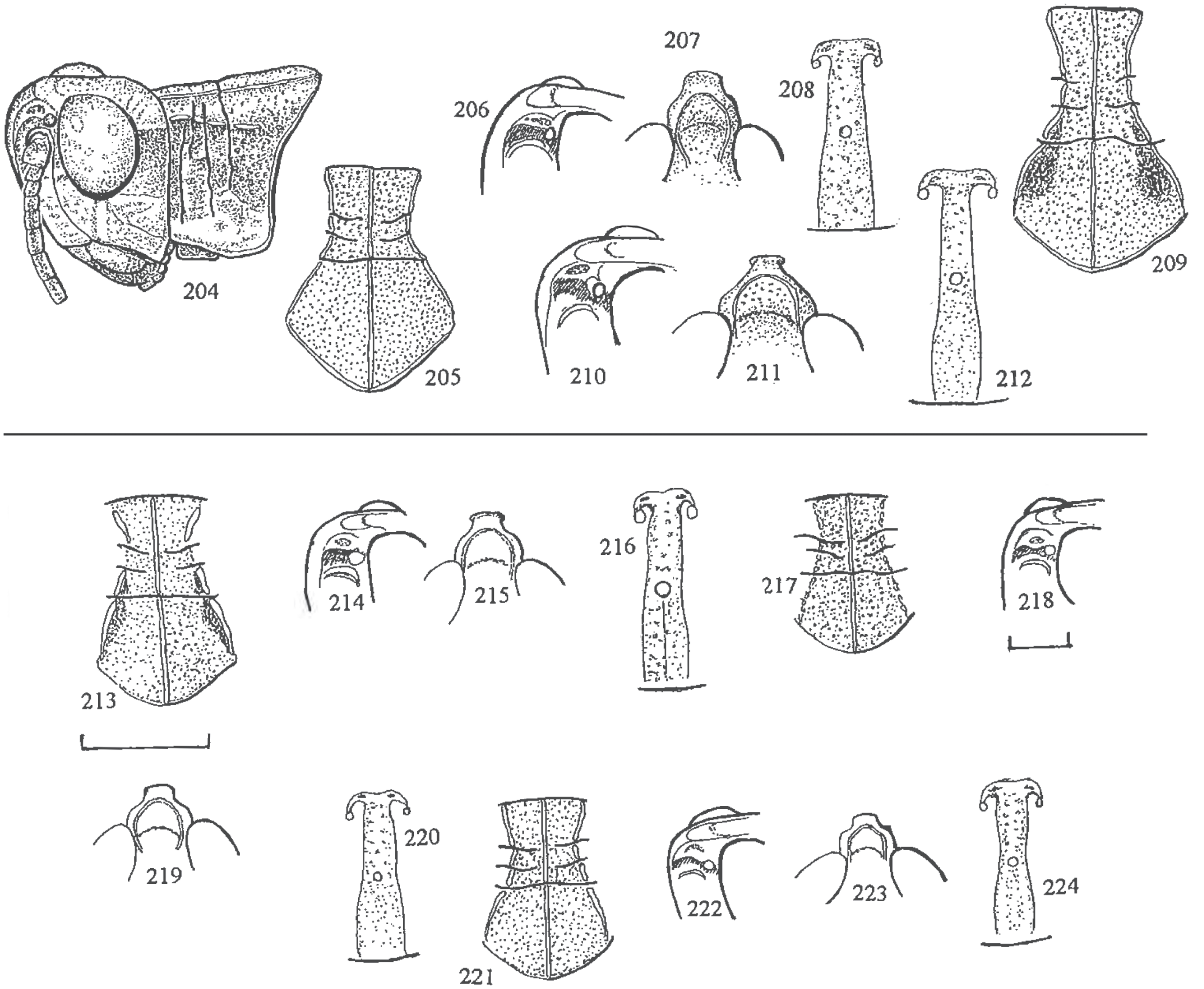
Distribution.—Found in the savannas and woodlands of the southern Sudanian and Guinean zones from SENEGAL and GAMBIA in the west to SUDAN and ETHIOPIA in eastern Africa, and southwards to southern Africa.

Gymnobothrus flexuosus (Schulthess, 1898)
Figs 213–224

Duronia flexuosa Schulthess, 1898: 186, pl.2, fig. 9, type male, SOMALIA: Banas, Geneva Mus.
Chirista flexuosa Kirby, 1910: 143.
Zacompsa brevipennis Miller, 1929: 70, pl. 9, fig. 42, type male TANZANIA: Kilosa, NHMUK (syn. Kevan 1950).
Ogmothela brevipennis Ramme, 1931: 928.

---

[2] Dirsh 1965: 446, fig. 357, whole insect.



Figs 204–224. Tribe Gymnobothrini. **Figs 204–212.** *Gymnobothrus temporalis* male: **204.** Oblique view head and pronotum. (205–208, topotype material *temporalis* from Namibia; 209–212, topotype material *emini*, D.R. Congo). **205, 209.** Pronotal disc; **206, 210.** Oblique view vertex; **207, 211.** Dorsal view vertex; **208, 212.** Frontal ridge. **Figs 213–224.** *Gymnobothrus flexuosus* male: (213–216, *brevipennis*; 217–220, Ethiopia, Wardere; 221–224, Angola). **213, 217, 221.** Pronotal disc; **214, 218, 222.** Oblique view vertex; **215, 219, 223.** Dorsal view vertex; **216, 220, 224.** Frontal ridge. Scale lines are all l mm: that under Fig. 218 applies to Figs 204, 205, 209, 213, 217, 221; that under Fig. 213 applies to Figs 206–208, 210–212, 214–216, 218–220 and 222–224.

Gymnobothrus subcarinatus (= *Pseudochirista subcarinata* I. Bolívar, 1922), type female. ETHIOPIA: Burka, MNHN, Paris. **syn. n.**

Material.— SOUTH SUDAN: Koalig hills; Imatong Mtns. SUDAN: Lomo. ETHIOPIA: Bourka (type locality of *Pseudochirista subcarinata* I. Bolívar); Lake Haramaia; Jigjiga; Bishoftu; Nr. Addis Abeba; Wardere; 15 mi. S.E. Harar. SOMALIA: Iscia Baidoa; Afmadu; Baun. KENYA: Moyale; Masai CIS Mara; Joroi; Orowa plain Kabete; Nairobi, Ngong Forest Res.; Mombasa; Turkana; Machakos; Athi; Thika; Diani Beach, Bura Garissa; Narossura R. Karura Forest; Lemek 01°07′S, 35°21′E; Mutomo-Mutha; Mutha hill; Sigiri Forest Res. 5350′ (1630 m); Nguni Kora; Baragoi; Dwa; Limuru 6000′ (1830 m); Kibwezi. I, II, III, Vl, VIII, X. UGANDA: Lake George; Toror Hills; Teso; Chukwani. I, III, V. TANZANIA: Arusha; Tubugwe; Msimbazi R. Tanga; Old Shinyanga; Mkomasi stn. 60 m W. Amani. Msimbasi R, Tanga distr.; Kilosa; Muheza; Mhindulo; Tubugwe; Chilangali; Wuguru (type localities of *G. brevipennis* Miller) Tanga; Milingano; Morogoro; Wuguru; Zanzibar: Bububu. Kisese. II, III, IV, VI, VIII, Xll.

Description.—Differs from *G. temporalis* in smaller size, shorter wings and different coloration. Size (in mm): total length males 12.5–15.0, females 20.0–25.0. Antenna filiform, in male longer than, in female as long as or slightly shorter than, length of head and pronotum. Fastigium of vertex oblong, trapezoidal, transverse sulcus slightly behind middle (Figs 215, 219, 223). Frontal ridge (Figs 216, 220, 224) and temporal foveolae (Figs 214, 218, 222) as *temporalis*. Pronotum less constricted and lateral carinae less divergent in metazona, latter only slightly longer than prozona (Figs 213, 217, 221). Wings short; folded apices level with, or only very slightly surpassing level of hind knee. Coloration differs from *G. temporalis* in more pronounced black markings on hind femora and color of lower areas being yellow-ochraceous and not reddish. Coloration somewhat resembles *G. anchietae* but can be distinguished from it by its heavier build, finer and longer antennae, more pronounced temporal foveolae, a shorter fastigium of vertex, and proportionately a longer metazona of pronotum.

Discussion.—Annual cycle similar to *G. temporalis*. Habitat described variously as: riverine forest; thicket and grass; banks of dry river; relic forest; scrub on waste ground. Life cycle probably continuous reproduction.

Distribution.—SUDAN, ETHIOPIA, KENYA, SOMALIA, UGANDA, TANZANIA: Zanzibar.

Macropterous group: The *anchietae* species sub-group

Discussion.—The species sub-group includes the nominate and three other taxa, which are here reduced to subspecies of *anchietae*. Synonymies and descriptions are given under each subspecies; full diagnosis of *Gymnobothrus anchietae bounites* (Jago, 1970), **stat. n. et comb**. is given under the brachypterous species group later in this paper.

Species notes

Gymnobothrus anchietae I. Bolívar, 1889
Figs 15, 225–246

Gymnobothrus anchietae I. Bolívar, 1889: 101.

Material.—See under nominate and other subspecies below.

Description.—Medium to slender build; size mostly small. Size (in mm): total length males 11.0–16.0, females 12.5–23.0. Integument punctured, finely to coarsely rugulose. Antennae short and incrassate, usually shorter than length of head and pronotum, but more elongate in *flaviventris*. Fastigium of vertex rounded-pentagonal, moderately (in *flaviventris,* considerably) longer than broad (Figs 227, 229, 241). Foveolae weak, usually narrow, punctured (Figs 240, 243). Pronotum moderately compressed, medial carina weak, cut by typical sulcus in its middle, with prozona slightly longer than metazona; lateral carinae regularly to irregularly incurved, mostly weak, and often obsolescent between first and second sulcus and partly or wholly in metazona, (in *inflexus* stronger and more angularly converging on first transverse sulcus (Fig. 244)). Tegminal apices extend slightly beyond hind knees in all subspecies, except *bounites*, in which they barely reach middle of abdomen. Genital structures show no differences between subspecies. Coloration in shades of brown, stramineous, ivory-white, grey and black, in mottled, striped and occasionally finely speckled patterns, which do not provide striking diagnostic features. In nominate subspecies face is often speckled and/or striped; dorsum is paler and occasionally with a narrow dorsomedial band edged with darker brown pigment. Lateral pronotal lobes are usually dark brownish in upper 2/3, with a contrasting large ivory-white spot in lower third (Figs 236, 239). Hind femur with faint dark bands on upper face; outer face brownish, and lower yellowish; hind knee brown, bordered by a pale ring which matches pale sub-basal ring on tibia. Tibiae otherwise ochraceous, somewhat blackened ventrally.

Key to subspecies in the *anchietae* species sub-group

1 Size exceptionally small, male <13mm, female <18mm; sculpturing pronounced; pronotal carinae thick and raised; lateral pronotal lobes with callose ridges in metazona. ETHIOPIAN highlands .... *anchietae inflexus* Uvarov 1934, **stat. n. et comb. n.**

– Size larger, sculpturing and pronotal carinae weaker 2

2 Brachypterous. TANZANIA: Ufipa plateau; ZAMBIA, MALAWI: Nyika plateau. .... *anchietae bounites* Jago, 1970, **stat. n. et comb.**

– Fully winged 3

3 Slender and elongate, fastigium of vertex much longer than broad (Fig. 241); antennae longer than head and pronotum; frontal ridge constricted at junction with fastigium. D.R. CONGO: Katanga, ZAMBIA, ANGOLA, BOTSWANA.. *anchietae flaviventris* Uvarov, 1953, **stat. n. et comb.**

– Antennae and fastigium shorter (Figs 228, 229); frontal ridge (Figs 230, 231). Widespread....... *anchietae anchietae* I. Bolívar, 1889, **stat. n.**

Subspecies notes

Gymnobothrus anchietae anchietae I. Bolívar, 1889, stat. n.
Figs 225–233

Gymnobothrus gracilis (Ramme, 1931) **syn. n**.
Ogmothela meruensis Ramme, 1931 (syn. with *G. gracilis* Uvarov 1953)
Ogmothela rammei Sjöstedt, 1931 (syn. with *G. gracilis* Uvarov 1953)
Gymnobothrus angolensis Uvarov, 1953 (syn. Dirsh 1966)

Material.—Holotype female *anchietae anchietae*: ANGOLA: Caconda, Quando. Moxico dist. Villa Luso (det. Uvarov after comparison with two cotypic females from Madrid Museum); type series *angolensis* Loanda. Also ANGOLA: S.W. Sa de Bandeira, 5600′ (l705 m); Bruco; Rocadas; 10 mi. N.E. Cacula; Salazar; Duque de Bragança; Mt. Lubiri, 6 mi. N.E. Alto Hama; 3 mi. N.E. Negola; 8 mi. N.E. Cacula; Ceilunge; Calondo. Amboim; Cachociras 20 mi. S.W. Gabela. (Adults II, III, V, VII, X). BOTSWANA: Kuke Pan 20°59′S 22°25′E. NAMIBIA: Oshikango. TANZANIA: Shinyanga; Old Shinyanga; Tinde 20 mi. S.W. Shinyanga; Sigi, Nr. Amani; Ushora; Mpwapwa; Bukeni; Tanga; Mingano; Rukwa. KENYA: Nairobi; Ngare na Nyuki. ZAMBIA: Mporokoso; Mweru wa Ntipa; Mbala (as Abercorn). MALAWI: Nyika Nat. Park; nr. Chilenga. D.R. CONGO: Katanga, Chinchoxo.

Description.—As in key and under species. Size (in mm) total length: males 13.0–16.0, females 16.0–23.0.

Distribution.—ANGOLA, BOTSWANA, NAMIBIA, TANZANIA, KENYA, ZAMBIA, MALAWI, D.R. CONGO.

Gymnobothrus anchietae bounites Jago, 1970, stat. n. et comb. n.
Figs 234–238

Description.—See key. Full treatment in the brachypterous species group section (pp. 86 below).

Gymnobothrus anchietae flaviventris Uvarov, 1953, stat. n. et comb. n.
Figs 239–242

Gymnobothrus flaviventris Uvarov, 1953: 126–127, fig. 135

Material.—Holotype *flaviventris*: ZAMBIA: Lueno valley, Chisorwe. D.R. CONGO: Katanga prov: Nasantoye. ANGOLA: Tundavala, 8–10 ml. N.W. Sa de Bandeira; 12 mi. S.W. Luimbale ca. 5500′ (1675 m). BOTSWANA: Moremi Res.19°23′S, 23°33′E. Adults II, III.

Description.—As in the key. Differs from nominate subspecies in its more elongate, slender build; longer antennae; more slender, sulcate frontal ridge; more elongate fastigium of vertex. General coloration similar to nominate subspecies. Measurements (in mm): Total length male 15, female 19.

Distribution.—ZAMBIA, D.R. CONGO, BOTSWANA.

***Gymnobothrus anchietae inflexus* Uvarov, 1934, stat. n. et comb. n.**

Figs 243–246

Gymnobothrus inflexus Uvarov, 1934: 603, fig. 6.

Material.—ETHIOPIA: Mt. Chillalo, moorland at 10,000′ (3050 m), XI.1926; Oinchu Park Lodge, 3170 m., short turf bush heath, V.1975; 07°57′N 39°08′E, 2400m., IV.1975.

Description.—As in key. Exceptionally small size. Size (in mm): males 11.5–12.0, females 17.0–18.0. Rugulose integument. Short thick antennae. Well-defined temporal foveolae. Shape of pronotum diagnostic, with weak second sulcus and strong callose carinae. Coloration (as in *bounites*), predominantly in shades of dark brown and black.

Discussion.—Records of *inflexus* in SOMALIA given by Johnsen and Schmidt (1982) and by Baccetti (1984) are probably misidentifications of *G. flexuosus* (Schulthess).

Distribution.—Limited localities in highland ETHIOPIA. Also recorded from KENYA (Emali Hills) by Kevan (1950), and from UGANDA (Kampala) by Jago and Rowell (unpublished).

Brachypterous group

Discussion.—There are only two members in the brachypterous species group of *Gymnobothrus: G. anchietae bounites* Jago, 1970 and *Gymnobothrus rimulatus* (Karsch, 1896). However, apart from their shared character of brachypterism, they belong to two separate and distinctive species groups of the genus: *bounites* is a subspecies of *G. anchietae* and its diagnosis is included in the key to the other subspecies, while *G. rimulatus* is a close relative of *G. inflexus* and is described in some detail below.

Species notes

***Gymnobothrus anchietae bounites* Jago, 1970, stat. n. et comb. n.**

Figs 234–238

Gymnobothrus bounites Jago, 1970: 123, 205.

Material.—Very large type series of *bounites*: S.W. TANZANIA: S.E. of Mbeya, Rungwe Mt., 2 mi. S.E. of Kiwira Forest Station; 4.7 mi. along Kiwira-Mbeya road; Ufipa plateau, 12 mi. E. of Sumbawanga; Mbisi Forest Reserve, S.E. of Rungwe Mt., tree fern gorge; Mbeya Mt. N.E. of Mbeya, 8000′ (2440 m). In addition: TANZANIA: Poroto Mts. ZAMBIA: Nyika Plateau 7300′ (2225 m). MALAWI: Nyika Nat. Pk. nr. Chilenga.

Description.—As in the key given above. Differs from nominate subspecies in its short wings; small size and slender build. Fastigium of vertex shorter, parabolic (Fig. 237). Coloration dark brown to blackish with medial dorsal brown or creamy stripe. Antennae black apically, light brown in basal half. A broad dark lateral band extends from antennal sockets across genae, upper 3/5 of pronotum to pleurae. Abdominal tergites shiny black. Hind femora reddish-brown, lighter below; knees dark brown to sooty black. Hind tibiae light to dark grey.

