zoosystema

2025 • 47 • 24

Out of sight, out of mind? Ixalidiidae, a new family of African forest grasshoppers (Orthoptera, Acridoidea) revealed by molecular phylogenetics and genital morphology

Claudia HEMP, J. Mark RITCHIE, Maria Marta CIGLIANO, Klaus-Gerhard HELLER, Elżbieta WARCHALOWSKA-ŚLIWA, Beata GRZYWACZ, Jackson LINDE, Onur ULUAR, Charly OUMAROU NGOUTE & Hojun SONG

art. 47 (24) — Published on 3 October 2025
www.zoosystema.com

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

Couverture / Cover :
Unusually colored female of *Ixalidium haematoscelis* from the Taita Hills, Kenya, with yellow markings instead of the typical uniform brownish coloration.

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Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / https://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9551/ ISSN (électronique / *electronic*) : 1638-9387

Out of sight, out of mind? Ixalidiidae, a new family of African forest grasshoppers (Orthoptera, Acridoidea) revealed by molecular phylogenetics and genital morphology

Claudia HEMP
University of Bayreuth, Department of Plant Systematics Universitaetsstr 30,
95447 Bayreuth (Germany)
and Helmholtz Centre for Environmental Research (UFZ)
Permoserstraße 15, 04318 Leipzig (Germany)
claudia.hemp@uni-bayreuth.de

J. Mark RITCHIE
The Natural History Museum,
Cromwell Road, London SW7 5BD (Great Britain)
mark.ritchie@nhm.ac.uk

Maria Marta CIGLIANO
Museo de La Plata, CEPAVE-CONICET – UNLP,
Paseo del Bosque 1900, La Plata (Argentina)
cigliano@fcnym.unlp.edu.ar

Klaus-Gerhard HELLER
Triesdorf Bahnhof 8, 91732 Merkendorf (Germany)
heller.volleth@t-online.de

Elżbieta WARCHALOWSKA-ŚLIWA
Beata GRZYWACZ
Institute of Systematics and Evolution of Animals, Polish Academy of Sciences,
Sławkowska 17, 31-016 Kraków (Poland)
warchalowska@isez.pan.krakow.pl; grzywacz13@gmail.com

Jackson LINDE
Department of Entomology, Texas A&M University, College Station, TX (United States)
jackson.linde@tamu.edu

Onur ULUAR
Department of Biology, Faculty of Science, Akdeniz University,
07058 Konyaaltı/Antalya (Turkey)
onuruluar@gmail.com

Charly OUMAROU NGOUTE
Laboratory of Zoology, Faculty of Science, University of Douala,
Laboratory of Zoology, Faculty of Science, University of Douala (Cameroon)
coumaroungoute@gmail.com

Hojun SONG
Department of Entomology, Texas A&M University,
College Station, TX (United States)
hojun.song@ag.tamu.edu

Submitted on 4 August 2024 | Accepted on 26 March 2025 | Published on 3 October 2025 urn:lsid:zoobank.org:pub:C09919D9-3256-4F31-AED4-C7A36A06326C

Hemp C., Ritchie J. M., Cigliano M. M., Heller K.-G., Warchalowska-Śliwa E., Grzywacz B., Linde J., Uluar O., Oumarou Ngoute C. & Song H. 2025. — Out of sight, out of mind? Ixalidiidae, a new family of African forest grasshoppers (Orthoptera, Acridoidea) revealed by molecular phylogenetics and genital morphology. *Zoosystema* 47 (24): 489-553. https://doi.org/10.5252/zoosystema2025v47a24. http://zoosystema.com/47/24

ABSTRACT

This paper presents the most comprehensive higher level phylogeny of the Acridomorpha to date, based on molecular data, clearly showing that the genera *Mazaea* Stål, 1876, *Ixalidium* Gerstäcker, 1869, *Tangana* Ramme, 1929 and *Rowellacris* Ritchie & Hemp n. gen., previously assigned to the Acrididae, belong to a single clade, constituting a previously unsuspected monophyletic family-level group that we are naming Ixalidiidae Hemp, Song & Ritchie n. fam. This paper combines molecular phylogenetics, morphotaxonomy, cytogenetics and bioacoustics to characterize this new family, and presents a comprehensive character table as context for its placement within the Acridoidea. The family Ixalidiidae Hemp, Song & Ritchie n. fam. currently comprises five genera, two from West and Central Africa: *Mazaea* and *Barombia* Karsch, 1891 and three from the montane and coastal forests of Tanzania and Kenya: *Ixalidium*, *Tangana* and *Rowellacris* Ritchie & Hemp n. gen. Three species originally described in *Ixalidium* are transferred to *Rowellacris* Ritchie & Hemp n. gen.: *R. usambarica* (Ramme, 1929) n. comb. (as type species), *R. transiens* (Ramme, 1929) n. comb. and *R. obscuripes* (Miller, 1929) n. comb. *R. usambarica* and *R. obscuripes* are recalled from synonymy under *Ixalidium haematoscelis* Gerstäcker, 1869. The monotypic genus *Eubocoana* Sjöstedt, 1931 is synonymised with *Mazaea* and the previously unknown male of *Mazaea tristis* (Sjostedt, 1931) n. comb. is described. Lectotypes are designated for *Barombia tuberculosa* Karsch, 1891 and for *Ixalidium haematoscelis* Gerstäcker, 1869. The paper describes the diverse and unusual morphology of the male and female genitalia and documents the exceptional chromosome number of Ixalidiidae Hemp, Song & Ritchie n. fam. and the drumming behaviour of *Rowellacris* Ritchie & Hemp n. gen. and *Tangana*. An unexpected sister-group relationship between the African Ixalidiidae Hemp, Song & Ritchie n. fam. and the South American Tristiridae revealed by the molecular phylogeny points to the existence of a common ancestor in Western Gondwana (Atlantica), predating the final separation of South America and Africa around the beginning of the late Cretaceous period 100 million years ago.

KEY WORDS
Acridoidea,
molecular phylogenetics,
phylogeny,
Tangana,
Eastern Arc Mountains,
Cretaceous,
new genus,
new family.

RÉSUMÉ

Loin des yeux, loin du cœur ? Ixalidiidae, une nouvelle famille des acridiens forestiers africains (Orthoptera, Acridoidea) révélée par la phylogénie moléculaire et la morphologie des genitalia.

Cet article présente la phylogénie de niveau supérieur la plus complète à ce jour des Acridomorpha, basée sur des données moléculaires, montrant clairement que les genres *Mazaea* Stål, 1876, *Ixalidium* Gerstäcker, 1869, *Tangana* Ramme, 1929 et *Rowellacris* Ritchie & Hemp n. gen., précédemment attribués aux Acrididae, appartiennent à un seul clade, constituant une famille monophylétique, jusqu'alors insoupçonnée, que nous nommons Ixalidiidae Hemp, Song & Ritchie n. fam. Cet article combine la phylogénie moléculaire, la morphotaxonomie, la cytogénétique et la bioacoustique pour caractériser cette nouvelle famille, et présente une table de caractères complète comme contexte pour son placement au sein des Acridoidea. La famille des Ixalidiidae Hemp, Song & Ritchie n. fam. comprend actuellement cinq genres, deux d'Afrique occidentale et centrale : *Mazaea* et *Barombia* Karsch, 1891 et trois des forêts d'altitude et côtières de Tanzanie et du Kenya : *Ixalidium*, *Tangana* et *Rowellacris* Ritchie & Hemp n. gen. Trois espèces initialement décrites dans *Ixalidium* sont transférées dans *Rowellacris* Ritchie & Hemp n. gen. : *R. usambarica* (Ramme, 1929) n. comb. (comme espèce type), *R. transiens* (Ramme, 1929) n. comb. et *R. obscuripes* (Miller, 1929) n. comb., *R. usambarica* et *R. obscuripes* sont rappelés de la synonymie sous *Ixalidium haematoscelis* Gerstäcker, 1869. Le genre monotypique *Eubocoana* Sjöstedt, 1931 est mis en synonymie avec *Mazaea* et le mâle précédemment inconnu de *Mazaea tristis* (Sjöstedt, 1931) n. comb. est décrit. Des lectotypes sont désignés pour *Barombia tuberculosa* Karsch, 1891 et pour *Ixalidium haematoscelis* Gerstäcker, 1869. L'article décrit la morphologie diversifiée et inhabituelle des genitalia mâles et femelles et documente le nombre exceptionnel de chromosomes des Ixalidiidae Hemp, Song & Ritchie n. fam. et la communication par tambourinage chez *Rowellacris* Ritchie & Hemp n. gen et *Tangana*. Une relation de groupe frère inattendue entre les Ixalidiidae Hemp, Song & Ritchie n. fam. africains et les Tristiridae sud-américains révélée par la phylogénie moléculaire montre l'existence d'un ancêtre commun dans l'ouest du Gondwana (Atlantica), antérieur à la séparation définitive de l'Amérique du Sud et de l'Afrique, vers le début de la fin du Crétacé, il y a 100 millions d'années.

MOTS CLÉS
Acridoidea,
phylogénie moléculaire,
phylogénie,
Ixalidium,
Tangana,
Montagnes de l'Arc Est Africain,
Crétacé,
genre nouveau,
famille nouvelle.

INTRODUCTION

The Acridoidea MacLeay, 1821 is the largest superfamily within Caelifera Ander, 1936, containing over 8 400 described species of grasshoppers defined by distinctive male phallic complex morphology and other traits (Roberts 1941; Amédégnato 1974; Kevan 1982; Song & Mariño-Pérez 2013). According to the Orthoptera Species File (Cigliano *et al.* 2024), Acridoidea includes ten families, of which the Acrididae Ander, 1936 are by far the largest, exceeding 6 800 species (Song *et al.* 2018). The phylogenetic relationships among these families are mostly well-understood from molecular phylogenetic studies (Leavitt *et al.* 2013; Song *et al.* 2015, 2020), although the positions of Dericorythidae Jacobson & Bianchi, 1905 and Lathiceridae Dirsh, 1954 have not been tested due to a lack of molecular-grade specimens. Previous studies consistently found Acridoidea to be monophyletic and sister to Pyrgomorphoidea Brunner von Wattenwyl, 1874, with a clade consisting of Pamphagodidae Bolívar, 1884 and Pamphagidae Burmeister, 1840 hypothesized as the earliest diverging lineage.

The taxonomy of the genus *Ixalidium* Gerstäcker, 1869 has historically been problematic, with incorrect synonymies and misidentifications complicating its classification (Uvarov 1941; Dirsh 1966). Its assignment to various subfamilies within Acrididae, based on dubious external characters and single genital characters, has added to the confusion. What we now know to be the related West African genera (*Mazaea* Stål, 1876, *Barombia* Karsch, 1891 and the former *Eubocoana* Sjöstedt, 1931) have also been understudied. However, recent molecular phylogenetic studies supported by genital morphology have clarified the phylogeny of *Ixalidium* and its allies. Grasshoppers, including several *Ixalidium* species, serve as important bioindicators and are critically impacted by environmental degradation (Jago *in* Rowell *et al.* 2015; Oumarou Ngoute *et al.* 2020). Some *Ixalidium* species are listed among globally threatened insects in the Eastern Arc Mountains and Coastal Forests (EACF) of Kenya and Tanzania (Gereau *et al.* 2016).

The current study builds on research and field collecting by the UK Natural Resources Institute (NRI) from 1980 to 1996, and collecting and ecological studies by CH in the forests of Mt Kilimanjaro and the Eastern Arc Mountains of Tanzania. This research has amassed extensive collections of *Ixalidium*, whose identification was challenging due to their nymph-like and conserved external morphology. Molecular techniques have been used to elucidate species boundaries and phylogenetic relationships. Collaboration between CH and HS, along with earlier unpublished morpho-taxonomic work by MR at NRI, have significantly advanced this study.

This paper presents a comprehensive higher-level phylogeny of the Acridomorpha, confirming that the genera *Mazaea*, *Ixalidium*, *Tangana*, and *Rowellacris* Ritchie & Hemp n. gen. form a monophyletic family-level group, here named Ixalidiidae Hemp, Song & Ritchie n. fam., to which the genus *Barombia* Karsch is added on morphological grounds. This is the first new family group within Caelifera to be based primarily on molecular phylogenetic evidence, supported by morphological data. Material from various collections, including newly collected DNA samples from Tanzania, was examined, and representatives were dissected and imaged to facilitate comparisons and characterizations. The study provides means to accurately distinguish included genera and previously described species and reveals previously unrecognized diversity within the group.

To contextualize the new family morphologically among other extant families, an extensive literature review was conducted to develop a character table for Acridoidea, showing the congruence of 24 morphological characters across Ixalidiidae Hemp, Song & Ritchie n. fam. and nine other acridoid families. The paper defines these characters, assesses their consistency within families, and highlights the unique combination of characters that define Ixalidiidae Hemp, Song & Ritchie n. fam. The phylogenetic tree also suggests a previously unsuspected sister relationship between Ixalidiidae Hemp, Song & Ritchie n. fam. and the South American family Tristiridae Rehn, 1906, though with low support value, indicating potential evolutionary significance.

MATERIAL AND METHODS

Molecular analyses

Taxon sampling

To reconstruct the phylogeny of Acridomorpha and to place Ixalidiidae Hemp, Song & Ritchie n. fam. in the phylogeny, we compiled taxon sampling that included representatives of all major families within the Acridomorpha, except Lathiceridae, for which we did not have access to DNA-grade specimens. We included representatives of the superfamilies Tanaoceroidea Rehn, 1948, Trigonopterygoidea Walker, 1870, Pneumoroidea Thunberg, 1810, Pyrgomorphoidea Brunner von Wattenwyl, 1874, and Acridoidea. Specifically for Acridoidea, we included 22 species of Acrididae, one species of Dericorythidae, six species of Ixalidiidae Hemp, Song & Ritchie n. fam., six species of Lentulidae Dirsh, 1956, five species of Ommexechidae Bolívar, 1884, five species of Pamphagidae, one species of Pamphagodidae, one species of Pyrgacrididae, three species of Romaleidae, and nine species of Tristiridae. Of the 75 species included in the analyses, sequence data for 26 species were generated for this study. Detailed information about taxon sampling is found in Appendix 1.

Sequence data generation

We sampled complete mitochondrial genomes, 18S rRNA, and 28S rRNA for character sampling. To generate the sequence data, four different methods were used. For four species of Tristiridae (*Atacamacris diminuta* Carbonell & Mesa, 1972, *Punacris peruviana* (Saussure, 1888), *Circacris auris* Ronderos & Cigliano, 1989 and *Eremopachys bergii* Brancsik, 1901), we performed shotgun sequencing of genomic DNA using the Illumina platform. Mitochondrial genomes and rRNA sequences were assembled as described in Song *et al.* (2018). For *Hoplolopha asina* (Saussure, 1887) and *Chromacris trogon* (Gerstäcker, 1873), we generated *de novo* transcriptomes and mitochondrial genome data were assembled using the methods described in Shin *et al.* (2024). For *Bacteracris* sp., *Usambilla sagonai* (Ramme, 1929), *Zulutettix tarranti* Otte & Armstrong, 2017 and *Bullacris membracioides* (Walker, 1870), we used non-target bycatch sequences obtained while capturing loci using the Orthoptera-specific Target Enrichment according to the method described in Shin *et al.* (2024). The mitochondrial and rRNA genes were obtained using Geneious Prime using sequences of closely related species as references. The sequence data for these seven species were generated as part of previous studies but have not been published yet. For six Ixalidiidae Hemp, Song & Ritchie n. fam. species, three species of Ommexechidae (*Aucacris bullocki* Rehn, 1943, *Spathalium audouinii* (Blanchard, 1836), *Tetrixocephalus willemsei* Gurney & Liebermann, 1963), two species of Tristiridae (*Elasmoderus lutescens* (Blanchard, 1851), *Peplacris rucutita* Rehn, 1942), and two species of the acridid subfamily Catantopinae Brunner von Wattenwyl, 1893 (*Coenona brevipedalis* Karsch, 1896, *Serpusia opacula* Karsch, 1891), we generated sequence data *de novo* using shotgun sequencing. To extract high molecular weight DNA required for Illumina sequencing, we used a MasterPure™ Complete DNA and RNA Purification Kit (LGC Biosearch Technologies, London, U.K.) following the manufacturer's guidelines. The quality and concentration of DNA extracts were initially measured using a Qubit Fluorometer (Thermo Fisher, Waltham, MA, U.S.A.). Short-inserts of 350 bp paired-end libraries were prepared for all samples using NEBNext® Ultra™ II FS DNA Library Prep Kit for Illumina® (Biolabs) and 6 PCR cycles. Size-selection and clean-up was applied using SPRI beads and the library was subsequently checked using a Tapestation DNA screentape and D1000 reagents kit (Agilent). All paired-end libraries were shotgun sequenced on one lane of Illumina HiSeq 4000 at Novogene Inc. in paired-end 150 cycle mode. For these 13 newly generated sequences, the complete mitochondrial genomes were obtained from raw shotgun sequences using the organelle genome assembly toolkit GetOrganelle v1.7.7.0 (Jin *et al.* 2020). The assembly of the mitogenomes were executed with the following commands: -F animal_mt, -R 10 and -k 21,45,65,85,105. Subsequently, the obtained mitochondrial genomes were submitted to MITOS2 webserver (http://mitos2.bioinf.uni-leipzig.de/index.py) (Donath *et al.* 2019) for annotation (reference: RefSeq 63). The annotated genomes were manually checked and adjusted via Geneious Prime®2022.1.1 (https://www.geneious.com) to ensure the accuracy. The 18S and 28S rRNA genes were obtained using Geneious Prime and closely related *Lentula callani* reference sequences for each gene respectively; KM853234.1, KM853456.1 and KM853632.1 (Song *et al.* 2015).

Phylogenetic analysis
For mitochondrial protein-coding genes, we aligned based on the conservation of reading frames by first translating into amino acids (using invertebrate mitochondrial genetic code) and aligning individually in MUSCLE (Edgar 2004) using default parameters in Geneious Prime (Dotmatics). For mitochondrial ribosomal RNA genes (16S and 12S) and nuclear ribosomal RNA genes (18S and 28S), each gene was individually aligned using MAFFT (Katoh & Standley 2013) using the E-INS-I option also in Geneious Prime. These individual alignments were concatenated into a single total evidence matrix using SequenceMatrix (Vaidya *et al.* 2011). We partitioned the data into 17 data blocks (13 mitochondrial protein-coding genes, 2 mitochondrial rRNAs and 2 nuclear rRNAs). We used IQ-TREE (Minh *et al.* 2020) to select a best-fit model for each partition, reconstruct the maximum likelihood (ML) tree, and assess branch supports using the ultrafast bootstrap (1 000 replications). *Tanaocerus koebelei* Bruner, 1906 (Tanaoceridae) was used to root the tree.

Divergence time estimation
Because there is no reliable fossil available for most lineages within Acridoidea, we opted to use the divergence time estimates from Song *et al.* (2018) and Song *et al.* (2020) as calibration points. We used five calibration points: (1) 48.56 to 75.15 mya for the common ancestor of Acrididae; (2) 127.88 to 189.44 mya for the common ancestor of Pamphagodidae and Pamphagidae; (3) 182.26 to 229.53 mya for the common ancestor of Acridoidea; (4) 89.37 to 133.66 mya for the common ancestor of Pyrgomorphidae Brunner von Wattenwyl, 1874; and (5) 222.46 to 277.86 mya for the common ancestor of all included taxa except Tanaoceridae. We performed divergence time analyses of the unpartitioned dataset using MCMCTree implemented in the software package PAML v4.9130 (Yang 2007). We set the model HKY85+G with five rate categories and set the root age as 298.97 mya. We conducted Hessian matrix calculations according to the above specifications with CODEML as implemented in PAML. MCMC chains ran for 100 000 generations (sfreq = 100) while discarding a burn-in of 25 000 generations. A total of two independent runs were done at using Texas A&M High Performance Research Computing. The effective sample size was checked with the Tracer v1.7.1131 (ESS > 200).

Morphology
Descriptions, dissection and imaging
Where descriptions have been provided for monotypic genera, these reflect the characters and character states visible in the material examined that have been attributed to the single described species. However, this material may include as yet unrecognised closely-related species, such that some characters may later prove to be species-specific, rather than generic, if further study reveals unrecognised speciation. Where possible measurements have been taken from viable samples from a limited area, named in the relevant table captions. Length of fastigium of vertex is measured from its apex to it base, which is considered to be a line constituting the shortest distance between the eyes (Dirsh 1965: 5).

Male genitalia were extracted and prepared for study using the method of Dirsh (1956). After removal of genitalia, compressed macerated paper tissue was substituted within the abdominal cavity so that the terminalia retained their natural position after drying. Female genitalia of representative species were dissected and prepared for study by the method described by Slifer (1940). The entire abdomen was removed at its junction with the metathorax after relaxing the specimen, then macerated in warm NaOH or KOH. Soft tissues were removed and the ovipositor and subgenital plate, together with any attached internal sclerotized structures, were separated from the other abdominal tergites and sternites, washed in distilled water and preserved in 75% ethanol. For digital imaging genitalia preparations were positioned in hand sanitizer gel beneath a layer of 75% ethanol in a glass cavity block. Subgenital plates were slightly flattened for imaging and drawing by placing pieces of glass coverslip over them. Image stacks were obtained with a Zeiss AxioZoom V.16 microscope and AxioCam HRc digital camera running Zen software. Stacked images were combined using Helicon Focus software and cleaned using Photoshop Elements 15. Drawings were made using a Wild M5Apo stereomicroscope with a drawing tube at approximately 30× magnification, then scanned, edited and assembled into plates using Photoshop Elements. Cut surfaces, when seen in side view are shown as a jagged line and when seen face-on are shown cross-hatched. Genitalia were stored in an 85% solution of 75% ethanol and 15% propylene glycol in polythene vials pinned with the respective insect specimens.

Relevance of acridoid genital morphology for phylogeny

The Acridoidea are the largest superfamily of Acridomorpha, and indeed of Caelifera, currently comprising 10 families (Acrididae, Dericorythidae, Lathiceridae, Lentulidae, Ommexechidae, Pamphagidae, Pamphagodidae, Pyrgacrididae, Romaleidae, and Tristiridae) with *c.* 8 400 valid species, of which more than 6 800 are currently classified as Acrididae (Cigliano *et al.* 2023). Roberts (1941), Dirsh (1956), and Amédégnato (1976, 1977) perceived genital morphology as the key to elucidating phylogeny, driven by an underlying evolutionary model that structures become more complex over time. Roberts (1941) and Dirsh (1956) considered genitalia to be unaffected by environmental selection pressures and therefore likely to show ancient patterns of relationship more clearly than external morphology. This view is also implicit in the classification based on genital structures proposed by Eades (2000).

However, the presumed reliability of genital morphology as a guide for phylogenetic reconstruction has been questioned in recent studies that show rapid genital differentiation in response to sexual selection pressures (e.g. Song & Bucheli 2010). A molecular phylogeny of the Pyrgomorphidae (Zahid *et al.* 2021) demonstrated widespread paraphyly among the tribes of both subfamilies based on morphology, owing to convergences both in external shape and in genitalic characters. This highlights the need for extensive taxon sampling and a large amount of molecular data to identify the most phylogenetically informative morphological traits. However, in both crickets and grasshoppers genitalic divergence has been shown to lead to speciation through creating reproductive isolation, either alone (Knowles *et al.* 2016; Huang *et al.* 2020), or in combination with ecological selection and isolation (Oneal & Knowles 2013). In the *Melanoplus scudderi* complex, Huang *et al.* (2020) found that "*distinct male genitalic shapes correspond to independently evolving lineages identified by the genomic data*", confirming the validity of utilizing variation in genitalic shape to delimit recently diverged evolutionary entities.

Song & Mariño-Pérez (2013) re-evaluated the taxonomic utility of characters of the male phallic complex across the higher-level classification of Acridomorpha in a phylogenetic framework provided by mitochondrial genomic data (Leavitt *et al.* 2013). Noting the difficulty of interpreting published images and incomplete or vague descriptions they augmented selective desk study of the synoptic literature on inter-family variation with their own dissections of single species representatives of 13 families of Acridomorpha to generate a character matrix, coding only the 26 characters that they considered were uniformly present in all members of a family (Song & Mariño-Pérez 2013: 246, Table 3). They then generated one phylogenetic tree using only the male genitalia characters and a second tree mapping/optimizing this morphological character information onto a family-level phylogenetic analysis of Acridomorpha derived from mitochondrial genome sequence data (Leavitt *et al.* 2013). Both trees generated by Song & Mariño-Pérez (2013) found the Acridoidea to be monophyletic, but they differed on the relationships among the included families. However, optimization of genitalic morphological characters onto the molecular phylogenetic tree revealed four uncontroverted synapomorphies, that define the branching of the acridoid family tree. These were the possession of epiphallic lophi, a sclerotised epiphallus, presence of the zygoma and presence of a gonopore. Song & Mariño-Pérez (2013) concluded that despite frequent homoplasies occasioned by sexual selection, many male genitalia characters have strong phylogenetic signal and are informative in inferring relationships at and above family level. This is because male genitalia are a composite character suite. Some parts may evolve rapidly (shape of aedeagus for example) and thus be informative at species level (Huang *et al.* 2020), while other parts may be conserved across phylogeny. Thus, the utility of genitalic characters may vary across different taxonomic levels and groups.

Terminology and abbreviations of male genitalia

The terminology of the acridoid genitalia used here follows, in some cases with modification, a number of sources, including Snodgrass (1935), Roberts (1941), Dirsh (1956), Amédégnato (1976, 1977) and Eades (1961, 1962, 2000). Many of these terms were defined by Song & Mariño-Pérez (2013) and extensively illustrated for *Melanoplus rotundipennis* (Scudder, 1878) by Woller & Song (2017).

Abbreviations

Male genitalia

Ac	arch of cingulum;
Ae	apodemes of endophallus;
As	apical sclerites of endophallus;
Av	valves of aedeagus;
B	bridge of epiphallus;
Ca	apodemes of cingulum;
Cr	rami of cingulum;

Cut	incision made during dissection of genitalia;
Df	dorsal fold (basal fold);
Dll	dorso-lateral lobes of endophallus (in Tangana);
Ead	dorsal epiphallic apodeme;
Eav	ventral epiphallic apodeme;
Ef	flanges of endophallic apodemes;
Ejd	ejaculatory duct;
Ejs	ejaculatory sac;
Fu	furcula;
Lo	lophi of epiphallus;
Lp	lateral plates of epiphallus;
Ls	lateral spur of cingular apodemes;
Lsc	lateral sclerite of epiphallus;
Ms	medial sclerites of endophallus;
Pa	pallium;
Pp	paraproct;
Sdl	sub-dorsal lobe of cingulum;
Sh	sheath of aedeagus;
Sps	spermatophore sac;
Vl	ventral lobe of ectophallus;
Vla	ventral lobe apodeme;
Zyg	Zygoma of cingulum.

Repositories

Coll. AH	A. Hochkirch collection, Bremen;
Coll. CH	C. Hemp collection, Bayreuth;
Coll. CHR	C. H. Rowell collection, Ayer;
MfN, Berlin	Museum für Naturkunde (MfN), Berlin;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMUK	Natural History Museum, London;
NR, Stockholm	Naturhistoriska Rijksmuseum, Stockholm;
SMNK	Staatliches Museum für Naturkunde, Karlsruhe.

Bioacoustics

To investigate acoustic and vibrational communication, both male and female specimens of selected species (*Rowellacris obscuripes* n. comb. (Kwale Island near Tanga), *R. usambarica* n. comb. (Ndelemai Forest Reserve), *Rowellacris* Ritchie & Hemp n. gen. sp. (Sigi, East Usambara), *Tangana asymmetrica* (Kimboza Forest Reserve, Morogoro), *Tangana* sp. (Tanzanian coast and Zanzibar) were subjected to video recording.

Subsequently, the sound was extracted from the video recordings, and the audio data were further processed using Amadeus II and Amadeus Pro software developed by Martin Hairer (http://www.hairersoft.com). Oscillograms depicting the acoustic characteristics of the songs were generated using Turbolab, a software tool from Bressner Technology, Germany. The impact period refers to the time measured from the initiation of one impact to the beginning of the subsequent one, with its reciprocal value denoted as impact repetition rate (IRR). Temperature was measured after each recording, ranging from 22 to 27°C.

Cytogenetics

The study involved cytogenetic analyses of several species, namely, four males of *Ixalidium sjostedti* from different elevations of Mt Kilimanjaro, the submontane zone at 1430 m a.s.l. (HE216, HE222) and lowland forest remnants at the Sugar Cane Plantations (TPC), (HE223, HE224), three males of an undescribed species of *Rowellacris* Ritchie & Hemp n. gen. from Sigi, East Usambara Mountains (HE218, HE220, HE221), a male of *R. usambarica* from Ndelemai Forest Reserve (HE227), and one male (HE247) and one female (HE246) of *Tangana asymmetrica* from Kimboza, Uluguru Mts. Chromosome preparations were made from males and freshly moulted females by dissecting out the testes and ovaries, incubating them in a hypotonic solution (0.9% sodium citrate), fixing them in ethanol: acetic acid (3: 1), and squashing them on slides in a drop of 45% acetic acid. The cover slips were then removed using the dry ice procedure, and the slides were dehydrated and air-dried. The C-banding technique, as described by Sumner (1972), was used to reveal the constitutive heterochromatin, and the silver staining method (AgNO3) was employed to locate the nucleolar organizer region (NOR) as previously reported (Warchałowska-Śliwa & Maryańska-Nadachowska 1992).

Furthermore, fluorescence in situ hybridization (FISH) was performed on four species, namely, *I. sjostedti* (HE216, HE223), *Rowellacris* Ritchie & Hemp n. gen. sp. (HE218, HE220, HE221), *R. usambaricum* (HE 227), and *T. asymmetrica* (HE247), using 18S ribosomal DNA (rDNA) and telomeric DNA (TTAGG)n probes. The FISH technique was applied as previously described in Grzywacz *et al.* (2018). The chromosomal localization of rDNA sequences was carried out using a biotin-16-dUTP-labeled probe containing a fragment of orthopteran 18S rDNA (Roche Diagnostics GmbH, Mannheim, Germany). The telomeric (TTAGG)n DNA probes were obtained by PCR in the absence of DNA template. The hybridization signals were detected using avidin-FITC (Invitrogen, Life Technologies INC., Carlsbad, California, USA) and anti-digoxigenin rhodamine (Roche Diagnostics GmbH, Mannheim, Germany). Chromosomes were mounted in ProLong Gold antifade reagent containing DAPI (Invitrogen, Life Technologies INC., Carlsbad, California, USA) and analyzed under a Nikon Eclipse 400 microscope fitted with a CCD DS-U1 camera using a set of standard filters and an NIS-Elements BR 3.0 image-analyzing system (Nikon). The images were processed and organized with Adobe Photoshop and Lucia Image 5.0 software.