Distribution.—S.W. TANZANIA, ZAMBIA, MALAWI. Inhabits plateau grasslands spanning the Mbeya valley, linking the hills of northern MALAWI and southern TANZANIA faunistically with those of the Ufipa Plateau (Jago 1970).

***Gymnobothrus rimulatus* (Karsch, 1896)**

Figs 247–258

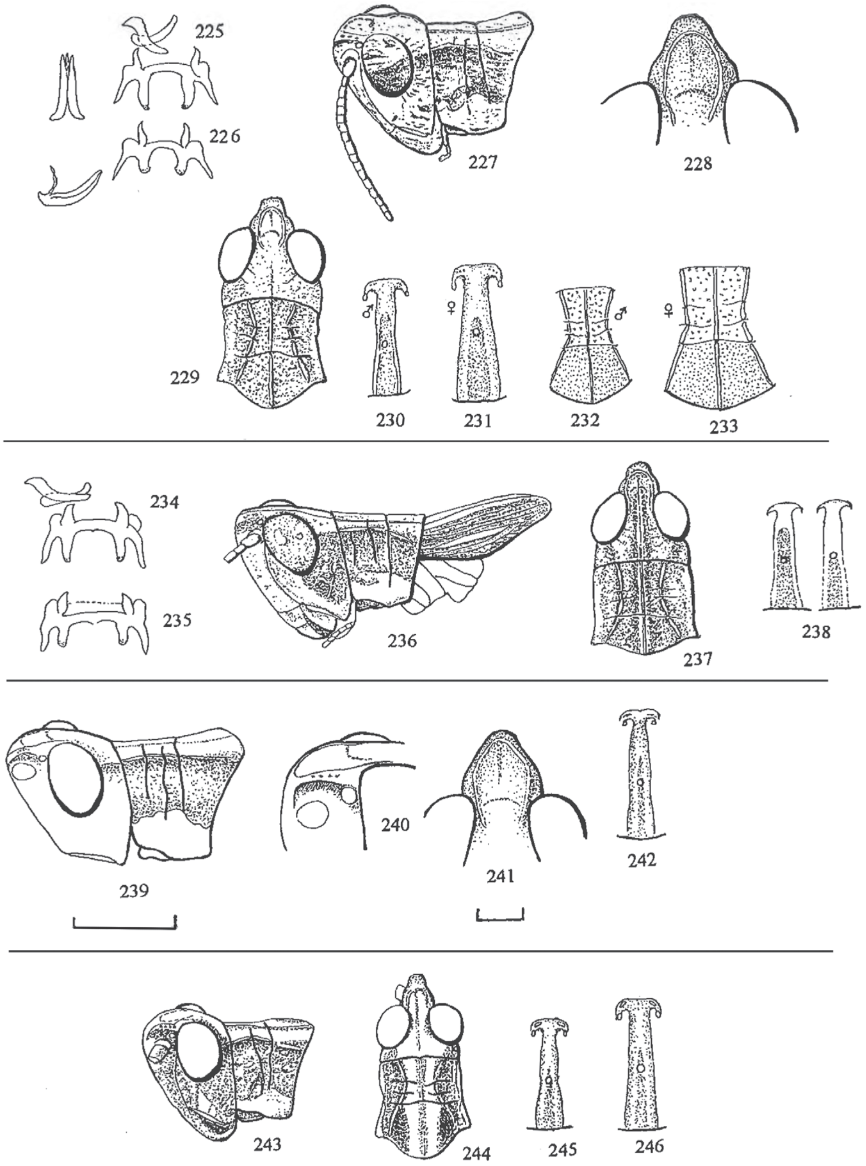
Ogmothela rimulata Karsch, 1896: 260.
Gymnobothrus rimulata Uvarov, 1953: 123–124.

Material.—Holotype *rimulata*: KENYA: Mombasa, Berlin; Kilindini; Watamu; Malindi, Driftwood Beach Club, grass, bushes and leaf litter behind beach; Kilifi dist., Arabuko-Sokoke, forest, clearings and path side; 20 km. N. Malindi, dunes N. of Mambrui; Lamu dist. 29 km. E. of Manjila, *Diospyros-Dobera* woodland; Kwale dist. Jombo hill, ca. 800–1000′, foot of slope, in clearings. Mwamberu stn.1000′ (305 m) 03°45′S, 39°13′E (I, II, III, IV, VI, VII, XI). TANZANIA: Victoria Nyanza, Ukerewe I.; Mahali Peninsula, Ujamba; Singida dist. 14 mi. N. of Mkalama; Old Shinyanga; Ngonghoo River; Manyara Nat. Park, groundwater forest and adjacent forest; Gibbs farm, Karatu; Ngorongoro (NHMUK) (Adults: VII, VIII, IX, XI).

Description.—Of medium size, robust build. Size (in mm): males 14–16, females 18–22. Integument finely pitted and rugose. Frontal ridge thick, barely sulcate, with subparallel, somewhat undulating, thick margins (Fig. 250). Fastigial constriction weak. Fastigium of vertex oblong/parabolic with weak margins (Figs 248, 249); transverse sulcus weak, roughly in mid-position. Structure of pronotum variable, from roughly the shape found in *G. flexuosa*, to that in *G. cruciatus* (Figs 251–253); transverse sulci strong; lateral carinae weak to strong, obsolescent towards rear of metazona and occasionally weaker between 1st and 2nd sulci; length of metazona equal to subequal to that of prozona. Tegmina with more or less rounded to attenuate apex, varying in length from equal to length of pronotum (as in coastal populations in Kenya) to more than twice its length (as in some specimens from Tanzania, notably those from Manyara) (Figs 255–257). Hind femora rather robust; arolia rather small (e.g. in comparison with *G. t. temporalis*).

Coloration rather similar to that in *G. t. flexuosus*, in shades of browns, ochraceous, stramineus and ivory-white with presence of light and dark forms; some of latter resemble a duller version of Tanzanian populations of *G. pullus*. Antennae dark brown, dorsum pale entirely or sometimes with a narrow dorso-medial band bordered with dark brown; costal area of tegmina dark brown; anal area stramineous. Body sides with a broad dark band in upper part extending from frons across genae, pronotal lobes and pleurae onto tegmina; lower third of lateral pronotal lobes and pleurae pale. Upper face of hind femur with a large pale sub-basal and a sub-apical spot; outer face brown, lower ferruginous to orange; hind knee black, hind tibia slate blue to brownish, with a broad sub-basal white ring, tarsi ivory; spines ivory, tipped black.

Distribution.—KENYA, TANZANIA.



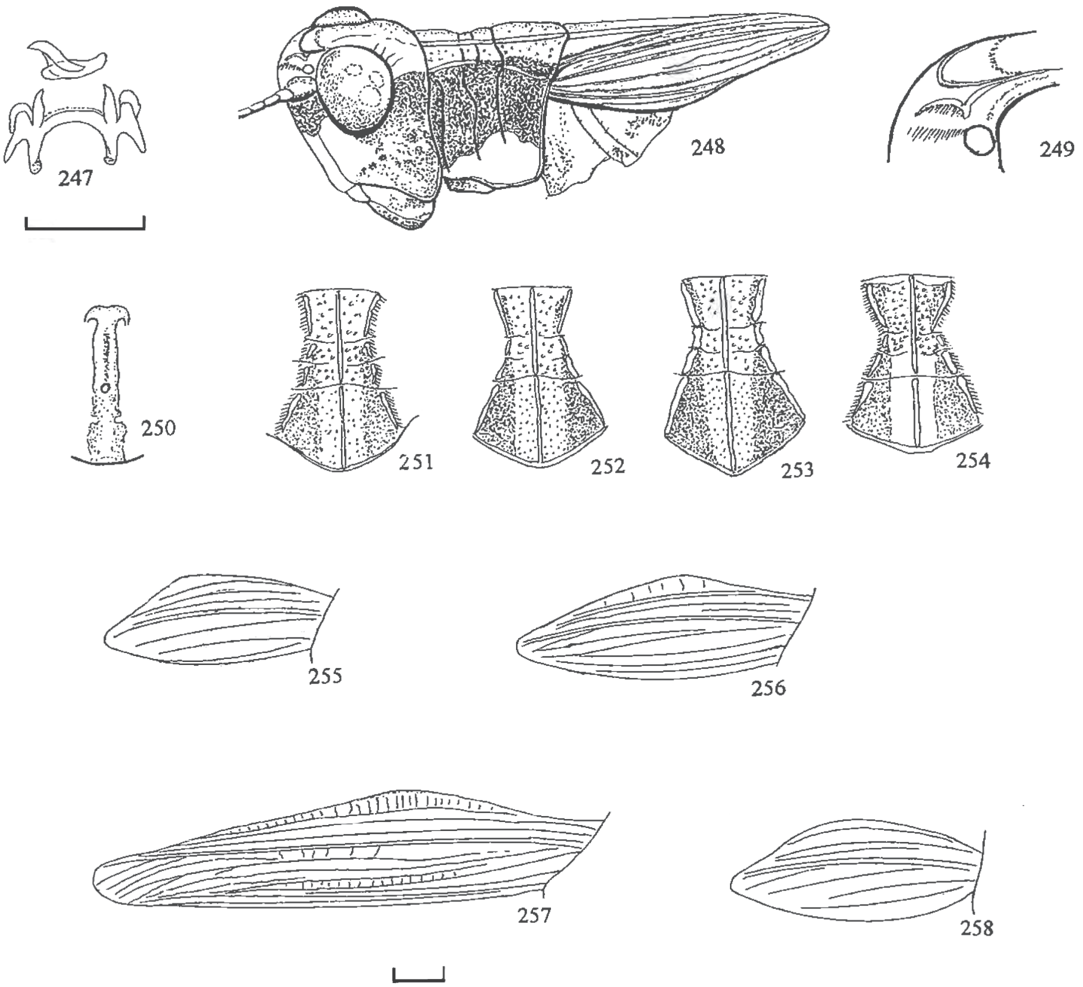
Figs 225–246. Tribe Gymnobothrini. *Gymnobothrus anchietae*. **Figs 225–233.** *Gymnobothrus anchietae anchietae*: **225, 226.** Epiphallus (Rukwa); **227.** Male oblique view head and pronotum; **228.** Male dorsal view vertex; **229.** Male dorsal aspect head and pronotum; **230, 231.** Male, female, frontal ridges; **232, 233.** Male, female pronotal discs. **Figs 234–238.** *Gymnobothrus anchietae bounites*: **234, 235.** Epiphallus; **236.** Male, oblique aspect head, pronotum and tegmina; **237.** Dorsal aspect head and pronotum; **238.** Male frontal ridge. **Figs 239–242.** *Gymnobothrus anchietae flaviventris*: **239.** Male oblique view head and pronotum; **240.** Oblique view vertex; **241.** Dorsal view vertex; **242.** Male frontal ridge. **Figs 243–246.** *Gymnobothrus anchietae inflexus:* **243.** Male oblique aspect head and pronotum; **244.** Same, dorsal aspect; **245.** Male frontal ridge; **246.** Female same. Scale lines all 1 mm: that under Fig. 239 applies to Figs 225, 226, 228, 230, 231, 234, 235, 238, 240–242, 245–246; that under Fig. 241 applies to Figs 227, 229, 232, 233, 236, 237, 239, 243, 244.

Micropterous group

Discussion.—This includes taxa previously included under *Gymnobothroides*. The affinities of the genus *Gymnobothroides* and the phylogenetic problems that it presents have been discussed by Uvarov (1953) and Jago (1968, 1970), both commenting on its close relationship to *Gymnobothrus* and that it is strictly definable at present only on the basis of tegminal abbreviation. The bridge afforded between the two genera provided by *G. rimulatus* removes the justification for continued maintenance of *Gymnobothroides* as a separate genus.

Of the taxa placed in *Gymnobothroides* by Jago (1968, 1970), *G. amplificata amplificata* Johnston and *G. amplificata morotoensis* Jago were transferred by Bouvy (1982) to *Rastafaria*. In this review (above) they have been reallocated to *Coryphosima*, to join *cytidonota*, Jago, already placed under that genus by its author. The following micropterous taxa previously in *Gymnobothroides* are here transferred to *Gymnobothrus*: *pullus pullus* Karny, 1915 (syn. *minutus* Ramme (Dirsh 1970), here reinstated as a subspecies of *pullus*); *pullus montanus* (Kevan, 1950); *levipes* (Karsch, 1896); *keniensis* Johnston, 1937; *hemipterus* Miller, 1932.

Only two full species are recognized here: *pullus* (Karny, 1915) and *levipes* (Karsch, 1896). The remaining taxa listed above considered as subspecies of one or the other.



Figs 247–258. Tribe Gymnobothrini. *Gymnobothrus rimulatus.* **Fig. 247.** Epiphallus; **248.** Female oblique view head, pronotum and tegmina; **249.** Male oblique view vertex; **250.** Male frontal ridge; **251–253.** Variation in male pronotal disc; **254.** Same, intermediate to subsp. *pullus*; **255–257.** Male tegminal variation; **258.** Male tegmen intermediate to subsp. *pullus*. Scale lines all represent l mm: that under Fig. 247 applies to Figs 247 and 249; that under Fig. 257 applies to all the rest.

Key to species in the micropterous group of *Gymnobothrus*

1 Larger and more robust; antennae elongate and slender, in males considerably longer than, in females as long as or only slightly shorter than length of head and pronotum. Compound eyes round and protruding (Fig. 278). Hind margin of pronotal disc rounded; lateral carinae interrupted by all three sulci (Figs 284–286). Tegmina broadly rounded, less than twice as long as broad (Figs 287, 288). Coloration in contrasting dark brown and cream, bands; tip of abdomen and underside of hind femora ferruginous-reddish or ochraceous. KENYA, TANZANIA, D.R. CONGO, RWANDA, SOUTH AFRICA....... .... *pullus* (Karny, 1915), **stat. n. et comb. n.**

– Smaller and more slender; antennae incrassate and somewhat dilated basally; in male barely as long as head and pronotum, in female much shorter. Compound eyes not unduly protruding, more elongate and pointed apically (Fig. 259). Hind margin of pronotum emarginate; lateral carinae rather less divergent and usually interrupted only by typical sulcus (Figs 261, 262). Tegmina more elongate and narrow (Fig. 258). Coloration in more cryptic shades of browns and greys (and rarely with some green pigmentation). TANZANIA, KENYA..............................*levipes* (Karsch, 1896), **stat. n. et comb. n.**

Gymnobothrus levipes (Karsch, 1896), comb. n.

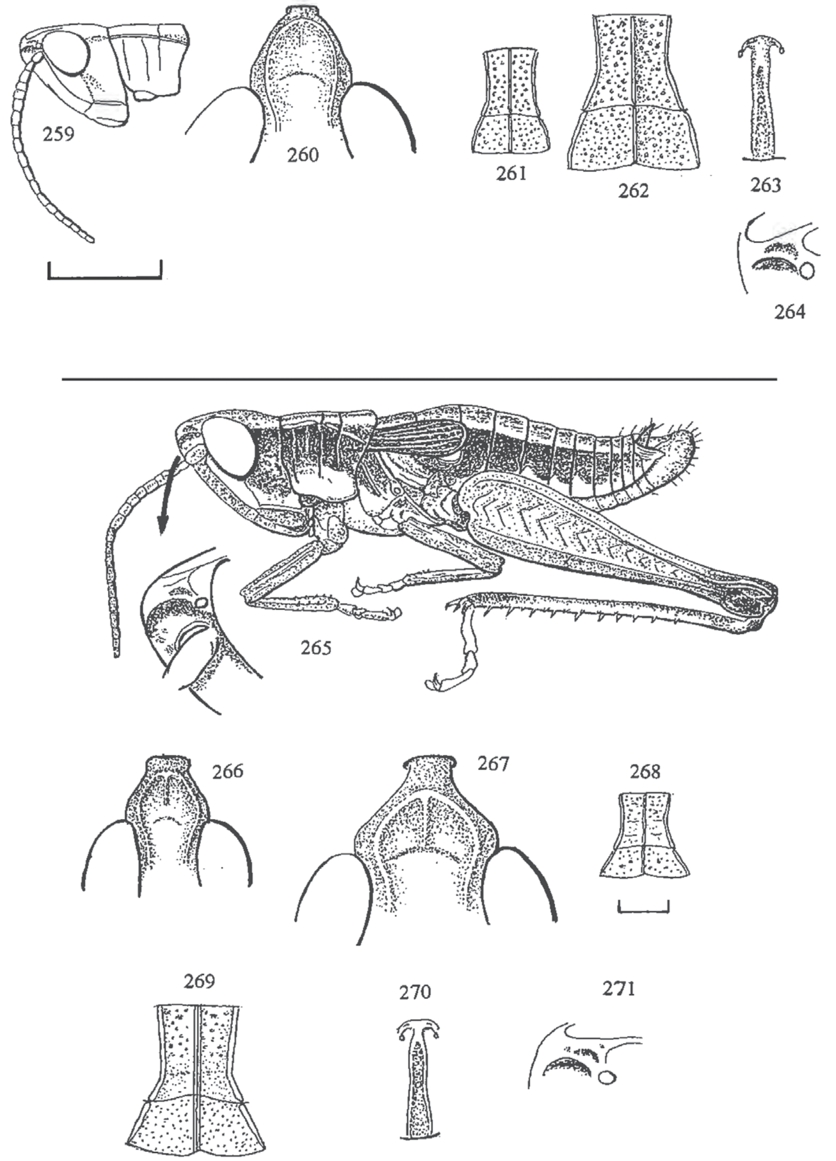
Figs 259–271

Chrysochraon levipes Karsch, 1896: 255. Types Kilimanjaro (MfN).