RESULTS

Molecular analyses

We recovered a topology that is largely congruent with the previous studies, and our analysis robustly recovered Ixalidiidae Hemp, Song & Ritchie n. fam. as a monophyletic group and determined its phylogenetic position within Acridomorpha (Fig. 1). In terms of superfamily-level relationships, the earliest diverging lineage within Acridomorpha is Tanaoceridae, the sole member of the superfamily Tanaoceroidea. Its basal position has been shown in all previous studies (Klee *et al.* 2000; Leavitt *et al.* 2013; Song *et al.* 2015, 2020). Then, we recovered a clade consisting of Xyronotidae, Pneumoridae, and Trigonopterygidae as the next diverging lineage. Currently, Xyronotidae and Trigonopterygidae are placed in the superfamily Trigonopterygoidea, but our analysis did not recover Trigonopterygoidea as monophyletic. Song *et al.* (2020) also did not recover monophyletic

Trigonopterygoidea. Xyronotidae is endemic to Mexico while Trigonopterygidae is endemic to Southeast Asia, and these two families are morphologically quite distinct from each other. It is likely that future studies including larger taxon sampling may result in reclassification of Trigonopterygoidea. We then recovered a sister relationship between Pyrgomorphoidea and Acridoidea, consistent with previous molecular phylogenetic studies (Leavitt *et al.* 2013; Song *et al.* 2015; 2020). Within Acridoidea, we recovered a clade consisting of Pamphagodidae and Pamphagidae as the earliest diverging lineage, consistent with the previous phylogenomic study (Song *et al.* 2020). Our study recovered the South African endemic family Lentulidae as the next diverging lineage. Otte (2024) recently synonymized Lithidiidae Dirsh, 1961 under Lentulidae, and we also found a member of Lithidiidae (*Lithidiopsis carinatus* Dirsh, 1956) nested within Lentulidae, consistent with Otte's reclassification. However, this finding is only based on the placement of a single taxon, and it remains to be seen if this reclassification holds up if additional members of the former Lithidiidae (such as *Eneremius* Saussure, 1888*, Lithidiopsis* Dirsh, 1956 and *Microtmethis* Karny, 1910) are included in the phylogenetic analysis. The phylogenetic position of Pyrgacrididae, which includes one genus with two species endemic to the Reunion Islands and Mauritius, is not clear although most agree that it is near the base of the Acridoidea. Leavitt *et al.* (2013) found Pyrgacrididae to be sister to Acridoidea (minus Pamphagodidae + Pamphagidae), while Song *et al.* (2015) found it to be at the base of Acridoidea. Song *et al.* (2020) found a relationship identical to Leavitt *et al.* (2013). However, none of these studies found the placement of Pyrgacrididae with a strong nodal support value. In the present study, we recovered a different placement of Pyrgacrididae compared to all previous studies and showed that it diverged after Lentulidae diverged. However, the nodal support value for this placement is again not strong, and we may need additional data to ascertain its phylogenetic position.

The family Lathiceridae was not included in this or in earlier studies (Leavitt *et al.* 2013; Song & Mariño-Pérez 2013; Song *et al.* 2015, 2020) owing to a lack of molecular data. Thus, the phylogenetic relationship of Lathiceridae to other Acridoidea remains unclear. We included a member of the family Dericorythidae, represented by *Dericorys annulata* (Fieber, 1853) in this study and found it to be nested deep within Acrididae, closely related to the acridid subfamily Hemiacridinae Dirsh, 1956. Recent studies by Chang *et al.* (2020) and Zhang *et al.* (2023) have suggested that the Dericorythidae are paraphyletic and closely allied to the Acrididae. A comprehensive revision of the Dericorythidae incorporating molecular analysis in parallel with genital morphology is needed to resolve this issue.

Building on earlier molecular studies (Flook & Rowell 1997; Leavitt *et al.* 2013; Song *et al.* 2015) a recent phylogenetic study of the Acridoidea (Song *et al.* 2018), using mitochondrial and nuclear DNA sequences, resulted in a phylogeny of the Acrididae which placed the family in a monophyletic group with Ommexechidae and Romaleidae, which in turn is sister to the Tristiridae. A more recent phylogeny (Song *et al.* 2020) using a larger taxon sampling recovered a similar relationship but had Ommexechidae more closely related to Acrididae than to Romaleidae. The enhanced and extended phylogeny presented here (Fig. 1) confirms that finding, with the Ixalidiidae Hemp, Song & Ritchie n. fam. recovered unambiguously as a monophyletic sister group of the Tristiridae and the two families together as a sister clade of the combined Ommexechidae, Acrididae, and Romaleidae.

Taxonomic treatment

This section provides the following elements: firstly a formal morphological description of the family Ixalidiidae Hemp, Song & Ritchie n. fam., followed by brief remarks and a key to the six genera currently included in the family. It should be noted that while *Mazaea*, *Ixalidium*, *Rowellacris* Ritchie & Hemp n. gen. and *Tangana* have all been shown to be members of the family based on molecular evidence, *Barombia* is included in the family because its male and female genitalia and other morphology are almost indistinguishable from those of *Mazaea*, indicating a very close relationship. Next a description is provided for each of the included genera, including the new genus *Rowellacris* Ritchie & Hemp n. gen. Where a genus comprises more than one described species the included species are listed and for *Rowellacris* Ritchie & Hemp n. gen. a diagnosis is provided for each of the previously described species transferred to it from *Ixalidium*.

Family Ixalidiidae Hemp, Song & Ritchie n. fam.

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Type genus. — *Ixalidium* Gerstäcker, 1869.

Etymology. — Ixalidiidae Hemp, Song & Ritchie n. fam. takes its name from the root of the oldest genus name in the family, *Ixalidium* Gerstäcker, 1869, which appears to have been derived from the Greek adjective ἴξαλος meaning "bounding, springing", combined with the final syllables of the old (and now suppressed) genus name *Acridium* Schaeffer, 1766.

Description

Small to medium sized grasshoppers (males 16.5-27.6 mm; females 23.6-39 mm), females more robust. Integument rugose and punctate to tuberculate and granulose, variably setose. Antennae with 17-23 segments, from slightly shorter than to slightly longer than head and pronotum together, basal half excluding scape and pedicel dorso-ventrally compressed, widening somewhat from segment three, widest between 3 and 6, with 8-9 distinctly less compressed and terminal segments filiform.

Head width across eyes distinctly less than pronotum length and less than pronotum width at its hind margin; head in lateral view obliquely slanted, with vertex produced and frons in profile sometimes shallowly incurved between antennae; eyes of moderate size, ovoid, narrower above, oblique; fastigium of vertex from above rounded angular, with raised lateral margins, forming an angle less than or equal to 90° (in males), projecting over lateral ocelli and antennal bases;

foveolar area obsolete; median carinula of occiput variably expressed, sometimes continuing on vertex; frontal ridge in anterior view narrowest immediately below vertex, widening between antennae, sometimes narrowing above median ocellus, obsolescent towards clypeus; lateral carinae widening below ocellus, sometimes becoming obsolete towards clypeus.

Pronotum low tectiform (*Ixalidium*) to inflated with projections (*Barombia*), median carina intersected by 2-3 sulci; prozona 3-5 times longer than metazona; dorsum from above widening from fore margin to hind margin. Prosternal tubercle conical (*Barombia*, *Mazaea*) (Fig. 6B) to transverse, spathulate (*Ixalidium, Rowellacris* Ritchie & Hemp n. gen.*, Tangana*). Meso- and metathorax shallowly tectiform to inflated (*Barombia*), with median carina; mesonotum usually lacking tegminal rudiments, but occasionally (in *Rowellacris* Ritchie & Hemp n. gen. species) with strap-like tegminal scars, just above lateral sutures separating dorsum from mesopleura. Metathorax raised posteriorly and with distinct lateral carinae above robust lateral projecting flanges which reinforce metapleura above hind coxae. Meso-sternal interspace medially slightly narrower than its length at outer margins, widening caudad (strongly in *Barombia*); minimum width of metasternal interspace approximately equal to its length.

Fore and mid legs of typical acridoid appearance, unspecialized. Hind femur in lateral view stocky (length/max. depth, males: 3.1-4.0, females; 3.34-3.9), with upper basal lobe larger than lower lobe, upper carina serrate; hind knee with upper and lower lobes bluntly to acutely rounded; hind tibia with 8-9 outer spines and 9 inner spines; external apical spine present but of reduced size (West African genera) or absent (East African genera); arolium large, rounded, length in ventral view less than or equal to claw; claws thickened at base, apically strongly curved.

Abdomen with median dorsal carina and with segments one and two distinctly raised, together with metathorax forming slight to large hump; tympanum large, sub-oval, sclerotised. External terminalia (Fig. 5A-H) with tergites 9 and 10 fused laterally; tergite 10 dorso-medially excised, fusing with the roughly trapezoid basal section of supra-anal plate, the latter with its lateral margins defined by oblique ridges and grooves, their interspace narrowing forwards, bounded anteriorly by tergite 9 and posteriorly by hinged movable section of supra-anal plate (epiproct); this area unmodified in *Ixalidium*, symmetrically modified in *Rowellacris* Ritchie & Hemp n. gen. and West African genera, asymmetrically modified in *Tangana*; cerci straight, unspecialised, narrowly conical, sometimes attenuated at apex, clothed with long sensory hairs; paraprocts triangular, partly exposed at lateral margins of supra-anal plate; subgenital plate conical, with distal apex varying from bluntly rounded to acute and attenuated; dorsal medial area usually membranous anteriorly, often forming a distinct medial longitudinal furrow bounded by lateral carinae (Fig. 5G).

Male genitalia. Morphology highly diverse (see figures). Epiphallus usually bridge-shaped (but with bridge elongated anteriorly into an apodeme in *Tangana*); without distinct ancorae and with pointed lophi; lateral (oval) sclerites present. Cingulum highly variable, forming a sclerotised dorsal shell with or without paired apodemes (*Rowellacris* Ritchie & Hemp n. gen.), less sclerotised (*Tangana*), or reduced to a narrow collar with elongated apodemes (*Ixalidium*, *Mazaea*, *Barombia*); zygoma present. Ventral lobe present as paired sclerotised plates below rami of cingulum, least developed and sclerotised in *Ixalidium*, massively developed and strongly sclerotised in *Rowellacris* Ritchie & Hemp n. gen. and *Tangana,* separated into elongated digitate lobes in *Tangana* (Figs 16D; 17G-L). Ventral infold present below endophallus, originating from anterior margin of ventral lobe, either forming a bi-layered sheet (Fig. 7F) (*Mazaea*, *Barombia*) or reduced to a whisker-like apodeme (*Ixalidium*, *Tangana*, *Rowellacris* Ritchie & Hemp n. gen.), sometimes bifurcating at a node anteriorly (Fig. 11B). Endophallus tripartite (except in *Rowellacris* Ritchie & Hemp n. gen.), with paired basal, medial and apical sclerites separate but conjoined; endophallic apodemes of variable development and shape, lacking evidence of gonopore processes (but see Discussion), apart from small flanges (Ef) on inner surface adjoining gonopore in West African genera and *Ixalidium* (Figs 7G; 9A; 10A-D); sclerites of medial section (analogous to, though not necessarily homologous with lateral plates of Roberts (1941) elongated and dorso-ventrally flattened in all genera except *Rowellacris* Ritchie & Hemp n. gen. (*q.v.*), with conjoined paired sclerites visible in West African genera (Figs 7H; 9B) and *Ixalidium* (Fig. 10E, F), but forming a single fused sclerite in *Tangana*; medial section of endophallus obsolete in *Rowellacris* Ritchie & Hemp n. gen.; apical endophallic sclerites enclosed within a membranous or sclerotised ectophallic sheath, sometimes laterally compressed (*Rowellacris* Ritchie & Hemp n. gen.), with a distinct arch arising basally and attaching to the cingulum, formed by a pair of sclerites in *Ixalidium* and W African genera, but with sclerites fused into a single pillar in *Rowellacris* Ritchie & Hemp n. gen. (Fig. 14J, L). Ejaculatory sac either present as a free antero-ventral elastic sac (Fig. 9B, C) (*Ixalidium*, *Barombia*, *Mazaea*) or reduced to a slight expansion of the ejaculatory duct (*Rowellacris* Ritchie & Hemp n. gen., *Tangana*). Spermatophore sac dorsal to the endophallus, of variable development.

Female genitalia. Spermatheca of diverse form, with two interconnected sac-like basal appendices or bursae, one short and one very long together with separate short narrow duct leading to well-developed apical diverticulum and ampullate or vermiform sub-apical diverticulum (*Rowellacris* Ritchie & Hemp n. gen. and *Tangana*) (Fig. 12); or with a simple robust duct, without bursa, with up to five loops and a short apical section, with flask-like pre-apical and short digitate apical diverticula (*Ixalidium*); or with a very long repeatedly coiled vermiform duct ending in a vermiform subapical diverticulum and a much longer vermiform apical diverticulum in *Mazaea* (Fig. 8A) and *Barombia*. Subgenital plate internally of typical acridoid form with floor pockets, postvaginal sclerites, egg guide and with or without medial pouch and columellae (Fig. 6C). Ovipositor valves of normal acridoid type, unspecialised (Figs 5C; 9), slenderer in *Ixalidium* and more robust in *Rowellacris* Ritchie & Hemp n. gen. and *Tangana*. Subgenital plate almost as wide as long in *Mazaea* (Fig. 6C) and *Ixalidium*; about 1.3 times

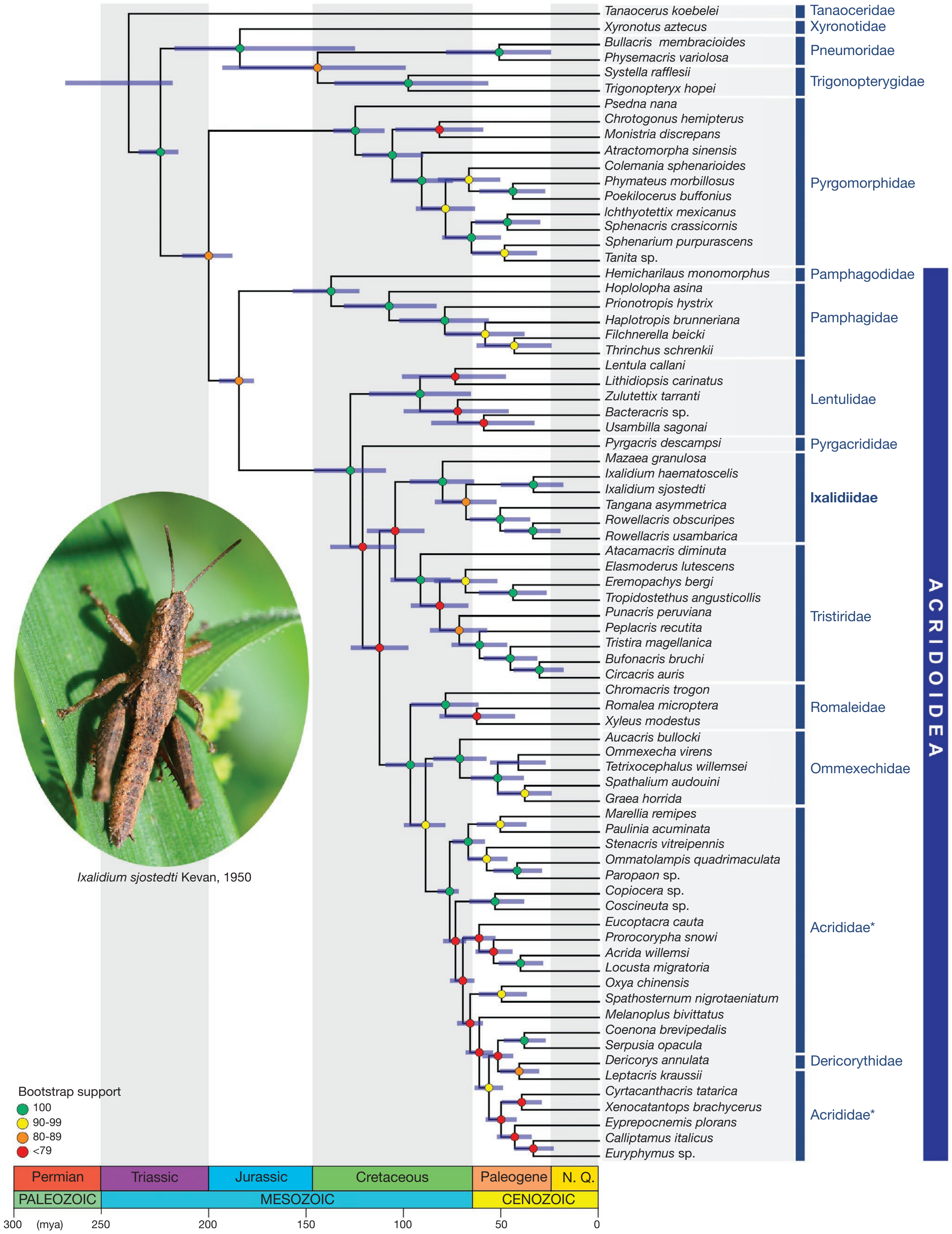

Fig. 1. — A time-calibrated phylogeny of the Acridomorpha derived from mitochondrial genome and two nuclear ribosomal RNA genes. Shown here is the result of MCMCTree analysis and light blue bar indicates 95% HPD for a time estimate. Bootstrap support values are from the maximum likelihood analysis of the same dataset.

as long as wide in *Rowellacris* Ritchie & Hemp n. gen. and 1.7 times as long as wide in *Tangana*.

General coloration typically drab brown (apart from *Barombia* which has lighter greenish yellow ground colour with reddish brown markings (Fig. 3A); internal surfaces of hind femora with some dark patches, with or without reddish shading ventrally; tibiae straw-coloured, grey, violet or pink at least in part.

Remarks

The genera assigned to the Ixalidiidae Hemp, Song & Ritchie n. fam. share few distinctive and consistent external morphological characters. Apart from their overall habitus, with matt and rugose cuticle, common to many ground-living acridoids across several families, the most distinctive external characters of Ixalidiidae Hemp, Song & Ritchie n. fam. are the absence of tegmina and wings, with the possession of a tympanum and the possession of a transversely divided supra-anal plate. These characters also occur in some genera across several other families, but only the Lentulidae are always apterous and they always lack a tympanum, while in Ixalidiidae Hemp, Song & Ritchie n. fam. the tympanum is always present and well-developed. A detailed comparison of the characters of both male and female internal genitalia reveals remarkable diversity across the family, with some unusual character states expressed in individual genera within the family, including the apparent loss of the medial section of the endophallus in *Rowellacris* Ritchie & Hemp n. gen. (Figs 14J-L; 15H-I), the fusion of the medial sclerites of the endophallus into a sclerotised casing enclosing the spermatic duct in *Tangana* (Figs 16; 17) and the development of a massive blind-ending sac at the mouth of the spermatheca in both *Rowellacris* Ritchie & Hemp n. gen. and *Tangana* (Fig. 12).

However, despite these unusual features expressed in individual genera of Ixalidiidae Hemp, Song & Ritchie n. fam., across the family as a whole there are no monomorphic character states that are not also found in one or more other families of Acridoidea (Table 13). Instead, Ixalidiidae Hemp, Song & Ritchie n. fam. are ultimately distinguishable from other families by the external characters mentioned above, together with a unique combination of characters of the male genitalia. These are the possession of a bridge-shaped epiphallus with pointed lophi (Fig. 7C, D), an arch sclerite or paired arch sclerites, a divided endophallus with basal and apical sclerites articulated (Fig. 11D) and the spermatophore sac situated dorsal to the (ventral) endophallic sclerites (Fig. 10E, F).

Included genera

The family Ixalidiidae Hemp, Song & Ritchie n. fam. comprises five genera, two from West and Central Africa: *Mazaea* Stål (including the former *Eubocoana* Sjöstedt n. syn.) and *Barombia* Karsch and three from the submontane and coastal forests of Tanzania and Kenya: *Ixalidium* Gerstäcker, *Tangana* Ramme and *Rowellacris* Ritchie & Hemp n. gen. These were all originally considered as Acrididae. Dirsh (1965) initially placed them all in the Catantopinae, but reassigned *Barombia*, *Mazaea* and *Ixalidium* to the Hemiacridinae (Dirsh 1966: 97).

Key to Genera of Ixalidiidae Hemp, Song & Ritchie n. fam. (males)

1. Prosternal tubercle conical (Fig. 6B), hind tibia with external apical spine (Fig. 3C); fastigium of vertex almost as long as, or longer than its basal width (Fig. 3D, F) 2
— Prosternal tubercle transverse, lamelliform; hind tibia lacking external apical spine; fastigium of vertex much shorter than its maximum basal width (Fig. 4A-C) 3

2. Pronotum with two subconical dorso-medial projections and two pairs of subconical dorso-lateral projections, variably expressed, in prozona and metazona (Fig. 3A) .... *Barombia* Karsch, 1891
— Pronotum lacking subconical dorso-medial projections and subconical dorso-lateral projections in prozona and metazona, but with variably expressed dorso-medial tubercles (Fig. 3B) .... *Mazaea* Stål, 1876

3. Small species (16-21 mm); abdominal apex slender, nymph-like, with tergites 9 and 10 slim, tapering; supra-anal plate bilaterally symmetrical; basal part rhomboid, deeply inset into tergite 10, with sharp lateral margins; transverse suture almost straight; apical portion acutely triangular, longer than its basal width (Fig. 5A-C); hind tibiae usually reddish at least in apical third .... *Ixalidium* Gerstäcker, 1869
— Larger species (18-27 mm); abdominal apex plump, with tergites 9 and 10 robust; supra-anal plate either not visible or with transverse suture medially incurved (Fig. 5D-H); hind tibiae of variable coloration (brown, grey, straw, violet), but never reddish 4

4. Abdominal apex bilaterally asymmetrical, tergites 9 and 10 dorsally fused and twisted, usually with short or elongated pointed process arising from basal section, normally on right side only; basal part of supra-anal plate not clearly distinct, apical portion either internalised or, if visible, then vestigial; subgenital plate acutely pointed in dorsal view (Fig. 5H) .... *Tangana* Ramme, 1929
— Abdominal apex bilaterally symmetrical; tergite 10 and anterior margin of supra-anal plate either forming raised median furcula (Fig. 5D, E) or flat (Fig. 5F, G); basal and apical portions of supra-anal plate clearly visible; transverse suture medially incurved, flanked by excurved and raised lateral flanges; subgenital plate broadly rounded with pointed tip (Fig. 5E-G) .... *Rowellacris* Ritchie & Hemp n. gen.

Fig. 2. — Ixalidiidae Hemp, Song & Ritchie n. fam., East African genera and species: **A**, **B**, *Ixalidium haematoscelis* Gerstäcker, 1869,Taita Hills, Kenya; **A**, mating pair; **B**, unusually coloured female; **C**, **D**, *Rowellacris usambarica* (Ramme, 1929) n. comb. from type locality, male and pair from Muafa, W. Usambara Mts, Tanzania (TZ); **E**, *R. obscuripes* (Miller, 1929) n. comb., Kwale sacred forest, TZ; **F**-**H**, *Tangana asymmetrica* Ramme, 1929, Tanzania; **F**, male, near Pangani; **G**, pair, Kimboza Forest, Uluguru Mts, TZ; **H**, unusually coloured female, Kazimzumbwi Forest, near Dar-es-Salaam, TZ.

Genus *Mazaea* Stål, 1876
(Figs 1; 3B, C, E, F; 6; 7B-H; 8A, B; 9; 18A, B; Tables 1; 2)

Mazaea Stål, 1876: 54.

Eubocoana Sjöstedt, 1931: 21-22, Plate 2, figs 7, 7a, 7b; **n. syn**.

TYPE SPECIES. — *Mazaea granulosa* Stål, 1876, by monotypy.

DESCRIPTION
Morphology as for family, but typically slightly larger than *Ixalidium* and *Rowellacris* Ritchie & Hemp n. gen., differing principally by characters given in key. Medium size (male *c.* 20-28 mm; female *c.* 27.5-39 mm).

Head
Antennae 22-segmented, slightly longer than, as long as, or slightly shorter than head and pronotum together. Integument strongly granulose, rugose and punctate. Head with fastigium and frons above median ocellus strongly projecting in front of eyes. Fastigium of vertex forming an ogival arch, longer than, as long as, or slightly shorter than its maximal basal width, with bluntly pointed apex, lateral carinae and variably expressed median carinula (Fig. 3E, F). Head width across eyes from slightly less to slightly more than three times vertex length. Eyes protuberant and globular when seen from above (Fig. 3E), ovoid in lateral view. Frons produced, blade-like above and between antennal bases, meeting lateral carinae of fastigium dorsally at about 120°; frontal ridge below antennae sulcate, becoming broader with irregular lateral carinae, constricted below median ocellus, widening and obsolescent ventrally; facial carinae irregular, diverging ventrally with acute lower angles.

Thorax
Pronotum tectiform (*M. granulosa*) to subcylindrical (*M. tristis* n. comb.), not or only partly covering mesonotum, strongly granulose, with distinct lateral carinae (*M. granulosa*) or coarsely rugose and granulose, with small tubercles and without distinct lateral carinae (*M. tristis* n. comb.), with one deep transverse sulcus dividing prozona, and another separating it from metazona; prozona more than three times length of metazona, with raised irregular dorso-medial triangular tuberculate area, widest at anterior margin, narrowing towards first transverse sulcus; second triangular dorso-medial tubercular area extending from anterior sulcus to hind margin of pronotum and traversed by posterior sulcus; posterior margin of pronotum scalloped, medially indented, ornamented with small tubercles. Mesonotum dorsally short, carinate, rugose and puncate in anterior half (when visible), granulate in posterior half; hind margin with small papillate tubercles and with medial raised tuberculate mass. Metanotum and abdominal tergite 1 somewhat humped, with hour-glass-shaped medial raised tuberculate areas, widest at anterior and posterior margins.

Prosternal tubercle acutely subconical, with dentate apex, subvertical anteriorly, but obliquely sloping and concave posteriorly. Mesosternal interspace open, trapezoidal, longer than its minimum width; mesosternal lobes smoothly curving. Metasternal interspace open, longer than its minimum width, metasternal lobes bluntly rectangular. Elytra and wings absent.

Abdomen
Abdominal tergites carinate; tergite 1 with distinctly angled shoulders marked by irregular line of granulate tubercles and with hour-glass-shaped raised medial tuberculate area, as for metanotum; tympanum large, suboval, sclerotised; tergite 2 and subsequent tergites progressively less raised and tuberculate in medial area. Supra-anal plate (Fig. 9F) divided into basal and apical portions by a transverse furrow, with basal part narrowly embedded into last abdominal tergite, with broad medial longitudinal groove; its hind margin slightly carinate, shallowly concave medially and with small, rounded flanges at its outer ends (Figs 7B; 9G). Hinged apical part shield-shaped with subacute apex. Subgenital plate conical, postero-ventrally slightly concave in lateral view, with papillate apex, with shallow dorso-medial furrow widening forwards and with its anterior medial margin forming a domed membranous cowl over apex of aedeagus. Cerci elongate conical, with digitate tips, clothed with long setae.

Legs
Hind femur moderately robust, male *c.* 3.4-4 times as long as maximum depth, female; 3.5-5.1 times (Tables 1; 2), with serrated upper carina, granulose upper and lower marginal areas, rounded knee lobes. Hind tibia with 8-9 inner and 7 outer spines, small external apical spine usually present (Fig. 3C), but sometimes obsolete. Arolium large, diameter less than claw length.

Male genitalia (Figs 7; 9)
Somewhat similar to those of *Ixalidium*, but much more robust, enclosed within a narrow membranous pouch. Epiphallus with bridge from above semi-circular (Figs 7D; 9E), with nascent ancorae (Figs 7C; 9F) and with pointed lophi, directed medially and dorsally. Ectophallus with ventral lobe small and distinct from rami, closely applied to base of aedeagus (Figs 7E, F; 9B, D). Ventral lobe apodeme (ventral infold of Dirsh, 1956) present as a narrow thin bi-layered sheet below endophallus, broadening and bifurcating capitad (Fig. 7F), not illustrated by Dirsh (1966, fig. 41). Dorsal (basal) fold of cingulum forming a trilobate membranous cushion appressed to anterior wall of aedeagus, with its medial lobe produced caudad into a stalked vesicle, normally overlapping lowered antero-dorsal rim of aedeagus, so as to lie within and partially plug lumen of aedeagus (shown dislodged in Fig. 18A); lateral wings of dorsal fold produced posteriorly, curving around each side of aedeagus. Zygoma and rami of cingulum reduced, collar-like. Separate caudally-directed rounded sclerotised dorso-lateral lobes (supra-rami of Eades 1962) with denticulate outer surfaces on postero-dorsal margins of rami. Apodemes of cingulum strongly elongated, slightly diverging towards apices; supra-rami with spur-like supplementary apodemes directed anteriorly, as in *Ixalidium*. Arch of cingulum formed by paired bilateral sclerites arising

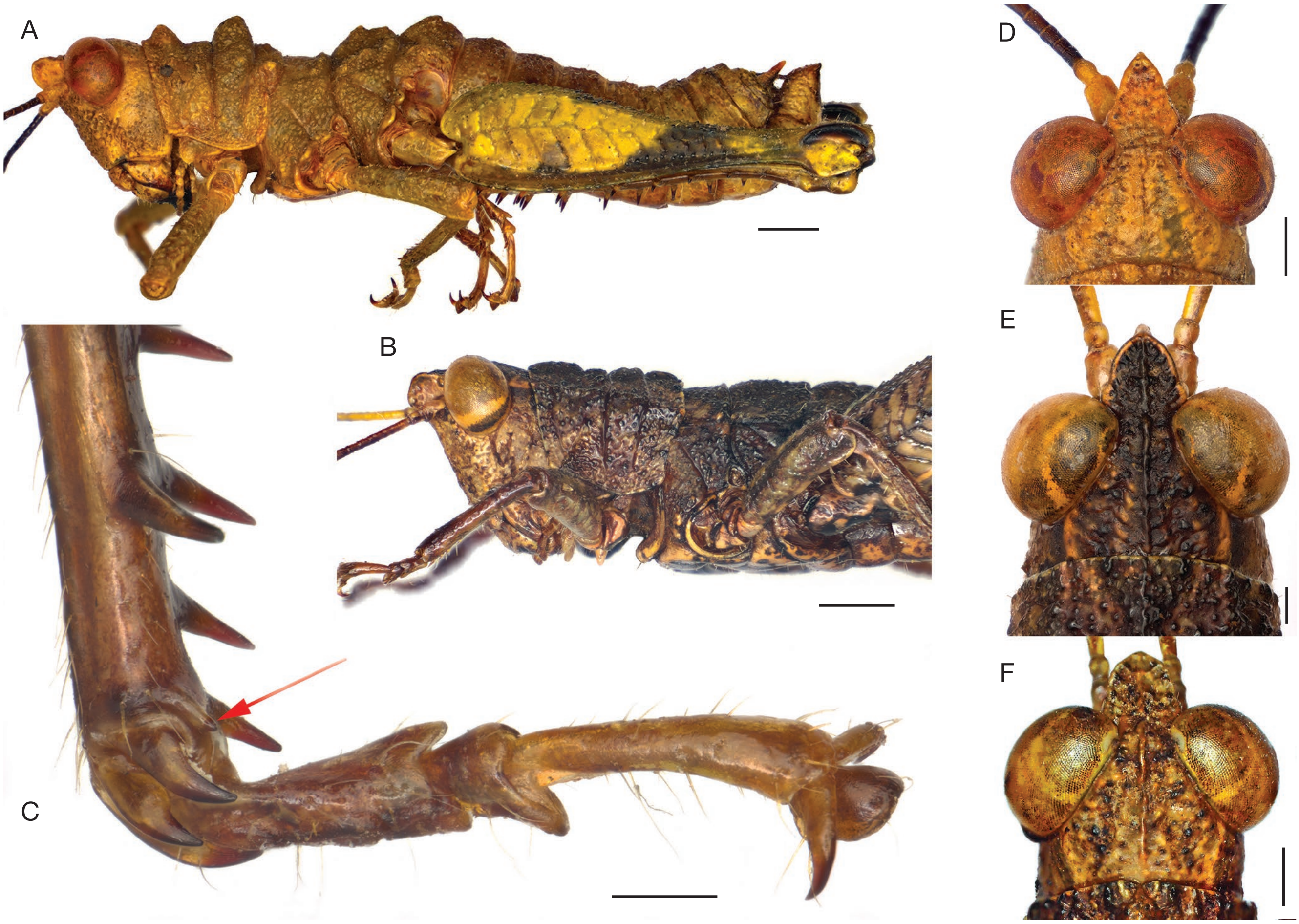

Fig. 3. — **A**, *Barombia tuberculosa* Karsch, 1891, whole insect, male, lateral view (Nigeria); **B**, *Mazaea granulosa* Stål, 1876, head and thorax, male, lateral view (Cameroon, Mt Fébé); **C**, apex of hind leg, *Mazaea granulosa*, external view (red arrow shows apical tibial spine); **D**-**F**, male heads, dorsal view; **D**, *Barombia tuberculosa* (Nigeria); **E**, *Mazaea granulosa* (Cameroon, Mt Fébé); **F**, *Mazaea tristis* (Sjöstedt, 1931) n. comb. (Congo Republic). Scale bars: A, B, 2 mm; C, E, 0.5 mm; D, F, 1 mm.

from sides of endophallus, with additional pair of slender apodemes of cingulum projecting anteriorly (Figs 7F; 9C) and with a bifurcated stout dentate process (incipient valves of cingulum?) projecting caudad (Fig. 18B, C), appressed to dorso-lateral surface of aedeagus, normally concealed by dorsal fold of ectophallic membrane. Endophallus similar to that of *Ixalidium*, in three sections (Fig. 7F-H); apodemes and medial sclerites separated from posterior section (apical sclerites) by articulated break; endophallic apodemes strongly-developed, proximally well-separated, upwardly curving, slightly excurved (smaller in *Ixalidium*), rising to their posterior point of fusion, then sharply recurved downwards and caudad. Flanges of endophallus visible as short, pointed, medially-directed projections on internal surfaces of endophallic apodemes (Figs 7G; 9A) anterior to their junction, adjoining confluence of ejaculatory duct and ventrally placed ejaculatory sac (Fig. 7F-G). Spermatophore sac forming flattened strip on dorsal surface of conjoined medial sclerites; ventral surface of medial sclerites of endophallus with alternating transverse striations of sclerotised (dark) and unsclerotised (light) cuticle (Fig. 7F, H). Posterior (apical) section of endophallus (aedeagal sclerites) fused, elongated and upcurved, separated from medial sclerites by hinged break and forming well-developed aedeagus with genital pore at its apex, dorso-ventrally compressed (Fig. 7G, H); anterior margin of aedeagal apex excavated to receive vesicle of medial lobe of dorsal fold of cingulum. Subgenital plate about as wide as long (when flattened); dorsal surface with medial pouch present, overlying common oviduct; egg guide narrow, continuous with inner margins of floor pouches; post-vaginal sclerites transverse, elongate reniform, with small, pigmented areas of columellae at their inner ends (Fig. 6C).

Female genitalia (Fig. 8)
Spermathecal duct extremely long (several times length of body) (Fig. 8A), repeatedly coiling and looping, forming two distinct clusters to left and right sides, occupying much of abdominal cavity between gut and ovaries as far forward as tergite 2, ending with short vermiform subapical diverticulum and vermiform apical diverticulum nearly ten times as long (Fig. 8B).

Measurements
Tables 1; 2.

Table 1. — Measurements in mm, *Mazaea* sp. (E Nigeria and S Cameroon).

	Antenna length	Head width	Pronotum length	Hind femur Length	Hind femur depth	Femur length / depth	Total body length	Vertex length	Vertex max width	Vertex length / max. width	Head + pronotum length (h+pl)	Antenna length / h+pl
Males												
n	12	13	13	11	11	11	13	13	13	13	13	12
Range	7.08-8.89	3.91-4.67	3.93-5.06	12.43-14.6	3.46-4.04	3.23-3.70	20.29-27.56	1.2-1.54	1.1-1.44	0.94-1.23	6.94-9.14	0.93-1.17
Mean	8.14	4.22	4.39	13.49	3.79	3.57	24.04	1.34	1.23	1.09	7.86	1.05
Females												
n	12	13	13	13	13	13	12	13	13	13	13	12
Range	9.1-11.75	4.38-5.09	5.02-6.5	15.49-19.51	4.13-5.11	3.56-3.97	27.7-38.96		1.47-1.79	0.9-1.31	8.74-11.47	0.91-1.12
Mean	10.05	4.78	5.77	17.28	4.59	3.77	33.21	1.79	1.67	1.07	10.00	1.02

Coloration (Figs 3B, E; 19C, D)

Male: General ground colour variable, especially in *M. granulosa*, light to dark brown with lighter banding and spotting and some darker brown to black areas. Antennae in basal half pale buff dorso-externally with darker speckling, pale buff or pale yellow ventro-internally (sometimes light red in *M. granulosa*), darkening to black towards tips on dorsal and ventral surfaces. Head light to dark brown, sometimes with darker speckling. Eyes light to dark brown with or without pale horizontal line across upper third, continuing caudad across occiput; second oblique curved pale line sometimes crossing lower third of eye, rising sharply caudad.

Dorsum of pronotum showing a range of pattern morphs in *M. granulosa*, some with dark brown medial longitudinal hour-glass marking framing median carina, alternately constricted and widened in prozona and metazona, bounded laterally by paler longitudinal areas of varying width, externally following inner edges of lateral carinae; others unicolorous lighter or darker brown dorsally, with or without pale buff to light brown longitudinal bands along inner margins of pronotal lateral carinae, continued obliquely downwards on meso- and metathoracic pleurae to episternum above hind coxae; dorsum in *M. tristis* n. comb. dull speckled mid brown, without pale lateral lines, with tubercles blackish except for pale buff tubercles on hind margin. Lateral lobes from light to dark brown, sometimes lacking clear markings, sometimes with pale oblique blotches in prozona, rising from antero-ventral angle caudad, interrupted by first transverse sulcus. Prosternum pale buff, sometimes with dark grey-brown spotting; meso- and metasternum anterior and lateral margins pale, becoming darker brown or grey-brown medially. Dorsum of meso-and metathoracic tergites mid brown medially (with greenish tinge towards lateral plates in *M. tristis* n. comb.); triangular epimeron on metathoracic pleura anterior to tympanum with large dark brown or black spot in caudal half.

Dorsum of abdominal tergite 1 often with pale tubercles at posterior margin; tergites 1-4 mid brown with paired dorso-lateral dark transverse dashes on hind margins; tergites 5 and 6 dorso-laterally paler; lateral lobes of tergite 2 with pale upper lateral area and dark shiny patch below; tergites 3-5 laterally with dark brown to blackish shiny areas, normally concealed by widest part of hind femur; tergites 7-10 darker (with olive greenish tinge dorso-laterally in *M. tristis* n. comb.). Abdominal sternites with lateral margins light brown with darker speckling, with dark brown or grey-brown patches medially, becoming chevrons pointing capitad on sternites 7-8. Cerci dorsally light to mid brown with subapical transverse black band, ventrally black with pale tips. Supra-anal plate mid brown, speckled with darker brown. Paraprocts blackish. Sternite 9 to tip of subgenital plate with continuous or interrupted irregular medial longitudinal dark grey-brown to black band, sometimes obsolescent.

Fore and mid legs mid dark grey-brown with lighter and darker speckling. All coxal joints blackish below. Hind femur externally and in upper internal area light to mid brown, with three indistinct oblique darker bands, interrupted in medial area, situated at base, 2/5 from base, and between 3/5 from base and knee; knee lunules dark brown. Hind femur internally with medial area dark brown to black throughout, apart from pale buff area in upper half at base, narrow irregular or incomplete pale transverse band half way from base sometimes reduced to small pale blotch on ventral internal carina and small pale mark just above knee; ventral internal area buff or greyish. Hind tibia dorsal and ventral surfaces buff to grey buff, with smoky blotches dorsally in basal half, becoming more evenly smoky grey brown towards tarsi; external spines and claws smoky buff with black tips, sometimes black at base or all black; internal spines usually darker with black tips or all black.

Female

Coloration similar to male but less contrasted. Triangular epimeron on metathoracic pleura anterior to tympanum without dark blotch; abdominal tergites 2-4 only with lateral dark brown to black shiny areas.

History

The genus *Mazaea* was described by Stål (1876) for his single female specimen of an apterous species that he named *M. granulosa* on account of the small granular tubercles covering the integument of the thorax and hind legs. Stål evidently did not know the provenance of his type specimen which must have been acquired in West Africa by a visiting European before 1876. Given the known geographical range of the genus and

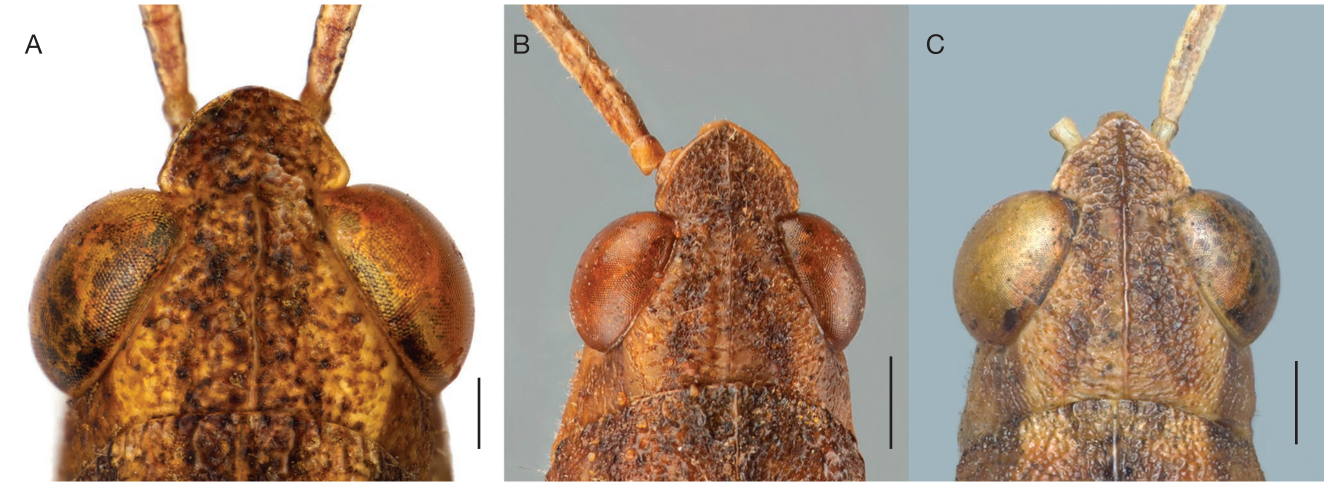

Fig. 4. — Male heads, dorsal view; **A**, *Ixalidium haematoscelis*, Kenya, Taita Hills (NHM, London); **B**, *Rowellacris usambarica* n. comb., paratype, Tanzania, Muafa, West Usambara Mts (MfN, Berlin) DORSA BA000802S03 (http://coll.mfn-berlin.de/u/d87ebc); **C**, *Tangana asymmetrica*, paratype, Tanzania, Tanga (MfN, Berlin) (http://coll.mfn-berlin.de/u/a08979). Scale bars: A, 0.5 mm; B, C, 1 mm.

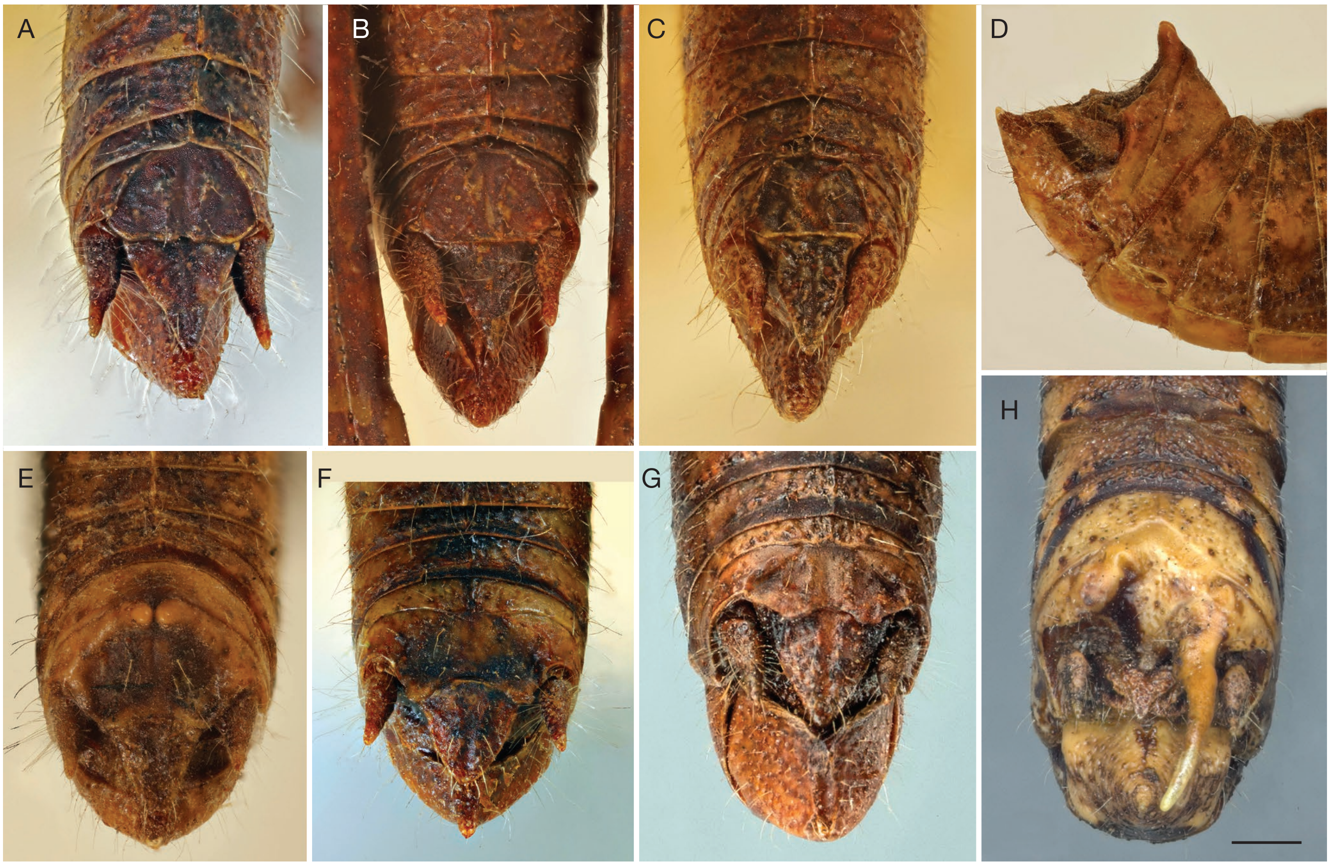

Fig. 5. — **A**-**H**. Male terminalia of *Ixalidium* spp. (**A**-**C**), *Rowellacri*s n. gen. spp. (**D**-**G**) and *Tangana asymmetrica* Ramme, 1929 (**H**), in dorsal view (apart from **D** which is in lateral view): **A**, *I. haematoscelis* (Taita Hills, Kenya, NHMUK 010594102); **B**, *I. bicoloripes* Uvarov, 1941 (holotype, Emali, Kenya, NHMUK 010595041); **C**, *I. sjostedti* Kevan, 1950 (holotype, Kilimanjaro, Tanzania, NHMUK 010594124); **D**, **E**, *R. transiens* Ramme, 1929, n. comb. (Usambara Mts, Tanzania, NHMUK 010594275); **F**, *R. obscuripes* Miller, 1929, n. comb. (holotype, Msimbazi River, Tanga District, Tanzania, NHMUK; 10594720); **G**, *R. usambarica* n. comb. (paratype, Muafa, West Usambara Mts, Tanzania, MFN, Berlin, DORSA BA000802S03); **H**, *T. asymmetrica* (paratype, Tanga, Tanzania, MfN, Berlin, (MfN URl http://coll.mfn-berlin.de/u/a08979). NHMUK numbers are barcode numbers for the UK Barcode of Life database https://www.ukbol.org/. Scale bar: 1 mm.

the fact that there were few European settlements on the coast of the Bight of Biafra at that time, it is likely that the type specimen came from a forested location close to what is now Douala in the littoral region of SW Cameroon. However a provenance from coastal areas of Congo, DR Congo, Gabon or Equatorial Guinea is also possible.

Bolívar (1908:105) described *M. granulosa* var. *cingulata* from "Loagna" [sic] (probably Loanga, Congo Republic), but this was synonymised by Kirby (1910) apparently as a cataloguing convenience, since he did not recognise varieties. Dirsh (1966:102) repeated the synonymy. All other published records of *Mazaea* have been attributed to *M. granulosa*. Sjöstedt (1931) assigned *Mazaea*, *Barombia* and his own *Eubocoana* to "*Acanthini*", an informal grouping possessing an external apical tibial spine, but he considered *Ixalidium* to belong to the "*Anacanthini*", which lacked this spine. Dirsh (1965) also used the presence or absence of this spine to organise his key to the genera of the Catantopinae. Today this character would be perceived as potentially subject to rapid evolution. Hollis (1975: 197) studied the presence or absence of the external apical tibial spine within and between different genera of Oxyinae Brunner von Wattenwyl, 1893. In *Thanmoia* Ramme, 1931 he noted that it could be present or absent and even show both conditions on the two hind legs of a single individual.

Remarks

Genomic evidence presented elsewhere in this paper (Fig. 1) now suggests that the West African *Mazaea* is the most basally-positioned subclade of the Ixalidiidae Hemp, Song & Ritchie n. fam., which agrees well with the ancestral character states that it exhibits (e.g. the large ejaculatory and spermatophore sacs, elongated apodemes of cingulum and recurved endophallus), that are shared with the East African *Ixalidium*. These characters have been lost or greatly modified in the other East African subclades of the family, *Tangana* and *Rowellacris* Ritchie & Hemp n. gen. *Mazaea* is also shown to be a member of the Ixalidiidae Hemp, Song & Ritchie n. fam. on the basis of its general habitus (Fig. 3) and especially its genitalia (Fig. 6). The external morphological features which distinguish *Mazaea* from the genus *Ixalidium* are its strongly granulose integument, more pointed vertex, pointed prosternal tubercle (spathulate in *Ixalidium*) and the presence (usually) of a small external apical spine on the hind tibia (absent in *Ixalidium* and other East African members of the family).

Included species

Mazaea granulosa Stål, 1876
Mazaea tristis (Sjöstedt, 1931) n. comb.

Mazaea granulosa Stål, 1876
(Figs 1; 3B, C, E; 6; 7B-H; 8A, B; 18A, B; 19C, D; 22C; Table 1)

Mazaea granulosa Stål, 1876: 54.

Type material. — **Holotype** • ♀; "Africa occidentalis"; [no further data] (NR, Stockholm).

Material examined. — **Nigeria** • 1 ♂; Eastern Province, 20 mls NE of Calabar, [Ekinta] Forest Reserve; [5°01'23"N, 8°28'43"E; 8.I.1961]; N. D. Jago leg.; NHMUK014035468 • 1 ♀; same collection data as for preceding, NHMUK.
Cameroon • 1 ♂, 1 ♀; Southern Bakundu Forest Reserve; 4°22'-4°27'N, 9°16'-9°16'E; 9.IX.1968; J. S. Gartlan leg.; #68015 (♂), #68014 (♀); Coll. CHR • 1 ♂; Lake Tissongo, Douala-Edéa National Park; 3°33'48"N, 9°53'9"E; 28.I.1975; T. E. Rowell leg.; #75025; Coll. CHR • 1 ♂; Dja [Faunal Reserve], 2°49'-3°23'N, 12°25'-13°35'E; 16.VII.1975; T. E. Rowell leg.; leaf litter in forest; #75024; Coll. CHR • 1 ♀ nymph; same collection data as for preceding; #75023; Coll. CHR • 1 ♂; Mt Fébé, nr Yaoundé; 3°54'47.99"N, 11°29'19.56"E; 1-11.VII.1975; N. D. Jago leg.; NHMUK 014035469 • 1 ♂; Yaoundé; 3°50'38.8284"N, 11°30'4.8456"E; 20.XII.1973; G. Popov leg.; NHMUK 014035470 • 1 ♀; same collection data as for preceding; NHMUK 014453740 • 2 ♂; Ongot Forest; *c.* 03°51'N, 11°25'E; VIII.2022; C. Oumarou Ngoute leg.; Coll. CH • 1 ♂; N Yaoundé, Nkométou II; 4°2'0"N, 11°33'0"E; 3.XI.1975; M. Descamps leg.; Coll. CH • 1 ♀; Edea [Forest Plantation], Mangombe Forest Reserve, 23-24.IX.1975; M. Descamps leg.; Coll. CH • 1 ♂; Ongot Forest; 03°51'57.28"N, 11°21'59.52"E; 887m a.s.l.; 5.XII.2021-20.III.2022; J. Yetchom-Fondjo leg.; SMNK • 1 ♂; Yingui, Deng-Deng National Park; 3°21'22"N, 12°44'37"E; 513 m a.s.l.; 12.VI.2022; J. Yetchom-Fondjo leg.; SMNK • 1 ♂, 3 ♀; Yingui, Iboti; 04°27'48"N, 10°27'32"E; 746 m a.s.l.; 7.I.2022; J. Yetchom-Fondjo leg.; SMNK • 2 ♂; Yingui, Iboti; but 04°27'47.76"N, 10°27'17.94"E; 7.I.2022; J. Yetchom-Fondjo leg.; SMNK • 1 ♂; Sanaga Maritime, Mouanko; 03°38'23"N, 09°46'37"E; 16.VII.2017; J. Yetchom-Fondjo leg.; SMNK • 1 ♂; Nkam, Solé; 04°36'00"N, 09°48'00"E; 28.II.2017; J. Yetchom-Fondjo leg.; SMNK • 2 ♂; Nkam, Djawara; 4°12'15.66"N, 9°50'16.01"E; 6 m a.s.l.; 13.III.2017; J. Yetchom-Fondjo leg.; SMNK • 2 ♂, 1 ♀; locality unknown; X.1938-VIII.1939; H. Jacques-Félix leg.; MNHN.
Congo Republic • 1 ♂; Dimonika [Biosphere Reserve]; [4°10'0.13"S, 12°25'0.12"E]; 28.V.1972; C. Morin leg.; MNHN • 1 ♂; N'go, [2°28'50.7144"S, 15°45'6.0732"E]; 12.III.1973; J. F. Cornic leg.; MNHN • 1 ♂, 1 ♀; Odzala; [*c.* 0.8°N, 14.9°E]; 9.XI.1977; S. Kelner-Pillault leg.; MNHN • 2 ♀; Mossendjo, Vouka [Vouga]; [2°34'08"S, 12°44'44"E]; 500 m a.s.l.; 14.XII.1973; J. C. Thibaud leg.; MNHN • 1 ♂; same locality as preceding; 2.XII.1973; J. C. Thibaud leg.; MNHN • 1 ♂; same locality as preceding; 2. II.1974; J. C. Thibaud leg.; MNHN.
Central African Republic • 1 ♀; La Maboke; [3°49'54"S, 17°50'45"E]; 16.I.1968; P. Teocchi leg.; MNHN • 1 ♀; same locality as preceding; 24.IV.1968; P. Teocchi leg.; MNHN • 1 ♂, same locality as preceding; 17.XII.1967; P. Teocchi leg.; MNHN.
Gabon • 2 ♂, 2 ♀; Ipassa; [c. 00°28'00"N, 12°43'00"E]; 30.IX.1974; A. Mougazi leg.; MNHN • 1 ♂, 1 ♀; Between Lastourville and Moanda; [between 0°49'2.71"N, 12°42'29.45"E and 1°34'0"S, 13°12'0"E]; 16.VI.1974; M. Donskoff and J. Le Breton leg.; MNHN.

Diagnosis. — Integument finely rugose and granulose, lacking larger papillate tubercles. Antennae in both sexes from 0.9 to 1.2 times as long as head and pronotum together. Pronotal shoulders in cross-section angular, with clear lateral carinae composed of granular tubercles forming a distinct angle between dorsum and lateral lobes. Pronotal shoulders widening evenly to hind margin, with acute hind angles. Dorso-medial tubercular areas of thoracic tergites and abdomen weakly raised.
Measurements: Table 1.

Distribution

Most records of *Mazaea granulosa* are from forested areas of Cameroon. Mestre & Chiffaud (2009) also reported it from the Republic of Congo (Congo Brazzaville), Equatorial Guinea and DR Congo (Congo Kinshasa, formerly Zaire), but without citing specific localities. However, they did not find any record of *Mazaea* or *Barombia* from the Central African Republic or from Gabon. Material of *M. granulosa* from all these countries has been examined for this study. Dirsh (1966: 103) reported a specimen from Dundo, Angola, close to the border with DR Congo.

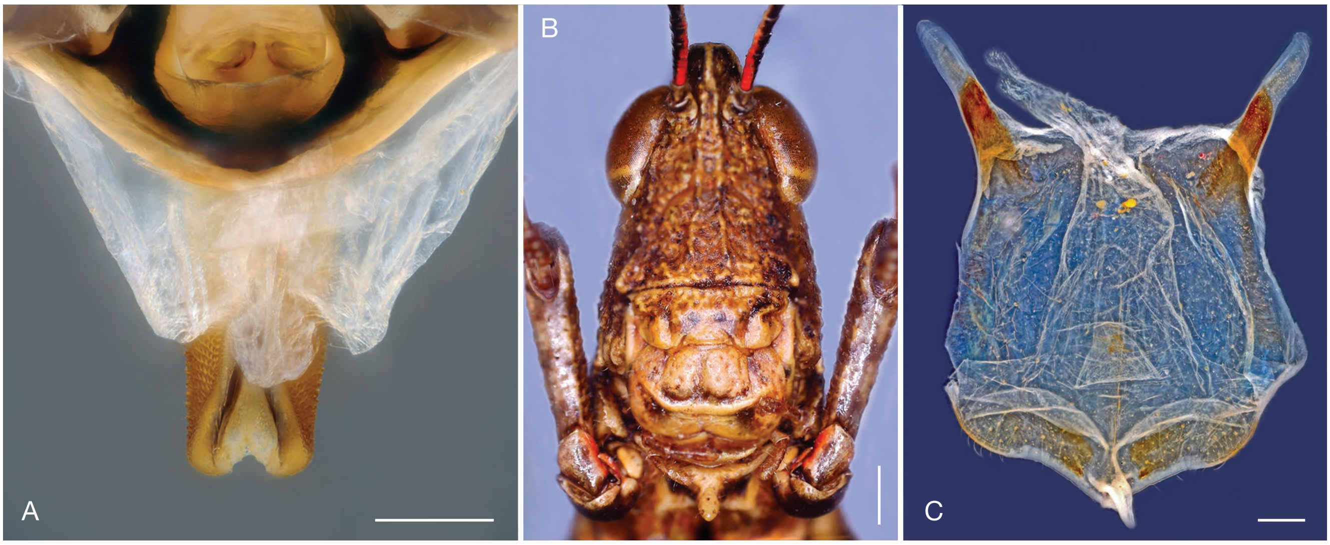

FIG. 6. — *Mazaea granulosa* Stål, 1876: **A**, male, zygoma and aedeagus with dorsal lobe membrane forming aedeagal plug, dorsal view (Cameroon, Ongot); **B**, female, head and prosternal tubercle, antero-ventral view (Cameroon, Mangombe); **C**, female, subgenital plate, cleared, dorsal view (Cameroon, Yaounde). Scale bars: A, 0.2 mm; B, 1 mm; C, 0.5 mm.

The occurrence of *Mazaea granulosa* in Nigeria, reported by Dirsh (1965, 1966, 1970) and Johnston (1968), but queried by Mestre & Chiffaud (2009), is based on specimens (collected in the Ekinta Forest Reserve in 1961 by N.D. Jago) in the NHMUK collection. This record is not surprising, given that the forested area of Cross River State, now included within the Eastern half of the Oban Group of Cross River National Park, was originally continuous with the Takamanda Forest Reserve in SW Cameroon which borders Nigeria and the Cross River NP. Mestre & Chiffaud (2009) indicated the importance for present-day distribution of forest species of the extreme dry period at the last glacial maximum (25000 to 15000 years BP), which left just two montane forest refugia in SW Cameroon, the western one extending into SE Nigeria.

Despite having been gazetted as a National Park, much of the Cross River forests are now within commercial estate concessions, and large parts of them have been cleared for oil palm production (Offiong 2017). In Cameroon, *Mazaea granulosa* was found to be the most common grasshopper species in three forested areas (Ongot forest, near Yaoundé; Zamakoe forest, near Mbalmayo; and Ngutadjap forest, near Ebolowa) and was most abundant where deforestation was highest (Oumarou Ngoute *et al.* 2020). It was found in agroforestry plots, crop fields, forest, and fallows in the SW Region and West Regions, but not in the Centre region (the forest-savannah transition zone) (Christel *et al.* 2019).

REMARKS

Unfortunately, the female holotype of *M. granulosa* in the Naturhistoriska Riksmuseet, Stockholm, lacks provenance and is not available for study. However, current investigations of the genitalia (Ritchie, unpublished) and mitochondrial genome (Yetchom-Fondjo, pers. comm.) of material presently assigned to *Mazaea granulosa* indicate a degree of geographical variation. Hence the specimens studied here and the measurements provided in Table 1 may ultimately be found to represent more than one closely-related species.

Mazaea tristis (Sjöstedt, 1931) n. comb.
(Figs 3F; 9; Table 2)

Eubocoana tristis Sjöstedt, 1931: 21-22, Plate 2, Figs 7, 7a, 7b.

Eubocoana tristis Sjöstedt, 1931 (Dirsh 1965: 308-309, fig. 235).

TYPE MATERIAL. — **Syntypes. Congo Republic** • 2 ♀; Boko - Kinkala, [c. 4°37'36"S, 14°37'11"E to 4°21'41.00"S, 14°45'51.98"E]; [M.] Lundgren leg.; NRM-ORTH0002426 [Type] and NRM-ORTH0002427 [Cotype] (NR, Stockholm).

MATERIAL EXAMINED. — **Congo Republic** • 1 ♀; Mossendjo, Vouka [Vouga]; [2°34'08"S, 12°44'44"E]; 500 m a.s.l.; 1-6.IX.1973; J. C. Thibaud leg.; MNHN • 1 ♂; same collection data as for preceding; 27.XI.1973; J. C. Thibaud leg.; MNHN • 1 ♂; same collection data as for preceding; 15.II.1975; J. C. Thibaud leg.; dense secondary forest; Coll. CH • 1 ♀; same collection data as for preceding; secondary forest; 13.III.1975; J. C. Thibaud leg.; Coll. CH. • 1 ♀; N'go; [2°28'50.7144"S, 15°45'6.0732"E]; 12.III.1973; J. F. Cornic leg.; MNHN.

DIAGNOSIS. — Integument coarsely rugose, granulose and pitted, with scattering of larger papillate tubercles. Antennae in female about same length as head and pronotum together; male antennae more than 1.2 times as long as head and pronotum together (based on small available sample). Pronotal shoulders in cross-section rounded, irregular, rugose and pitted, lacking clear lateral carinae. Pronotal shoulders widest in prozona, between transverse sulci, maintaining same width, or narrowing slightly, towards hind margin, with rounded hind angles. Dorso-medial tubercular areas of thoracic tergites and abdomen strongly raised.
Measurements: Table 2.

DISTRIBUTION

M. tristis n. comb, was until recently only known from two female syntypes, collected by a Swedish missionary, Manne

TABLE 2. — Measurements in mm, *Mazaea tristis* (Sjöstedt, 1931) n. comb. Congo Republic, Vouka (Vouga) and N'go.

	Antenna length	Head width	Pronotum length	Hind femur Length	Hind femur depth	Femur length / depth	Total body length	Vertex length	Vertex max width	Vertex length / max. width	Head + pronotum length (h+pl)	Antenna length / h+pl
Males												
n	2	2	2	2	2	2	2	2	2	2	2	2
Range	9.62-9.82	4.38-4.43	4.33-4.54	13.39-13.64	3.63-3.75	3.64-3.69	22.39-25.61	1.44-1.49	1.23-1.48	1.01-1.17	7.86-7.88	1.22-1.25
Mean	9.72	4.41	4.44	13.52	3.69	3.66	24.00	1.47	1.36	1.09	7.87	1.24
Females												
n	3	3	3	3	3	3	3	3	3	3	3	3
Range	10.24-10.99	4.4-4.98	5.37-5.70	17.35-18.08	4.48-4.66	3.87-4.01	33.44-34.21	1.6-1.9	1.66-1.82	0.90-1.04	9.91-10.31	1.01-1.09
Mean	10.68	4.72	5.56	17.79	4.54	3.92	33.89	1.71	1.77	0.97	10.12	1.06

Lundgren, based at Musana Mission Station in Boko-Kinkala Subdivision, about 120 kms W of Brazzaville, Republic of Congo. Recently further males and females have been examined from Republic of Congo, (Vouka [Vouga] and N'go), together with sympatric specimens of *M. granulosa*.