Key to subspecies of *G. levipes* in the micropterous group

1 Slightly larger and more slender, frontal ridge broader and less deeply sulcate; tegmina broader, more rounded apically. More uniform coloration in shades of brown and ochraceous; lower sulcus of hind femur orange-ochraceous. TANZANIA: Kilimanjaro and Taita hills; KENYA....................*levipes levipes* (Karsch, 1896), **stat. n. et comb. n.**

– Slightly smaller and more robust, frontal ridge narrower and more deeply sulcate; tegmina narrower, width little more than half the length. Coloration more varied and contrasting in marbled patterns of grey and dark brown. C. KENYA, notably the slopes of Mt. Kenya ....*levipes abbreviatus* (Chopard, 1921), **stat n. et comb. n.**



Figs 259–271. Tribe Gymnobothrini. *Gymnobothrus levipes.* **Figs 259–264.** *Gymnobothrus levipes levipes* male: **259.** Lateral aspect head and pronotum; **260.** Dorsal view apex of head; **261, 262.** Male, female pronotal discs; **263.** Frontal ridge; **264**. Temporal foveolus. **Figs 265–271.** *Gymnobothrus levipes abbreviatus* male: **265.** Entire insect (*Gymnobothroides keniensis* Johnston 1937**, n. syn.**); inset below an enlargement of apex of head showing temporal foveolus; **266, 267.** Male, female, dorsal view vertices; **268, 269.** Male, female pronotal discs; **270.** Frontal ridge; **271.** Temporal foveolus. All scale lines represent l mm: that below Fig. 259 applies to Figs 260, 264, 266, 267, 271; that below Fig. 268 applies to Figs 259, 261–263, 265, 268–270.

Species notes

Gymnobothrus levipes levipes (Karsch, 1896), stat. n. et comb. n.

Figs 259–264

Chrysochraon levipes Karsch, 1896: 255
Gymnobothroides levipes (Karsch, 1896) (syn. Johnston 1956)
Gymnobothroides montanus Kevan, 1950 **syn. n.**
including *Gymnobothroides pullus montanus* Jago, 1968

Material and discussion.—Lectotype male *levipes* here designated: TANZANIA: Mt. Kilimanjaro, Djagga, Madjame. MfN. 2 female paralectotypes, same data, MfN. Additional specimens: TANZANIA: Arusha, Grevillea Plantation, II; E. of Mt. Meru, Ngurdoto Lake Crater, XI; E. side of Mt. Meru, 6150′ (1875 m), Ngurdoto Nat. Park VI. KENYA: Type locality of *montanus* Kevan: Taita hills, 4500–5500′ (1370–1675 m), grass and bushes, 25.XII.1945; Taita Farmer Training Centre, 8 km. S. of Wundanyi (03°26′S 38°20′E), 5400′ (1645 m), V.1975. Following material from KENYA exhibits clinal links with *abbreviatus*: Machakos, Malili Ranch, IV; Nairobi, Karen-Ngong Rd. II. These are generally of smaller size with shorter antennae narrower tegmina and brighter coloration (NHMUK).

Description.—Synonymy and species diagnosis as above. Differs from subsp. *abbreviatus* as follows: proportionately slightly larger size, more slender build; size (in mm): total length males 11–14, females 18–20; slightly longer antennae; somewhat broader and less sulcate frontal ridge; slightly less constricted pronotum (but similar otherwise in that lateral carinae are interrupted only by typical sulcus and hind margin of metazona is emarginate) (Figs 261, 262); broader, more rounded tegmina (Fig. 258) and a more uniform coloration, in type material of *levipes* from 'Kilimanjaro', specimens from Arusha in Tanzania and types of *montanus* from Kenya, Taita hills in southern Kenya, general coloration is reddish-brown; lateral dark band is faint and lower area of hind femur is in shades of orange; this may, however, be in other shades of brown and stramineous; lower area of hind femur is ochraceous.

Discussion.—Study of the three syntypes of *Chrysochraon levipes* Karsch, 1896 has shown them to be conspecific with the two types of *Gymnobothroides montanus* Kevan, 1950, differing only in the slightly smaller size of the former. The male syntype is here designated as lectotype and the two females as paralectotypes. The closest match with the lectotype specimens of *levipes* are specimens from Mt. Meru-Ngurdoto National Park, Momella Lakes and W. Usambara, Mazumbai Forest Res.

Distribution.—S. KENYA; N. E. TANZANIA.

Gymnobothrus levipes abbreviatus (Chopard, 1921), stat. n. et comb. n.

Figs 265–271

Phloeobida abbreviata Chopard, 1921: 48–50, figs 28, 29
Phloeochopardia abbreviata (Dirsh, 1958)
Gymnobothroides keniensis Johnston, 1937 **syn. n.**

Material.—KENYA: (as Brit. E. Africa), Nairobi, 1 male, 1 female types of *Phloeobida abbreviata* Chopard 1921 (MNHN). 1 male, 3 females, types of *Gymnobothroides keniensis* Mt. Kenya, (above 8,000′, 2440 m) (NHMUK); Brit. E. Africa, 1 male, Karati Kikuya; 1 female, Ngalano, (Gregory Coll. 94–94), both bearing Ramme, det. "*Chortoicetes levipes*"; Kijabe section, Kikuyu Escarpment, 8200′ (2500 m), VI; Nairobi, Sigiri For. Res. Stn., Limuru rd 5350′, XI; E.A.A.F.R.O„ Muguga, 14 mi. N. Nairobi, 6800′ (2070 m), V. Limuru, VI; Nairobi, Balmoral/Ngong rd. 01°17′S 36°45′E, 5500′ (1675 m); Nara Moru 00°9′S 37°02′E, 6000′ (1830 m), III; 49 kms. N.W. Nairobi, hillside forest path, VI; 1°23′N 36°38′E, grass/bush/shrubs, IV; S. side of Mt. Kenya, Ragati For. Res. XII; Limuru, VI; Nakuru rd., Kenya Nat. Agric. Inst. relict forest, I; Kitibo Coffee Est., Makuyu 00°53′S, 37°17′E, 1550 m, IV; 48 km E Makutano, 5600′ (1705 m) *Ficus* forest, IX; homotypes *P. abbreviata* Chopard, Karen-Ngong rd, forest, II ; homotypes of *G. keniensis* Johnston; Thika rd. 38°41′E 00°44 ′S, 8400′ (2560 m) grassland and degraded forest; Ngong hills, 8000′ (2440 m), V; Mfunguni hill, Tulia, Kitui, 01°12′S, 38°02′E, *Combretum-Commiphora-Acacia* woodland; Ol Donyo Sapuk, nr. mt. summit, 7040′, 01°08′S, 37°15′E, V, cleared bush; Chyulu hills, 38 kms E. of Makutano 4900′ (1495 m), forest on old lava mountain, savanna/woodland mosaic, IX; Karen, XI; Ngong hills, 7000′ (2135 m), XI; between Nairobi and Limuru, VIII; Karura forest, VII; Mt. Kenya, VIII–X; Kabete, nr. Nairobi, IV.

Description.—Synonymy and recognition as above. Size small; see measurements in Table 9; of medium build; integument rugulose, shiny. Antennae short, incrassate, flattened and often weakly expanded basally, barely as long as head and pronotum in male, distinctly shorter and more slender in female. Frontal ridge narrow, sulcate, narrowed at junction with fastigium, divergent below ocellus. Fastigium of vertex moderately concave, elongate-parabolic in male, rounded in female, margins low but distinct; medial carinula distinct sometimes continuing onto occiput, transverse sulcus very weak; fastigial rim narrow. Foveolae weak, often as disjunct scattered pits of varying size, occasionally coalescing into an elongate shallow depression, usually open towards antennal socket. Pronotum somewhat constricted in middle, expanding caudad; typical sulcus strong, others weak or obsolete; medial carina broad, occasionally very narrowly divided lengthways, especially in females; lateral carinae strong, roundly converging towards first sulcus, broadly diverging thereafter, but incurving and weakening or disappearing towards the rear of metazona (latter a little more than half length of prozona, its hind margin broadly emarginate (Figs 268, 269)). Tegmina scale-like, convex, with raised callose veins, about as long as, or very slightly longer than, pronotum; width little more than half their length (Fig. 265). External and internal genital structures typical for group, without marked distinctive features. Hind femora of moderate build, length-width ratio about 4. General coloration striped and marbled in cryptic shades of browns and greys, usually paler dorsally with a more or less marked broad lateral dark fascia extending from antennal socket across genae, upper half of lateral pronotal lobes to pleurae and on to sides of abdomen, where pigmentation often becomes more intense; underside pale ochraceous-yellow, more brightly so in males; femora brownish-rusty-brown above, paler below, with lower area orange-yellow; hind tibiae brownish, with inner face darker.

Discussion.—Color pattern and morphology seem to vary with habitat terrain, as follows: Chyulu hills with forest on old lava, savanna/woodland mosaic (very rugose and exceptionally dark, frontal ridge broad, sulcate, foveolae narrow, crescentic, antennae rather long and dilated at base); Ol Donyo Sapuk, near mountain summit, cleared bush (frontal ridge deeply sulcate, foveolae large, strong); Nakuru Rd. relict forest (strongly rugose and pitted; frontal ridge moderately sulcate, with wavy margins, foveolae weak, coloration brown-stramineous to blackish-brown); 49 km. NW Nairobi, hillside, forest path (occiput, disc of pronotum and anal area of tegmina with greenish pigmentation); Naro Moru (more robust, distinct temporal foveolae and straighter pronotal carinae; brighter coloration; larger (male 13–14 mm) and generally paler, more brightly colored specimens; frontal ridge less sulcate); Kikuyu Escarpment – small, dark specimens (close match of types of *keniensis* Johnston and *abbreviata* Chopard).

The two specimens in the NHMUK det. '*Chortoicetes levipes* Karsch' by Ramme, in very poor condition, both from KENYA, are misidentifications; they closely resemble the types of *Gymnobothroides keniensis* Johnston, 1937 (NHMUK), which themselves are junior synonyms of *Phloeochopardia abbreviata* (Dirsh, 1958) (= *Phloeobida abbreviata* Chopard, 1921, types (MNHN) examined).

There is some geographical and ecological variation; as a rule, specimens from altitudes above about 7000′ (2135 m) tend to be smaller and darker with a more rugulose and sculptured integument than those from lower altitudes. Some of the latter, particularly from southern Kenya towards Tanzanian border, exhibit clinal changes towards *G. l. levipes*, (e.g. in their larger size and longer, more slender antennae).

Distribution.—KENYA.

Table 9. Morphometric measurements of *Gynmobothrus levipes abbreviatus*.

	M (mm)	F (mm)
Antennae	4.5	4.5
Tegminal length	2.1	3
Tegminal width	1	1.4
Hind femur length	8–9	9–11
Hind femur depth *	2	2.7
Hind femur L/D ratio *	4–4.5	3.3–4.1
Total length	10.5–13	14–17
Total length *	10.5–12*	14–15.5*

*Kikuyu road material

Gymnobothrus pullus (Karny, 1915), comb. n.

Gymnobothroides pullus Karny, 1915: 134.

Description.—As in key to species.

Discussion.—See below.

Key to subspecies of *G. pullus* in the micropterous group

1 Larger (male 12–14 mm, female 16–22 mm), structurally more variable, lateral pronotal carinae vary from roundly inflexed (as in *G. temporalis*) to angularly converging (as in *G. cruciatus*). Tegmina vary in size and shape (Figs 280–281, 287–288). C. and E. TANZANIA; C. and S. KENYA............ *Gymnobothrus pullus pullus* (Karny, 1915), **stat. n. et comb. n.**

– Smaller (male 12–13, female 15–20 mm) 2

2 Coloration strongly contrasting; frontal ridge narrower. D.R. CONGO: Lake Kivu; RWANDA: Kisenye....................... *G. pullus minutus* (Ramme, 1929), **stat. n. et comb. n.**

– Coloration less contrasting, in lighter shades of brown; frontal ridge broader. SOUTH AFRICA: Kwazulu-Natal; LESOTHO...................... *G. pullus hemipterus* (Miller, 1932), **stat. n. et comb. n.**

Species notes

Gymnobothrus pullus pullus (Karny, 1915), stat. n. et comb. n.[3]

Figs 272–288

Material.—TANZANIA: Type locality Dar es Salaam; Sigi, near Amani, 1500′ (460 m), V, XI; Morogoro; Mahange dist, Kakara, VI; 2 mi. E. Gilodari, S. of Yasda R.; Ngurdoto, edge of forest, I, IV; Munega Magna; Ngorongoro; Morogoro dist. Bunduki, IX,II,III; Lushoto dist. Soni, 3000′ (920 m); Arusha; Usambara; Mpwapwa, 5500′ (1675 m); Mwanza; Old Shinyanga; Gibbs Farm, Manyara; Ngorongoro, III, IV, X. KENYA: Samburu dist; Ngong hills, 7000′ (2135 m), XI; Nairobi-Limuru, 6000′ (1830 m) VII; Karura forest VIII; Lasenie VIII. (NHMUK).

Description.—Recognition as in key to species. Size (in mm): total length males 12–14, females 16–22. Integument rugulose, prozona coarsely, metazona finely, punctured. Antennae slender, slightly flattened basally; in male longer than, in female subequal to, length of head and pronotum. Compound eye large, protruding and rounded (Fig. 278). Frontal ridge (Fig. 282) rather broad with thick margins. Fastigium of vertex pentagonal, elongate in male (Fig. 279), round in female; foveolae as small shallow pits (Fig. 283). Pronotum weakly compressed in middle, somewhat variable in shape; lateral carinae vary from weak to strong and from roundly inflexed (as in *G. temporalis*), to straight and angularly converging (as in *G. cruciatus*) (Figs 280, 281, 284–286) and interrupted by all three strong transverse sulci; metazona proportionately broader than in *levipes*, its hind margin broadly rounded, not emarginate. Tegmina broad, somewhat varying in size and shape (Figs 287, 288). At extremes of tegminal and pronotal variation (Figs 254, 258), some specimens, e.g. from Shinyanga and Manyara, exhibit clinal links with *G. rimulatus*, which constitutes a remarkable example of a connection between two taxa originally attributed to two different genera. Genital structures typical of group and diagnostically not distinctive.

Coloration in bright contrasting pattern of broad dark and light longitudinal stripes, similar to that in *Zacompsa festa*; a dorsomedial ivory-white stripe extending whole length from fastigium to tip of abdomen is flanked by broad dorso-lateral black to blackish-brown stripes extending from antennal socket and including antennae, across genae, pronotal lobes and tegmina, gradually narrowing towards tip of abdomen; below this there is another somewhat narrower pale stripe, extending from lower genae, lower third of pronotal lobes to pleurae; underside is yellowish suffused with a ferruginous tinge, becoming a brighter reddish orange towards tip of abdomen and lower face of hind femora, which are a darker brown above with a black knee; hind tibiae slate-grey to brownish, with a pale sub-basal ring.

Discussion.—Nominate subspecies is larger and more robust than *G. levipes* (Karsch, 1896) and also larger than the other two subspecies, *pullus minutus* (Ramme, 1931) and *pullus hemipterus* (Miller, 1932).

Gymnobothrus pullus minutus (Ramme, 1929), stat. n. et comb., nom. res.

Figs 289–292

Gymnobothroides minutus Ramme, 1929.
Gymnobothroides pullus (Karny, 1915, 1929) (syn. Dirsh 1970).

Material.—D.R. CONGO: Lake Kivu: Goma, 05°19′S 14°24′E. Lwiro River, 47 km N. of Bukavu. RWANDA: Kisenye. Adults II, VIII, XII.

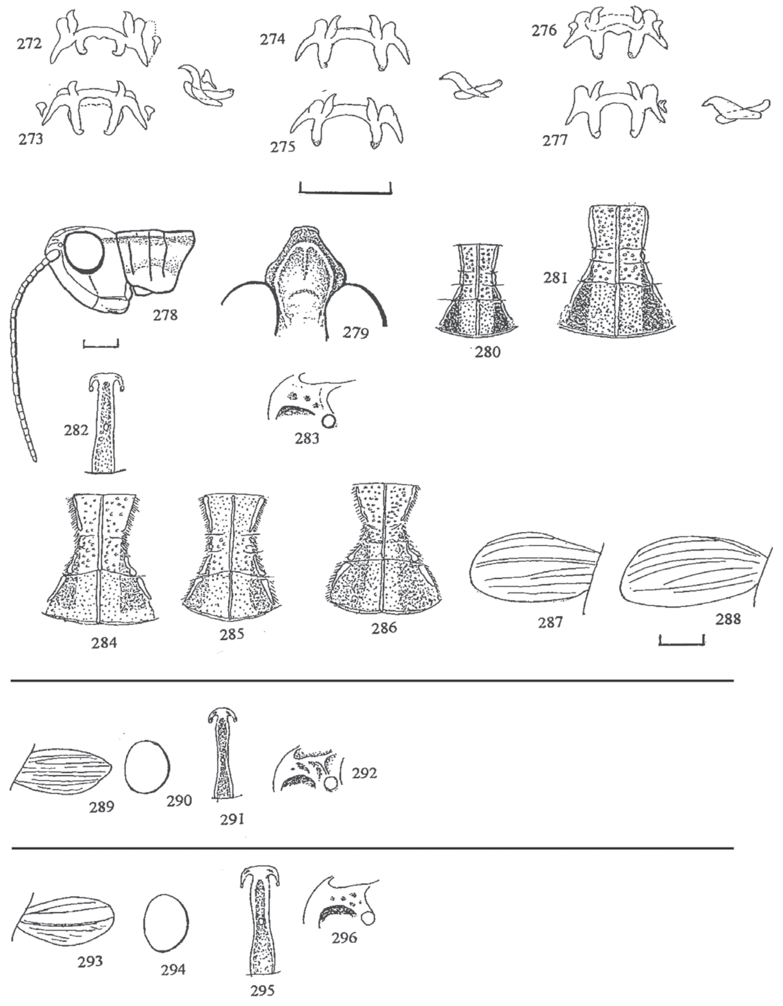
Description.—Differs from nominate subspecies in its smaller size (in mm: total length males 12–13, females 15–20); narrower, more deeply sulcate frontal ridge (Fig. 291); more elongate, apically pointed eye and apically attenuate tegmina (Figs 289, 290). Coloration very similar to nominate subspecies.