REMARKS

Sjöstedt (1931) did not designate a holotype for *Eubocoana tristis*, so despite being labelled as Type and Cotype, the original specimens in the Naturhistoriska Riksmuseet, Stockholm are syntypes. Sjöstedt (1931: 21) also listed females of *Mazaea granulosa* collected from the type locality of *E. tristis* by the same collector. Since the original description of *Eubocoana*, *Mazaea tristis* n. comb. has not been mentioned in primary taxonomic literature, featuring only in catalogues and in Dirsh's *African genera of Acridoidea* (Dirsh 1965: 308-309). Unfortunately, repeated requests for detailed imagery of the type specimens have received no response. However, descriptions and illustrations based on the female syntypes exist (Sjöstedt 1931: 21; Dirsh 1965: 308-309; Cigliano *et al.* 2023). The only characters adduced by Dirsh (1965) to separate females of *Eubocoana tristis* from *M. granulosa* were the fastigium of vertex shorter than wide in *E. tristis* rather than longer than wide in *M. granulosa*, the more rugose and tuberculate integument of *E. tristis* compared to *M. granulosa* and the absence of pronotal lateral carinae in *E. tristis*. The male of *Mazaea tristis* (Sjöstedt, 1931) n. comb. has not previously been described. However, comparison of the vertex measurements of a sample of *M. granulosa* (Table 1) with the newly studied specimens of *M. tristis* n. comb. (Table 2) indicates that there is no consistent difference in proportions between the two taxa, with length / width varying from around 0.9 to 1.3 in *M. granulosa* and from around 0.9 to 1.2 in *M. tristis* n.comb. Other standard metrics for *M. tristis* n. comb. are mostly well within the range for *M. granulosa*, apart from antenna length in males. Male antennae (in a sample of two) are more than 1.2 times the length of head and pronotum together in *M. tristis* n. comb., whereas they are either slightly shorter than, or barely longer than head and pronotum together in *M. granulosa.* However, the lack of distinct pronotal lateral carinae in *Mazaea tristis* n. comb. and the more tuberculate and rugose integument are confirmed for both sexes. The male genitalia of *M. tristis* n. comb. (Fig. 9A-F) are indistinguishable from those of *M. granulosa*, while the female spermatheca shows exactly the same complex structure in both taxa. Based on the original description (Sjöstedt 1931: 21), published illustrations of one of the two female syntypes (Dirsh 1965: 309; Cigliano *et al.* 2023) and examination and dissection of newly available males and females, the genus *Eubocoana* Sjöstedt, 1931 is therefore here synonymised with *Mazaea*.

Genus *Barombia* Karsch, 1891

Barombia Karsch 1891: 180.

TYPE SPECIES. — *Barombia tuberculosa* Karsch, 1891, by monotypy.

Barombia tuberculosa Karsch, 1891
(Figs 3A, D; 7A; Table 3)

Barombia tuberculosa Karsch 1891: 180.

Barombia tuberculosa var. *sublaevis* Bolívar, 1905: 226. Synonymised by Kirby (1910: 386).

Barombia nassaui Rehn, 1958: 3-5. Synonymised by Dirsh (1966: 101).

TYPE MATERIAL. — **Holotype of *Barombia nassaui*. Cameroon** • ♂; Ja River, Bitje [= Bitye]; [3°01'00"N, 12°22'00"E]; G. L. Bates leg.; Holotype 5808; ANSP, Philadelphia.
Lectotype of *Barombia tuberculosa*. Cameroon • ♂; Barombi Station; Preuss leg.; DORSA BA 000504S01; MfN, Berlin; here designated.
Types (status not confirmed) of *Barombia tuberculosa* var. *sublaevis*. Equatorial Guinea • "Biafra"; [Cape San Juan; 1°10'29"N, 9°20'31"E];[VI-XI.1901]; [M.] Martinez de la Escalera leg.; [Sex and status of Type(s) not confirmed, Repository not confirmed].

MATERIAL EXAMINED. — **Nigeria** • 1 ♂, Cross River State, Calabar, 30 kms E on Akansako road; 13.XII.1979; J. C. Reid leg.; NHMUK014453739.
Central African Republic • 1 ♀; La Maboke; [3°49'54"S, 17°50'45"E]; 12.IV.1968; P. Teocchi leg.; MNHN • 1 ♂; La Maboke; [3°49'54"S, 17°50'45"E]; 10.I.1966; R. Pujol leg.; #42; MNHN.
Cameroon • 1 ♂; Koupongo (Edea); [c. 3°48'N, 10°08'E]; 25.XI.1975; M. Descamps leg.; MNHN.
[**Equatorial Guinea**] • 1 ♂; "Congo, Riv. San Benito"; 27.II.1905; L. Guiral leg.; [determined as *Barombia tuberculosa* by W. Ramme]; MNHN.
Congo Republic • 1 ♂; Bassin N'gogo-Sanga, Region d'Ouésso; [*c.* 1°36'38"N, 16°03'05"E]; 20.III.1905; J. Gravot leg.; [determined

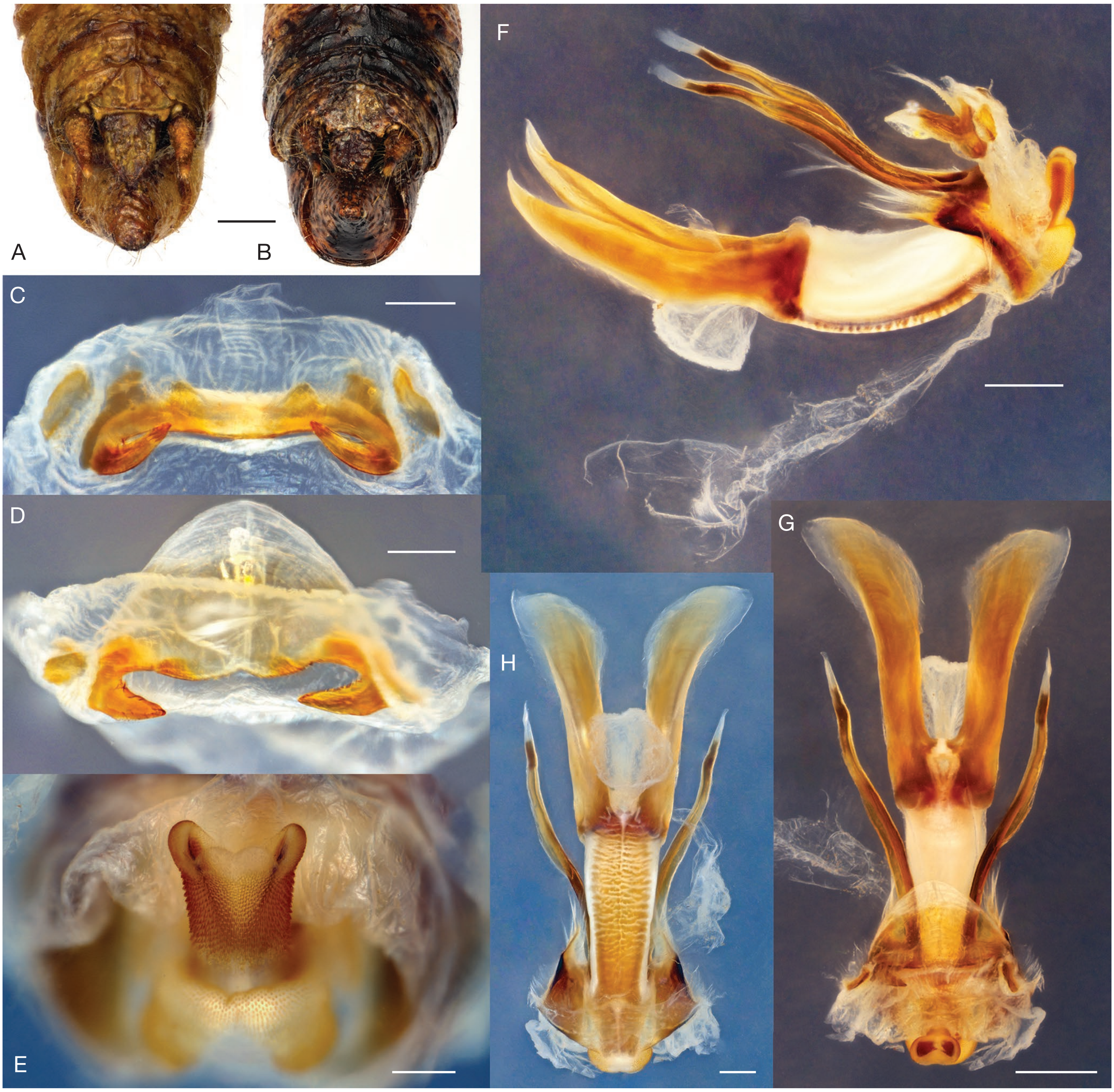

Fig. 7. — *Barombia* Karsch, 1891 and *Mazea* Stål, 1876 male terminalia and genitalia: **A**, **B**, male terminalia, dorsal view; **A**, *Barombia tuberculosa* Karsch, 1891 (Nigeria, Cross River State); **B**, *Mazaea granulosa* Stål, 1876 (Cameroon, Mt Fébé); **C**, **H**, male genitalia, *Mazaea granulosa* (Nigeria, Cross River State, NHMUK 014035468); **C**, epiphallus, posterior view; **D**, same dorsal view; **E**, aedeagus, posterior view; **F**, phallic complex, lateral (epiphallus removed); **G**, same, dorsal (epiphallus in place); **H**, same, ventral. Scale bars: A, B, F, G, 1 mm; C, D, 0.4 mm; E, 0.2 mm; H, 0.5 mm.

as *Barombia tuberculosa* by W. Ramme]; MNHN • 1 ♂; [Niari Department], Mossendjo [District], Vouka [Vouga]; [2°34'08"S, 12°44'44"E]; 500 m a.s.l.; 1-2.XII.1973; J. C. Thibaud leg.; MNHN • 1 ♀; same locality as preceding; 4.II.1974; J. C. Thibaud leg.; MNHN.
Gabon • 1 ♂; Fernan Vaz; [0°27'0"S, 10°28'0"E]; 1.I.1990; E. Cherlonneix leg.; MNHN-EO-CAELIF 11142; MNHN • 1 ♂; Cap Estérias; [c. 0°37'0"N, 9°19'60"E]; 15-16.V.1974; M. Donskoff and J. Le Breton; MNHN-EO-CAELIF 11141; MNHN • 1 ♂; Ipassa; [0°28'0"N, 12°43'0"E]; 3-30.V.1974; M. Donskoff and J. Le Breton leg.; quadrat; Coll. CH • 1 ♀; Ipassa; [0°28'0"N, 12°43'0"E]; 450-550 m a.s.l.; 28-30.IV.1974; M. Donskoff and J. Le Breton leg.; leopard trail; Coll. CH.

Redescription

Appearance distinctive (Figs 3A; 19G, H). Medium size (male, *c.* 23.5-27 mm; female *c.* 32-36 mm). Integument coarsely rugose, granulose and punctate.

Head

Antenna filiform, with 23 articles (Dirsh, 1965), about 1.45-1.6 times (male), 1.3-1.4 times (female) as long as head and pronotum together. Head conical; frons in profile oblique and indented at median ocellus; fastigium of vertex strongly

TABLE 3. — Measurements in mm, *Barombia tuberculosa* (Karsch, 1891). E Nigeria, S Cameroon, Congo Republic, Equatorial Guinea, Central African Republic and Gabon.

	Antenna length	Head width	Pronotum length	Hind femur Length	Hind femur depth	Femur length / depth	Total body length	Vertex length	Vertex max. width	Vertex length / max. width	Head + pronotum length (h+pl)	Antenna length / h+pl
Males												
n	5	9	9	9	9	9	9	9	9	9	9	5
Range	11.29-13.57	4.23-4.67	3.85-5.06	12.79-14.61	3.37-3.87	3.66-3.96	22.7-27.12	1.27-1.5	1.05-1.39	0.99-1.21	7.45-8.85	1.48-1.58
Mean	12.23	4.43	4.40	13.74	3.61	3.81	24.78	1.39	1.24	1.12	8.03	1.54
Females												
n	3	3	3	3	3	3	3	3	3	3	3	3
Range	12.91-13.8	5.05-5.12	4.85-5.68	15.61-18.89	4.18-4.44	3.73-4.25	31.02-35.47	1.72-1.94	1.64-1.73	1.0-1.18	9.37-10.14	1.31-1.39
Mean	13.33	5.09	5.26	17.48	4.34	4.02	33.24	1.82	1.69	1.12	9.81	1.36

projecting beyond eyes, horizontal, acutangular, as long as or slightly longer than its basal width, with marginal carinae in apical half but with medial carinula obsolete (Fig. 3D). Face and lower genae coarsely rugose and punctate. Frontal ridge medially produced, narrow, bladelike above antennae, becoming shallow with carinulae present between antennae and median ocellus, obsolete ventrally. Head width across eyes *c.* 2.9-3.5 times length of vertex (males), *c.* 2.6-2.9 times (females) (measured to narrowest point between eyes). Lateral ocelli barely visible from above. Eyes from above protuberant and globular (Fig. 3D).

Thorax

Pronotum short, not covering mesonotum, with deep transverse sulci dividing prozona into anterior and posterior sections and separating prozona from much reduced metazona; prozona about 4.8 times as long as metazona, with both sections having strongly raised and bluntly pointed dorso-medial lobes, of variable development, the posterior lobe somewhat larger; anterior and posterior sections of prozona and metazona with pointed dorso-lateral tubercular lobes, small or obsolescent in anterior section of prozona, but larger in posterior section of prozona and in metazona; metazona not raised but with very small medial pointed lobe; hind margin of metazona medially indented; prosternal process acutely conical. Mesonotum low, with fore margin medially indented, as broad as or broader than pronotum, hind margin ridged and tuberculate. Mesosternal interspace open, longer than its minimum width; mesosternal lobes with smoothly curving posterior margins. Elytra and wings absent. Metanotum and first abdominal tergite inflated (Fig. 3A), coarsely granulose, with median carina forming irregular raised arcuate or pointed medial lobes, subtriangular in dorsal view.

Abdomen

Dorsally carinate. Tympanum large, oval, sclerotised. Supra-anal plate divided into basal and apical portions by a transverse furrow, its basal portion narrowly embedded into last abdominal tergite, with broad medial longitudinal groove and with shallowly concave carinate hind margin with papillate flanges at its outer ends (Fig. 7A); hinged apical portion shield-shaped, longer than its basal width. Subgenital plate subconical, postero-ventrally slightly concave in lateral view, with acutely conical apex. Cerci elongate conical, with digitate tips, clothed with long setae.

Legs

Hind femur of moderate depth (*c.* 3.7-3.9 times as long as maximum depth, male; *c.* 3.7 times, females), with serrated upper carina, tuberculate upper and lower marginal areas, rounded knee lobes. Hind tibia with 8 inner and 7 outer spines, small external apical spine usually present (as in *Mazaea*, Fig. 3C). Arolium large, diameter less than claw length.

Male genitalia

Very similar to those of *Mazaea* in all respects (Fig. 7).

Female

Internal genitalia with spermatheca of similar configuration to that found in *Mazaea*, with long duct repeatedly looped and coiled in two distinct clusters to left and right sides of abdomen, becoming narrower in its apical section and ending with short vermiform subapical diverticulum and longer looping vermiform apical diverticulum; overall length of spermathecal duct shorter than in *Mazaea* spp. and with proportionately shorter apical diverticulum. Subgenital plate similar in shape to that in *Mazaea* species, as described above.

Measurements

Table 3.

Coloration (Figs 3A; 19G, H)

In contrast to other genera of Ixalidiidae Hemp, Song & Ritchie n. fam., ground colour olivaceous green to buff, variegated with light rufous brown markings, with some tubercles yellowish; antennae black with apical segments usually white; abdominal tergites 2-5 laterally with black shiny patches; abdominal sternites 2-7 variably infused with black; hind femora externally yellowish buff in basal half, with dark grey to blackish oblique transverse banding in apical half; black patches in basal half on upper and lower outer areas and internal medial area; ventral internal area brownish to blackish; knee lunules black; tibiae mottled brown and dark grey with spines black-tipped.

Fig. 8. — Female genitalia: **A**, *Mazaea granulosa* Stål, 1876, ovipositor valves and spermatheca, duct partially unravelled, ventral view; **B**, same, apex of spermatheca enlarged; **C**, *Ixalidium sjostedti* Kevan, 1950, ovipositor valves and spermatheca, ventral view; **D**, same, apex of spermatheca, enlarged, dorsal view. Scale bars: A, 2 mm; B, 0.5 mm; C, D, 1 mm.

Distribution

The genus *Barombia* was described by Karsch (1891: 180) for his species *B. tuberculosa* collected from Barombi Station, Cameroon, by the botanist Paul Preuss, who also collected material of *Mazaea granulosa* at the same location (Karsch 1891: 179). Mestre & Chiffaud (2009) suggest that Barombi Station was close to present-day Kumba. The type locality for var. *sublaevis* Bolívar, 1905, was initially given as"Biafra". Bolívar omitted to mention any specific locality, or the sex of his type material. However, it was actually from Cape San Juan, as indicated in the catalogue of species from Spanish Guinea (Anonymous 1910: 580). It seems possible that he did not intend to formally designate a type for his record of this variety. The location of Bolívar's material has not been confirmed, but may be the MNCN, Madrid (Mestre & Chiffaud 2009: 25). Further specimens from Cameroon were reported from Bibundi (Massa 2020) and from "Bonge" (Bong?) by Sjöstedt (1910). In Cross River State, Nigeria a male was collected from Ekinta Forest Reserve (NHMUK 014453739). Dirsh (1965, 1966, 1970) reported *Barombia* as present in Congo Republic and Congo Democratic Republic, in addition to Cameroon and Equatorial Guinea. Recently material from Congo Republic and Gabon (Ipassa) has been examined (MNHN). The large protuberant eyes, long antennae and overall greenish coloration of *Barombia* suggest that it inhabits the field layer rather than the leaf litter where the more sombre *Mazaea* is normally found.

History

Karsch (1891: 180) made clear in his description that he considered *Barombia* and *Mazaea* closely allied. Dirsh (1965: 302) also demonstrated their close relationship in his key to the Catantopinae and in his drawings of their genitalia (Dirsh 1966, 1970) which clearly showed the supplementary apodemes of cingulum that link these two genera to *Ixalidium*, though he did not mention them in his text. Bolívar (1905: 226) characterized *Barombia tuberculosa var. sublaevis* in a single line of Latin text as *"colour grass green, pronotal tubercles sub-obsolete"*. Var. *sublaevis* was automatically synonymised with *B. tuberculosa* by Kirby (1910: 386). Ramme (1929: 311) repeated the synonymy without citing Kirby (1910) and listed material from Ouésso, Congo Republic. Otte (1995: 277) ignored the synonymy of var. *sublaevis*, making it a subspecies, but Mestre & Chiffaud (2009: 25) reinstated the synonymy (referencing the earlier synonymies of Kirby and Ramme). Bolívar (1908: 106) listed material of *B. tuberculosa* from Mukonje Farm, Cameroon, collected by R. Rhode (Zoological Museum, Hamburg University), that Massa (2020: 49-50) stated to be three females, one of which Massa considered to be typical "var. *sublaevis*". Massa concluded that the degree of tuberculation was variable within a population, reconfirming the synonymy of var. *sublaevis* with *B. tuberculosa*. Rehn (1958: 3-5) described *B. nassaui* from a single specimen from Bitje (Bitye) on the basis of its more pronounced tubercular development of the thoracic dorsum relative to material of *B. tuberculosa* he had studied, which was in fact somewhat atypical. *Barombia nassaui* was synonymised by Dirsh (1966: 101). The increased production of the dorsal thoracic crest reported by Rehn may have resulted from allometric growth, since the hind femur length of his holotype male (16.3 mm) is 12% larger than that of the material of *B. tuberculosa* (14.1-14.3 mm) to which he compared it.

Remarks

Karsch's type series of one male and two females are all syntypes, since Karsch did not designate holotypes when more than one specimen was present (Holier 2010). This reality is not altered by the subsequent labelling of the male as holotype (DORSA BA 000504S01) and the two females as allotype and paratype (respectively DORSA BA 000504S02 and DORSA BA 000504S03). Accordingly, the single male syntype (DORSA BA 000504S01) is here designated as lectotype of *Barombia tuberculosa* Karsch. Images of the syntypes and their labels are shown in OSF (Cigliano *et al.* 2023). No revision of the genus *Barombia* has been undertaken. The genus is probably known from fewer than 30 specimens in museum collections globally. In line with the foregoing record of synonymies, critical examination of material, including male genitalia, from across the geographical range of *Barombia* has not so far yielded clear evidence that more than one species exists.

Genus *Ixalidium* Gerstäcker, 1869

Ixalidium Gerstäcker, 1869: 220. Table III, figs 6 and 6a.

Type species. — *Ixalidium haematoscelis* Gerstäcker, 1869 by monotypy.

Redescription

Small to medium size (Tables 4-6). Males 16.5-20.2 mm; females 23.6-29, with body length up to 50% greater than males and with more robust habitus (Fig. 11A). Integument rugose and punctate, variably setose.

Head

Antennae: 17-segmented, about as long as or slightly longer than head and pronotum together, basal segments (apart from scape and pedicel) dorso-ventrally compressed, widening markedly at segment three, widest between 3 and 6, with 8-9 distinctly less compressed and 10-17 filiform. Head width across eyes distinctly less than pronotum length and less than pronotum width at its hind margin; head obliquely slanted in lateral view, with vertex produced and frons sometimes shallowly incurved between antennae; eyes ovoid, narrower above, oblique. Fastigium of vertex from above (Fig. 4A) projecting over lateral ocelli and antennal bases, shorter than its maximal basal width, with obtusely rounded apex and median carinula continuing on occiput; foveolar area obsolete; frontal ridge in anterior view narrowest immediately below vertex, widening between antennae, then narrowing above median ocellus; lateral carinae widening below ocellus and becoming obsolete towards clypeus.

Thorax

Pronotum low tectiform, median carina crossed by 2-3 sulci; prozona 3-4 times longer than metazona; dorsum from above widening steadily from fore margin to hind margin. Prosternal tubercle transverse, spathulate, almost straight-sided, sparsely to densely setose, anterior face flat to slightly concave, posterior face flat to slight convex; apical margin straight or slightly uneven, with rounded angles. Meso- and metathorax tectiform, with median carina; mesonotum without visible tegminal rudiments; metathorax raised posteriorly and with distinct lateral carinae above robust lateral projections which stiffen its lateral lobes above hind coxae; Mesosternal interspace broader than its length, widening posteriorly; mesosternal furcal suture with deep medial and lateral pits. Metaster-

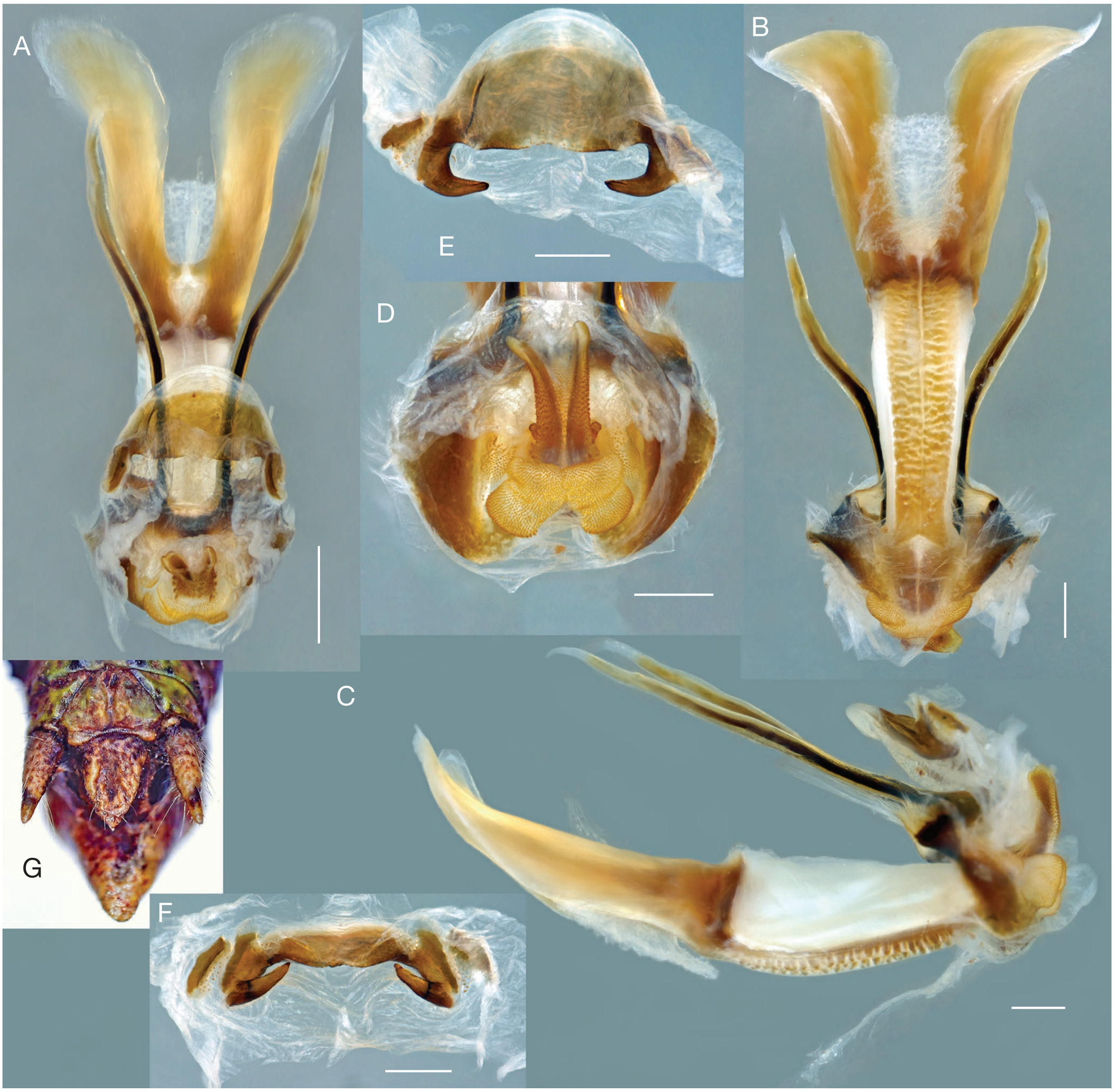

FIG. 9. — Male terminalia and genitalia, *Mazaea tristis* (Sjöstedt, 1931) n. comb., Congo Republic. **A**, phallic complex, dorsal; **C**, same, lateral; **B**, same, ventral, epiphallus removed; **D**, aedeagus, posterior view; **E**, epiphallus, dorsal view; **F**, same, posterior view; **G**, terminalia, dorsal view. Scale bars: A, 1 mm; B-F, 0.5 mm; G, not to scale.

nal interspace slightly broader than its length, narrowing posteriorly, tending to form two separate pits with medial portion of interspace continuous anteriorly with anterior portion of metasternum.

Legs
Fore and mid legs of typical acridoid appearance, unspecialized. Hind femur moderately robust, 3.1-3.9 times as long as maximum depth, male; 3.3-4.1 times, female (Tables 4-6); hind knee with upper and lower lobes bluntly or acutely rounded; hind tibia with 8 outer and 9 inner spines; external apical spine absent; arolium large, rounded, in ventral view about as long as claw; claws thickened at base, apically strongly curved.

Abdomen
With median dorsal carina and with segments one and two distinctly raised, together with metathorax forming slight hump; tympanum large and sub-oval; tergites 9 and 10 fused laterally.

External terminalia (Fig. 5A-C) presenting nymph-like appearance, without specialised structures; supra-anal plate (epiproct) in two sections, articulating at transverse hinge; basal section forming roughly trapezoid area, narrowing anteriorly, on dorsum of tergite 10, and bounded anteriorly by tergite 9; its lateral margins formed by oblique cuticular ridges and its posterior margin carinate, undulating or straight, overlying a transverse groove adjoining movable triangular apical portion, with its sides slightly incurved, tip acutely rounded; supra-anal plate rugose and sculptured, with shallow median longitudinal groove; cerci straight, acutely conical, sometimes attenuated at apex, clothed with long sensory hairs; paraprocts triangular, partly exposed at lateral margins of supra-anal plate; subgenital plate conical, with apex varying from bluntly rounded to acute and attenuated; dorsal medial area usually membranous anteriorly, sometimes bounded by lateral carinae forming a distinct longitudinal groove.

Male genitalia

Epiphallus (Figs 10G, H, I; 11E, F) much wider than endophallus (Fig. 11C); bridge-shaped, without ancorae, but with distinct shoulders bearing sclerotised denticles along their anterior margin; bridge with large circular sensory pores, possibly campaniform or coeloconic sensilla, clustered in medial area (Figs 10G-I; 11F); lateral sclerites irregular in outline, laterally compressed and curved; lophi strongly developed, pointed, projecting caudad, hook-like in lateral view, weakly bilobate, with short externo-lateral spur near base (Figs 10G-I; 11B); bridge with filamentous medial retractor apodeme situated antero-ventrally (Fig. 11B, E).

Cingulum (Figs 10A, B, E; 11B, C) with narrow, elongated and divergent apodemes, similar to those in Ommexechidae and Lentulidae, joined by narrow v-shaped zygoma carrying delicate anteriorly-directed lateral spurs (secondary apodemes) at ventrolateral margins (Figs 10A, B, E; 11C); rami of cingulum forming pair of laterally compressed spoon-like plates, flanking apical valves of aedeagus, externo-laterally convex and internally concave, heavily sclerotised and denticulate along their dorsal surface (presumed to be homologous with dorso-lateral lobes in *Mazaea*) but lightly sclerotised or membranous in their externo-medial part (Figs 10E; 11B), with numerous sensory pores; their antero-ventral margins narrowly sclerotised.

Ventral lobe much reduced, present medially as narrow lightly sclerotised paired plates underlying apical valves of endophallus; homology of these structures with ventral lobe in other genera of Ixalidiidae Hemp, Song & Ritchie n. fam. confirmed by presence in each case of delicate whisker-like medial apodeme (residual ventral infold) (Figs 10B; 11B) running forward from postero-ventral margin of ventral lobe below endophallus, dividing at node below spermatophore sac into two hair-like branches (Fig. 11B).

Arch of cingulum formed by two separate struts, joining lateral margins of proximal end of apical endophallic sclerites to underside of zygoma at bases of cingular apodemes, rather than at centre of zygoma; supplementary pair of delicate narrow apodemes (Fig. 10A; 11B, C) running capitad from point of origin of suprarami of cingulum, above spermatophore sac and between apodemes of cingulum, reaching as far forward as junction of spermatophore sac with fused section of endophallic apodemes; post-zygomal area overlain by lightly-sclerotised extension of dorsal fold (basal fold) of epiphallic membrane, covering anterior (basal) half of aedeagus, suprarami and rami of cingulum (Figs 10A, D; 11C), and concealing additional shorter transverse fold of membrane, also covering bases of rami and aedeagus; main dorsal fold continuous laterally with pallium beneath rami and ventral lobe; pallium shown covering the whole aedeagus in Figure 11B, C, but folded back during copulation during eversion of the aedeagus and then forming ventral cushion below genitalia.