Discussion.—Described originally as *Gymnobothroides minutus* Ramme, 1929, and synonymized by Dirsh (1970) under *Gymnobothroides pullus* Karny, 1915, this taxon is recalled here as a valid subspecies.

Distribution.—Known from eastern D.R. CONGO and RWANDA.

---

[3] Dirsh 1965: 447, fig. 358, whole insect, male, and epiphallus (as *Gymnobothroides pullus* Karny).



Figs 272–296. Tribe Gymnobothrini. *Gymnobothrus pullus.* **Figs 272–288.** *Gymnobothrus pullus pullus*: **272–277.** Variation in epiphallus (272, 273, Tanzania, Amani; 274, 275, Tanzania, Mwanza; 276, 277, Malawi); **278.** Male, lateral aspect head and pronotum; **279.** Dorsal view male vertex; **280, 281.** Male, female pronotal discs; **282.** Frontal ridge; **283.** Temporal foveolus; **284–286.** Variation in male pronotal disc; **287, 288.** Variation in male tegmen. **Figs 289–292.** *Gymnobothrus pullus minutus* male: **289.** Tegmen; **290.** Compound eye; **291.** Frontal ridge; **292.** Temporal foveolus. **Figs 293–296.** *Gymnobothrus pullus hemipterus* male: **293.** Tegmen; **294.** Compound eye; **295.** Frontal ridge; **296.** Temporal foveolus. All scale lines represent l mm: that below Fig. 275 applies to Figs 272–277, 279, 283, 292, 296; that below Fig. 288 applies to Figs 280–282, 284–288, 291, 293–295, 289, 290; that under Fig. 278 applies to 278 only.

Gymnobothrus pullus hemipterus **(Miller, 1932), stat. n. et comb. n.**
Figs 293–296

Gymnobothroides hemipterus Miller, 1932.

Material.—SOUTH AFRICA: Kwa-Zulu Natal, nr. Weenen, N'Kolombe Mt., 5000′ (1525 m). LESOTHO: Maputo (NHMUK).

Description.—Similar in size to *minutus*, size (in mm): total length males 12–14, females 16–20) but differs in a broader, deeply sulcate frontal ridge. Eye elongate as in *minutus* (Fig. 294). Tegmina rounded apically as in *pullus* (Fig. 293). Fastigium of vertex similar to that in *pullus*; foveolae as scattered small pits (Fig. 296). Lateral pronotal carinae, said to be obsolete in original description, are in fact fairly well-developed in some specimens from both KwaZulu-Natal and Lesotho. Coloration less contrasting than in other subspecies, in duller, paler shades of brown; underside and lower area of hind femora reddish brown, hind knee black; hind tibiae black basally, remainder blackish brown.

Discussion.—Here reduced in rank from species to subspecies.

Distribution.—SOUTH AFRICA: KwaZulu-Natal; LESOTHO.

Generic diagnosis

Brachybothrus gen. n.

http://zoobank.org/4326112F-5DD3-40EF-9FC1-C67CCFD98DEC

Type species.—*Brachybothrus phyllopterus* **sp. n.** here designated.

Description.—Small, integument rugose and callose. Antennae as long as, or slightly shorter than, head and pronotum, weakly compressed basally and incrassate apically. Head somewhat inflated and rounded in profile; frontal ridge narrowly sulcate above ocellus, with margins below thick and divergent. Fastigium deeply concave, pentagonal, pointed apically, with sharp raised margins; transverse sulcus slightly behind middle. Foveolae elongate and shallow, concealed from above. Pronotum short, sellate and compressed in middle; dorsum traversed by three strong sulci, only typical sulcus interrupting median carina, but all three crossing lateral carinae. These consist of interrupted raised callosities, strong and convergent in front of 1st sulcus, obsolescent between 1st and 2nd and strongly divergent and progressively weaker thereafter; metazona much shorter than prozona, its hind angle broadly rounded. Lateral lobes of equal height and length, with a sinuous ascending lower margin and a rounded lower posterior angle. Mesosternal interspace transverse in both sexes. Tegmina and wings with more or less attenuate apices, abridged to half length of abdomen, or less. Hind femur moderately robust, knee lobes rounded; arolia much shorter than claw. External and internal genital structures unspecialized, typical of *Gymnobothrus* genus group.

Discussion.—This new genus has affinities both with *Gymnobothrus* – notably *Gymnobothrus rimulatus* (Karsch) and also with *Guichardippus somalicus* Dirsh. Its rugose integument and reduced arolia testify to a terricolous mode of existence, separating it from members of *Gymnobothrus* with their much larger arolia and graminicole to terri-graminicole habits. It includes two species: *Brachybothrus phyllopterus* **sp. n.** from SOMALIA and *B. hola* **sp. n.** from KENYA, which can be diagnosed by means of the key below.

Distribution.—SOMALIA, KENYA.

Key to species in the genus *Brachybothrus*

1 Of heavier build, head proportionately larger. Lateral pronotal carinae distinct in metazona in both sexes; prozona/metazona ratio 1.8 in the male, 1.6 in female. Tegmina with elongate, sharply attenuate apices (Figs 297, 302). SOMALIA............................*phyllopterus* **sp. n.**

– Of more slender build, head proportionately smaller. Lateral carinae in metazona weak in male and obliterated in female. Prozona-metazona ratio 1.5 in male, 1.25 in female. Tegmina narrowed, but not sharply attenuate apically (Fig. 304). KENYA .... *hola* **sp. n.**

Species notes

Brachybothrus phyllopterus sp. n.

http://zoobank.org/A0E83A68-E9C0-450F-9123-9056799B239A
Figs 297–303

Material.—Holotype male: SOMALIA: 5 km S. of Dinsor, 31.VII.1981, broad-leaf bush and *Acacia* on red sand. All paratypes: 3 males, 1 female, same data as holotype; 5 males, 6 females, 5 km S. of Bardera, 30.VII.1981, thorn scrub and loose stones on silt, Ritchie (NHMUK).

Description.—As in key and generic description. Coloration speckled in shades of fawn, brown and blackish-brown. Dorsally, an ochraceous stripe of varying width runs from fastigium to tip of abdomen. This is flanked by a broader subdorsal, contrasting dark-brown band extending from antennal sockets across postocular area and upper pronotal lobes to anal areas of tegmina, and contrasts with pale-ivory of lower cheeks and large spot in lower part of lateral pronotal lobe. Underside pale fawn. Outer face of hind femur fawn, upper ferruginous, with two brown transverse bands; hind knee and adjacent basal part of tibia blackish-brown, outlined by pale sub-basal rings; rest of tibia and lower area of femur slate-grey. Coloration of females more uniform in less contrasting shades of ferruginous-brown. Some specimens have large dark spots in metazona and upper face of hind femur.

Measurements.—See Table 10.

Discussion.—As under genus; marked terricole mode of life.

Distribution.—SOMALIA.

Brachybothrus hola sp. n.

http://zoobank.org/FF360752-C3BD-45D9-8FB4-C291CC5566DE
Figs 304–309

Material.—Holotype male: KENYA: Hola 01°30'S 40°00'E, 29.XII.1972, coll. ?; allotype female, same data as holotype. All paratypes: l male, l female, 17 kms N.E. of Mambeala Rock Rd., Nguni-Kora 00°20'S, 38°32'E 1800'. 28.V.1975, Robertson and Robertson (NHMUK).

Description.—Diagnosis as under genus and key to species. Size small. Coloration of similar pattern to *phyllopterus*, but in more vivid, contrasting shades and hues.

Measurements.—See Table 10.

Discussion.—As under genus; marked terricole mode of life.

Distribution.—KENYA.

Generic diagnosis

Guichardippus Dirsh, 1959

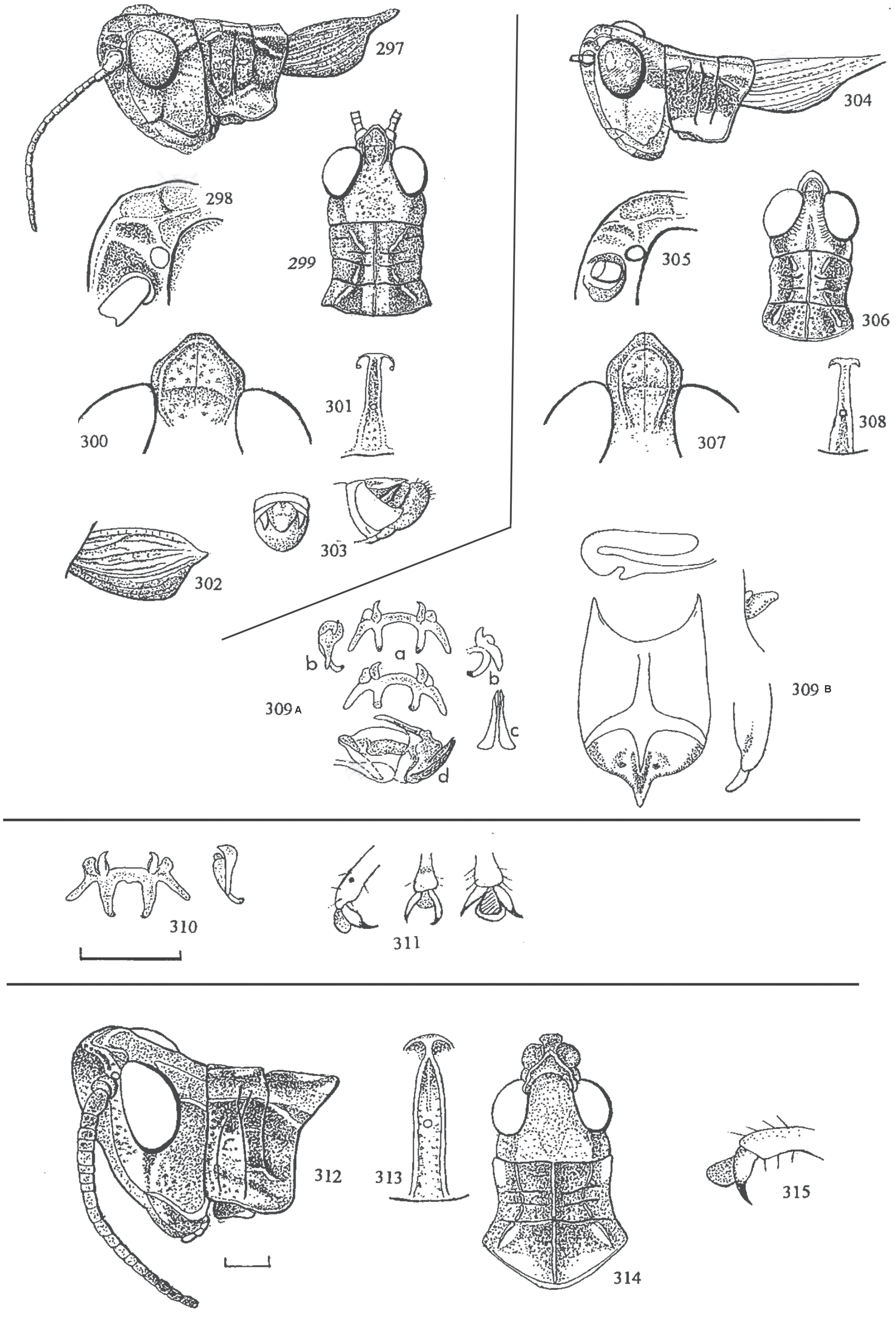
Guichardippus Dirsh, 1959: 37.

Type species.—*Guichardippus somalicus* Dirsh, 1959: 38, fig. 8, by original designation.

Description.—As in the key to genera (p. 67). Structure of antennae and dorsum of pronotum particularly diagnostic. Antennae shorter than head and pronotum in both sexes; in male basally compressed and apically incrassate. Frontal ridge oblique, nar-

Table 10. Measurements of *Brachybothrus* spp.

	phyllopterus (mm)		*hola* (mm)	
	M	F	M	F
Antennal length	4.5–5.0	4.5–5.0	4.8	4.5–5.0
Antennal width	0.2	0.22	0.22	0.28
Pronotal length	2	3	2.4	3.2
Prozona/metazona ratio	1.7	1.65	1.4	1.35
Tegminal length	3.4	2.7	3.7	2.8
Tegminal width	1.2	1.8	1.5	1.6
Tegminal length/width ratio	2.5	1.8	2.5	1.75
Hind femur length	7.5–8.5	9.5–10.7	8.2	8.9
Hind femur depth	2.2–2.5	2.9–3.3	2.4	3.1
Hind fenur length/depth ratio	3.3–3.4	3.2–3.27	3.4	2.9
Total length	10.0–11.2	14.0–16.0	11.5	14.4



Figs 297–315. Tribe Gymnobothrini. **Figs 297–303.** *Brachybothrus phyllopterus* **n. gen. et sp. n.**, male: **297.** Oblique view head, pronotum and tegmen; **298.** Oblique view vertex; **299.** Dorsal view head and pronotum; **300.** Dorsal view vertex; **301.** Frontal ridge; **302.** Tegmen; **303.** Abdominal apex laterally and dorsally. **Figs 304–309.** *Brachybothrus hola* **sp. nov.:** **304.** Oblique view head, pronotum and tegmen; **305.** Oblique view vertex; **306.** Dorsal view head and pronotum; **307.** Dorsal view vertex; **308.** Frontal ridge; **309.** Genitalic structures, **A.** Male, **B.** Female elements. **Figs 310–311.** *Guichardippus somalicus*: **310.** Epiphallus; **311.** Tarsal claws and pulvillus (lateral view), compared with *B. phyllopterus* (smallest) and *G. rimulatus* (larger, seen dorsally). **Figs 312–315.** *Malcolmburria angolensis* male: **312.** Oblique view head and pronotum; **313.** Frontal ridge; **314.** Head and pronotum from above; **315.** Tarsal claw and pulvillus. Scale lines all l mm: that below Fig. 310 applies to Figs 298, 300, 305, 307, 309–311, 315; that below Fig. 312 applies to Figs 297, 299, 301–304, 308, 312–314.

rowly sulcate with raised margins. Fastigium of vertex elongate-parabolic, deeply concave with raised carinulae, transverse sulcus well behind middle; fastigial foveolae crescent-shaped, with rough surface. Pronotum elongate with deep transverse sulci, medial carina sharp, lateral disrupted, converging towards middle in an X pattern, raised in front of first sulcus and behind typical, obliterate in middle; metazona slightly more than half length of prozona its hind margin obtuse-angular, broadly rounded. Genital structures characteristic of genus group. Coloration mottled in cryptic shades of browns and greys without distinctive bright pigmentation.

Discussion.—A distinctive monotypic Somali endemic genus, with *somalicus* Dirsh, 1959 as its unique species.

Species notes

***Guichardippus somalicus* Dirsh, 1959**[4]
Figs 310–311

Guichardippus somalicus Dirsh, 1959: 38, fig. 8.

Material.—SOMALIA: Hargeisa-Borama region and Sheikh (NHMUK).

Description.—As for genus above. Size (in mm): total length males 12–14, females 18–20. Epiphallus as in Fig. 310.

Discussion.—Terri-graminicole, on dry stony hillsides and in gullies with short grass, scattered bushes and aloes, acacias as well as other shrubs and small trees. Frequently found on open ground but never far from shelter of vegetation where it hides on disturbance.

Distribution.—SOMALIA.

Generic diagnosis

***Malcolmburria* Uvarov, 1953**

Malcolmburria Uvarov, 1953: 130.

Type species.—*Malcolmburria angolensis* Uvarov, 1953: 130–132, figs 141–144, by original designation.

Description.—Size below medium; total length: male 13–14 mm, female 18–20 mm. Head acute apically (Fig. 312), ascending above level of pronotum; frontal ridge very narrow apically, evenly widening towards clypeus. Fastigium of vertex (Fig. 313) triangular, concave, with widely arched transverse sulcus, margins raised, overhanging compound eyes; foveolae vertical, broad, their surface coarsely and irregularly pitted. Pronotum saddle-shaped with strongly raised, laminate medial carina (Fig. 314), deeply notched by typical sulcus; lateral carinae narrow, interrupted by all three sulci, excurved and partly obsolescent in metazona. Tegmina narrow with dense venation and weak to obsolescent intercalary vein in medial area. Epiphallus with incurving, apically pointed, digitiform lophi typical of the *Gymnobothrus* genus group. Coloration marbled in cryptic shades of chestnut to light-brown and stramineous with charcoal-black and slate grey maculation, but details of pattern variable. Antennae dark basally and apically, paler in middle or, as in most females, barely darkened apically. Hind femur slate-grey-brown basally, charcoal-black apically, corresponding part of hind tibia similarly dark. In some specimens outer face of hind femur is stramineous with a faint dark stripe and only the genicular crescent black. Tegmina clear in apical part and with 4–5 evenly spaced large dark spots in basal half. Hind wing with remigium infumate and vannus light yellowish or pinkish.

Discussion.—Monotypic genus originally described from ANGOLA. A distinctive genus superficially resembling the oedipodine genus *Calephorus*, but readily distinguished from it. Fire melanism evident; its color always provides protective crypsis.

Species notes

***Malcolmburria angolensis* Uvarov, 1953**[5]
Figs 312–315

Material.—Holotype male: ANGOLA: Luchase distr., Quangu R., X. Further material: ANGOLA: Moxico dist; Huamba, V; river Luena, Katula, V; river Langiliko, VI. TANZANIA: Sumbawanga (NHMUK).

Description.—As in diagnosis of genus, above.

Discussion.—According to its collector, Dr. M. Burr, the insects have some terricolous tendencies. Their mottled coloration blended closely with the black and grey sand on which they were found.

Distribution.—E. ANGOLA; S.W. TANZANIA.

Generic diagnosis

***Tenuihippus* Willemse, 1994**

Tenuihippus Willemse, 1994: 454–456, figs 31–32, 36, 40–43.

Type species.—Tenuihippus parvus Willemse, 1994: 454, by original designation.

Description.—Very small and slender with smooth integument and fully developed wings. Head acutely conical, somewhat ascending and about as long as pronotum. Antenna narrowly ensiform, slightly longer than length of head and pronotum (Fig. 316). Fastigium as in Figs 316, 317; fastigial foveolae absent. Frons strongly oblique, frontal ridge as in Fig. 318. Pronotum weakly tectiform; carinae sharp over entire length (Fig. 316), metazona longer than prozona, posterior margin obtuse-angular. Lateral lobes higher than long, their lower hind angle broadly rounded. Hind femur slender (Fig. 319), surpassing tip of abdomen. Hind tibia slightly shorter than femur; arolium large. Abdominal appendages unspecialized; internal genital structures as in Fig. 322, typical of *Gymnobothrus* genus group, with epiphallic lobes relatively short and bent inwards.

Discussion.—A monotypic genus and a distinctive member of the *Gymnobothrus* genus group. Known only from the male holotype and paratype from the type locality on the banks of the Zambezi in ZAMBIA. Phallic characters clearly indicate that *Tenuihippus* belongs to the *Gymnobothrus* group of genera. Willemse (1994) states that it most closely resembles *Roduniella*, *Coryphosima*, and

---

[4] Dirsh 1965: 449, fig. 360 whole insect, male, head and pronotum, antenna, tip of male abdomen, epiphallus.

[5] Dirsh 1965: 453, fig. 364, whole insect, male, pronotum, apex of head, epiphallus.

Chirista, but differs from them and the other genera principally in its very small size, slender build and elongate metazona of pronotum.

Species notes

Tenuihippus parvus Willemse, 1994

Figs 316–322

Material.—ZAMBIA: Holotype male (W. Prov.) Kasize (E. bank of Zambezi) opposite Sioma, 70 km S. of Senanga, 16.VI.1987, L. Willemse; Paratype female, same data as holotype.

Description.—As for genus: General coloration uniform dull brownish, paler yellowish ventrally. Postocular area and adjacent part of lateral pronotal lobes may be darkened, also narrow triangular area along sides of pronotal disc; proximal half or upper side of hind femur with faint dark fascia.

Measurements.—See Table 11.

Distribution.—ZAMBIA. Collected in a small marshy plot with reeds, adjoining the Zambezi river.

Table 11. Morphometric measurements of *Tenuihippus parvus.*

	M (mm)
Antennal length/length head and pronotum	1.2
Pronotal length	2.0–2.3
Metazona/prozona ratio	1.4
Tegminal length	12.0–12.2
Hind femur length	8.7–9.0
Hind femur length/depth ratio	4.7–4.9
Total length	11.7–12.3

Generic diagnosis

Zacompsa Karsch, 1893

Zacompsa Karsch, 1893: 54, 74.

Type species.—*Zacompsa festa* Karsch, 1893: 74, by original designation.

Description.—Size small to medium (males 15–24, females 22–31 mm); moderately robust. Integument shiny, finely dotted. Antennae filiform, somewhat compressed in basal third. Frons oblique, weakly convex in profile; frontal ridge shallowly sulcate, margins obtuse, partly obliterate and divergent below ocellus. Fastigium more or less concave, trapezoidal to oblong; lateral carinulae distinct, but medial carinula obsolescent; transverse arcuate sulcus weak. Temporal foveolae concealed from above, elongate, shallow and indistinct, sometimes obliterate. Pronotum subcylindrical; medial carina thick and strong, lateral carinae usually weak, especially in metazona and between first and second transverse sulci, while strongest and somewhat convergent in prozona. All three transverse sulci distinct, the third, and sometimes the first, interrupting medial carina. Metazona distinctly shorter than prozona, its hind margin obtuse-angular, or broadly rounded. Mesosternal interspace open. Tegmina and wings fully developed or shortened. Membrane of tegmen parchment-like, reticulation moderately dense, intercalary vein present but weak. Hind femur of medium build, genicular lobes of equal length, rounded. Arolium large. Male supra-anal plate elongate-cordate, sulcate; cercus narrow, tapering and obtuse apically. Epiphallus with moderately narrow, arcuate bridge, large ancorae, elongate, pointed posterior processes and elongate, finger-shaped lophi (Fig. 24). Spermathecal duct (Figs 327, 329) of usual structure for Gymnobothrini. Ovipositor short with robust valves; lower pair with rounded external lateral projections. Coloration in all taxa bold contrasting pattern of alternating pale and dark stripes on dorsum and sides of body (Fig. 323). Three pale stripes may vary in shade from ivory-white to darker yellowish. One is a broad stripe on dorsum extending from fastigium to tip of tegmina, and other two lie one each on lower half of body, including sides of abdomen; between them are two dark stripes in shades of blackish-brown one each in upper half of body, extending from antennal sockets to tip of tegmina. Hind knee also black, but hind femur is otherwise yellowish-orange. A typical speckled coloration may occasionally occur in some females.

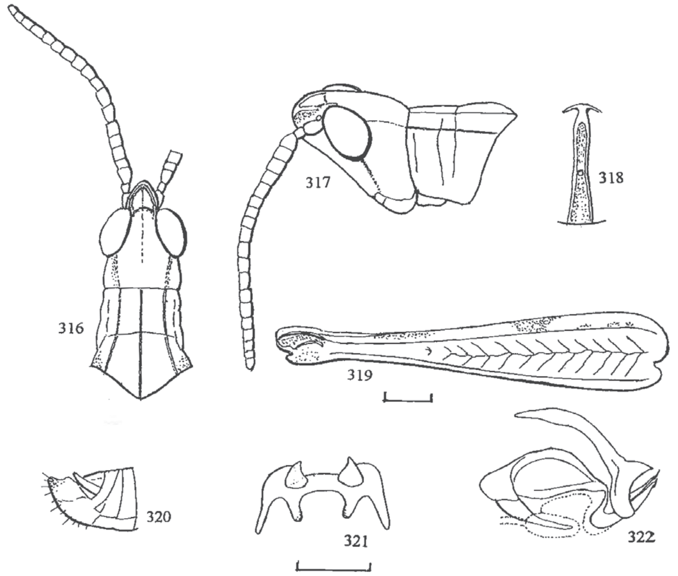
Discussion.—In reviewing the African Gymnobothrini, Uvarov (1953) diagnosed *Zacompsa*, based on *festa*, Karsch, as distinct, on the basis of its non-constricted, almost cylindrical pronotum with typical sulcus placed distinctly behind middle and its peculiar striped patterning. Certain genera, previously attributed by him to *Zacompsa* as synonyms (Uvarov 1926), were reallocated to *Gymnobothroides* Karny, whilst others became synonyms of *Gymnobothrus* I. Bolívar (*Pseudochirista* Karsch, *Ogmothela* I. Bolívar).

Five species have at different times been attributed to *Zacompsa* by different authors:

1. *Z. festa* Karsch, 1893: male, female types, TOGO: Bismarckburg (MfN).
2. *Z. bivittata* Uvarov, 1926: Holotype female, N. NIGERIA (NHMUK) as *Z. festa* var. *bivittata*, subsequently elevated to species rank *Z. bivittata* by Ramme, 1931: 931.
3. *Z. karschi* Ramme, 1929: Holotype male, CAMEROON: Benue (MfN). Ramme (1931) later changed its status to *Z. bivittata karschi*. Subsequently, Dirsh (1970) rendered it a synonym of *Z. bivittata*.
4. *Z. pedestris* Uvarov, 1953: 132. Holotype male, TANZANIA: Rukwa valley, Ikuu forest (NHMUK).
5. *Z. helonoma* Jago, 1966: 351. Holotype male, GHANA: N. Region (NHMUK).

The present review recognises only two species: the highly localized *Z. pedestris* Uvarov, 1953 (W. Tanzania, Ufipa-Rukwa) and the widespread *festa* Karsch, 1893 (W. Africa to Sudan and Eritrea). Within the latter, three geographically distinct subspecies can be identified: (i) the typical *Z. festa festa* Karsch, 1893 (Guinea savanna zone from Sierra Leone to Nigeria and Cameroon in moist grasslands within thickets (also montane, upland forests and riverine habitats); (ii) *Z. festa bivittata* Uvarov, 1926, Sahelian and Sudanian Zones from Senegal to Ethiopia and Eritrea (rather localized meso-hygrotypic grassland habitats often in association with woodlands and watercourses, but occasionally, e.g. in South Sudan, in open grasslands); (iii) *Z. festa helonoma* (Jago, 1966) which is apparently an intermediate form between (i) and (ii) above; known so far only from northern Ghana.

Editorial note.—No author has at any time doubted the validity or the specific distinctiveness of either *Z. festa* or *Z. pedestris.* The other species (*bivittata*, *karschi*, and *helonoma*) have, however, a more



Figs 316–322. Tribe Gymnobothrini. *Tenuihippus.* **Figs 316–322.** *Tenuihippus parvus* male: **316.** Dorsal view head, pronotum and antennae; **317.** Idem oblique lateral view showing temporal foveolae; **318.** Frontal ridge; **319.** Hind femur, outer side; **320.** Tip of male abdomen laterally; **321.** Epiphallus; **322.** Phallic complex without epiphallus from left side. Scale lines all 1 mm: that below Fig. 321 applies to Figs 321, 322; that under Fig. 319 applies to Figs 316–320.

uncertain history (e.g. Ramme 1931, Dirsh 1970). Popov, as seen above, considered their distinctive characters to be insufficient for species status, and so proposed to reduce them all to subspecies of *festa.* Mestre (2001) independently came to the same conclusions but went further. After a study of specimens from all of West Africa, and of the original type specimens, he synonymized all *Zacompsa* species, other than *Z. pedestris,* with *Z. festa*. Accordingly, we follow Mestre (2001) and so omit Popov's key to subspecies and his treatments of them.

Key to species within the genus *Zacompsa*

1 Tegmina reduced to small pads barely length of pronotum. TANZANIA: Ufipa-Rukwa area................................*Z. pedestris* Uvarov, 1953

– Tegmina and wings more fully developed, macropterous, or brachypterous, wings half length of abdomen or longer. Coloration darker, brighter and more contrasting; upper face of hind femur often with a distinctive white spot in basal third. Both sexes usually macropterous, folded wings reaching hind knees. Guinea savanna from MAURITANIA and SENEGAL, through SIERRA LEONE and CAMEROON, to SUDAN and ERITREA............................ *Z. festa festa* Karsch, 1893

Species notes

Zacompsa festa Karsch, 1893

Figs 323–327

Zacompsa festa Karsch, 1893: 74, fig. 11.
Zacompsa karschi Ramme, 1929 (syn. Dirsh 1970).
Zacompsa helonoma Jago, 1966: 351. (syn. Mestre 2001).
Zacompsa festa var. *bivittata* Uvarov, 1926 (syn. Mestre 2001).

Material.—Lectotype male, *festa*: TOGO: Bismarckburg, 20.IX-31.X.1890, R. Büttner, Zool. Mus. Berlin, no. 5543 (MfN). Paralectotypes – 1 female, same data as lectotype; 1 female, same as lectotype but I.XI–15.XII.1890; 1 male, 1 female, same as lectotype but 20.IX–15.X.1890. Holotype male *helonoma*: GHANA: N. Region, 6 mi. N. Mole R. Bosum-Daboya Road, [09°20′N, 1°30W], 26.XII.1963. All paratypes – 9 males, 2 females, same data as holotype; 2 males, 2 mi. W. of Daboya, 24.XII.1963, Jago. (all NHMUK). Holotype female *festa var. bivittata*: NIGERIA: Azare (NHMUK). Holotype male *karschi*: CAMEROON: Benue (MfN). SENEGAL: Bambey; Ziguinchor, (rizières); Tambacounda (long grass, bush). MAURITANIA: Timbedra; Aioun el Atrouss. MALI: Nr. Darou, Gourma; Kara. NIGER: Agadez (smallest and palest specimens); Niger river valley S. of Niamey, several localities. SIERRA LEONE: Msala (NHMUK). TOGO: Misahohe (NHMUK). GHANA: Volta region, Chiara, Nkwanta, Kpandu; Northern region, Yeji (NHMUK). NIGERIA and CAMEROON: Obokamaji (nr. Ibadan) (NHMUK); Azare (type series of *Z. f. bivittata*), Ba Sidderi (1 male paratype of *Z. bivittata karschi* Ramme); Karim; Wurge; Kalkala (at light); Kianje. SUDAN: Singa; Suki; MCPS (Gedaref); Basunda. ETHIOPIA: Meisso (near station); Lake Bishoftu; River Hawash. ERITREA: nr. Ducumbia; Keren.

Description.—Wings are usually about same length in both sexes; when folded, tips of tegmina vary from falling short of the tip of the abdomen to more or less level with, or even surpassing, the hind knees. Coloration variable; bright and contrasting in some, with face and medial stripe on occiput dark and pale spots on upper face of hind femur. In others, paler, particularly on the face and with uniformly pale rusty-brown upper and outer face of hind femur, without notable maculation.

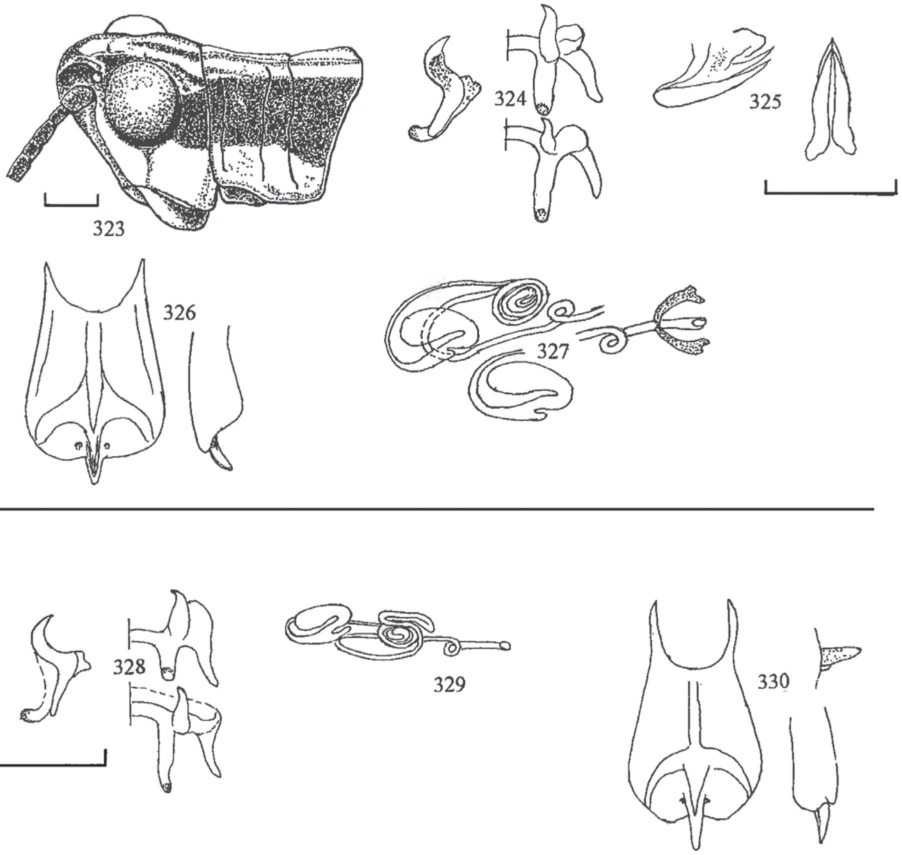
Measurements.—Table 12. This table shows the considerable variation in size over the range of the species *festa* as now understood

Distribution.—MAURITANIA, SENEGAL, SIERRA LEONE, IVORY COAST, GHANA, MALI, BURKINA FASO, BENIN, TOGO, NIGER, NIGERIA, CAMEROON, CHAD, SUDAN, ETHIOPIA, ERITREA. Not so far recorded from Uganda, Tanzania or Kenya.

Discussion.—The species shows a remarkable stability of characters throughout its considerable range. It is likely, as Jago (1966) comments, that this stability of characters is an expression of the general similarity of environmental conditions in habitats across the Guinean zone. The only significant variation is associated with latitude, whereby coloration of populations in the Sahel/Sudanian zones (SENEGAL to SUDAN and ERITREA), is often duller and less contrasting; white spot in basal third of hind femur indistinct or absent; length of wings variable, even in same locality.