Endophallus (Fig. 11D) elongated, in three sections; anterior section (endophallic apodemes) laterally flared anteriorly, convergent posteriorly; in lateral view (Figs 10E, F; 11B, D) distal (posterior) ends of apodemes project caudad above spermatophore sac, well beyond junction of apodemes with medial sclerites of endophallus ventrally; paired medial sclerites fused, dorso-ventrally compressed, emerging from ventral surface of conjoined apodemes downwards and turning sharply caudad; ejaculatory sac situated antero-ventrally to point of fusion of endophallic apodemes; paired medially-directed flanges of endophallic apodemes flanking ejaculatory duct adjacent to gonopore, appear analogous (though perhaps not homologous) to gonopore processes of other Acridoidea (see discussion of that character below), but situated medially rather than ventrally; mid section of endophallus after flexure with transversely striated cuticle basally, with spermatophore sac situated above it, followed by break or "hinge" between medial sclerites and apical sclerites; aedeagus formed by slender, laterally compressed, distinctly paired apical sclerites of endophallus, with sheath of ectophallic origin (Amédégnato, 1976), with dense denticulation on exposed apical portion (Fig. 11D), narrowing distally, slightly flared at apex.

Female genitalia (Fig. 8)

Spermatheca with simple robust duct, without bursa, with up to five loops and a short apical section, with flask-like preapical and short digitate apical diverticulum (Fig. 8C, D).

Measurements

Tables 4-6.

Coloration (Figs 2A; 11A)

Males, generally drab brown, more or less contrasted, varying from light to dark, with pale specks. Pronotum often marked by paired dorso-lateral pale striae (sometimes obsolete), starting behind eyes, converging towards median carina in anterior half of prozona before diverging and slanting obliquely downwards towards hind margin, continuing at a steeper downward slant onto lateral lobes of meso- and metanotum and coxae of hind femur; dorsum of meso- and metathorax and abdominal tergites with truncated dark triangles, narrowing capitad, on mid brown ground; hind margin of thoracic nota and abdominal tergites with paired black raised pustules bearing sensilla, less obvious in darker specimens; metathoracic

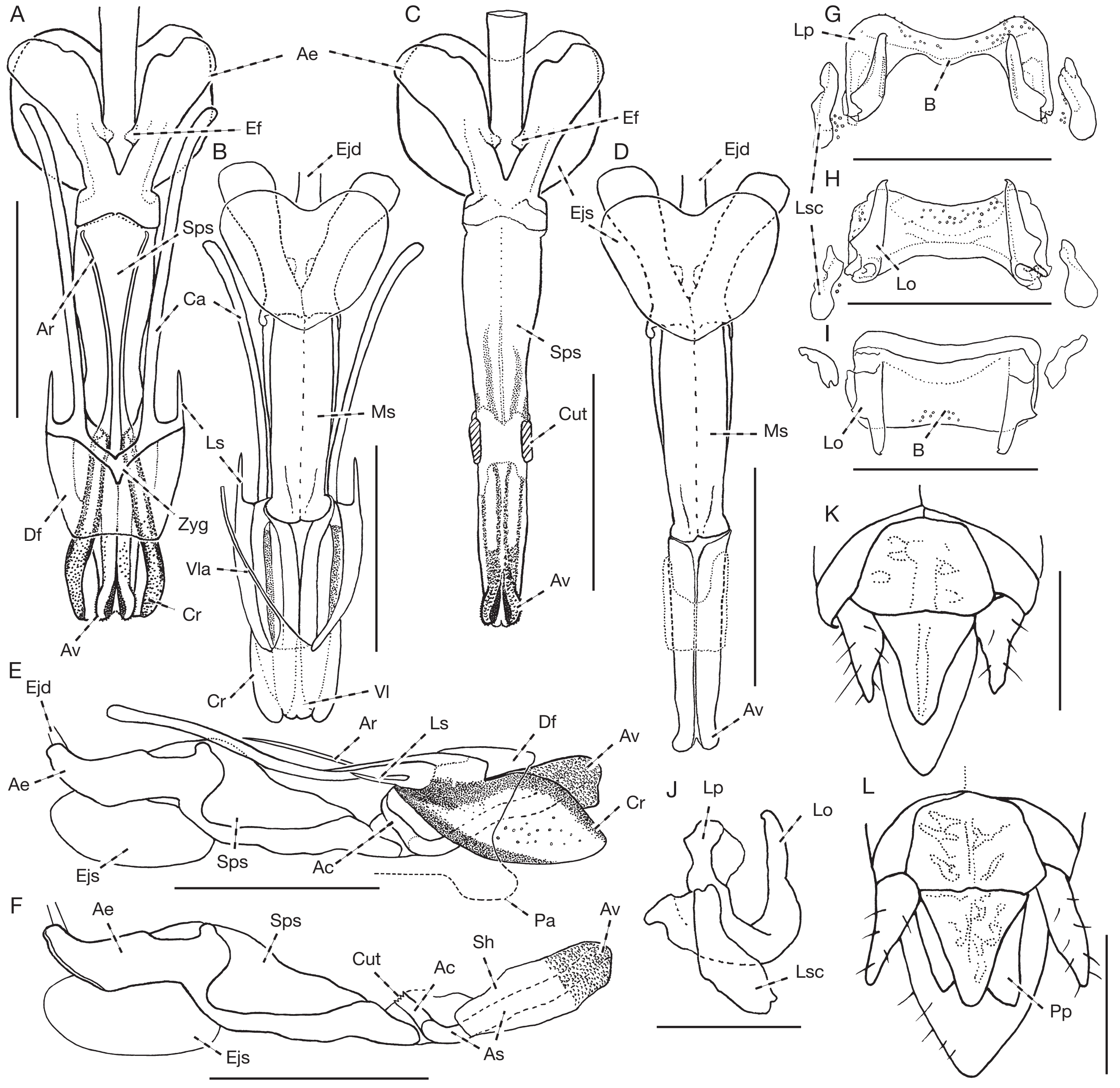

Fig. 10. — *Ixalidium haematoscelis* Gerstäcker, 1869, male genitalia: **A**-**F**, genital complex (epiphallus removed): **A**, dorsal view; **B**, ventral view (pallium removed); **E**, lateral view, left side; **C**, **D**, **F**, endophallus (cingulum and ventral lobe removed): **C**, dorsal view; **D**, ventral view; **E**, lateral view, left side; **G**, **J**, epiphallus: **G**, dorsal view; **H**, postero-dorsal view; **I**, antero-dorsal view; **J**, lateral view, left side; **K**, **L**, end of abdomen, dorsal view. Provenance: **A**-**J**, **L**, Kenya, Dwa Estate, Kibwezi; **K**, holotype, Kenya, Bura, Taita Hills. Abbreviations: see Material and methods. Scale bars: A-F, K-L, 1 mm; J, 0.5 mm.

pleura with triangular area of metaepimeron usually glossy black, bounded by lateral carina above, pleural suture and metaepisternum below and anteriorly and tympanum caudad; coxal joints ventrally blackish. Hind femur with internal medial area black at least in part, often extending onto upper and lower carinulae; lower internal carinula, lower internal carina and lower internal marginal area suffused with red, at least in basal area; upper internal marginal area in basal half with pale patch continuing on upper carina and outer upper marginal area; outer upper marginal and medial areas drab brown with faint dark patches before and after the pale patch; external medial area olivaceous, lower external margin blackish, greyish or olivaceous, with dense dark speckling; hind tibiae brownish to blackish basally becoming reddish in apical half. Abdominal tergites 2-4 laterally with glossy black longitudinal band above junction with sternites, extending dorsally as far as upper margin of tympanum, continuous with black triangle on metaepimeron, weakening progressively on tergites 5 to 8, often restricted to ventral and posterior margin of tergites, sometimes reaching only to tergite 5; this characteristic marking

TABLE 4. — Measurements in mm, *Ixalidium haematoscelis* Gerstäcker, 1869 Kenya, Chyulu Hills (NHMUK).

	Antenna length	Head width	Pronotum length	Hind femur length	Hind femur depth	Femur length/ depth	Total body length
Males							
n	10	10	10	10	10	10	10
Range	5.05-6.4	3.3-3.6	3.8-4.4	9.5-10.4	2.85-3.15	3.11-3.53	18.45-20.15
Mean	5.76	3.43	3.95	9.87	3.01	3.29	19.18
Females							
n	10	10	10	10	10	10	10
Range	6.3-7.15	4.05-4.35	4.9-5.8	12.2-13.05	3.5-3.85	3.34-3.61	24.6-27.3
Mean	6.88	4.13	5.41	12.75	3.69	3.46	26.21

TABLE 5. — Measurements in mm, *Ixalidium sjostedti* Kevan, 1950, Tanzania, Kilimanjaro and environs (NHMUK).

	Antenna length	Head width	Pronotum length	Hind femur length	Hind femur depth	Femur length/ depth	Total body length
Males							
n	10	10	10	10	10	10	10
Range	5.35-6.5	3.05-3.35	2.75-4.2	9.65-10.3	2.5-2.9	3.45-3.9	16.5-19.7
Mean	6.02	3.25	3.6	9.95	2.76	3.61	18.03
Females							
n	10	10	10	10	10	10	10
Range	6.9-7.8	3.7-4.15	4.65-5.65	12.25-13.65	3.05-3.6	3.71-4.08	23.65-29
Mean	7.3	3.9	5.22	13	3.33	3.91	26

usually concealed by hind femur when at rest; thoric sterna and abdominal tergites largely pale brown, darkening at lateral margins to match colour of tergites. Females with more uniform, less contrasting coloration overall; dark banding on abdomen obsolete. Occasional green morph occurs (Fig. 2B) with entire dorsum of head, thorax and abdomen, and dorsal and inner and outer lateral surfaces of hind femora yellowish green, apart from basal sixth and apical third; remainder of body shades of brown.

HISTORY

Although Gerstäcker had already briefly described *Ixalidium* and *I. haematoscelis* as new (Gerstäcker 1869: 220), he repeated and extended his descriptions four years later (Gerstäcker 1873: 46-47). We have designated the male syntype, labelled ambiguously as from "Bura, Endara" (DORSA BA000505S01), as the lectotype of *I. haematoscelis* Gerstäcker, 1869.

A second species, *Acridium gabonense* Brisout, 1851 from Gabon was later attributed to *Ixalidium* by Kirby (1910: 385), quite inexplicably, since Brisout himself had suggested that his new species was allied to *Podisma*. However, the original description of *A. gabonense* mentions the presence of elytra: *"elytres trés courtes, oblongues-obovales"* (Brisout 1851: lxviii), which eliminates this taxon from *Ixalidium*. Its true identity and the current whereabouts of any type specimen are unknown. In 1929 three further species of *Ixalidium* were described from Tanzania: *I. obscuripes* Miller, *I. transiens* Ramme and *I. usambaricum* Ramme. These are here referred to the new genus *Rowellacris* Ritchie & Hemp n. gen. Uvarov (1941) described a further species, *Ixalidium bicoloripes*, from Kenya and Kevan (1950) reviewed Sjöstedt's material from Kilimanjaro, originally determined as *I. haematoscelis* (Sjöstedt 1909: 186, 190), referring it to a new species, *I. sjostedti* Kevan. Johnston (1956: 294) catalogued *Ixalidium* as a member of the Catantopinae, but Dirsh (1966) transferred the genus from the Catantopinae to the Hemiacridinae Dirsh, 1956.

INCLUDED SPECIES

Ixalidium haematoscelis Gerstäcker, 1869
Ixalidium bicoloripes Uvarov, 1941
Ixalidium sjostedti Kevan, 1950

Ixalidium haematoscelis Gerstäcker, 1869
(Figs 1; 2A, B; 4A; 5A; 10; 22E; Table 4)

Ixalidium haematoscelis Gerstäcker, 1869: 220; Table III, Figs 6 and 6a.

TYPE MATERIAL EXAMINED. — **Lectotype. Kenya** • ♂; "Bura, Endara" [Bura Mts (North Taita Hills) and/or Endara (Ndara Mountain, NW Taita Hills)]; [3°27'S, 38°19'E and/or 3°30'23.18"S, 38°35'37.7"E]; XII.1862; K. K. von der Decken leg.; DORSA BA000505S01; MfN, Berlin. Here designated.
Paralectotype. Kenya • ♀; Endara [=Ndara Mountain, NW Taita Hills]; [3°30'23.18"S, 38°35'37.7"E]; XII.1862; K. K. von der Decken leg.; DORSA BA000505S02; MfN, Berlin.

OTHER MATERIAL EXAMINED. — **Kenya** • 2 ♀; Taita Hills, south; VIII.1947; V. G. L. Van Someren leg.; NHMUK • 1 ♂, 1 ♀; Taita Hills, Taita Farmers' Training Centre; 8 km S of Wundanyi; 3°26'S, 38°28'E; 5400 ft a.s.l.; 6.V.1975; I. A. D. & A. Robertson leg.; lush grass and herbs; NHMUK • 1 ♂, 1 ♀; Taita Hills; 15 kms along route C104; 3 500 ft a.s.l.; 17.IX.1982; N. D. Jago leg.; road edge forest remnant; NHMUK • 1 ♀; Taita Hills, Ngangao

Forest reserve; 1700-1800 m a.s.l.; II.2018; C. Hemp leg.; montane forest; Coll. CH • 1 ♂; Taita Hills, Mt Vuria; 1950 m a.s.l.; XI.2010; C. Hemp leg.; forest floor; Coll. CH • 2 ♀; S of Voi, Sagala Hills; 3°27'S, 38°25'E; 2600 ft a.s.l.; 17.IX.1982; N. D. Jago leg.; dry grass and *Euphorbia* thicket on stoney slopes; NHMUK • 2 ♂; Chyulu Hills, East end, 66 km from Makutano; 2°35'S, 37°50'E; 4500 ft a.s.l.; 16.IX.1982; N. D. Jago leg.; NHMUK • 4 ♂, 1 ♀; Kwale District, Kilibasi Hill, SW side, upper slopes; 3°57'S, 38°57'E; 1800-2700 ft a.s.l.; 27.I.1990; J. M. Ritchie & M. N. Mungai leg.; mist forest; NHMUK • 12 ♂, 11 ♀, 2 nymphs; Kenya, Near Kibwezi, Dwa, N of Brooke Bond Sisal Estate Rest House, 21.XI.1988; N. D. Jago, J. P. Grunshaw, J. Muli leg.; riverine forest near dam; NHMUK.

Measurements. — Table 4.

Ixalidium sjostedti Kevan, 1950
(Figs 1; 5C; 8C, D; 11; 21A-C; Table 5)

Ixalidium haematoscelis – Sjöstedt 1909: 186, 190.

Ixalidium sjostedti Kevan, 1950: 211.

Type material examined. — **Holotype**. **Tanzania** • ♂; Kilimanjaro; Kibonoto [= Kibongoto]; "kultur z" [cultivation zone]; [3°11'S, 37°06'E]; 12.X.1905-06; Y. Sjöstedt leg.; NHMUK. 'Allotype' [= Paratype] ♀; Kilimanjaro; Kibonoto [= Kibongoto] nieder [= base]; [3°11'S, 37°06'E]; 7.I.1906; Y. Sjöstedt leg.; NHMUK.
Paratypes. **Tanzania** • 1 ♀; Kilimanjaro, Kibonoto [= Kibongoto] nieder [= base]; [3°11'S, 37°06'E]; 2.i.1906; Y. Sjöstedt leg.; NHMUK • 1 ♂; Kilimanjaro; VIII.1905; Y. Sjöstedt leg.; NHMUK • 1 ♂; Kilimanjaro, Kibonoto [= Kibongoto]; [3°11'S, 37°06'E]; 1000-1200 m a.s.l.; 1905-06; Y. Sjöstedt leg.; NHMUK.

Other material examined. — **Tanzania** • 2 ♂; Kilimanjaro; 8.IX.1905; Y. Sjöstedt leg.; NR, Stockholm • 1 ♂; Kilimanjaro; 30.ix.1905; Y. Sjöstedt leg.; NR, Stockholm • 1 ♂; Kilimanjaro; IX.1905; Y. Sjöstedt leg.; NR, Stockholm • 1 ♂, 1 nymph; Kilimanjaro; 7.IX.1905; Y. Sjöstedt leg.; NR, Stockholm • 3 ♂; Kilimanjaro; VIII.1905; Y. Sjöstedt leg.; NR, Stockholm • 1 ♂; Kilimanjaro; 5.X.1905; Y. Sjöstedt leg.; NR, Stockholm • 2 ♂, 1 nymph; Kilimanjaro, Kibonoto [= Kibongoto]; [3°11'S, 37°06'E]; 1000-1200 m a.s.l.; VIII.1905; Y. Sjöstedt leg.; NR, Stockholm • 2 ♂; Kilimanjaro, Kibonoto [= Kibongoto]; [3°11'S, 37°06'E]; 1000-1200 m a.s.l.; IX.1905; Y. Sjöstedt leg.; NR, Stockholm • 2 ♂, 1 nymph; Kilimanjaro, Kibonoto [= Kibongoto], kultur z (cultivation zone); [3°11'S, 37°06'E]; VIII.1905; Y. Sjöstedt leg.; NR, Stockholm. • 1 ♂; Kilimanjaro, Kibonoto [= Kibongoto]; stäpp [= steppe]; [3°11'S, 37°06'E]; 1000-1200 m a.s.l.; Y. Sjöstedt leg.; NR, Stockholm • 1 ♂; Kilimanjaro, Kibonoto [= Kibongoto] nieder [= base]; [3°11'S, 37°06'E]; 2.I.1906; Y. Sjöstedt leg.; NR, Stockholm • 1 ♂; Mt Kilimanjaro, Nkweseko, montane grassland; 1660 m a.s.l.; XII.2013; C. Hemp leg.; Coll. CH. • 1 ♂, 1 ♀; Nr Mt Kilimanjaro, TPC Sugar Plantation; 3°33'30"S, 37°21'58"E; 700 m a.s.l.; III.2022; C. Hemp leg.; Coll. CH • 1 ♂; Mt Kilimanjaro, Masoka; 1150 m a.s.l.; I.2014; C. Hemp leg.; Home garden, Hom 2; Coll. CH • 1 ♂; Mt Kilimanjaro, Lyamungu; 1600 m a.s.l.; XII.2000; C. Hemp leg.; plantation; Coll. CH • 1 ♀; Mt Kilimanjaro, Mweka; 1030 m a.s.l.; XII.2000; C. Hemp leg.; plantation; Coll. CH • 1 ♀; Mt Kilimanjaro, Masoka; 1150 m a.s.l.; X.2013; C. Hemp leg.; Home garden, Hom 2; Coll. CH • 2 ♂, 5 ♀, 1 nymph; Moshi District, Kirua Vunja [= Kirua Vunjo Magharibi]; 3°20'S, 37°27'E; 6000 ft a.s.l.; 28.IX.1952; K. Guichard leg.; NHMUK • 1 ♂, 1 ♀; Moshi District, Marangu; 3°17'S, 37°31'E; 4000 ft a.s.l.; XI.1949; J. Phipps leg.; NHMUK • 1 ♂; Moshi District, Moshi; 3°20'S, 37°20'E; 20.XI.1943; E. Burtt leg.; NHMUK • 7 ♂, 4 ♀, 1 nymph; Ngurdoto Crater, Arusha National Park, E of Mt Meru, Crater Lake rim; 3°17'20"S, 36°55'36"E; 11.VI.1967; N. D. Jago leg.; NHMUK • 2 ♂, 2 ♀; Ngurdoto Crater, Arusha National Park, E of Mt Meru, Crater Lake rim; 3°17'20"S, 36°55'36"E; 14.VI.1967; N. D. Jago leg.; NHMUK • 16 ♂, 10 ♀, 5 nymphs; Ngurdoto Crater, Arusha National Park, E of Mt Meru, Crater Lake rim; 3°17'20"S, 36°55'36"E; 22.XI.1964; N. D. Jago leg.; NHMUK • 4 ♂, 1 ♀, 1 nymph; Ngurdoto Crater, Arusha National Park, E of Mt Meru, Kusari Lake; 22.XI.1965; N. D. Jago leg.; NHMUK • 1 ♀; Ngurdoto Crater, Arusha National Park, Forest SE of Ngurdoto Crater; 4000 ft a.s.l.; 12.VI.1967; N. D. Jago leg.; sunny forest margins; NHMUK • 3 ♂, 1 ♀; Ngurdoto; 3°18'S, 36°56'E; 3.VI.1972; I. A. D. & A. Robertson leg.; NHMUK • 2 ♂, 1 ♀; Meru; 3°14'48"S, 36°44'54"E; 14.I.1990; A. W. Harvey leg.; NHMUK • 2 ♂, 1 ♀, 1 nymph; Arusha, Grevillea plantation; 3°22'S, 36°41'E; 19.II.1948; E. Burtt leg.; NHMUK • 1 ♀; Arusha; 3°22'S, 36°41'E; 1.III.1969; P. Ward leg.; scrub on wasteland; NHMUK • 2 ♂, 1 ♀; Tengeru area, East of Arusha; 3°22'27"S, 36°47'7"E; 26.IX.1982; N. D. Jago leg.; NHMUK • 1 ♀; Arusha National Park; 3°15'S, 36°50'E; 2.V.1970; C. F. Dewhurst leg.; NHMUK.

Measurements. — Table 5.

Ixalidium bicoloripes Uvarov, 1941
(Fig. 5B; Table 6)

Ixalidium bicoloripes Uvarov, 1941: 28-30.

Type material examined. — **Holotype**. **Kenya** • ♂; Emali Range, Sultan Hamud; 4900-5900 ft a.s.l.; 13.III.1940; V. G. L. Van Someren leg.; NHMUK.
Paratypes. **Kenya** • 2 ♂, 2 ♀; same collection data as for preceding; NHMUK.

Other material examined. — **Kenya** • 1 ♂; Machakos District, NNE of Emali, Nzaui Hill; 1°55'S, 37°33'E; 5900 ft a.s.l.; 26.I.1990; J. M. Ritchie & M. N. Mungai leg.; mature pine plantation forest; NHMUK.

Measurements. — Table 6.

Distribution

Ixalidium haematoscelis is known from the Taita Hills and Sagala, Kenya. The same or closely related species occur in riverine forest near Kibwezi, in the Chyulu Hills and on Kilibasi Hill. *Ixalidium sjostedti* is found on the slopes of Mt Kilimanjaro and Mt Meru, Tanzania, in forest and montane grassland up to 1660 m a.s.l. Closely related species, as yet undescribed, occur in the North and South Pare Mountains. *Ixalidium bicoloripes* is known only from the Emali Hills, but it has not been collected since 1941 and the exact type locality is unidentified. Similar specimens are known from Nzaui Hill and from the northern foot slope of Mt Kenya.

Remarks

The male genitalia of *Ixalidium sjostedti* Kevan (Fig. 11) are closely similar to those of *I. haematoscelis* (Fig. 10) and other undescribed putative species of *Ixalidium*. The genitalia of *I. bicoloripes* are not available for study, but examination of material from other mountains in Kenya suggests they will

Fig. 11. — *Ixalidium sjostedti* Kevan, 1950 (Tanzania, Kilimanjaro): **A**, habitus, male (above) and female (below); **B**-**F**, genitalia: **B**, phallic complex, lateral view; **C**, same, dorsal view, epiphallus removed; **D**, Endophallus, lateral view, cingulum removed; **E**, **F**, Epiphallus; **E**, dorsal view; **F**, posterior view. Scale bars: B-D, 0.5 mm; E, F, 0.2 mm.

also be closely similar. The genitalia of *Ixalidium* have numerous similarities with those of *Mazaea* and *Barombia* but are radically different from those of *Tangana* and *Rowellacris* Ritchie & Hemp n. gen., as well as being conspicuously smaller and more slender than those of any other genus in the family. In fact, each of the three East African genera, while individually consistent, is quite distinct from the others.

Gerstäcker's male syntype of *Ixalidium haematoscelis* is not available for dissection, but the identity of the species is not in doubt as there is only one species of this family present in the Taita Hills. The genitalia erroneously figured for *I. haematoscelis* by Dirsh (1966) were in reality those of an undescribed species of *Rowellacris* Ritchie & Hemp n. gen. from the East Usambara Mountains, while the specimen

TABLE 6. — Measurements in mm, *Ixalidium bicoloripes* Uvarov, 1941. Kenya. Emali Range.

	Antenna length	Head width	Pronotum length	Hind femur length	Hind femur depth	Femur length/ depth	Total body length
Male	7.3	3.35	4.85	10.85	2.95	3.68	17.95
Female	–	4.1	5.45	14.15	3.8	3.72	27.4

TABLE 7. — Characters stated by Uvarov (1941) and Kevan (1950) to separate *I. haematoscelis* Gerstäcker, 1869, *I. bicoloripes* Uvarov, 1941 and *I. sjostedti* Kevan, 1950.

	***I. haematoscelis* Gerstäcker, 1869**	***I. bicoloripes* Uvarov, 1941**
Size	slightly smaller [than *I. bicoloripes*]; very slightly larger [than *I. sjostedti*] (Kevan 1950).	–
Fastigium of vertex	very slightly narrower [than *I. bicoloripes*]; rather wider [than *I. sjostedti*] (Kevan 1950).	almost twice as wide as its length (males), more than twice as wide as its length (females) (Uvarov 1941); wider than *I. haematoscelis* (Uvarov 1941: 29).
Hind tibiae colour	almost wholly red, becoming brownish in basal third (Uvarov 1941: 28); less extensively and less intensely dark basally [than *I. bicoloripes*] (Kevan 1950).	brownish black in basal half and red in the apical half (Uvarov 1941: 28-29).
Puncturation of integument	finer [than *I. bicoloripes*] (Kevan 1950).	head, pronotum and abdomen coarsely punctured and rugose; punctures and rugosities becoming less pronounced posteriorly (Uvarov 1941).
Abdominal tergites	differs from *I. sjostedti* in the gibbose [swollen] abdominal terga; less gibbose abdominal terga than *I. bicoloripes* (Kevan 1950).	abdominal tergites gibbose in profile; median carina acute throughout, distinctly convex in profile on each segment (Uvarov 1941).
Last abdominal tergite	differs from *I. bicoloripes* in trapezoidal excision of the last abdominal tergum (Kevan 1950).	with a broad and deep incision (Uvarov 1941).
Male supra-anal plate	basal portion less broad than *I. bicoloripes*, with straight sides, apical portion less acutely pointed than *I. bicoloripes* (Uvarov 1941); wider than *I. sjostedti*, though more acutely pointed; basal portion slightly narrower than *I. bicoloripes*; apical portion slightly shorter with straight (not slightly concave) sides and more distinct median sulcus than *I. bicoloripes*; impression on base narrower and better defined than *I. bicoloripes*, being a sulcus rather than an impression between two widely spaced ridges (Kevan 1950).	very long and acute, basal part wider than long, with pair of very irregular rugose ridges parallel to middle line; apical part acutely triangular, distinctly longer than its basal width (Uvarov 1941).

from Jadini Beach, Kenya, figured by Johnsen & Forchhammer (1975: 41, figs 15-18) as representing *I. haematoscelis*, probably belongs (as they suspected) to *Rowellacris obscuripes* (Miller, 1929) n. comb.

To our knowledge the supplementary apodemes of cingulum found in *Ixalidium* (Fig. 11B, C), *Mazaea* and *Barombia* have not previously been described in Acridoidea, though they were faithfully illustrated by Dirsh (1966) in *Mazaea* and *Barombia*. These additional muscle attachment points presumably enhance manoeuvrability of the exserted genitalia during mating in species with relatively weak apodemes of cingulum. The medial section of the endophallus is apparently very flexible in life, as dissected specimens have been found to exhibit widely differing angles between the basal valves and the aedeagus, especially in *Mazaea*. The alternating bands of more and less sclerotised cuticle visible ventrally at the base of the middle section of the endophallus (Fig. 7F; 9D; 11B, D) may facilitate this flexibility.

At present we are not able reliably to separate the described species of *Ixalidium* morphologically, hence no key or differential diagnosis is offered here. Kevan (1950: 211) and Uvarov (1941: 28-29) attempted to distinguish *I. sjostedti* and *I. bicoloripes*, respectively, from *I. haematoscelis* on the basis of minor features of the sculpturing, coloration, abdominal profile, supra-anal plate morphology and size (Table 7). Comparison of measurements of available material (Tables 4; 6) indicates that the size range and bodily proportions of different populations overlap. Hind tibial colour also varies within populations. Nonetheless, the shape of the subgenital plate, though variable, does appear to differ between species (Fig. 5A-C). In general *I. haematoscelis* has a somewhat wider and shorter apical section of the supra-anal plate than the other described species, but this has not been assessed with large samples. From molecular evidence (unpublished data) it appears probable that the three described species are all valid and that widely separated populations of *Ixalidium* found in different mountainous areas of east Africa, including the North and South Pare Mountains, Mt Kasigau (a mountain adjacent to the Taita Hills) and Mt Kenya may represent closely related species.

Genus *Rowellacris* Ritchie & Hemp n. gen.

urn:lsid:zoobank.org:act:216ED37B-FAC1-49B8-A046-BB3988AB4EE5

Type species. — *Ixalidium usambaricum* Ramme, 1929.

Etymology. — This new genus is named in honour of Charles Hugh Fraser Rowell in grateful recognition of his outstanding contributions to the biology and systematics of tropical locusts and grasshoppers over more than sixty years.

Description

See family description. Small to medium size (see Measurements, Tables 8; 10; 11). Males 18.5-24.75; Females 27.5-33.95. Integument rugose and punctate.

Head

Antennae ensiform, with *c.* 16-17 segments, from 80% to 115% of combined length of head and pronotum. Fastigium of vertex 1.3 to 1.6 times as long as its basal width, with irregular transverse sulcus at base.

Thorax

Pronotum low tectiform, median carina intersected by 3 sulci, the first often indistinct. Prosternal tubercle transverse, chisel like, with anterior face oblique, apex widening, lateral edges rounded to slightly bilobate, sometimes slightly crescentic in cross-section with anterior margin shallowly concave. Mesonotum, short, occasionally (*R. transiens* (Ramme, 1929) n. comb.) with narrow strap-like tegminal scars, completely fused to integument, sometimes visible projecting from beneath hind margin of pronotum, on one or both sides just above lateral sutures separating dorsum from mesopleura. Metanotum slightly inflated.

Legs

Hind femora moderately stocky (length / max. depth, males: 3.1-3.75, females; 3.35-3.85); hind tibiae with seven outer and nine inner spines; external apical spine absent.

Abdomen

Tergites medially carinate with each segment in lateral view dorsally convex, tergites 1 and 2 slightly inflated; tympanum large, suboval, with ventral margin flattened or slightly concave.

External terminalia (Fig. 5D-G) with supra-anal plate divided into basal polygonal portion and movable triangular apical portion. Hind margin of basal portion distinctly sinuous with paired rounded flanges. In *R. usambarica* (Ramme, 1929) n. comb. last abdominal tergite (tergite 10) interrupted dorso-medially by basal portion of supra-anal plate; in *R. transiens* n. comb. tergite 10 continuous and thickened dorsally, with dorsally-projecting digitate median furcula; supra-anal plate strongly rugose; cerci simple, conical, densely covered in sensilla. Subgenital plate bulbous (by comparison to *Ixalidium*), of variable length (short in *R. obscuripes* n. comb.), with attenuate apex.

Male genitalia

Epiphallus (Figs 13E, F; 14M-O; 15K-M) bridge-shaped, without ancorae; lateral plates concave in dorsal view; lateral sclerites elongated, irregular in outline, somewhat deflexed postero-dorsally; lophi bilobate, lobes pointed with inner pair directed medially and postero-dorsally, outer pair smaller and laterally directed; ventral margin of bridge forming a membranous cushion; bridge, lateral plates and adjoining membrane with numerous sensory pores.

Cingulum (Figs 13B, D; 14E, G, H; 15B, C, G). Having sclerotised shell-like zygoma with anteriorly placed paired apodemes distinct (in *R. usambarica* n. comb. and *R. transiens* n. comb.), obsolescent (in *R. obscu*ripes (Miller) n. comb., or absent (in undescribed species from East Usambara Mts); zygoma hind margin medially incurved in *R. usambarica* n. comb., and *R. transiens* n. comb., and forming sclerotised lateral horns in *R. usambarica* n. comb., or roundly excurved (*R. obscuripes* n. comb. and *R. transiens* n. comb.); rami of cingulum, covered by epiphallic membrane, forming inflated mitten-like lateral lobes with sclerotised ectophallic structures visible within, medially concave and externally convex; rami continuous with zygoma dorsally and fusing ventrolaterally with dorso-lateral margins of inflated bulbous ventral lobe. Arch of cingulum present, well-developed, joining zygoma to apical valves of endophallus; dorsolateral margins of cingular arch bilaterally inflated to form bulbous sub-dorsal lobe, strongly developed and visibly projecting caudad from beneath cingulum in dorsal view in *R. usambaricum* n. comb. and *R. transiens* n. comb., less developed and somewhat variable in different populations of *R. obscuripes* n. comb.

Endophallus (Figs 13D; 14E, J-L; 15F, H-J). In two sections with visible articulated break, paired endophallic apodemes separated apically, laterally flared dorsally, fused and medially ridged throughout most of their length; ejaculatory sac obsolete, reduced to a slight widening of the ejaculatory duct, before entering fused endophallic apodemes; apical endophallic sclerites fused, laterally compressed, slightly to moderately upcurved, forming tubular aedeagus enfolding phallotreme, within membranous sheath continuous with rami of cingulum; apex of aedeagus excurved, projecting dorsally beyond rami and ventral lobe; spermatophore sac reduced, situated dorsally at proximal end of apical sclerites, anterior to arch of cingulum.

Female genitalia (Fig. 12).

Spermatheca with three diverticula (Fig. 12A-C) arising from vestibule one above another: most ventral one short, sac-like, widening distally; middle one elongate sac-like, almost as long as dorsal ovipositor valves and apodemes together; dorsal one thin tubular, shorter than dorsal ovipositor valves, with apical and subapical diverticula, each ending in an apical ampulla (Fig. 12A-C); vestibule with elongate open slit ventrally between ventral valves of ovipositor (Fig. 12B).

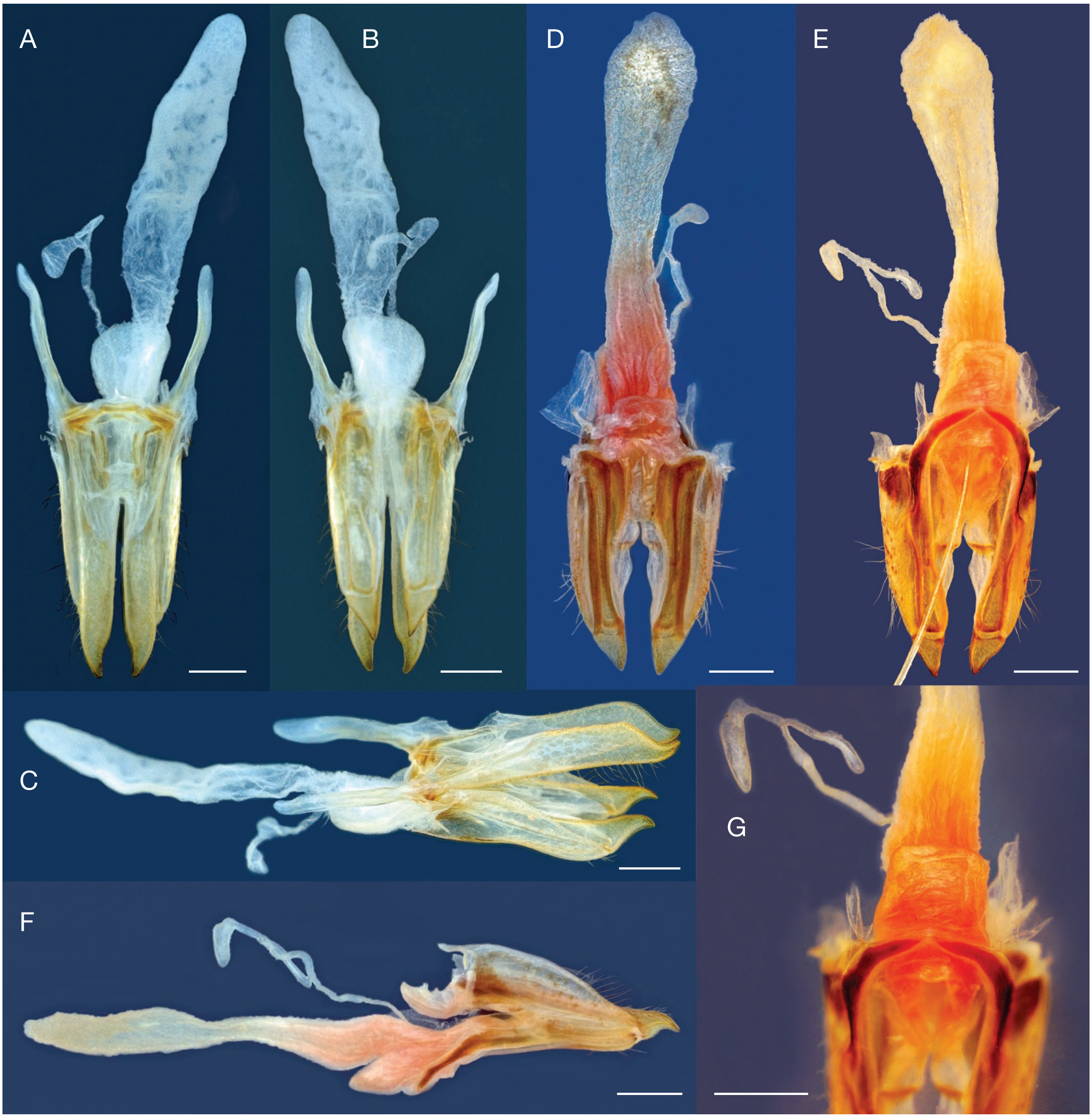

Fig. 12. — Female genitalia: **A**-**C**, *Rowellacris* n. gen. sp. (Tanzania, E Usambara Mts, Sigi); **D**-**G**, *Tangana asymmetrica* Ramme, 1929 (Tanzania, Pangani Coast): **A**, Spermatheca and ovipositor valves, dorsal view; **B**, same, ventral view; **C**, same, lateral view; **D**, Spermatheca and ventral ovipositor valves (dorsal valves removed), dorsal view; **E**, same, ventral view, with bristle inserted through vestibule into lumen of spermathecal bursa; **F**, same, lateral view; **G**, spermathecal vestibule, duct and diverticula, ventral view, enlarged. Scale bars: 1 mm.

Coloration (Figs 2C-E; 19E, F).
Rowellacris Ritchie & Hemp n. gen. males have similar range of overall patterning to *Ixalidium*, with paler morphs dorsally buff-coloured, contrasting with darker brown lateral parts of thorax and darker morphs having all paler markings indistinct. Typical patterning includes dorsal longitudinal lateral pale bands beginning behind eyes, converging towards median carina in prozona of pronotum, then either continuous or interrupted by darker pigment, before diverging and continuing obliquely downwards across thoracic pleura to hind coxae; metaepimeron black. Hind femora externally mottled brown or olive grey, darker on upper and lower marginal areas; internal upper marginal area mottled olive grey proximally, becoming darker towards knee, sometimes with pale buff oval marking in proximal half; internal medial area mainly black with pale mark towards knee, sometimes with paler area medially; lower

TABLE 8. — Measurements in mm, *Rowellacris usambarica* (Ramme, 1929) n. comb., Tanzania, West Usambara Mts.

	Antenna length	Head width	Pronotum length	Hind femur length	Hind femur depth	Femur length / depth	Total body length
Males							
n	4	4	4	4	4	4	4
Range	6.11-6.93	3.31-3.51	4.2-4.63	10.22-11.66	3.26-3.59	3.13-3.25	18.52-22.85
Mean	6.57	3.42	4.38	10.91	3.43	3.18	20.2

TABLE 9. — Assignment to species of Ramme's type series of *Rowellacris usambarica* (Ramme, 1929) n. comb. (**MfN**, Berlin).

Localities (collector)	Species	Type specimens
West Usambara, Muafa (J. Buchwald)	*Rowellacris usambarica* n. comb. [based on dissection of topotypic paratype]	Holotype male, 1 paratype male (MfN)
East Usambara, Amani (Vosseler)	*Rowellacris* sp. 1 [only species known from Amani]	Paratypes, 1 male, 2 females (MfN); 1 female (NHMUK)
Tanga (Karasek)	*Rowellacris* cf. *obscuripes* n. comb. [based on dissection of male paratype]	Paratype, 1 male (MfN)
Buloa, nr Tanga (P. Lucker)	Uncertain, not seen, but most likely *R.* cf. *obscuripes* n. comb., if not *Tangana asymmetrica*	Paratype, 1 female (MfN)

internal carinula and carina and lower marginal area red in proximal three fifths, fading or darkening towards knee. Hind tibia varying from pale greyish buff to grey brown, pale mauve, violet or blackish, but never red; tibial spines black-tipped. Abdomen with lateral shiny black bands reaching from tergite 2 to tergites 5 or 6, fading caudad. Ventral surface of thorax and abdomen pale buff to light brown.

INCLUDED SPECIES

Rowellacris usambarica (Ramme, 1929) nom. rev., n. comb.
Rowellacris transiens (Ramme, 1929) n. comb.
Rowellacris obscuripes (Miller, 1929) nom. rev., n. comb.

Rowellacris usambarica (Ramme, 1929) nom. rev., n. comb. (Figs 1; 2C, D; 4B; 5G; 13; 21D; Tables 8; 9)

Ixalidium usambaricum Ramme, 1929: 307.

Ixalidium haematoscelis – Dirsh 1966: 103 (incorrectly synonymised; here recalled from synonymy).

TYPE MATERIAL EXAMINED. — **Holotype. Tanzania** • ♂; [Lushoto District], [West] Usambara Mountains, Muafa; [c 1200-1300 m a.s.l.]; J. Buchwald leg.; DORSA BA000802S01; Collection Object 1501239; 1d78f5f7-d185-4827-87e9-ed12890fc309; MfN, Berlin. **Paratype. Tanzania** • ♂; same collection data as for preceding; DORSA BA000802S03; MfN, Berlin; MfN URI: http://coll.mfn-berlin.de/u/d87ebc.

OTHER MATERIAL EXAMINED. — **Tanzania** • 2 ♂; West Usambara Mts, Wilhelmstal [= Lushoto]; F. E. Zeuner leg.; NHMUK • 1 ♂; West Usambara Mts, West foot of mountains, Mombo, Riverine forest; 9.VI.1967; N. D. Jago; DNA voucher B5, extracted 19.X.2022, Box: SA00924142, Tube: FD18757457; NHMUK 015134149 • 1 ♂; West Usambara Mts, Ndelemai Forest; III.2022; C. Hemp leg.; Coll. CH • 1 ♂; West Usambara Mts, Muafa [Lushoto District]; III.2022; C. Hemp leg.; Coll. CH.

DIAGNOSIS. — Basal portion of supra-anal plate with flanges on posterior margin not continuous with outer edges (Figs 5, G; 13A). Cingulum with well-developed apodemes (Fig. 13B-D). Posterior margin of cingulum medially excavated with pointed and sclerotised lateral processes (Fig. 13B). Sub-dorsal lobe prominently inflated and exposed dorsally, slightly bilobate (Fig. 13B).
Measurements: Table 8.

DISTRIBUTION

Known only from submontane forest sites at Muafa, Ndelemai Forest, Lushoto and riverine forest at Mombo, West Usambara Mountains. Dissection of the genitalia of the male paratype from Muafa and comparison with recently collected specimens of this species from Muafa and the nearby Ndelemai Forest indicate that *R. usambarica* n. comb. (Fig. 13A-H) has a restricted distribution within the West Usambara Mountains. It is replaced by several other closely-related *Rowellacris* Ritchie & Hemp n. gen. species, both on neighbouring Eastern Arc mountains and within the West Usambara Mts. The single male paratype collected, along with three females, by Vosseler from Amani (East Usambara Mts) has not been dissected, but numerous other specimens from Amani and its environs, both in the NHMUK collection and collected recently have been dissected. These all show character states in the morphology of the cingulum that are consistently distinct from West Usambara material and all evidently belong to a single species. Accordingly, this Amani material has been assigned to a third, as yet undescribed species of *Rowellacris* Ritchie & Hemp n. gen. (unpublished data). The single male paratype of *I. usambaricum* collected by Karasek from Tanga has been

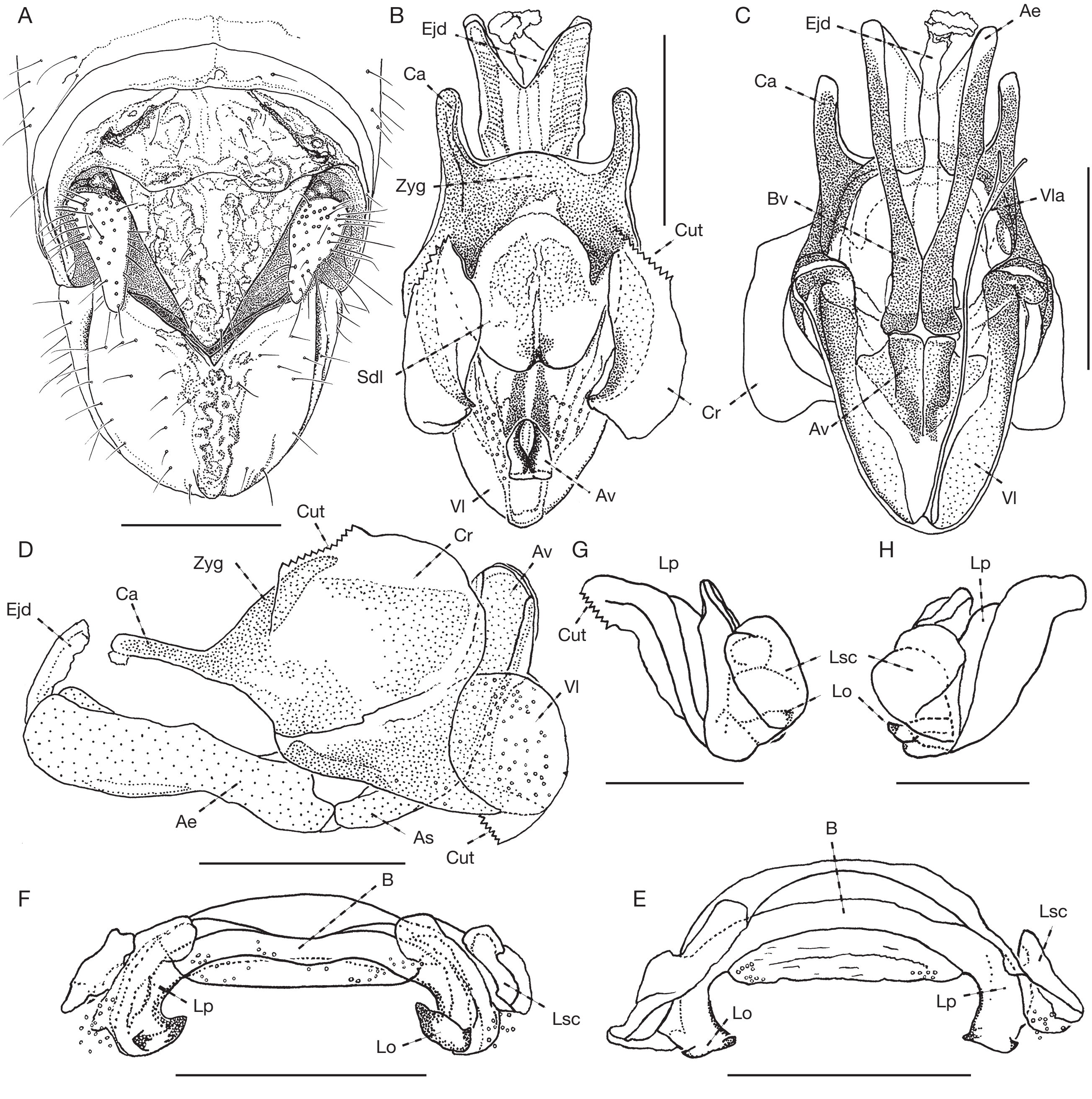

Fig. 13. — *Rowellacris usambarica* (Ramme, 1929) n. comb., male genitalia: **A**, end of abdomen, dorsal view; **B**-**D**, phallic complex (epiphallus removed); **B**, dorsal view (rami slightly separated); **C**, ventral view (pallium removed); **D**, lateral view, left side; **E**-**H**, epiphallus: **E**, dorsal view; **F**, postero-dorsal view; **G**, lateral view, left side; **H**, same, right side. Provenance: **A**-**H**, West Usambara Mountains, Tanzania; **A**, paratype, Muafa, **B**-**H**, Ndelemai Forest. Scale bars: 0.5 mm, except under Figure A, where 1 mm. Abbreviations: see Material and Methods.

dissected and found to belong to the related coastal forest species *Rowellacris obscuripes* (Miller, 1929) n. comb. The records of *R. usambarica* n. comb. from East Usambaras and Mlinga Mountain (Magroto) by Hochkirch (1996: 204) are misidentifications of two different undescribed species of *Rowellacris* Ritchie & Hemp n. gen. (material studied). The record of *I. usambaricum* from Lutindi Forest (Hemp *et al.* 2016: 216) represents yet another undescribed species of *Rowellacris* Ritchie & Hemp n. gen. Yet another undescribed species of this genus occurs in the Irente area west of Lushoto.

Remarks

Ramme (1929: 307-308) described *I. usambaricum* from a mixed species series here recognised as comprising three distinct species (Table 9). The holotype male and two paratypes, one male and one female, were collected by J. Buchwald at Muafa (West Usambara Mountains).

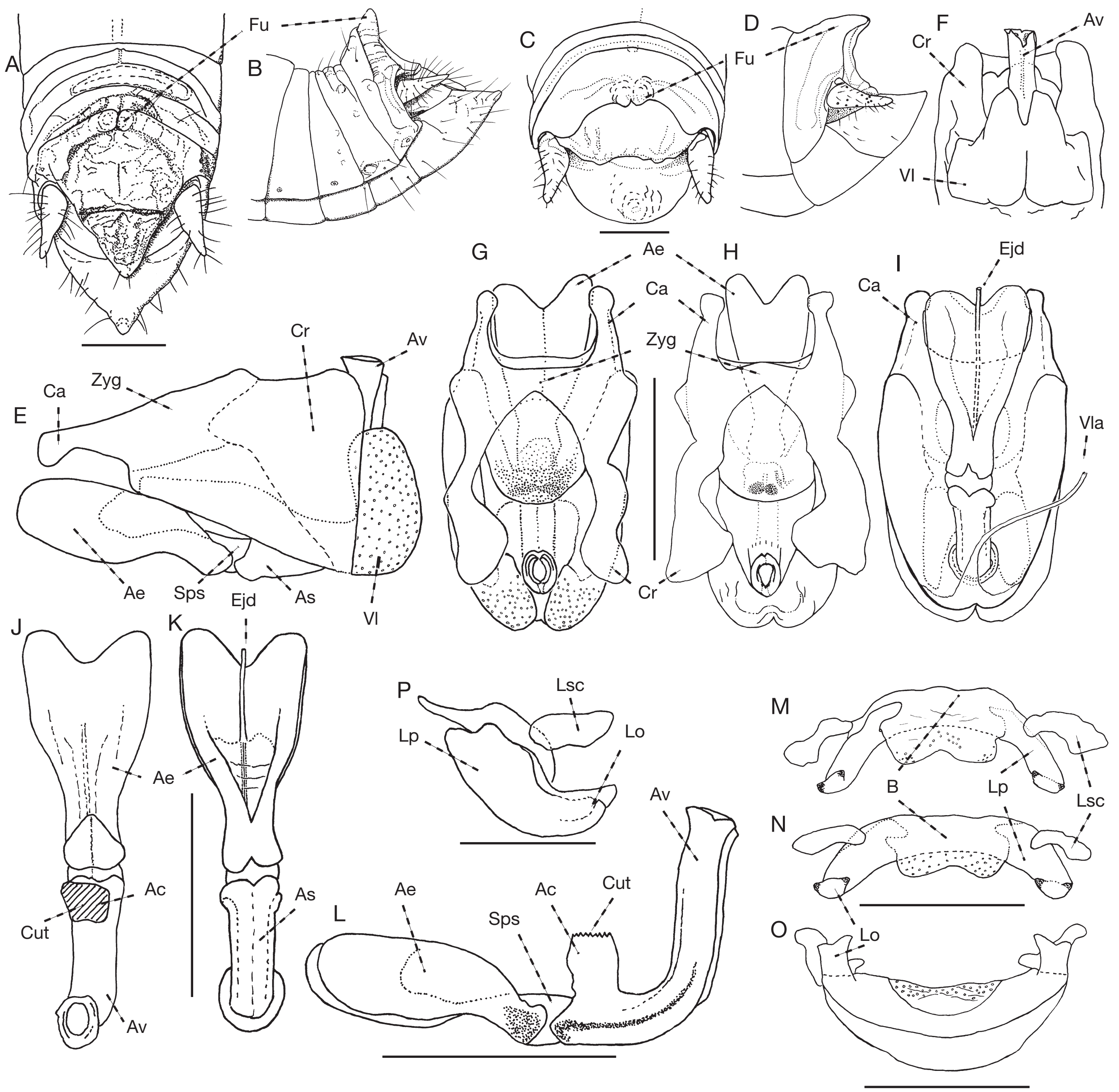

Fig. 14. — *Rowellacris transiens* (Ramme, 1929) n. comb., male genitalia: **A**-**D**, end of abdomen: **A**, dorsal view; **B**, lateral view, left side; **C**, holotype, dorsal view (with tip of supra-anal plate covered by subgenital plate); **D**, same, lateral view, left side; **E**-**L**, internal genitalia; **E**-**I**, genitalia with epiphallus removed; **E**, lateral view, left side; **F**, posterior view; **G**, **H**, dorsal view; **I**, ventral view; **J**-**L**, Endophallus with cingulum and ventral lobe removed: **J**, dorsal view; **K**, ventral view (only basal portion of apical valves visible); **L**, lateral view, left side; **M**-**P**, epiphallus; **M**, dorsal view; **N**, dorso-posterior view; **O**, ventral view; **P**, later view, left side. Provenance: **A**-**O**, East Usambara Mountains. Scale bars: 1 mm, except under figure **P**, where 0.5 mm. Abbreviations: see Material and Methods.

Rowellacris transiens (Ramme, 1929) n. comb. (Figs 5D, E; 14; Table 10)

Ixalidium transiens Ramme, 1929: 308-309.

Ixalidium haematoscelis – Dirsh 1966: 103 (incorrectly synonymised. Recalled from synonymy by Johnsen & Forchhammer [1975: 38-41]).

Type material examined. — **Holotype. Tanzania** • ♂; [Lushoto District], [East] Usambara, Nguelo [Ngwelo]; [4°44'S, 38°29'E]; [Ernst?] Heinsen leg.; MfN.
'Allotype' [Paratype]. Tanzania • ♀ [Lushoto District], [East] Usambara, Nguelo [Ngwelo]; [4°44'S, 38°29'E]; [Ernst?] Heinsen leg.; MfN.

Other material examined. — **Tanzania** • All material: Lushoto District, East Usambara Mountains • 6♂, 3♀, 3 nymphs; Soni; 4°51'S, 38°22'E; 17.IX.1950; J. Phipps leg.; NHMUK • 2♂, 1♀; Kihuhwi Bridge, 7 miles East of Amani; 5°13'S, 38°41'E;

Table 10. — Measurements in mm, *Rowellacris transiens* (Ramme, 1929) n. comb., Tanzania, East Usambara Mts (NHMUK).

	Antenna length	Head width	Pronotum length	Hind femur Length	Hind femur depth	Femur length/ depth	Total body length
Males							
n	9	10	10	10	10	10	10
Range	7.15-7.7	3.35-3.55	4.25-4.85	11.55-12.65	3.3-3.55	3.4-3.72	19.6-23.2
Mean	7.47	3.47	4.52	12.05	3.42	3.52	21.58
Females							
n	6	6	6	6	6	6	6
Range	7.3-8.7	4.05-4.45	5.95-7.1	15.65-17.6	4.2-4.6	3.65-3.83	28.4-32.75
Mean	7.93	4.26	6.43	16.38	4.38	3.74	30.74

Table 11. — Measurements in mm, *Rowellacris* cf. *obscuripes* (Miller. 1929) n. comb., Kenya, Mrima Hill (NHMUK).

	Antenna length	Head width	Pronotum length	Hind femur length	Hind femur depth	Femur length/ depth	Total body length
Males							
n	10	9	10	10	10	10	10
Range	5.75-6.7	3.4-4.35	4.05-4.35	11.2-12.0	3.35-3.65	3.21-3.36	19-20.65
Mean	6.08	4.06	4.25	11.56	3.53	3.28	19.91
Females							
n	10	10	10	10	10	10	10
Range	6.1-7.5	4.15-4.4	5.8-6.3	14.5-15.75	4.2-4.55	3.37-3.62	27.55-31.85
Mean	6.69	4.26	6.07	15.28	4.42	3.46	29.19

27.VIII.1937; E. Burtt leg.; NHMUK • 1 ♂; Kihuhwi Bridge, 7 miles East of Amani; 5°13'S, 38°41'E; 28.VIII.1938; E. Burtt leg., NHMUK. • 1 ♂; Kwamtili Plantation; 4°55'S, 38°44'E; III.1952; J. Phipps leg.; NHMUK • 5 ♂, 4 ♀, 2 nymphs; Sigi, nr Amani; 5°6'S, 38°39'E; 18-31.XII.1965; N. D. Jago leg.; NHMUK • 2 ♂, 1 ♀; Sigi, nr Amani; 5°6'S, 38°39'E; 2-11.IV.1966; N. D. Jago leg.; NHMUK • 1 ♂; Bomole Summit, near Amani; 5°6'S, 38°37'E; 3.IV.1966; N. D. Jago leg.; NHMUK • 1 ♂, 1 ♀; Longuza Forest Reserve; 5°4'S, 38°41'E; 15.IV.1966; N. D. Jago leg.; NHMUK • 1 ♂; Derema Forest; 5°38'S, 37°30'E; 24.XII.1965; N. D. Jago leg.; NHMUK • 1 ♂; Amani, Amani Nature Reserve, nr HQ; 5°5'S, 38°40'E; VII.2016; C. Hemp leg.; submontane forest; Coll. CH • 1 ♂; Amani, Waldrand (forest edge); 5°5'S, 38°40'E; X.2002; C. Hemp leg.; Coll. CH • 1 ♂; Sigi, trail at night; 5°6'S, 38°39'E; III.2012; C. Hemp leg.; Coll. CH.

Diagnosis. — Male terminalia of unique form, with projecting medial furcula (Fig. 5D, E). Cingulum with well-developed apodemes with expanded tips (Fig. 14G-I). Posterior margin of cingulum medially excavated but lacking lateral processes (Fig. 14G, H). Sub-dorsal lobe prominently inflated and exposed dorsally, but unilobate (Fig. 14G, H).
Measurements: Table 10.

Distribution

R. transiens n. comb. is known only from relict forest patches around Amani, East Usambara Mountains, where Hochkirch (1996) reported the species from 11 different survey sites and considered *R. transiens* n. comb. to be an indicator species for intact forest canopy (Hochkirch 1996: 209). Hochkirch (2014) gave the name drumming grasshoppers to members of the genus *Ixalidium*, based on drumming observed in *R. transiens* n. comb. However drumming behaviour has not been observed in *Ixalidium sjostedti* and *Ixalidium* sp. from the North Pare Mts. in recent experiments by one of us (CH), whereas it is has been observed in both *Rowellacris* Ritchie & Hemp n. gen. and *Tangana* (see Bioacoustics). The conservation status of *R. transiens* n. comb. was assessed as vulnerable by Hochkirch (2014, 2020) and Gereau *et al.* (2016) due to forest destruction.

History

Ramme (1929: 311) reported that his *Ixalidium* (now *Rowellacris* Ritchie & Hemp n. gen.) *transiens* represented a transitional stage between *Ixalidium usambaricum* and *Tangana asymmetrica*, because of the presence of a furcula on tergite 10 (Fig. 5D, E), which he considered a precursor to the asymmetric prong in *Tangana* (Fig. 5H). However the furcula is an autapomorphy of *R. transiens* and the genital morphology of this species and all other *Rowellacris* Ritchie & Hemp n. gen. species is otherwise very consistent and quite distinct from that of *Tangana*. Johnsen & Forchhammer (1975: 38-41) correctly recalled this species from Dirsh's (1966: 103) synonymy under *I. haematoscelis* and figured the distinctive male external and internal genitalia. Ramme's unique holotype male of *I. transiens* has the apical section of the supra-anal plate deflexed into the abdomen (Ramme 1929: fig. 31) and completely covered by the subgenital plate (see Fig. 14C, D), which led Johnsen & Forchhammer (1975) to believe that the tip was missing.

Rowellacris obscuripes (Miller, 1929) nom. rev., n. comb. (Figs 1; 2E; 5F; 15;Tables 9; 11)

Ixalidium obscuripes Miller, 1929: 80.

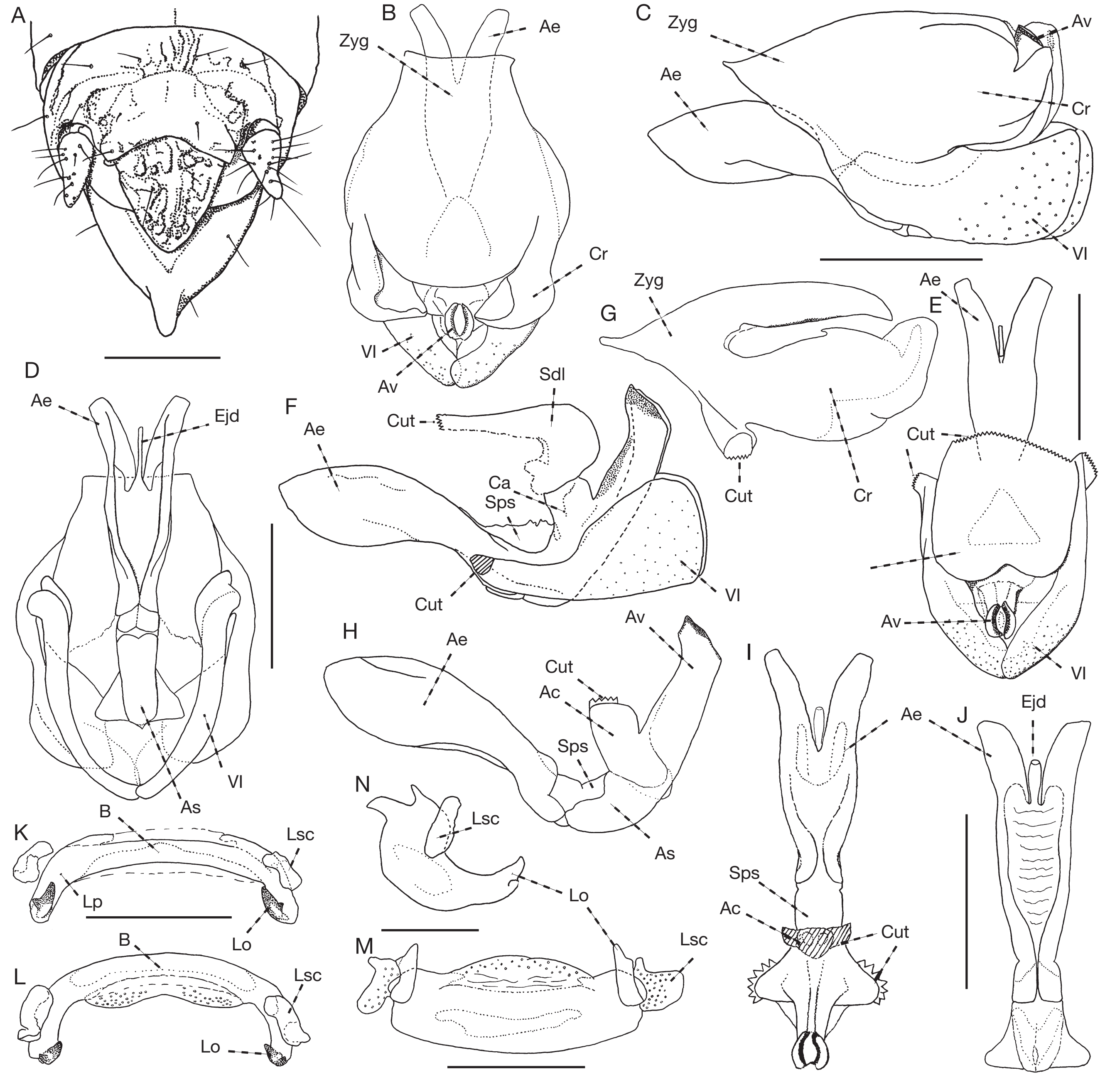

FIG. 15. — *Rowellacris obscuripes* (Miller, 1929) n. comb., male genitalia: **A**, end of abdomen, dorsal view; **B**-**N**, Internal genitalia; **B**-**J**, genitalia with epiphallus removed: **B**, dorsal view; **C**, lateral view, left side; **D**, ventral view; **E**, **F**, Endophallus with ventral lobe attached and with cingulum removed, showing sub-dorsal lobe underlying cingulum; **E**, dorsal view, **F**, lateral view; **G**, cingulum after removal, lateral view, left side; **H**-**J**, Endophallus with ventral lobe removed: **H**, lateral view, left side; **I**, dorsal view, **J**, ventral view (only basal portion of apical valves visible); **K**-**N**, Epiphallus: **K**, dorsal view; **L**, dorso-posterior view; **M**, postero-ventral view; **N**, lateral view, left side. Scale bars: A-M, 1 mm; N, 0.5 mm. Provenance: A-N, Diani, Kenya. For key to abbreviations, see Material and Methods.