Table 12. Measurements of *Zacompsa festa.*

	Zacompsa festa (mm)	
	M	F
Antennal length	11.5–13.0	9.0–11.0
Pronotal length	3.0–4.0	4.1–5.0
Tegminal length	14.0–16.0	17.5–18.5
Hind femur length	12.7–13.2	14.0–15.8
Hind femur length	15.0–20.5	22.0–26.5



Figs 323–330. Tribe Gymnobothrini. *Zacompsa* spp. **Figs 323–327**. *Z. festa festa*: **323.** Head and pronotum obliquely; **324.** Epiphallus dorsally and laterally; **325**. Apical valves of aedeagus; **326**. Female subgenital plate from above and side; **327**. Spermathecal duct and spermatheca. **Figs 328–330.** *Zacompsa pedestris*: **328.** Epiphallus from above and left side; **329.** Female spermathecal duct; **330.** Female sub-genital plate from above and right side and left female cercus. All scales represent 1 mm; that under Fig. 325 applies to Figs 324, 325, 328; that under Fig. 323 applies to Figs 323, 326, 327, 330, 329, and 330.

Zacompsa pedestris Uvarov, 1953
Figs 328–330

Zacompsa pedestris Uvarov, 1953: 132.

Material.—Holotype male, *pedestris*: TANZANIA: Rukwa valley, Ikuu forest, 1.IV.1950 (NHMUK); Paratype female, Muze, 26.IV.1950, Bredo. 5 males, Rukwa Rift, 5.II.1962; 1 female, Ufipa, Ilemba gap, 12.III.1959, Vesey-Fitzgerald (NHMUK).

Description.—Differs from *Z. festa* Karsch in the following respects: shorter and more obtuse fastigium; broader meso- and metasternal interspaces; relatively minor differences of genital structures (Figs 328, 329); abbreviated tegmina reduced to short, leathery apically pointed pads, which just meet dorsally, and just reach middle of abdomen; in *festa* wings overlap and extend beyond mid-line of abdomen; details of coloration similar to *festa*, but even darker and more contrasting; pale femoral spots of *festa*, however, are lacking. Two color forms in local populations in both sexes: in one pale dorsal stripe is widened, as in *festa,* and contains a dark but even more contrasting elongate spot on occiput; in the other, dorsal stripe is much narrower and has no dark spot. However, there are no structural differences to warrant taxonomic recognition.

Distribution.—S.W. TANZANIA.

2.3 The tribe Pargaini and its genera

Description.—Defined in the diagnosis of tribes and genus groups (p. 67).

Discussion.—Dirsh (1975) erected the subfamily Pargainae, (type genus *Parga* Walker, 1870), which he placed in the family Catantopidae. He included in the subfamily the following genera: *Acteana* Karsch, 1896, *Amphicremna* Karsch, 1896, *Machaeridia* Stål, 1873, *Paraparga* I. Bolívar, 1909, *Pargaella* I. Bolívar, 1909, and the Madagascan genus *Pseudopargaella* Descamps & Wintrebert, 1966. According to Dirsh (*loc. cit.*) the main difference of the Pargainae from other Acridoidea is a very characteristic structure of epiphallus, which is bridge-shaped, the bridge is narrow, ancorae absent or short, rudimentary, not articulated; lophi short, mostly bilobate, lateral plates well developed (cf. Figs 31–34). However, Jago (1983b) questioned Dirsh's treatment and reduced Pargainae to the status of a genus group within Acridinae. He also argued, correctly, that on the basis of its genital structures, the genus *Odontomelus* I. Bolívar, 1890 should also be included in the group, but then added eight other genera allied to *Gymnobothrus* I. Bolívar, 1889 (originally placed by Dirsh (1975) in his subfamily Gymnobothrinae), regardless of the fact that in these the structure of the epiphallus is quite different—the ancorae are well-developed and articulated with the bridge, while the lophi are finger-shaped, elongate and never bilobate (Figs 24–30). Subsequently, Jago (1994), in his revision of genus *Odontomelus* I. Bolívar, 1890, reiterated his 1983 arrangement, while synonymizing the genera *Amphicremna*, *Paraparga*, and *Pargaella* under *Odontomelus.*

Here, *Gymnobothrus* and its allies are treated as a separate tribe Gymnobothrini. Consequently, the *Parga* group becomes the tribe Pargaini and contains the following genera recorded in East Africa: *Acteana* Karsch, 1896, *Parga* Walker, 1870, *Machaeridia* Stål, 1873, *Odontomelus* I. Bolívar, 1890, and *Phryganomelus* Jago, 1983.

Key to the genera in the tribe *Pargaini*

1 Small and robust; micropterous; antennae clearly divided into basal broad and flat, medial narrow and flat, and apical cylindrical tapering parts (Fig. 339). TANZANIA: coastal areas .... *Acteana* Karsch, 1896

– Small to medium, elongate and slender; micropterous, short, or fully winged. Antennae not modified as above, except in *Parga,* which is fully winged 2

2 Both upper lobes of hind knee strongly elongate (Figs 351, 352). Integument with deep longitudinal ridges. Fully winged. Antennae short and broad and modified as described under couplet 1, their outer margin serrate (Figs 341–350). Widespread .... *Parga* Walker, 1870

– Knee lobes only moderately or weakly elongate, integument smooth or only moderately sculptured. Antennae unmodified, usually somewhat ensiform 3

3 Integument very smooth, without marked sculpturing, pronotal disc very narrow with sharply defined parallel lateral carinae. Fully winged, but never with a pre-anal speculum in hind-wing. Widespread .... *Machaeridia* Stål, 1873

– Integument more or less sculptured and coriaceous, fully winged or more or less micropterous. When fully winged, often but not always with a hind-wing pre-anal speculum in males and/or females 4

4 Of larger size, coarsely sculptured, micropterous. West to East Africa, forest .... *Phryganomelus* Jago, 1983

– Of smaller size; most species micropterous, but some brachypterous or fully winged, with or without a speculum. Sub-Saharan Africa .... *Odontomelus* I. Bolívar, 1890

Generic diagnosis

Acteana Karsch, 1896

Acteana Karsch, 1896: 255.

Type species.—*Acteana alazonica* Karsch, 1896: 255, by original designation.

Description.—Phallic structures in *Acteana* are typical for the *Parga* genus group; structure of epiphallus with its vestigial ancorae and elongate, bilobate lophi (Figs 31, 340) is particularly diagnostic. For details see under species, below.

Discussion.—Genus monotypic.

Species notes

Acteana alazonica Karsch, 1896

Figs 67, 331–340

Acteana alazonica Karsch, 1896: 255, fig. 7.

Material.—Holotype female, Zanzibar (MfN): TANZANIA: 5 males, 3 females, Dar es Salaam, III.1936, K. H. Key (NHMUK); 3 males, 1 female, University College Campus, 8 ml. W. Dar es Salaam, 4.IV.1967; 1 female, Pugu hills SW of Dar es Salaam airport, 500′, 28.IV.1982; 1 male, 1 female, Korogwe-Msata Rd., 103 km. N. of Msata, summit of Kopje, 27.IX.1982; 1 male, 1 female, Korogwe-Handeri Rd., 24 km. N.E. of Sindeni, 3.X.1982, riverine grassland, degraded woodland, all Jago (NHMUK).

Description.—Male antennae slightly longer and, in female, slightly shorter, than combined length of head and pronotum together; flagellum divided into basal, medial and apical parts, (basal moderately widened, flattened and serrated, particularly in female; medial slightly widened and compressed; apical cylindrical and somewhat inflated distally in male). Head short, conical; frons oblique and weakly concave in profile; frontal ridge shallowly sulcate with raised lateral margins, parallel above, divergent below ocellus. Fastigium of vertex widely parabolic, about as long as wide, with weak, but distinct median and lateral carinulae and a shallow arcuate sulcus behind middle. Dorsum of pronotum narrow; medial carina thick and somewhat raised, lateral carinae inflexed and weaker, particularly in metazona. Only typical sulcus distinct; metazona half length of prozona, its hind margin obtuse-angularly incurved. Mesosternal interspace quadrate in male, weakly transverse in female; metasternal interspace narrow in male, broadly open in female (Figs 67A, B). Tegmina lobiform, lateral, narrowly elongate, only a fifth as wide as long, barely covering tympanum, the latter fully developed. Male supra-anal plate triangular, with obtusely rounded apex and without a marked medial sulcus. Cerci small, obtusely conical; subgenital plate simple, short, subconical with obtuse apex. Phallic complex similar in structure to that in *Parga* genus group: epiphallus with moderately narrow, arcuate bridge with a marked medial projection, without ancorae, and with moderately elongate posterior projections. Lophi directed inwards, and divided into an elongate, finger-like outer, and a shorter, abruptly rounded, inner lobe. Penis valves slender, upturned. Integument finely and uniformly pitted, structure of head and pronotum as in Figs 331, 333. Antenna as in Fig. 339 and genital structures as in Figs 31 and 340. Generally dark-testaceous to rusty brown, often, but not always and more usually in males, paler dorsally; sometimes, more often in females, there is some fine, dark speckling. Cryptic coloring, probably associated with substrate homochromy, covers most of body, including underside, antennae, and legs. Sometimes with a striking large, ivory-white, flat, smooth callosity on lower half of lateral pronotal lobe, and bright, rusty-red coloration of lower outer sulcus of hind femur. In some specimens underside is also suffused with rusty-red which could be associated with sexual maturation.

Discussion.—Note that the shape of the lateral pronotal lobe differs from that in *Anacteana* species, and the tegmina are much narrower.

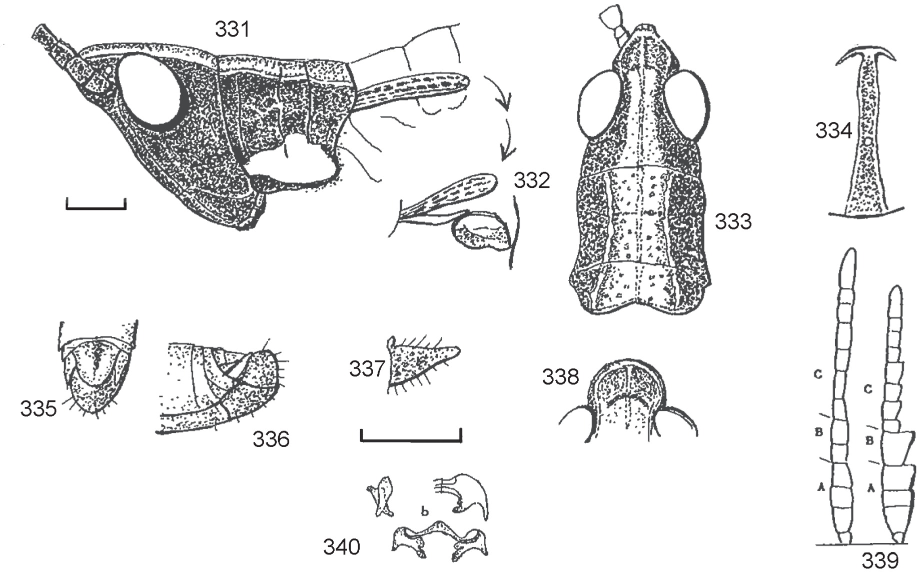
Distribution.—TANZANIA: Zanzibar (holotype only); coastal and close hinterland areas of TANZANIA (S.W. of Dar es Salaam to the KENYA border).

Generic diagnosis

Parga Walker, 1870

Parga Walker, 1870: 504 (replacement for *Amycus* Stål, 1855: 353).

Type species.—*Amycus xanthopterus* Stål, 1855: 353.



Figs 331–340. Tribe Pargaini. *Acteana.* **Figs 331–340.** *Acteana alazonica* male: See also Fig. 67: **331.** Lateral view head, pronotum, and tegmen; **332.** Tegmen raised to show tympanum and wing; **333.** Head and pronotum from above; **334.** Frontal ridge; **335.** Abdominal apex from above; **336.** Abdominal apex from side; **337.** Left cercus; **338.** Female, apex of head from above; **339.** Male, female antennae; **340.** Epiphallus from dorsal and lateral angles. Scale lines represent 1 mm: that next to Fig. 340 applies to Fig. 340 and 337; that below Fig. 331 applies to all the rest.

Description.—Of medium size, slender and elongate. Integument strongly carinate and rugose. Antenna short and broad, clearly divided into basal, medial and apical part, with acutely serrated outer edge (Figs 341–350). Head elongate and acutely conical, strongly carinate above. Fastigium elongate, parabolic, foveolae absent. Pronotum with well developed median and parallel lateral carinae; metazona shorter than prozona, its hind margin obtuse-angular. Tegmina and wings fully developed with acute apices and dense, rough venation and reticulation and numerous intercalary veins. Hind femur narrow; upper lobes of hind knee elongate, lower lobes acute (Figs 351, 352). Apex of male abdomen (Fig. 353) elongated, acute. Internal genital structures in male (Figs 354–356).

Discussion.—The genus *Parga* is in need of revision. Three species are known from eastern Africa: *P. xanthoptera* (Stål, 1855), *P. taeniata* (I. Bolívar, 1889), and *P. musanae* Sjöstedt, 1931 with the possibility that a fourth, *P. cyanoptera* Uvarov, 1926 (recorded from South Sudan and southern Africa), could also occur there. A tentative key to species is given below.

Key to East African species in the genus *Parga*

1 Upper internal lobe of hind knee only slightly longer than outer lobe (Fig. 351). Antenna broad and only slightly longer than head (Figs 346–349) .... *xanthoptera* (Stål, 1855)

– Upper internal lobe of hind knee considerably longer than outer lobe (Fig. 352). Antenna proportionately longer than head (Figs 341–345).. 2

2 Outer side of male antennal flagellum moderately serrated, frons in profile incurved; head no longer than pronotum ....*musanae* Sjöstedt, 1931

– Outer side of male antennal flagellum strongly serrated. Frons in profile straight, or weakly incurved, head distinctly longer than pronotum... *taeniata* (I. Bolívar, 1889)

Note: *P. cyanoptera* Uvarov is similar to *P. xanthoptera* but differs in having proportionately longer and narrower antennae (Fig. 350).

Species notes

No taxonomic changes to the treatment by Dirsh (1970) are proposed, so redefinition of the East African species is not attempted here.

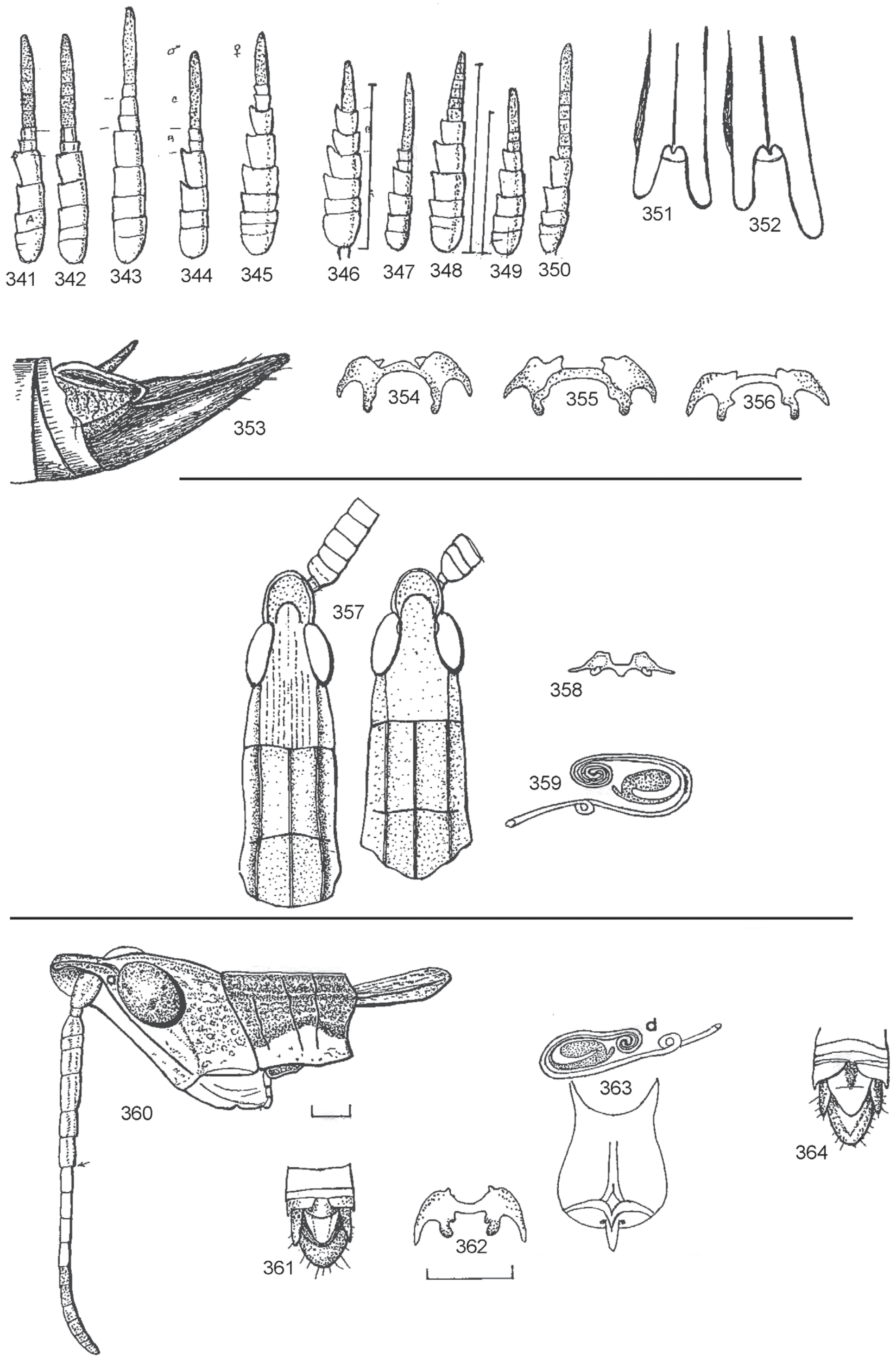
Generic diagnosis

Machaeridia Stål, 1873

Machaeridia Stål, 1873: 90, 100.