Ixalidium haematoscelis – Dirsh 1966: 103 (incorrectly synonymised; here recalled from synonymy).

TYPE MATERIAL EXAMINED. — **Holotype. Tanzania** • ♂; Tanga District, Msimbazi River; 5.XII.1926; N. C. E. Miller leg.; NHMUK.

OTHER MATERIAL EXAMINED. — **Tanzania** • 1 ♂; Tanga; A. Karasek leg.; paratype of *Ixalidium usambaricum*; MfN URI: http://coll.mfn-berlin.de/u/44d6c4; DORSA BA000802S05; MfN • 1 ♂; [Tanga Region, Muheza District], [Mlinga Mountain], Magrotto [=Magoroto Forest Estate]]; 05°07'0"S, 38°45'0"E; [700-1069 m a.s.l.]; 27.VII.1994; A. Hochkirch leg.; on forest path; DNA voucher E2, extracted 19.X.2022, Box SA00924142, Tube: FD18757436; NHMUK 015134130; Coll. AH • 1 ♂; Tanga Region, nr Tanga, Amboni Caves; 05°03'60"S, 39°2'60"E; 27.I.1998.; ground litter under tree; Coll. AH • 2 ♂, 1 ♀; Manza Bay, Kwale Island; 4°57'30"S, 39°10'17"E; 1-2 m a.s.l.; IV. 2021; C. Hemp leg.; coastal forest leaf litter; Coll. CH • 1 ♀; Manza Bay, Kwale Island, Sacred Forest; 4°57'43"S, 39°8'28"E; 12 m a.s.l.; X.2021; C. Hemp leg.; Coll. CH. **Kenya** • 10 ♂, 21 ♀; Shimba Hills; III.1941; V. G. L. Van Someren leg.; NHMUK • 4 ♀; Shimba Hills; VII.1939; V. G. L. Van

Someren leg.; NHMUK • 1 ♂, 1 ♀, 1 nymph; Shimba Hills, W side, scarp road, 4°15'26"S, 39°23'16"E; 19.IX.1982; N. D. Jago leg.; forest; NHMUK • 1 ♂; Tiwi; III.1941; V. G. L. Van Someren leg.; NHMUK • 1 ♂, 1 ♀; Diani Beach, 22 miles S of Mombasa; 27.III.1953; E. S. Brown leg.; NHMUK • 1 ♂; Diani Beach, 22 miles S of Mombasa; 30.III.1953; E. S. Brown leg.; *Julbernardia* /*Manilkara* forest; NHMUK • 3 ♂, 7 ♀, 2 nymphs; Mangea Hill, nr summit; 03°16'S, 39°43'E; 1500 feet a.s.l.; 1.III.1988; N. D. Jago, J. P. Grunshaw, I. A. D. Robertson leg.; NHMUK • 4 ♂, 2 ♀; Kwale District, Mrima Hill, S of Kikoneni, forest; 4°29'9"S, 39°16'10"E; 800 feet a.s.l.; 21.IX.1982; N. D. Jago leg.; NHMUK • 11 ♂, 12 ♀, 4 nymphs; Kwale District, Mrima Hill, SW side, upper slope, forest; 4°29'9"S, 39°16'10"E; 500-800 feet a.s.l.; 29.1.1990; J. M. Ritchie, M. N. Mungai, J. Muli leg.; NHMUK • 2 ♂, 2 ♀; North Diani Beach, 20 miles S of Mombasa, 1 km N of Tradewinds Hotel; 16.IV.1975; 100 metres wide foreshore and exploited coastal thicket, 100-500 metres from beach; 4°18'S, 39°35'E; *c.* 20 ft a.s.l.; I. A. D. & A. Robertson leg.; NHMUK • 5 ♂, 6 ♀; W of Gazi, Mombasa to Ramisi road, Gogoni Forest; 21.IX.1982; N. D. Jago leg.; NHMUK • 1 ♂, 3 ♀, 3 nymphs; Kwale District, Kilibasi Hill, SW side, upper and lower slopes; 3°57'S, 38°57'E; 1400-2700 ft a.s.l.; 27.I.1990; J. M. Ritchie & M. N. Mungai leg.; forest and mist forest; NHMUK • 8 ♂, 13 ♀, 1 nymph; Dzombo [Jombo] Hill, upper slope, N side; 4°26'S, 39°13'E; 1000-1300 feet a.s.l.; 30.I.1990; J. M. Ritchie & M. N. Mungai leg.; forest; NHMUK • 1 ♂; Kwale District, 20 kms N of Lunga Lunga; 4°33'S, 39°08'E; 31.I. 1990, J. M. Ritchie & M. N. Mungai leg.; lowland dry forest; NHMUK • 1 ♀; Cha Simba Limestone outcrop; 03°44'S, 39°42'E; 650 feet a.s.l.; 29.II.1988; N. D. Jago, J. P. Grunshaw, I. A. D. Robertson leg.; *Gymnocarpus* / *Pandanus* (*Ficus*) / *Euphorbia* forest; NHMUK • 4 ♀; plain between Linango and Kwale, Route C106, Godoni Forest; 4°09'S, 39°26'E; 18.IX.1982; N. D. Jago leg.; NHMUK • 2 ♀; 3.5 kms NW of Jaribuni; 3°38'S, 39°44'E; N. D. Jago leg.; savanna woodland with cycads and aloes; NHMUK.

Diagnosis. — Subgenital plate shorter than other species of *Rowellacris* Ritchie & Hemp n. gen. (Fig. 5F). Posterior margin of basal section of supra-anal plate strongly concave, with flanges at outer edges (Figs 5F; 15A). Cingulum hind margin strongly convex, largely or completely covering sub-dorsal lobe (Fig. 15B). Sub-dorsal lobe strongly bilobate posteriorly (Fig. 15E).
Measurements: Table 11.

Distribution

Originally described by Miller (1929) from the riverine forest bordering the lower Msimbazi River which flows through the centre of Dar Es Salaam, the type locality of *R. obscuripes* n. comb. has not yielded any further specimens since then. The type locality is now severely affected by urban encroachment entailing habitat destruction, waste dumping and pollution as well as bi-annual flooding worsened by upstream deforestation in the Pugu Hills and land-use change (World Bank 2022). Morphologically similar specimens are known from patches of woodland, dry forest and thicket at Magoroto, Amboni, Tanga (paratype of *R. usambaricum* n. comb.), from coastal scrub forest on coral on Kwale Island (Manza Bay) and Fish Eagle Point and coastal forest on Kilulu Hill in Tanzania, as well as from Mrima Hill, Jombo Hill, Kilibasi Hill (co-occurring with *I. haematoscelis*), Shimba Hills, Diani, Cha Simba, Godoni Forest, Gogoni Forest, Tiwi, among other sites in Kenya. The measurements given (Table 11) are derived from the long series from Mrima Hill, while drawings of morphology are from the Diani population.

Remarks

The terminalia of *R. obscuripes* n. comb. are distinctive (see diagnosis). Minor variations in male genital morphology occur between the different populations assigned to this species, but they all share the widely-spaced and protuberant flanges on the male supra-anal plate (Fig. 5F). The male specimen from Jadini, Kenya, figured by Johnsen & Forchhammer (1975: 41, fig. 18) as *I. haematoscelis*, has been assigned to *R. obscuripes* n. comb. by this character. The genitalia of the unique holotype of *R. obscuripes* n. comb. are not available for dissection. However, recently collected specimens from Kwale Island in Manza Bay are close to the holotype in terms both of their external morphology and their Mt DNA profile (Price et al, in preparation). Specimens from sub-coastal localities in Kenya (Shimba Hills, Mangea Hill) are also genetically and morphologically more closely similar to this taxon than to any other. Continuing research to characterize the various populations currently assigned to *R. obscuripes* n. comb. based on DNA and genital morphology, may lead to the recognition of new species.

In synonymizing three species now assigned to *Rowellacris* Ritchie & Hemp n. gen. under *Ixalidium haematoscelis* Dirsh (1966: 103-104, fig. 42) substituted a drawing of the highly characteristic genitalia of an undescribed *Rowellacris* Ritchie & Hemp n. gen. species from Amani, East Usambara Mts, for the very different genitalia of *Ixalidium haematoscelis*, which he had apparently never dissected, since no genitalia preparations of his exist in the collections of the NHMUK. This error misled later workers, including Johnsen & Forchhammer (1975).

Genus *Tangana* Ramme, 1929

Tangana Ramme, 1929: 309.

Ixalidium – Uvarov 1941: 30 (incorrect synonymy). — Johnston 1956: 294.

Tangana – Dirsh 1965: 320 (ignoring Uvarov's synonymy). — Johnsen & Forchhammer 1975: 38 (recalled from synonymy). — Hemp 2017: 188.

Type species. — *Tangana asymmetrica* Ramme, 1929, by monotypy.

Tangana asymmetrica Ramme, 1929
(Figs 1; 4C; 5H; 12D-G; 16; 17; 20B; 21H-J; 22F; Table 12)

Tangana asymmetrica Ramme, 1929: 310.

Ixalidium asymmetricum – Ramme 1929; incorrectly synonymised by Uvarov (1941: 30); recalled from synonymy by Johnsen & Forchhammer (1975: 38).

Type material examined. — **Holotype**. **Tanzania** • ♂; Tanga; A. Karasek*;* MfN.
Paratype. Tanzania • ♀; Tanga; [5°4'S, 39°6'E]; A. Karasek leg.; NHMUK • 2 ♂; Tanga; [5°4'S, 39°6'E]; A. Karasek leg.; MfN, Berlin.

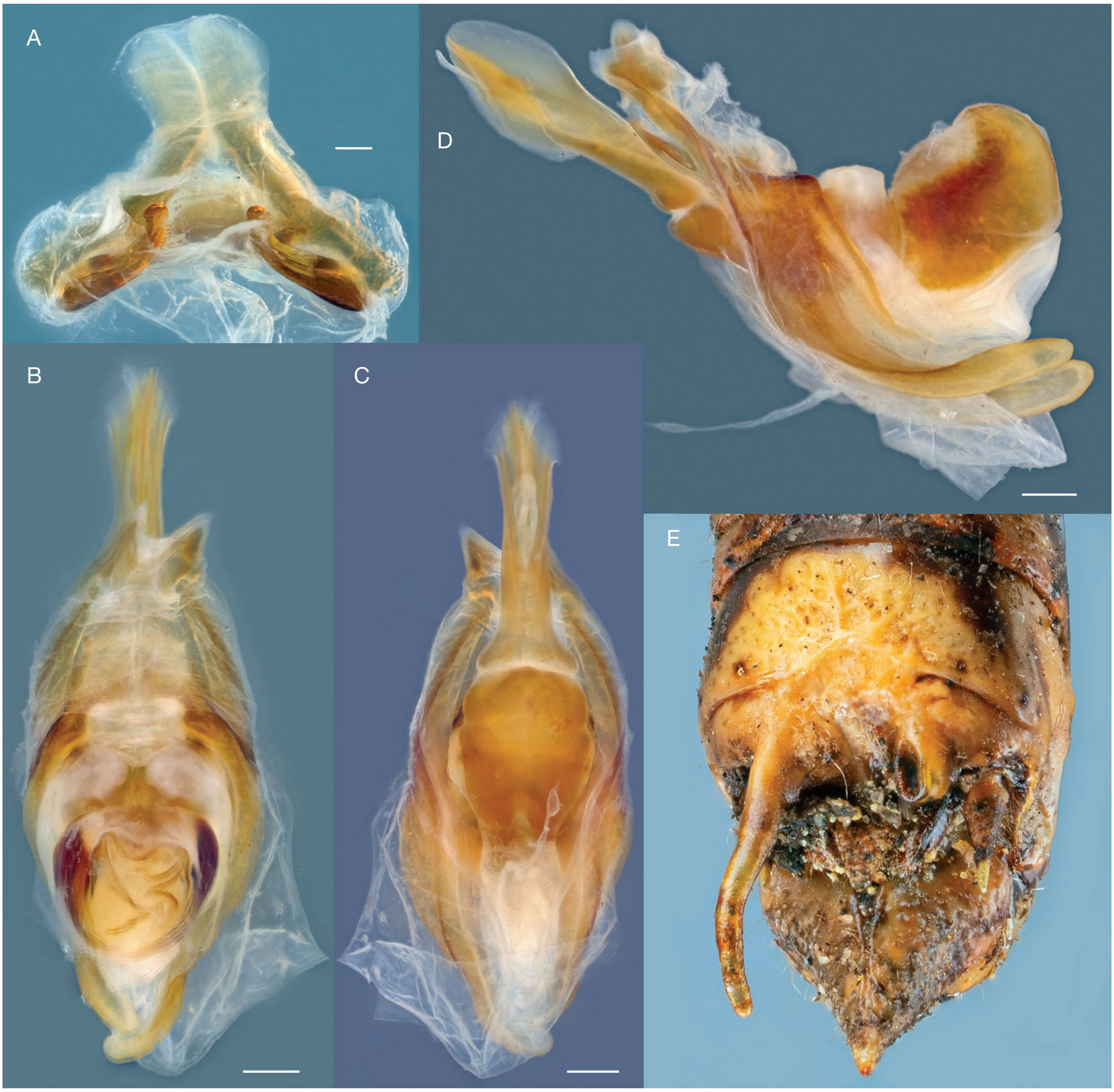

FIG. 16. — **A**-**E**, *Tangana asymmetrica* Ramme, 1929, male paratypes, Tanzania, Tanga (*A. Karasek*), MFN, Berlin. **A**-**D**, internal genitalia, dextral paratype (MfN URI http://coll.mfn-berlin.de/u/a08979): **A**, Epiphallus, postero-dorsal view; **B**-**D**, genital complex (epiphallus removed); **B**, dorsal view; **C**, ventral view; **D**, lateral view, left side. **E**, terminalia, sinistral paratype, dorsal view (MfN URI http://coll.mfn-berlin.de/u/9aa74a). Image E by courtesy of MfN, Berlin. Scale bars: A, 0.2 mm; B-D, 0.5 mm; E, not to scale.

OTHER MATERIAL EXAMINED. — **Tanzania** • 4♂; Korogwe, Handeni, Kwa Mbisi; 5°25'27"S, 38°1'10"E; 18.IX.1952; E. Burtt leg.; NHMUK • 6♂, 3♀; Korogwe, Handeni, Kwa Mbisi; 5°25'27"S, 38°1'10"E; 20.IX.1952; E. Burtt leg.; NHMUK • 1♀; Tanzania, Korogwe, Handeni, Kwa Mbisi; 5°25'27"S, 38°1'10"E; 19.IX.1952; E. Burtt leg.; NHMUK • 1♂; Morogoro District, Kingolwera [Kingolwira]; 6°47'S, 37°46'E; 7.XII.1953; E. Burtt leg.; NHMUK • 1♂; Morogoro District, same collection data as for preceding; 10.IX.1952; E. Burtt leg.; NHMUK • 1♀; same collection data as for preceding; 18.XII.1953; E. Burtt leg.; NHMUK • 2♀, 1 nymph; Muheza District, Mlingano, Ngomeni; 5°09'00"S, 38°53'60.0"E; IV.1952; J. Phipps leg.; NHMUK • 1♂; same collection data as for preceding; III.1952; J. Phipps leg.; rubber bush; NHMUK • 2♀; same collection data as for preceding; 9.IV.1952; J. Phipps leg.; NHMUK • 1♀; same collection data as for preceding; 30.III.1952; J. Phipps leg.; NHMUK • 1♀; same collection data as for preceding; V.1953; J. Phipps leg.; NHMUK • 1♂, 1♀; Dar es Salaam; 6°48'S, 39°17'E; 24.I.1964; E. Burtt leg.; NHMUK • 1♂, 1♀; same collection data as for preceding; 26.I.1964; E. Burtt leg.; NHMUK • 3♂, 7♀; same collection data as for preceding; 27.I.1964; E. Burtt leg.; NHMUK • 1♂, 2♀; same collection data as for preceding; 28.I.1964; E. Burtt leg.; NHMUK • 1♂, 3♀; same collection

TABLE 12. — Measurements in mm, *Tangana* cf. *asymmetrica* (Ramme, 1929) (Tanzania, Nguru Mts) (NHMUK).

	Antenna length	Head width	Pronotum length	Hind femur Length	Hind femur depth	Femur length/ depth	Total body length
Males							
n	9	10	10	10	10	10	10
Range	6.9-8.6	3.8-4.1	4.8-5.15	12.45-14.35	3.75-4.1	3.2-3.63	22.35-25.85
Mean	7.92	3.95	4.94	13.58	3.89	3.49	23.84
Females							
n	8	10	10	10	10	10	10
Range	6.6-8.1	4.2-4.5	5.95-6.5	15.05-16.55	4.2-4.5	3.48-3.73	27.95-31.25
Mean	7.45	4.29	6.16	16.02	4.41	3.63	29.33

data as for preceding; 29.I.1964; E. Burtt leg.; NHMUK • 1 ♂, 1 ♀; same collection data as for preceding; 30.I.1964; E. Burtt leg.; NHMUK • 2 ♂, 5 ♀; same collection data as for preceding; 31.I.1964; E. Burtt leg.; NHMUK • 4 ♀; same collection data as for preceding; 1.II.1964; E. Burtt leg.; NHMUK • 1 ♀; same collection data as for preceding; 27.II.1964; E. Burtt leg., NHMUK • 1 ♂; Dar es Salaam, University Campus; 17.II.1998; A. Hochkirch leg.; under trees; Coll. AH • 1 ♂; Pangani District, Kigombe [Sisal] Estate; 5°19'S, 39°1'59"E; III.1952; J. Phipps leg.; NHMUK • 14 ♂, 9 ♀, 3 nymphs; Nguru Mountains, above Turiani; 6°09'S, 37°36'E; 5-7.XI.1964; N. D. Jago leg.; montane forest; NHMUK • 12 ♂, 7 ♀, 3 nymphs; Nguru Mountains, east foot, Mtibwa Forest Reserve, near Turiani; 6°07'S, 37°39'E; 5.XI.1964; N. D. Jago leg.; dry woodland; NHMUK • 1 ♂, 1 ♀; Kisarawe, Kazimzumbwi Forest Reserve; I.2016; C. Hemp leg.; lowland wet forest; Coll. CH • 1 ♂; same collection data as for preceding; V.2016; C. Hemp leg.; Coll. CH • 1 ♀; same collection data as for preceding; VIII.2017; C. Hemp leg.; Coll. CH • 1 ♀; Pangani Coast, Turtle Beach; <100 m a.s.l.; 5°24'S, 38°59'E; I.2000; C. Hemp leg.; Küstenwaldboden [coastal forest floor]; Coll. CH • 2 ♂; Pangani Coast, Turtle Beach; <100 m a.s.l.; XII.2000; C. Hemp leg.; Waldrest [forest remnant]; Coll. CH • 1 ♀; Pangani Coast, zw. Kabuko-Mwera; 300 m a.s.l.; II.2000; C. Hemp leg.; Küstenwald [coastal forest]; Coll. CH • 1 ♂; Pangani Coast, Caspary Grundstück [Caspary property]; IX.2011; C. Hemp leg.; Waldboden [forest floor]; Coll. CH • 3 ♂, 1 nymph; Udzungwa Mts, Sanje trail; 7°45'54.3"S, 36°53'23.9"E; [886 m a.s.l.]; 5.XII.1997; A. Hochkirch leg; grasses; Coll. AH • 1 ♂; Nguru Mts, Site T1; 30.I.1998; A. Hochkirch leg.; litter under mango tree; Coll. AH • 1 ♂; same collection data as for preceding; 3.II.1998; A. Hochkirch; Coll. AH.
Kenya • 7 ♂, 6 ♀; Tana River District, Tana River Primate National Reserve, Mchelelo Forest; 1°53'S, 40°08'E; 4-6.II.1990; J. M. Ritchie, M. N. Mungai, J. Muli leg.; NHMUK • 1 ♂; Kwale District, Dzombo [Jombo] Hill, upper slope, north side; 4°26'S, 39°13'E; 1000-1300 ft a.s.l.; 30.I.1990; J. M. Ritchie, M. N. Mungai, J. Muli leg.; forest; NHMUK • 2 ♂, 5 ♀; Lamu District, Witu Forest Reserve, 5 km E of Witu; 2°23'S, 40°29'E; 150 ft a.s.l.; 10.VI.1975; I. A. D. & A. Robertson leg.; NHMUK.

REDESCRIPTION
Small to medium size (Table 12), but typically larger than *Ixalidium*. Males 22-26 mm; females 27.5-31.5. Integument rugose and punctate.

Head
Antennae differentiated (Dirsh 1965), 17-segmented, about as long as head and pronotum together, basal segments (apart from scape and pedicel) dorso-ventrally compressed, ensiform, widening markedly at segment three, widest between 3 and 6, with 8-9 distinctly less compressed and 10-17 filiform.

Head width across eyes distinctly less than pronotum length and less than pronotum width at its hind margin; head obliquely slanted in lateral view, with vertex produced and frons forming shallow obtuse angle between antennae; eyes ovoid, narrower above, oblique. Fastigium of vertex from above (Fig. 4C) projecting over lateral ocelli and antennal bases, its maximal basal width about 1.5 times its length, with narrowly rounded rectangular apex, more angular than *Ixalidium* and *Rowellacris* Ritchie & Hemp n. gen.; median carinula cut by indistinct irregular transverse sulcus at base of fastigium, continuing onto occiput; foveolar area obsolete; frontal ridge in anterior view narrowest immediately below vertex, becoming sulcate with lateral carinae, widening between antennae, then narrowing above median ocellus; carinae subparallel below ocellus, becoming divergent and obsolete towards clypeus.

Thorax
Pronotum low tectiform, median carina crossed by 2 sulci; prozona 3-4 times longer than metazona; dorsum from above widening steadily from fore margin to hind margin. Prosternal tubercle transverse, tapered, wedge-shaped, widening laterally towards apex, sparsely setose, anterior face oblique, flat to slightly concave, posterior face vertical, flat to slight convex; apical margin slightly trilobate, with rounded angles. Meso- and metanotum tectiform, slightly raised, with median carina; mesonotum short, partly covered by metazona of pronotum, with lateral tegminal rudiments often concealed by metazona; metanotum with distinct longitudinal lateral carinae forming sharp angle at upper margin of epimeron 3; episternum 3 forming robust lateral projections above hind coxae. Mesosternal interspace broader than its length, widening posteriorly; mesosternal furcal suture with medial and lateral pits narrow. Metasternal interspace slightly broader than its length, narrowing posteriorly, tending to form two separate pits with medial portion of interspace continuous anteriorly with anterior portion of metasternum.

Legs
Fore and mid legs of typical acridoid appearance, unspecialized. Hind femur moderately robust, 3.2-3.7 times as long as maximum depth, male; 3.4-3.8 times, female (Table 12); hind knee with upper and lower lobes bluntly

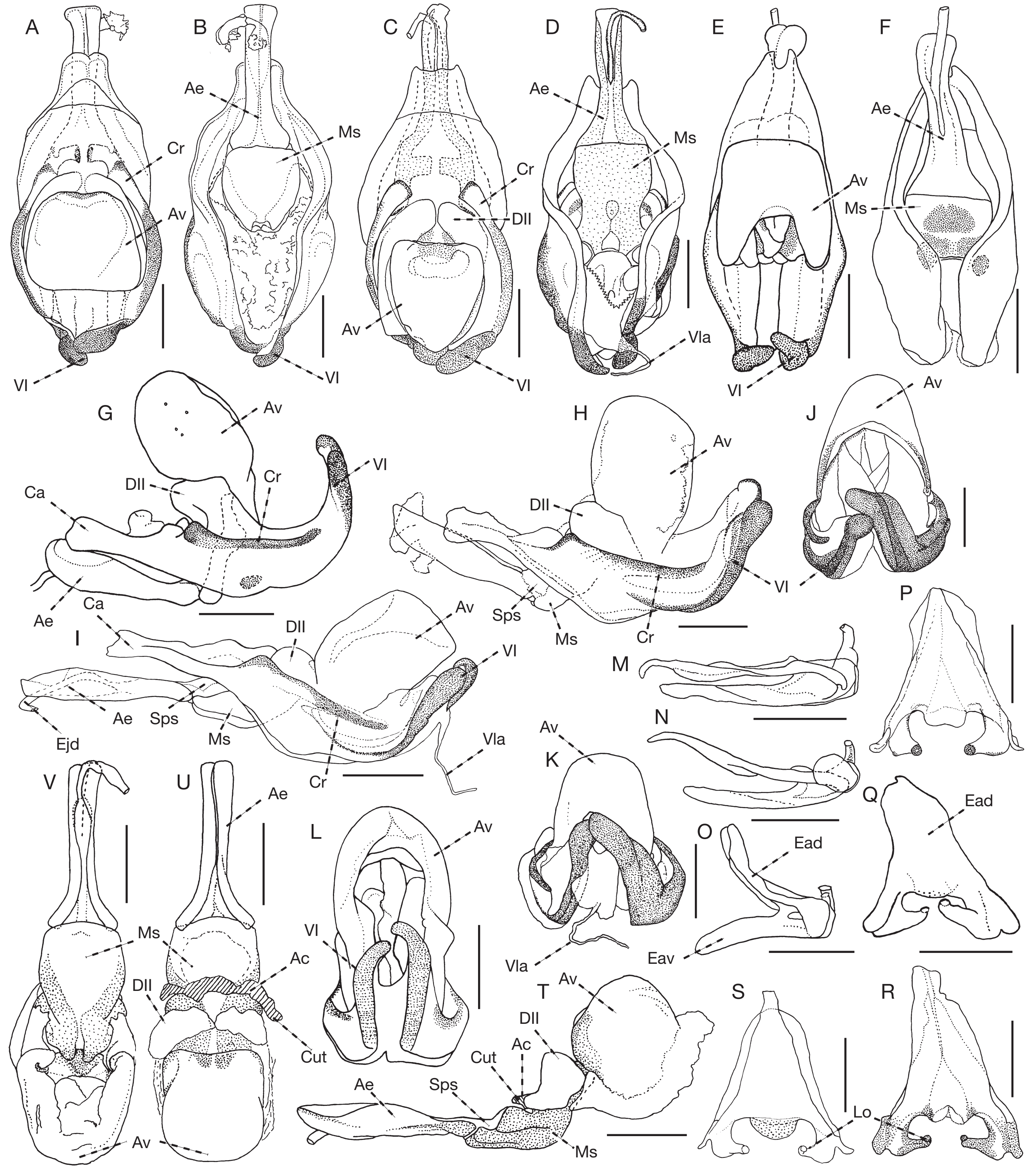

FIG. 17. — **A**-**V**, *Tangana asymmetrica* Ramme, 1929, male internal genitalia: **A**-**L**, genital complex (epiphallus removed): **A**, **C**, **E**, dorsal view; **B**, **D**, **F**, ventral view; **G**-**I**, lateral view, left side; **J**-**L**, posterior view; **M**-**S**, Epiphallus: **M**-**O**, lateral view; **P**-**S**, dorsal view; **T**-**V**, Endophallus (cingulum and ventral lobe removed); **T**, lateral view, left side; **U**, dorsal view; **V**, ventral view. Provenance: Tanzania, Nguru Mountains (**A**-**D**, **H**-**K**, **S**); Tanzania: Dar-es-Salaam (**N**, **R**); Kenya, Mchelelo Forest (**E**-**G**, **L**, **M**, **O**, **P**, **T**-**V**). Scale bars: 1 mm. Abbreviations, see Material and Methods.

rounded; hind tibia with 7-8 outer and 9-10 inner spines; external apical spine absent; arolium large, rounded, in ventral view about as long as claw; claws thickened at base, apically strongly curved.

Abdomen

Tergites tergites medially carinate, each segment in lateral view dorsally convex, tergites 1 and 2 slightly inflated, together with metathorax forming slight hump; tympanum large, sub-oval, with ventral margin flattened or slightly concave; tergites 9 and 10 fused laterally.

External terminalia (Fig. 5H). Abdominal tergites 9 and 10 and corresponding sternites heavily sclerotised, somewhat inflated, fused with basal portion of supra-anal plate (Fig. 5H), which is distinctly asymmetrical, displaced to right side, overlaying and largely obscuring right cercus, its dorsal surface produced into long curved tapering process or prong; junction between basal and apical portions of supra-anal plate reflexed antero-ventrally beneath basal portion; reduced apical portion of supra-anal plate projecting caudad between tips of paraprocts, or concealed to a variable degree by antero-dorsal margin of subgenital plate; subgenital plate subconical, upwardly directed, with ventral margin concave, in lateral view tapering to acute point at apex, with short dorso-medial longitudinal sulcus broadening into marginal cleft on anterior edge.

Male genitalia

Epiphallus (Figs 16A; 17M-S) recessed within invagination of epiphallic membrane (epiphallic infold (Eades 2000)), folding around and partially obscuring it when genital complex initially exposed; bridge of epiphallus extending internally capitad into two dorso-ventrally flattened spathulate apodemes, one above the other, arising from antero-dorsal and antero-ventral edges of bridge; apodemes approximately triangular viewed from above, with bridge and lateral plates of epiphallus forming short base of triangle distally; epiphallic apodemes in dorsal view (Fig. 17P, Q, R) often markedly asymmetric, more developed on left side; In lateral view dorsal and ventral epiphallic apodemes either parallel with narrow interspace between them (Fig. 17M) or dorsal apodeme diverging from ventral apodeme by about 20° (Fig. 17N), or both apodemes curving away from each other by up to 45° (Fig. 17O); epiphallic infold of ectophallic membrane divided by bridge of epiphallus and its apodemes into two subtriangular horizontal pouches, one above dorsal epiphallic apodeme and one below ventral apodeme; both pouches follow triangular form of dorsal and ventral epiphallic apodemes (Fig. 17P-S), but ventral pouch larger; postero-medial surface of bridge (Fig. 17P-S) forms cushion-like membranous bulge with many circular pits, presumably of sensory function; lateral sclerites of epiphallus fused to outer edges of lateral plates (Fig. 17P-S).