Type species.—*Machaeridia bilineata* Stål, 1873: 100, 216, by original designation.

Description.—As in key to genera, above (p. 99). A genus closely related to *Parga* with genitalia of fairly similar structure. Slightly more elongate; integument finely rugose and dotted, not ridged. Antenna broadly ensiform, serrated segments along external edge unspecialized, evenly tapering apically; as long as, or slightly longer than, head and pronotum. Fastigium parabolic, as long as, or slightly longer than broad (Fig. 357). Temporal foveolae absent. Dorsum of pronotum narrow, its surface smooth, weakly tectiform to almost flat; carinae sharp, well developed; lateral carinae straight parallel. Metazona shorter than prozona, its hind margin obtuse-angular, almost rounded. Tegmina and wings fully developed, venation and reticulation dense, intercalary vein of medial area present. Hind wings without a preanal speculum. Hind femur narrow, upper knee lobes much shorter than in *Parga*, their apices acute. Male subgenital plate acute, of similar structure, but shorter than in *Parga*. Genital structures (Figs 358, 359) similar to those in *Parga*.



Figs 341–364. Tribe Pargaini: morphology. **Figs 341–356.** *Parga* spp.: **341–350.** Antennae: **341–343.** *P. musanae:* **341**. Male (Uganda, Soroti); **342.** Male (Tanzania, Mkomasi); **343.** Female, same; **344, 345.** *P. taeniata*: **344.** Male (Tanzania, Old Shinyanga); **345.** Female (Tanzania, Kisulu); **346–349.** *P. xanthoptera*: **346.** Female, (Tanzania, 8ml. S. of Chala mission); **347.** Male (Tanzania, Ufipa); **348.** Female, (Uganda, Tororo); **349.** Female, (Tanzania, S. of Chala mission); (line alongside 348 and 349 indicates length of head and pronotum); **350.** *P. cyanoptera,* male. **Figs 351, 352.** Posterior femoral knee lobes from dorsal view (left leg): **351.** *P. xanthoptera*; **352.** *P. musanae*; **353.** *P. xanthoptera*, apex of abdomen. **Figs 354–356.** Male epiphalli: **354.** *P. xanthoptera*; **355.** *P. musanae*; **356.** *P. taeniata.* **Figs 357–359.** *Machaeridia bilineata*: **357.** Male head and pronotum, dorsal view left, compared with *Machaeridia conspersa* right; **358.** Epiphallus (from Hollis 1966); **359.** Female spermathecal duct. **Figs 360–364.** *Phryganomelus* spp. *Ph. phalangidus:* **360.** Head, pronotum, antennae and tegmen in profile; **361.** Abdominal apex from above; **362.** Epiphallus. *Ph. romi*: **363.** Female spermatheca and dorsal aspect of subgenital plate. *Ph. auriventer:* **364.** Male abdominal apex from above. All scale lines represent 1 mm: Scale line under Fig. 360 applies also to Figs 341–353, 357, 359–361, 362, 364; that under Fig. 362 also applies to Figs 354–356, 358.

Discussion.—*Machaeridia* Stål contains two species, *M. bilineata* Stål, 1873 and *M. conspersa* I. Bolívar, 1889. Both are common throughout eastern Africa.

Key to species in the genus *Machaeridia*

1 Of more slender build. Fastigium of vertex longer than wide. Tegmen narrow, more than 9 times as long as wide; wing relatively narrow, colorless or basally bluish. Hind femur narrow, its length/depth ratio about 8 .... *bilineata* Stål, 1873

– Of more robust build. Fastigium of vertex as long as wide. Tegmen wider, length/width ratio about 7.5; wing proportionately broader, colorless, or yellowish at base. Hind femur broader, length/depth ratio about 6.5 ....*conspersa* I. Bolívar, 1889

Species notes

No taxonomic changes are proposed, so redefinition of the East African species is not attempted here.

Generic diagnosis

Odontomelus I. Bolívar, 1890

Odontomelus I. Bolívar, 1890: 309.

Type species.—*Opomala brachyptera* Gerstaecker, 1869: 216, by monotypy.

Amphicremna Karsch, 1896: 250. Type species: *Amphicremna scalata* Karsch, 1896, by monotypy (syn. Jago 1994).

Paraparga I. Bolívar, 1909: 286. Type species: *Machaeridia strigosa* I. Bolívar, 1889 by monotypy (syn. Jago 1994).

Pargaella I. Bolívar, 1909: 287. Type species: *Pargaella luctuosa* I. Bolívar, 1909, by monotypy (syn. Jago 1994).

Description.—Differentiated as in key to genera, above.

Discussion.—Full revision published by Jago (1994). The genus now contains four winged species, two brachypterous species and 28 flightless micropterous species, including the recently described *O. ancestrus* Hugel, 2014 from Mauritius.

Species notes

As no taxonomic changes are proposed, redefinition of the East African species is not attempted here.

Generic diagnosis

Phryganomelus Jago, 1983

Phryganomelus Jago (1983a): 151–159.

Type species.—*Odontomelus fullonius* Karsch, 1896: 215, by subsequent designation Jago (1983a).

Description.—See Jago (1983a).

Discussion.—Very closely related to *Odontomelus* I. Bolívar, from which it differs in larger size, coarser integument, some details of coloration, but particularly in marked elongation of the head, with frons concave in profile, as also rather weak lateral pronotal carinae (Fig. 360). Currently five species, all micropterous, are attributed to this genus: *P. fullonius* (Karsch, 1896) from D.R. CONGO (synonymized with *olivescens* Sjöstedt, 1923 by Ramme (1929)), *P. biafrensis* (I. Bolívar, 1905) from EQUATORIAL GUINEA and CAMEROON; *P. romi* (I. Bolívar, 1908a) from D.R. CONGO and ANGOLA; *P. phalangidus* Jago, 1983 from UGANDA and E. D.R. CONGO; and *P. auriventer* Jago, 1983 from UGANDA.

Species notes

Only the last two species mentioned above have a known East African distribution and are discussed below.

Phryganomelus phalangidus Jago, 1983

Figs 360–362

Phryganomelus phalangidus Jago, 1983a: 157.

Material.—N.E. D.R. CONGO: Bas-Uélé, valley of the Semliki river. UGANDA: Budongo Forest, Bugoma Forest, Mabira Forest, Mpanga Forest (ml. 21 Kampala-Masaka road), and Bwamba Forest, L. Albert (Butiaba), and Kigezi.

Description.—Of medium size for genus. Male: Antennae longer than combined length of head and pronotum; flattened basal part shorter than rounded apical part (Fig. 360). Head more elongate than pronotum, apex very prominent (Fig. 360). Tegminal apices not surpassing back edge of abdominal tergite 1. Tip of abdomen as in Fig. 361; epiphallus as in Fig. 362. Coloration distinctive, underside of thorax and base of abdomen orange-red. Fore and mid-legs light red-brown. Hind femora orange-red below, shading to dark-brown apically; outer and dorsal areas brown. Hind tibiae dark-brown, black near knee. Female: spermathecal duct as in Fig. 363 (*P. romi*). Vertex and tegmina structurally similar to male. Underside of body orange-red. Hind femora shortest in genus and distinctly more stocky than in *P. auriventer*.

Discussion.—Its range of distribution broadly overlaps with *Odontomelus kwidschwianus* to which it bears a slight superficial resemblance. While both species occur in the same forests (from Bas Uélé in N.E. D.R. CONGO, the valley of the Semliki river and forests from the western rift of UGANDA east to the Nile (fig. 15 in Jago (1983a): Budongo, Bugoma, Mpanga, and Bwamba Forest Reserves), *P. phalangidus* favors the sunlit forest floor and litter along forest paths, while *O. kwidschwianus* inhabits the leaves and stems of forest grasses above ground level.

Distribution.—N.E. D.R. CONGO; W. and C. UGANDA.

Phryganomelus auriventer Jago, 1983

Fig. 364

Phryganomelus auriventer Jago, 1983a: 155.

Material.—Holotype male: UGANDA: Mabira forest, nr. Jinja, 33°00'E 00°25'N, 28.IV.67, and paratypes.

Description.—Closely resembles *P. phalangidus* Jago, 1983, but differs from it as follows: slightly larger size (in mm: total length males 23–28, females 32–36), and more massive hind femora; fore and mid-legs olive green; hind femora light brown above, outer areas olive green, lower surfaces yellow to pale green; underside of thorax and proximal sternites of abdomen yellow to pale green, not orange. Detailed structure of apex of male abdomen differs between the two species (compare Figs 364 and 361).

Distribution.—UGANDA: In forests west of the Nile outlet from Lake Victoria, but always much rarer than *P. phalangidus.*

2.4 Transitional genera of uncertain position

Genus group diagnosis

The *Aiolopus-Uganda* genus group and *Dorsthippus*

Description.—Outlined in Diagnosis of Tribes and Genus Groups, above, Page 39. Defined on basis of male and female genitalia.

Discussion.—This assemblage contains a group of four genera – *Aiolopus, Jasomenia, Paracinema, Uganda* – and *Dorsthippus*. Their peculiarity lies in that they fit the definitions of neither of the two subfamilies Oedipodinae or Acridinae. The Oedipodinae are considered to be characterized by their femoral/tegminal sound-producing mechanism, the sound being produced by the rubbing of a sharp carinula on the inner side of the hind femur against a prominent serrated inter-calary vein, usually in the medial area of tegmina; the Acridinae lack this mechanism, or it is vestigial and said to be incapable of sound-production. Generally, there is little ambiguity in attributing a given genus to one or other of these two subfamilies on the basis of the above distinction. The four genera listed possess a well-developed intercalary vein but in some it lacks the necessary serrations for sound production. Also, their rather slender build and hygrotypic habitat associations are more characteristic of the Acridinae than the Oedipodinae. They are thus at the root of the controversy surrounding the separate identity of the two subfamilies.

Importantly, Slifer (1939) described the presence of a loop at the proximal end of the female spermathecal duct in Acridinae, but which is absent in Oedipodinae. All the four genera considered here lack the proximal loop, and should, therefore, be placed in the Oedipodinae rather than Acridinae. Absence of serrations on the intercalary vein may thus be attributable to secondary loss.

Editorial note.—As discussed in the Introduction (p. 42) we consider these four genera to be most usefully classified as Oedipodinae, rather than Acridinae, and omit further treatment of them here. *Dorsthippus* is also discussed on p. 42.

Acknowledgements

G. Popov's thanks go to the curators and collection managers who provided specimens on loan to facilitate this publication. Colleagues at the Natural Resources Institute, University of Greenwich (Drs N.D. Jago, S.V. Green, J.M. Ritchie) and the Natural History Museum, London (Mrs. J.A. Marshall, Mr. D. Hollis) are especially thanked for their assistance. This paper is an output from a project funded by the UK Department for International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID. (DFID/ODA project code R5306/CPP).

C.H.F. Rowell and L.D.C. Fishpool thank the Drs. C. Hemp and A. Hochkirch for their help in preparing Popov's manuscript for publication. We further acknowledge gratefully the valuable help of the referees, Drs M. Lecoq and J. Mestre, in checking the submitted version of the manuscript.

References

Baccetti B (1984) Notulae Orthopterologicae 39. New or little known East African grasshoppers. Redia 67: 367–400. https://doi.org/10.1080/03749444.1985.10736701

Baccetti B (1985) Notulae Orthopterologicae 39. New or little known Phlaeobinae of Somalia (Orthoptera, Acrididae). Monitore zoologico italiano (N.S.) Suppl. 20; 14: 299–323.

Baccetti B (1997) Notulae Orthopterologicae 52. La collezione di ortotteri acridomorphi dell'Africa orientale conservata nel Museo Civico di Storia Naturale G. Doria di Genova. Annali del Museo civico di storia naturale di Genova 91: 227–292.

Baccetti B, Abukar MM (1987) Notulae Orthopterologicae 44. The Orthopterans present in sorghum, maize and rice in the area of lower Uebi Seebeile and upper Jubba. Monitore Zoologico Italiano Supplemento 22: 129–176. https://doi.org/10.1080/03749444.1987.10736726

Bolívar I (1881) Notas entomológicas V. Nuevas especies de ortópteros sudamericanos del viaje al Pacífico. Annales de la Sociedad Española de Historia Natural 10: 477–507.

Bolívar I (1889) Ortópteros de Africa del Museo de Lisboa. Jornal de sciências mathemáticas, physicas e naturaes (Ser. 2) 1: 73–112. https://doi.org/10.5962/bhl.part.9541

Bolívar I (1890) Diagnosis de ortópteros nuevos. Anales de la Sociedad Española de Historia Natural 19: 299–333.

Bolívar I (1898) Contribution à l'etude des Acridiens espèces de la faune indo et austro-malaisienne du Museo civivo di Storia Naturale di Genova. Annali del Museo civico di storia naturale di Genova Ser. 2 19: 66–101.

Bolívar I (1906) Rectificaciones y observaciones ortopterológicas. Boletín de la Real Sociedad Española de Historia Natural 6: 384–393.

Bolívar I (1908a) Acridiens d'Afrique du Musée Royal d'Histoire Naturelle de Belgique. Mémoires de la Société Entomologique de Belgique 16: 83–126. https://doi.org/10.5962/bhl.part.5613

Bolívar I (1908b) *Acridarachnea* gen.nov. Nuevo genero proximo al Acrida (L.) Stål. Boletín de la Real Sociedad Española de Historia Natural 8: 418–420.

Bolívar I (1909) Observaciones sobre los Truxalinos. Boletín de la Real Sociedad Española de Historia Natural 9: 285–296.

Bolívar I (1912) Orthoptères nouveaux recueillis par Dr. Sheffield-Neave dans la Katanga. Mémoires de la Société entomologique de Belgique 19: 73–99.

Bolívar I (1914) Estudios entomológicos. Segunda parte. I. El grupo de los Euprepocnemes. II. Los Truxalinos del antiguo mundo. Trabajos del Museo de Ciencias Naturales (Serie Zoológica) 20: 1–110.

Bouvy EH (1982) Five new Acridoidea from Lubumbashi, D.R. Congo and redescriptions of one species and genus (Orthoptera). Revue Zoologique Africaine 96: 399–435.

Brunner von Wattenwyl C (1893) Révision du système des orthoptères et description des espèces rapportées par M. Leonardo Fea de Birmanie. Annali del Museo Civico di Storia Naturale 'Giacomo Doria', Genova 33: 1–230. [pls 1–6] https://doi.org/10.5962/bhl.title.5121

Burmeister H (1838) Handbuch der Entomologie. Zweiter Band. Berlin, 1050 pp.

Chopard L (1921) Orthoptères. In: Voyage de M. Guy Barbault dans l' Afrique Orientale Anglaise. Result. Sci. (Paris) 1921: 1–64.

Chopard L (1958) La Réserve Naturelle Intégrale du Mont Nimba. III. Acridiens. Mémoire de l' Institut Français d' Afrique Noire 53: 127–153.

Cigliano MM, Braun H, Eades DC, Otte D (2018) Orthoptera Species File. Version 5.0/5.0. http://orthoptera.speciesfile.org [01–02–2018]

C.O.P.R. (1982) The Locust and Grasshopper Agricultural Manual. Centre for Overseas Pest Research, London, 690pp.

Descamps M (1965) Acridoides du Mali (deuxième contribution). Regions de San et Sikasso (zone soudanaise) (1 partie) et (2 partie). Bulletin de l'Institut Fondamental d'Afrique Noire (IFAN). Série A: Sciences Naturelles 27: 922–962, 1259–1314.

Descamps M, Donskoff M (1968) Contribution à la faune du Congo (Brazzaville). Mission A. Villiers et A. Descarpentiers. 77. Orthoptères Pyrgomorphidae et Acrididae. Bulletin de l'Institut fondamental d'Afrique noire 30A: 1198–1235.

Descamps M, Wintrebert A (1966) Pyrgomorphidae et Acrididae de Madagascar. Observations biologiques et diagnoses (Orth. Acridoidea). Eos, Revista española de Entomología 42: 41–263.

Dirsh VM (1951) Revision of the group Truxales (Orthoptera, Acrididae). Eos, Revista Española de Entomología tomo extraord (Madrid) 1951: 119–248.

Dirsh VM (1956) The phallic complex in Acridoidea (Orthoptera) in relation to taxonomy. Transactions of the Royal Entomological Society of London 108: 223–356. [pls 1–66] https://doi.org/10.1111/j.1365-2311.1956.tb02270.x

Dirsh VM (1958) Acridological notes. Tijdschrift voor Entomologie 101: 51–63.

Dirsh VM (1959) New genera and species of Acridoidea from tropical Africa (Orthoptera). Eos, Revista española de Entomología 35: 21–39.

Dirsh VM (1962) Synonymic notes on African Acridoidea (Orthoptera). Revue de Zoologie et de Botanique africaines 65: 81–89.

Dirsh VM (1963) The Acridoidea (Orthoptera) of Madagascar. II Acrididae, Acridinae. Bulletin of the British Museum (Natural History) Entomology 13: 245–286. http://biostor.org/reference/86053

Dirsh VM (1965) The African Genera of Acridoidea. Cambridge University Press, for the Anti-Locust Research Centre, Cambridge, 579 pp.

Dirsh VM (1966) Acridoidea of Angola. Publicações Culturais de Companhia de Diamantes de Angola 74, 527 pp.

Dirsh VM (1970) Acridoidea of the Congo (Orthoptera). Annales du Musée Royal de l'Afrique Centrale (série Sciences zoologiques) 182, 605 pp.

Dirsh VM (1975) Classification of the Acridomorphoid Insects. E.W. Classey Ltd., Faringdon, 171 pp.

Fabricius JC (1775) Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. Flensburg & Leipzig, 832 pp. https://doi.org/10.5962/bhl.title.36510

Felix RPWH, Massa B (2016) Orthoptera (Insecta: Tettigonioidea, Pyrgomorphoidea, Acridoidea) of Kafa Biosphere Reserve, Bale Mountains National Park and other areas of conservation interest in Ethiopia. Zootaxa 4189: 001–059. https://doi.org/10.11646/zootaxa.4189.1.1

Fishpool LDC, Popov GB (1984) The grasshopper faunas of the savannas of Mali, Niger, Benin and Togo. Bulletin de l'Institut Fondamental d'Afrique Noire 43[1981]: 275–410.

Gerstaecker A (1869) Beitrag zur Insekten-Fauna von Zanzibar. No. II. Orthoptera et Neuroptera. Archiv für Naturgeschichte 35: 201–223. https://doi.org/10.5962/bhl.part.12294

Hochkirch A (1998) *Parodontomelus luci* sp. n., a new grasshopper species from the Udzungwa Mountains, Tanzania (Orthoptera, Acrididae, Acridinae). Journal of Orthoptera Research 8: 39–44. https://doi.org/10.2307/3503423

Hollis D (1965) A revision of the genus *Machaeridia* (Orth. Acridoidea). Eos, Revista Española de Entomología 40: 495–505; Madrid.

Hollis D (1968) A revision of the genus *Aiolopus* Fieber (Orthoptera: Acridoidea). Bulletin of the British Museum (Natural History) (Entomology) 22: 309–355.

Hugel S (2014) Grasshoppers of the Mascarene Islands: new species and new records (Orthoptera, Caelifera). Zootaxa 3900: 399–414. https://doi.org/10.11646/zootaxa.3900.3.4

Jago ND (1966) Descriptions of new species of West African grasshoppers with taxonomic notes on some species recently mentioned in the literature. (Orth. Acrididae). Eos, Revista española de Entomología, 1965 41: 343–371.

Jago ND (1968) New East African taxa in the genus *Gymnobothroides* (Acridinae; Acrididae; Orthoptera). Notulae Naturae 417: 1–14.

Jago ND (1970) New East African grasshopper species (Acridinae, Acrididae, Orthoptera) with discussion of problems of generic designation. Notulae Naturae 433: 1–7.

Jago ND (1983a) A new genus of African forest grasshoppers and its differentiation from the genus *Odontomelus* I. Bolívar (Orthoptera, Acrididae). Entomologists' Monthly Magazine 119: 151–159.

Jago ND (1983b) Flightless members of the *Phlaeoba* genus group in eastern and north-eastern Africa and their evolutionary convergence with the genus *Odontomelus* and its allies (Orthoptera, Acridoidea, Acrididae, Acridinae). Transactions of the American Entomological Society 109: 77–126.

Jago ND (1994) *Odontomelus* I. Bolívar 1890 (Orthoptera, Acridoidea, Acrididae, Acridinae): savanna-woodland grasshoppers with a major radiation of flightless species in Eastern Africa. Tropical Zoology 7: 367–450. https://doi.org/10.1080/03946975.1994.10539266

Jago ND (1996) Song, sex and synonymy: the Palaearctic genus *Acrida* Linnaeus (Orthoptera, Acrididae, Acridinae) and synonymy of the subfamily Truxalinae under the subfamily Acridinae. Journal of Orthopteran Research 5: 125–129. https://doi.org/10.2307/3503586

Johnsen P (1983) Description of a new genus, three new species and the hitherto unknown sex of three species of Orthoptera: Acridomorpha from tropical Africa. Natura Jutlandica 21: 49–60.

Johnsen P (1984) Acridoidea of Zambia. Volume 5. Zoological Laboratory, Aarhus University, Aarhus, 267–354.

Johnsen P (1990) A new genus and three new species of Acridoidea with notes on some lesser known species from southern Africa (Orthoptera). Natura Jutlandica 23: 1–22.

Johnsen P (1991) Acridoidea of Botswana. Aarhus University, Aarhus, Denmark, part 2, 130–284.

Johnsen P, Schmidt GH (1982) Notes on and a check-list of Acridoidea (Saltatoria) collected in Somalia (East Africa). Monitore zoologico italiano, (N.S.) Suppl. 16: 69–119. https://doi.org/10.1080/00269786.1982.11758559

Johnston HB (1937) The Acrididae of Mt. Kenya, East Africa. Proceedings of the Royal Entomological Society of London (B) 6: 217–223. https://doi.org/10.1111/j.1365-3113.1937.tb01678.x

Johnston HB (1956) Annotated Catalogue of African Grasshoppers. University Press, Cambridge, 833 pp.

Johnston HB (1968) Annotated Catalogue of African Grasshoppers (Supplemental). University Press, Cambridge, 445 pp.

Karny HH (1907) Ergebnisse der mit Subvention aus der Erbschaft Treitl unternommen zoologischen Forschungsreise Dr. Franz Werner's nach dem ägyptischen Sudan und Nord-Uganda. IX. Die Orthopterenfauna des ägyptischen Sudans und von Nord-Uganda (Saltatoria, Gressoria, Dermaptera) mit besonderer Berücksichtigung der Acridoideengattung *Catantops*. Sitzungsberichte der Österreichischen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse (Abt. 1). 116: 267–378. [Taf. 1–3]

Karny HH (1915) Ergebnisse der Forschungsreise des Herrn Dr. Adalbert Klaptocz nach Französisch Guinea. Zoologische Jahrbücher. Abt. Syst. Geogr. und Biol. der Tiere 40: 119–146.

Karsch F (1893) Die Insecten der Berglandschaft Adeli im Hinterlande von Togo (Westafrika) nach dem von den Herren Hauptmann Eugen Kling (1888 und 1889) und Dr. Richard Büttner 1890 und 1891 gesammelten Materiale bearbeitet. – Berliner Entomologische Zeitschrift 38: 1–266. [pls 1–6; mit einem Vorworte von Dr. Richard Büttner und einer Uebersichtskarte des Togogebietes. 1. Abteilung: Apterygota, Odonata, Orthoptera Saltatoria, Lepidoptera Rhopalocera.] https://doi.org/10.5962/bhl.title.8524

Karsch F (1896) Neue Orthopteren aus dem tropischen Afrika. Stettiner ent. Zeitung 57: 242–359.

Karsch F (1900) Vorarbeiten zu einer Orthopterologie Ostafrika's II. Einige Gattungen Feldheuschrecken, Acridodea. Entomologische Nachrichten 26: 274–287.

Kevan DKMcE (1950) Orthoptera from the hills of South-East Kenya. Journal of the East Africa Natural History Society 19: 192–221.

Kirby WF (1910) A synonymic catalogue of Orthoptera. Vol. 3. Orthoptera Saltatoria. Part. 2. (Locustidae vel Acrididae). British Museum, London, 674 pp.

McNeill J (1897) Revision of the Truxalinæ of North America. Proceedings of the Davenport Academy of Natural Sciences 6: 179–274.

Macleay WS (1821) Chapter VI. On the orders of the Annulosa; Chapter VII. On the tribes of Mandibulata. Horae Entomol. (S. Bagster, London) 1: 341–417, 428–458.

Mestre J (1988) Les Acridiens des formations herbeuses d'Afrique de l'Ouest. Centre de Cooperation Internationale en Recherche Agronomique pour le Developpement, Paris, 331 pp.

Mestre J (2001) Notes systématiques sur les genres *Epistaurus*, *Bryophyma*, *Zacompsa* et *Acrotylus* en Afrique de l'Ouest (Orthoptera, Acrididae). Bulletin de la Société Entomologique de France 106: 483–495.

Mestre J, Chiffaud J (2006) Catalogue et atlas des acridiens d'Afrique de l'Ouest. http://www.acrida.info/bib/catog1.htm

Miller NCE (1929) Acrididae collected in Tanganyika Territory. Transactions of the Entomological Society of London 77: 61–97. https://doi.org/10.1111/j.1365-2311.1929.tb00680.x

Miller NCE (1932) New African Acrididae in the collection of the British Museum. Transactions of the Royal Entomological Society of London 80: 19–45. https://doi.org/10.1111/j.1365-2311.1932.tb00080.x

Miller NCE (1949) A new genus and new species of Acrididae from Southern Rhodesia. Annals and Magazine of Natural History 2: 679–687. https://doi.org/10.1080/00222934908654016

Otte D (1981) The North American Grasshoppers. Vol. I. Acrididae, Gomphocerinae and Acridinae. Cambridge, Massachusetts and London, England, Harvard University Press.

Otte D (1984) The North American Grasshoppers. Vol. II. Acrididae – Oedipodinae. Harvard University Press, 376 pp.

Otte D (1995) Orthoptera Species File 5. Grasshoppers [Acridomorpha] D. Acridoidea: Acrididae. The Orthopterists' Society & the Academy of Natural Sciences of Philadelphia, USA.

Popov GB, Fishpool LDC (1992) A revision of the grasshopper genus *Orthochtha* and allies (Orthoptera: Acrididae: Acridinae). Natural Resources Institute (Chatham, Bulletin) 54: 1–154.

Ramme W (1929) Afrikanische Acrididae. Revisionen und Beschreibungen wenig bekannter und neuer Gattungen und Arten. Mitteilungen aus dem Zoologischen Museum in Berlin 15: 247–492.

Ramme W (1931) Ergänzungen und Berichtigungen zu meiner Arbeit Afrikanische Acrididae. Mitteilungen aus dem Zoologischen Museum in Berlin 16: 918–945.

Rehn JAG (1914) Orthoptera. I. Mantidae, Phasmidae, Acrididae, Tettigoniidae und Gryllidae aus dem Zentral-Afrikanischengebiet, Uganda und dem Ituri-Becken des Kongos. Wiss. Ergebn. dtsch. Zent.-Afr. Exped. 1907–1908, 5: 1–223.

Rowell CHF, Hemp C, Harvey AW (2015) Jago's Grasshoppers of East and North East Africa, Vol. 1: Pneumoridae, Pyrgomorphidae, Lentulidae, Pamphagidae, and Dericorythidae. Blurb Publishers, San Francisco, 237 pp.

Rowell CHF, Hemp C (2017) Jago's Grasshoppers of East and North East Africa, Vol. 2. Acrididae: Teratodinae, Hemiacridinae, Spathosterninae, Tropidopolinae, Calliptaminae, Oxyinae, Coptacrinae and Eyprepocnemidinae. Blurb Publishers, San Francisco, 237 pp.

Rowell CHF, Hemp C (2018) Jago's Grasshoppers of East and North East Africa, Vol. 3. Acrididae: Catantopinae. Blurb Publ., San Francisco, 230 pp.

Roy R (2003) Les Acridiens du Nimba et de sa région. In: Lamotte M, Roy R (Eds) Le peuplement animal du mont Nimba (Guinée, Côte d'Ivoire, Liberia). Muséum national d'Histoire naturelle, Paris, 311–391. [Mémoires du Muséum national d'Histoire naturelle 190]

de Saussure H (1862) Etudes sur quelques orthoptères du Musée de Genève. Annales de la Société Entomologique de France 41: 469–494.

Schaum H (1853) In Peters. Übersicht der von ihm in Mossambique beobachteten Orthopteren nebst Beschreibung der neu entdeckten Gattungen und Arten durch Hrn. Dr. Hermann Schaum. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der königlich Preussischen Akademie Wissenschaften zu Berlin, 775–780.

von Schulthess A (1898) Orthoptères du pays des Somalis, recueillis par L. Robecchi–Brichetti en 1891 et par le Prince E. Ruspoli en 1892–93. Annali del Museo Civico di Storia Naturale 'Giacomo Doria', Genova (2) 19: 161–216. [pl. 2]

Serville JGA (1838) Histoire naturelle des Insectes. Orthoptères. Librairie Encyclopédique de Roret [Collection des suites a Buffon]; Paris (Roret): 776 pp. [pls 1–14]

Shumakov EM (1963) Les acridiens et les autres orthoptères de l'Afghanistan et de l'Iran [in Russian] Trudy Vsesoyeiznogo Entomologichesko-jo Obshchestva, Moskva [= Horae Societatis Entomologicae Unionis Soveticae] 49: 3–248.

Sjöstedt Y (1909) Wissenschaftliche Ergebnisse der schwedischen zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massaisteppen Deutsch-Ostafrikas, 1905–1906 unter Leitung von Prof. Dr. Yngve Sjöstedt. 17. Orthoptera, 7. Acridoidea: 149–199.

Sjöstedt Y (1929) Acridiodea aus Zentralafrika gesammelt von R. Grauer während seiner Expedition 1909–1911. Arkiv för Zoologi 20A: 1–41.

Sjöstedt Y (1931) Acridoidea aus Kongo and anderen Teilen von Afrika. Arkiv för Zoologi 22A: 64 pp. [6 pls., 40 figs]

Sjöstedt Y (1933a) Neue Acrididen von dem Mt. Elgon und dem Britischen Ostafrika. Vorläufige Diagnosen. Entomologisk Tidskrift 54: 215–216.

Sjöstedt Y (1933b) Sammlungen der Schwedischen Elgon-Expedition im Jahre 1920. Acrididae, Mantidae und Phasmidae. Arkiv für Zoologi (Stockholm) 26A: 1–27.

Slifer EH (1939) The internal genitalia of female Acridinae, Oedipodinae and Pauliniinae (Orthoptera, Acrididae). Journal of Morphology 65: 437–470. https://doi.org/10.1002/jmor.1050650304

Stål C (1855) Nya Orthoptera. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlinger 12: 348–353.

Stål C (1861) Orthoptera species novas descripsit. In: Kongliga Svenska Fregatten Eugenies Resa, Omkring Jorden under befal af C.A. Virgin, aren 1851–1853, Vetenskapliga Lakttagelser på H. M. Konung Oscar der Forstes Befallning, vol. 2, Zoologi. 1. Insecta. Utgifna of K. Svenska Vetanskaps Akademien 3 (P.A. Norstedt & Söner, Stockholm) [1858–1868]: 299–350 (1–617).

Stål C (1873) Recensio orthopterorum. Revue critique des Orthoptères décrits par Linné, De Geer et Thunberg. 1. Öfversigt Kongliga Vetenskaps-akademiens Förhandlingar 30: 1–153. [Acridiodea]

Stål C (1875) Recensio orthopterorum. Revue critique des Orthoptères décrits par Linné, De Geer et Thunberg. 3. Öfversigt Kongliga Vetenskaps-akademiens Förhandlingar 32: 1–105. [Gryllidae, Phasmidae]

Stål C (1876) Bidrag till södra Afrikas Orthopter-fauna. Öfversigt Köngliga Vetenskaps-akademiens Förhandlingar (Stockholm) 33: 31–58.

Thomas C (1872) Notes on the saltatorial Orthoptera of the Rocky Mountain regions. In Hayden, U.S. Geological Survey of Montana and Adjacent Territory 1871. Preliminary Report of the United States Geological Survey of Montana and Portions of Adjacent Territories; being a Fifth Annual Report of Progress 5: 423–466. [2 pls]

Uvarov BP (1926) Grasshoppers (Orthoptera, Acrididae) from Northern Nigeria. Transactions of the Entomological Society of London 1925: 413–453.

Uvarov BP (1930) A new alpine grasshopper (Orthoptera, Acrididae) from Mount Elgon. Annals and Magazine of Natural History 5: 249–250. https://doi.org/10.1080/00222933008673129

Uvarov BP (1934) Entomological expedition to Abyssinia 1926–7. Orthoptera of the families Mantidae, Gryllidae, Tettigoniidae, and Acrididae. Zoological Journal of the Linnean Society 38: 591–614, 10 figs. https://doi.org/10.1111/j.1096-3642.1934.tb00998.x

Uvarov BP (1938) Mission scientifique de l'Omo, Tome IV, Fascicule 35. Orthoptera III: Acrididae. Mém. Mus. Natn. d'Hist .nat. Paris, Numéro special 8: 145–176.

Uvarov BP (1941) New African Acrididae. Journal of the Entomological Society of Southern Africa 4: 47–71.

Uvarov BP (1952) Studies in the Arabian Orthoptera III. New genera, species and subspecies collected by the Anti-Locust Missions. Zoological Journal of the Linnean Society 42: 176–194. https://doi.org/10.1111/j.1096-3642.1952.tb01857.x

Uvarov BP (1953) Grasshoppers (Orthoptera, Acrididae) of Angola and Northern Rhodesia collected by Dr. Malcolm Burr in 1927–28. Publicações Culturais da Companhia de Diamantes de Angola 21: 9–217.

Uvarov BP (1966) Grasshoppers and Locusts. A Handbook of General Acridology. Volume 1, Cambridge: Cambridge University Press, for the Anti-Locust Research Centre.

Walker F (1870) Catalogue of the specimens of Dermaptera Saltatoria in the collection of the British Museum. Part III, British Museum of Natural History, London, 425–604.

Willemse L (1994) Additional records of Acridoidea (Orthoptera: Caelifera) from Zambia with a description of a new genus and two new species. Journal of African Zoology 108: 454–456.