Cingulum (Figs 16B-D; 17C) forming low, sclerotized, but partly translucent sheath covering endophallic apodemes dorsally, tapering proximally with its anterior margin medially indented with lateral margins incorporating converging cingular apodemes (Fig. 17A, C, E); rami of cingulum with raised and sclerotised shoulders (?suprarami of Eades 2000), flanking lightly sclerotised zygoma and enfolding endophallus laterally, fusing ventro-laterally with bilaterally separated sclerites of ventral lobe, which form two upcurved elongate compressed tapering digitate sclerotized processes directed caudad and dorsad, with their raised tips slightly overlapping, right arm slightly longer than left (Fig. 17G-L); both rami and ventral lobe arms heavily sclerotised and sculptured on their external surfaces with rows of fine denticles, neither continuous nor bilaterally symmetrical (Figs 16B-D; 17G-L); left side of rami and ventral lobe sclerites with longitudinal patches lacking denticles, but right side denticulation continuous between surfaces of rami above and ventral lobe sclerites below (Fig. 17, J, K); vestigial remains of ventral infold visible as short ventral lobe apodeme (Fig. 16D); arch of cingulum short, wide, joining zygoma closely to fused apical sclerites of endophallus (Fig. 17T, U).

Endophallus (Fig. 16B-D; 17T) tripartite, with apodemes formed of two distinct but continuously fused sclerites, lacking visible gonopore processes or endophallic flanges, with a longitudinal medial keel marking their junction dorsally (Fig. 17U); ejaculatory duct with sharp bend and ancillary tissue mass (vestigial ejaculatory sac) sometimes visible anterior to its junction with endophallus (Fig. 17A, B), duct partly enclosed below proximal portion of apodemes (Fig. 17D, F, V) and fully enclosed and widening within their distal half (Fig. 17V). Spermatophore sac (Sps) reduced, visible medially on dorsal surface of junction between diverging posterior ends of endophallic apodemes, anterior to arch of cingulum (Fig. 17H, T). Endophallic apodemes (Ae) with articulated break or hinge at junction with medial sclerites (Ms) (Fig. 17G, T), permitting considerable range of relative movement; medial and apical sclerites of endophallus continuous, proximally fused into single broad dorsal and ventral plates, of complex shape, dorso-ventrally compressed, with paired lightly sclerotised rounded dorso-lateral lobes (Dll), of unknown function, just posterior to arch of cingulum (Fig. 17T, U) and flanking inconspicuous dorsal opening of phallotreme, hidden within short medial longitudinal groove anterior to transverse cleft between dorso-lateral lobes and inflated fused apex of endophallus; distal section of fused apical sclerites of endophallus expanding into a single hollow bulbous domed bilayered sclerite, curving upwards, with arched cavity on its postero-ventral side, partly filled by folded membranes (Fig. 17L, V).

Female genitalia

Spermatheca (Fig. 12) with three basal diverticula (Fig. 12C, F) arising from vestibule one above another; most ventral one sac-like, short and wide; middle one elongate sac-like, almost as long as dorsal ovipositor valves and apodemes together; dorsal one thin tubular, uncoiled, shorter than dorsal ovipositor valves, with apical and subapical diverticula, one ending in an apical ampulla, the other swollen vermiform (Fig. 12E-G); vestibule with a wide lenticular cleft ventrally between ventral valves of ovipositor (Fig. 12E-G).

Measurements

Table 12

Coloration (Fig. 2F-H)

Males with similar patterning to *Ixalidium*, as illustrated by Hemp (2017, fig. 42 A). Lateral dark bands on flanks of thorax and abdomen strongly marked up to and including tergite 8; abdominal segments 9 and 10 distinctly paler than rest of body, with contrasting dark longitudinal striae on expanded tergite 9 and darkly pigmented spots around setae on tergite 9 and subgenital plate. Venter pale, mottled, or with darker patches in medial area of sternites 1-5, reaching hind margin of sternites, but leaving fore margins pale. Hind femur with lower internal area, lower carinula and lower carina light red in basal three fifths. Tibiae violet to dirty grey brown, sometimes with pinkish tinge on internal surface. Females with more uniform, less contrasting coloration. Occasionally with contrasting blocks of rufous brown on upper body (from head to abdominal segment 1) and pale buff (abdominal segments and wide band across hind femora) (Fig. 2H and Hemp 2017, fig. 42B) resembling dead leaves.

History

The genus *Tangana* was created by Ramme (1929: 309) for his species *T. asymmetrica* described from material collected by A. Karasek from "Tanga". Though it was presumably collected from the lowland coastal forest zone, the exact location(s) and date(s) of collection are unknown. *Tangana* was synonymised under *Ixalidium* by Uvarov (1941) on the grounds that there were no generic characters which separated females. This synonymy was tacitly ignored but not formally recalled by Dirsh (1965). This position was followed by later catalogues and checklists (Johnston 1968; Otte 1995) but the synonymy was explicitly contradicted by Johnsen & Forchhammer (1975) whose paper was not catalogued by Otte (1995).

Distribution

T. asymmetrica and undescribed species of the genus are now found in isolated populations in remnants of lowland and sub-montane forest in northeast Tanzania and eastern Kenya from close to sea level up to around 880 m (at Sanje Falls, Udzungwa Mountains, Tanzania). There is significant variation in morphology between populations (Fig. 17) which most probably represents as yet unrecognised vicariant speciation. However, there is also a high degree of morphological variability within populations, as shown by dorsal and lateral views of the epiphalli of two individuals from Mchelelo Forest (Fig. 17M, O, P, Q) and various views of the genitalia of two individuals from the Nguru Mountains, Tanzania (Fig. 17A-D and H-K). There are further species of *Tangana* from Tanzania, Kenya and Somalia awaiting description (Ritchie *et al.* pers. comm.) which have similar internal genitalia to *T. asymmetrica*, but with an intermediate level of asymmetric development of the external terminalia and inflation of the endophallic sclerites.

Remarks

The female spermathecae (Fig. 12) of *Tangana* and *Rowellacris* Ritchie & Hemp n. gen., not previously studied, are here shown to be radically different from those of *Ixalidium* species, as here defined, or of any other acridoid, and the status of *Tangana* as a valid genus is confirmed, based both on molecular evidence and on striking divergence in characters of the genitalia in both sexes from those in *Ixalidium.*

This account of the morphology of *Tangana* is based on the only described species, *Tangana asymmetrica* Ramme (paratype male, Fig. 16). The crumpled appearance of the tip of the aedeagus of this paratype, shown in dorsal view in Figure 16B may be a result of trauma sustained by the living insect. Other specimens seen, from a wide range of localities (Fig. 17), do not show this wrinkled effect. The male terminalia in *Tangana* are the most heavily modified and specialised in the family Ixalidiidae Hemp, Song & Ritchie n. fam. In addition to the unique asymmetry of the external terminalia, the most striking features of the male genital complex in *T. asymmetrica* are its overall size in relation to body length (up to 5.6 mm out of around 23 mm), the inflated and fused distal endophallic sclerites (apical valves of endophallus), the epiphallic apodemes and the finger-like paired arms of the ventral lobe. The homology of the modified ventral lobe in *Tangana* with the same paired sclerite in *Ixalidium* and all other members of the family is largely proven by the consistent presence of the ventral lobe apodeme, representing the reduced ventral infold which arises from the anterior ventro-internal margin of the lobe. The anterior dorsal positioning of the genital pore at the base of the inflated aedeagus, rather than at its tip, is an autapomorphy of the genus *Tangana*.

The epiphallus with its long asymmetrically placed apodemes, differs from that of all other Acridoidea, including its nearest relatives in Ixalidiidae Hemp, Song & Ritchie n. fam. Males typically adopt a dorsal mating position and copulate from the left side of the female. Since the male abdominal apex is turned upwards and forwards to connect with the underside of the female abdominal tip at a slight angle, the asymmetric form and alignment of the epiphallus allows the male to achieve the correct alignment to grip the female subgenital plate and egg-guide from the left side. During mating, when the epiphallus grasps the female subgenital plate, the egg guide probably slides over the sensory cushion on the posterior surface of the epiphallic bridge and docks within the dorsal epiphallic pouch. Fusion of the normally separate lateral sclerites of the epiphallus with the lateral plate (Fig. 17P-S) presumably gives the epiphallus greater rigidity to resist bending when the lophi are under tension, grasping the female subgenital plate. Given the considerable force with which the lophi would be inserted into the female genital cavity, their flattened button-like tips (Fig. 16A) may be an adaptation to prevent damage to the internal surface of the female subgenital plate.

Although the hinged endophallus seems quite rigid in alcohol-preserved specimens, it appears that in life considerable mobility is possible. In lateral view the long axis of the aedeagus (apical endophallic sclerites) may form an obtuse angle of about 135° to the basal valves, such that the aedeagus is depressed to lie close to the ventral lobe (Fig. 17I). However in some cases the aedeagus is found to have become flexed upwards and forwards (capitad) to an acute angle of between 80° and 60° with the endophallic apodemes (Fig. 17G). When the fused apical sclerites are flexed upwards, a large space is created between the aedeagus

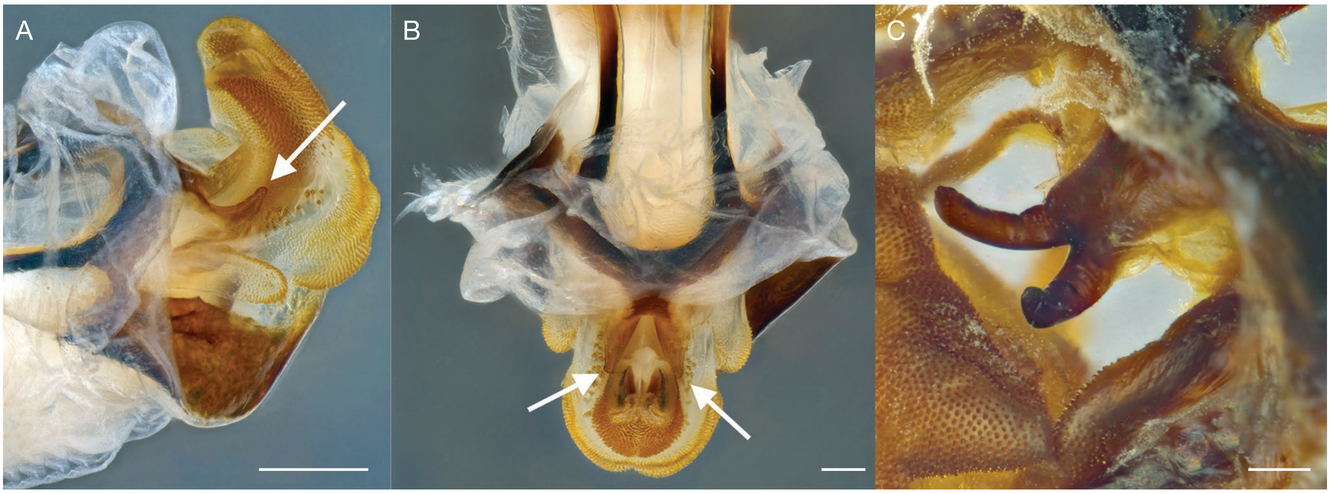

Fig. 18. — Bifurcated medial projection of the arch of cingulum in some Ixalidiidae Hemp, Song & Ritchie n. fam.: **A**, **B**, *Mazaea granulosa* Stål, 1876 (Cameroon), posterior section of phallic complex with epiphallus removed and epiphallic membrane pulled back. **White arrows** indicate position of bifurcated medial projection of arch of cingulum: **A**, dorso-lateral view; **B**, dorsal view. **C**, *Barombia tuberculosa* Karsch, 1891 (Nigeria), oblique dorsal view of zygoma and rami of cingulum with endophallus removed. Scale bars: A, 0.5 mm; B, C, 0.2 mm.

and the two upcurved arms of the ventral lobe. Membranes folded below the inflated tip of the aedeagus in its lowered position (Fig. 17I) are unfurled and drawn taut when it is fully raised (Fig. 17G). In dead specimens this variation in relative angle between cingulum and aedeagus and in the angle of flexion of the endophallus at its hinged break can present a strikingly different appearance. This may give a false impression of taxonomically significant character differences, where in reality none exist.

During mating it is likely that the tips of the ventral lobe arms are thrust upwards and forwards between the ventral ovipositor valves of the female as the epiphallic lophi pull downwards and backwards against the tip of the subgenital plate and egg guide, opening up the female genital chamber between the lower surface of the ventral ovipositor valves and the dorsal surface of the subgenital plate; the domed aedeagus could then be driven forward into the genital chamber; vertical rotation of the genitalia would mean that the spermatophore would be extruded ventrally onto the floor of the female genital chamber. It would then need to move upwards and forwards to reach the vestibule of the spermatheca.

The presence of the asymmetric prong arising from the right side of the massively reinforced supra-anal plate (Fig. 5H) narrows the space available for the aedeagus and ventral lobe arms to be everted for copulation. It is unclear whether during mating the prong ends up pointing vertically upwards or forwards over the male abdomen. If it was near vertical, it could perhaps be inserted upwards between the ovipositor ventral valves, or even between both ventral and dorsal valves, to keep the male and female locked together during mating. If it can be deployed horizontally it could perhaps enter the genital chamber. Whichever is the case, the genitalia must be everted past it and rotated upwards and forwards over the male abdomen to perform spermatophore transfer to the female genital chamber.

Genital asymmetry in Tangana

Bilateral asymmetry is common in the male genitalia of insects (Huber *et al.* 2007) and a few striking examples of internal genital asymmetry occur in Acridoidea, most notably in the aedeagus of the Central American acridid genus *Rhachicreagra* Rehn, 1905 (Ommatolampidinae Brunner von Wattenwyl, 1893) (Jago & Rowell 1981) and the epiphallus of the genus *Stolzia* Willemse, 1930 (Oxyinae Brunner von Wattenwyl, 1893) (Hollis 1975: 212). However, pronounced external asymmetry within the Acridoidea appears to be restricted to the genus *Tangana*. Huber *et al.* (2007) proposed that one major evolutionary driver of asymmetry is sexual selection in males for the capacity to adopt a dorsal mating position which requires asymmetric contact between male and female genitalia. In *Tangana*, the development of novel structures is predominantly to the right side of the male (dextral), corresponding to a left-sided approach to the female genitalia. Only one example is known of a *Tangana asymmetrica* male with sinistrally asymmetric terminalia. This is a paratype specimen in the Museum für Naturkunde Berlin, mentioned by Ramme (1929) in his original description of *T. asymmetrica*. This sinistral paratype male has a prong on the left side, but it is not a mirror-image of the dextral morphotype since it also has traces of a short process at the corresponding point on the right side of the abdomen (Fig. 16E). The extreme rarity of sinistral variants in *Tangana* suggests that either the morphological change itself or a concomitant change in mating position are highly disadvantageous for mating success. The condition of the internal genitalia in this sinistral specimen is unknown. The functional morphology of the male and female genitalia in *Tangana asymmetrica* in relation to mating and spermatophore formation and transfer requires further research using the methodology employed by Woller & Song (2017).

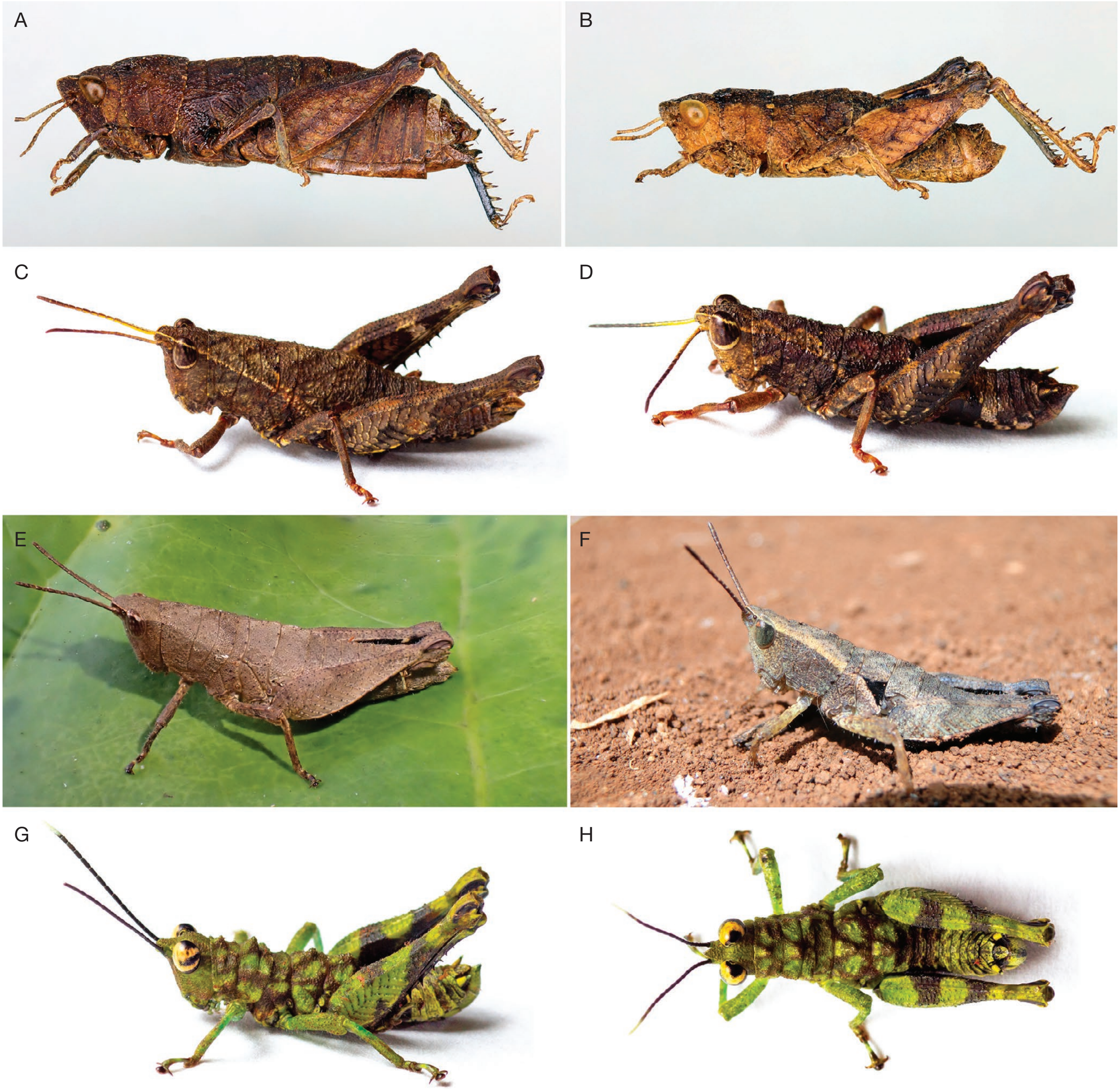

Fig. 19. — Members of related families of Acridoidea: **A**, **B**, Tristiridae Rehn, 1906: female and male *Peplacris recutita* Rehn, 1942 (from Orthoptera Species File, Cigliano *et al.* 2024); **C**-**H**, Ixalidiidae Hemp, Song & Ritchie n. fam.: **C**, **D**, *Mazaea granulosa* Stål, 1876, female and male (Cameroon); **E**, **F**, *Rowellacris* n. gen. sp., female and male (Tanzania, East Usambara Mountains); **G**, **H**, *Barombia tuberculosa* Karsch, 1891, male, lateral and dorsal views (Cameroon). Photos C, D, G, H, by courtesy of Brandon Woo.

CONTEXTUALIZING IXALIDIIDAE HEMP, SONG & RITCHIE N. FAM. WITHIN THE ACRIDOIDEA

Having established the value, or "phylogenetic signal" of male genital morphology in reconstructing phylogeny in Acridoidea, this section examines the individual characters and compares the character states that are found across the Acridoidea, including the new family Ixalidiidae Hemp, Song & Ritchie n. fam., in a summary table (Table 13) before looking in more detail at a few of these families to clarify the distinct identity of the Ixalidiidae Hemp, Song & Ritchie n. fam. The following comparison of Ixalidiidae Hemp, Song & Ritchie n. fam. with its nearest neighbours in the phylogenetic tree on the basis of genital morphology builds on Song & Mariño-Pérez (2013) with some minor areas of divergence. Table 13 presents twenty-four significant genitalic and other morphological characters with potential to shed light on the relationships of Ixalidiidae Hemp, Song & Ritchie n. fam. within the core clade of the Acridoidea, which (excepting Pamphagodidae and Pamphagidae) all share the possession of a bridge-shaped epiphallus with lophi (Song & Mariño-Pérez 2013; Song *et al.* 2015).

Characters of the male genitalia in Acridoidea, including Ixalidiidae Hemp, Song & Ritchie n. fam.

Supra-anal plate
The form of the supra-anal plate or epiproct, though not an internal genitalic structure, is included here and in Table 13 because it is evidently under sexual selection (e.g. see *Tangana*). It is divided into basal and apical portions by a transverse sulcus in the Ixalidiidae Hemp, Song & Ritchie n. fam. (see Figs 5; 7) as well as in Tristiridae (Cigliano 1989), all three subfamilies of Ommexechidae (Ronderos 1973, 1978; Carbonell & Mesa 1972), and many genera of Lentulidae. Among Romaleidae most Romaleinae have the supra-anal plate divided, except for *Diponthus* Stål, 1861, *Gurneyacris* Liebermann, 1958 and *Zoniopoda* Stål, 1873, while the Acrididae in general appear to lack the transverse division.

Epiphallus
Possession of a bridge-shaped epiphallus is shared by Pyrgacrididae, Tristiridae, Lentulidae, Ommexechidae, Romaleidae and Acrididae, and also by the Ixalidiidae Hemp, Song & Ritchie n. fam. The possession of epiphallic lophi (Roberts 1941: 244) characterizes all Acridoidea apart from the Pamphagodidae and Pamphagidae. However, the shape of the lophi (pointed in Tristiridae and Ommexechidae, polymorphic in Lentulidae, or lobiform in Romaleidae and Acrididae) is evidently homoplasious above family level (Song & Mariño-Pérez 2013). The lophi are pointed in Ixalidiidae Hemp, Song & Ritchie n. fam. (though with a flattened tip in *Tangana*).

The presence of epiphallic ancorae (Roberts 1941: 241) is found in all families of Acridoidea apart from the basal groups, Pamphagodidae and Pyrgacrididae (Song & Mariño-Pérez 2013, figure 5). However, when morphological characters are mapped onto the mitochondrial genome tree the character appears homoplasious, having developed independently in Pamphagidae as well as in the common ancestor of the Lentulidae, Tristiridae, Ommexechidae, Romaleidae and Acrididae. Ancorae must subsequently have been lost in the Ommexechidae (Song & Mariño-Pérez 2013, figure 5) and they are also largely absent from the Ixalidiidae Hemp, Song & Ritchie n. fam., though possibly incipient in *Mazaea* (Fig. 7C).

The lateral sclerites (Roberts 1941: 245) (= oval sclerites (Snodgrass 1935)) flanking the epiphallus are present in the eight core acridoid families included in Table 13, but absent in Pamphagidae and of uncertain homology in Pamphagodidae (Dirsh 1956). They are also present in the family Ixalidiidae Hemp, Song & Ritchie n. fam., though sometimes closely articulated or partly fused with the lateral plates of the epiphallus.

Lateral evaginations of the epiphallic membrane (*poches dorso-latérales* and *poches latérales*) have been noted in Pyrgacrididae (Descamps 1968: 34 35; Fig. 11). Similar and possibly homologous lateral lobes have been illustrated in the epiphallic membrane of *Tropidostethus* Philippi, 1863 and *Elysiacris* Rehn, 1942 (Tristiridae) (Cigliano 1989: figures 172, 187). Amédégnato (1976: 7) indicated the occasional presence of latero-ventral sclerites of the epiphallic layer. These have also been shown in *Paulinia acuminata* (De Geer, 1773) (Acrididae, Pauliniinae) by Carbonell (2000: 174; Figs 18; 19). These latero-ventral sclerites of the epiphallic membrane are quite distinct from the paired sclerites of the ventral lobe (ectophallic) (Snodgrass 1935; Roberts 1941; Dirsh 1956) found in most Acrididae and also in Ixalidiidae Hemp, Song & Ritchie n. fam. Too little is known about the occurrence of these epiphallic structures across the Acridoidea for them to be included in Table 13. They have not been found in Ixalidiidae Hemp, Song & Ritchie n. fam.

Ectophallus
This layer is largely constituted by the cingulum (Roberts 1941) a dorsal covering over the endophallus with differentiation of apodemes, rami, and in some families an arch, with or without a dorsal pair of aedeagal sclerites, all of which are discussed below. The degree of sclerotization of the ectophallus was said by Song & Mariño-Pérez (2013) to distinguish the Acridoidea (fully sclerotised) from all other superfamilies (partly sclerotised). However, in the Ommexechidae the ectophallus is visibly not fully sclerotized (Song & Mariño-Pérez 2013; Fig. 3G) as earlier indicated by Dirsh (1956: 247). In Tristiridae (Cigliano 1989b: 56) described the ectophallus in Tristirinae Rehn, 1906 as having "a lower degree of sclerification". In Ixalidiidae Hemp, Song & Ritchie n. fam. the ectophallus is mostly sclerotized, heavily so in *Rowellacris* Ritchie & Hemp n. gen. but less so in *Tangana*. The cingulum is reduced to a sclerotized skeletal framework in *Ixalidium*, *Mazaea*, *Eubocoana* and *Barombia*.

The apodemes of cingulum may be present or absent and, when present, may be long or short. Both Tristiridae and Ixalidiidae Hemp, Song & Ritchie n. fam. have species or genera in which although the cingulum is present as a sclerotised plate, it lacks differentiation into distinct paired apodemes, while in other genera there are taxa with either short or elongated apodemes (e.g. *Atacamacris* Carbonell & Mesa, 1972 in Tristiridae (Cigliano 1989: 53, Fig 5) and *Mazaea*, *Eubocoana*, *Barombia* and *Ixalidium* in Ixalidiidae Hemp, Song & Ritchie n. fam. have elongate apodemes). Both families therefore are considered as polymorphic for these characters (Table 13).

The presence of blade-like secondary cingular apodemes underlying and parallel to the main apodemes of cingulum has been illustrated for a few taxa, both in line drawings and in photographic images, but their presence has not previously been remarked upon. Dirsh (1966: 100, 102) figured these apodemes clearly in the male genitalia of *Mazaea* and *Barombia* (Ixalidiidae Hemp, Song & Ritchie n. fam.) (C. H. Rowell, personal communication, June 2020). In this study they have also been found in *Ixalidium s. str.* (Fig. 11B), and their presence confirmed in *Mazaea* (Fig. 7F), *Eubocoana tristis* (Fig. 9C) and *Barombia*. Similar structures have also been illustrated in *Eneremius desertorum* Saussure, 1888

TABLE 13. — Major morphological characters of female and male genitalia of the family Ixalidiidae Hemp, Song & Ritchie n. fam. and related families of Acridoidea. Symbols: **–**, inapplicable character; **?**, missing data; **0/1**, polymorphic character. 'Traffic light' colour coding indicates character states believed to be consistently shared with Ixalidiidae Hemp, Song & Ritchie n. fam. (**green**); partially shared (**orange**); or not shared (**red**).

Characters (described state = 1 unless otherwise stated)	**Ixalidiidae n. fam.**	**Pamphagodidae**	**Pamphagidae**	**Pyrgacrididae**	**Lentulidae**	**Tristiridae**	**Ommexechidae**	**Romaleidae**	**Acrididae**	**Notes and references**
Female Genitalia										
Two basal branches to spermathecal duct	0*/1	0†	0	0	0**	0§	0**	0**	0**	*0 in *Ixalidium*; **data incomplete; §Cigliano (1989a); †Descamps (1966).
More than 2 distal spermathecal diverticula	0*/1	0§	0	0	0	0	0/1**	0	0	*0 in *Ixalidium*; **Slifer (1940: 217); Amédégnato (1977); Ronderos (1979); §Descamps (1966).
Male genitalia										
Supra-anal plate										
Basal and apical parts separated by transverse suture/furrow	1	1‡	1¶	0	0/1**	1	1§	0/1†	0	**present in several genera, see text; §see text (Ronderos 1979; Amédégnato 1977); †present in *Brasilacris*, *Staleochlora*, and some Bactrophorinae; ‡Descamps (1966); ¶*Pamphagus* Cigliano *et al.* (2023).
Epiphallus										
Epiphallus bridge-shaped, in one or two parts	1*	0	0	1	1	1	-**	1	1	*modified in *Tangana*; **epiphallus in three parts (Eades, 1961: 167; Amédégnato 1977; Ronderos 1979).
Ancorae present	0/1*	0	1	0	1**	1	0**/1§	1	1	*incipient in *Mazaea*; **Dirsh (1956: 244, 247; Song & Mariño-Pérez 2013); §ancorae present in Aucacrinae (Ronderos 1979).
Lophi present	1	0	0	1	1	1	1	1	1	
Lophi pointed (not lobiform)	1	-	-	1	1*	1	1	0	0	*predominantly (Otte 2014a).
Lateral sclerites (oval sclerites) of epiphallus present	1	1**	0	1	1	1	1*	1	1	*Dirsh (1956, Plate 28A), Amédégnato (1977); Ronderos (1979); **homology uncertain (Dirsh 1956).
Ectophallus										
Ectophallus fully sclerotized	1	1	1	1	1	0†/1**	0*	0§/1	1	*Dirsh (1956: 247); **Atacamacridinae (Cigliano 1989a); † Tristirinae (Cigliano 1989a); §Bactrophorinae and *Tropidacris*.
Valves of cingulum present	0/1*	0	0	0	0	0	0	0	1	*incipient in *Mazaea*, *Barombia*; see text (Figure 17)
Rami of cingulum present	1	0	1	0*	1	1**	1	1	1	*Descamps (1968); **Cigliano (1989a).
Zygoma of cingulum differentiated	0¶/1	0§	1	1	1	0**	0†/1*	0‡/1	1	*Dirsh (1956: 247); "not clearly defined" (Eades 1961: 162) ** Cigliano (1989a); §Dirsh (1956); †Amédégnato (1977), Ronderos (1979); ‡e.g. Elaeochlorini (capsule-like cingulum); ¶diffuse in *Rowellacris* n. gen.
Apodemes of cingulum differentiated	0*/1	1	1	1	1	0**/1§	1	1	1	*variable in *Rowellacris* n. gen.; **Song & Mariño-Pérez (2013); §Atacamacridinae Cigliano (1989a: 53, Fig. 5).
Apodemes of cingulum short	0/1	0	1	1	0	-/1*	1	1	0/1	*Cigliano (1989a: 53, fig. 5), inapplicable (Song & Mariño-Pérez 2013).
Secondary apodemes of cingulum present	0/1*	0	0	0	0/1**	0	0	0	0	* Dirsh (1966: 100, 102); ** Dirsh (1961: 396, fig. 21); Brown (1962: fig. 4); Otte (2014a, figs 15, 17) ; see text.
Arch sclerite present	1	1†	0‡	0	0	0/1§	0	0*/1**	1*	*most prevalent state; ***Diponthus* (Pocco 2013); §see text; †Dirsh (1956); ‡zygoma connects direct to endophallus bilaterally (Dirsh 1956).
Endophallus										
Endophallus with dorsal branch	0*	0	0	0	0	1	0	0	0	*?incipient in *Ixalidium*, *Mazaea* & *Barombia*; see text.
Endophallus divided	1	1	1	1	0**/1§	0/1†	0‡	0*	0*/1†	*mostly undivided, flexured, but divided in *Hemiacridinae* (Dirsh 1956);**e.g. *Lentula* (Dirsh 1956; §Brown 1970; ‡Dirsh 1961: 384); †polymorphic, see text.
Endophallus with basal and apical sclerites articulated	1	0‡	1	? ‡	0**/1§	0/1†	0*	0*	0*/1§	*basal and apical valves with flexure; **endophallus undivided (Dirsh 1961); §valves separated in *Eneremius* (= *Lithidium*) (Dirsh 1961) and in Hemiacridinae (Dirsh 1956); †polymorphic, see text; ‡unclear.

Table 13. — Continuation.

Characters (described state = 1 unless otherwise stated)	Ixalidiidae n. fam.	Pamphagodidae	Pamphagidae	Pyrgacrididae	Lentulidae	Tristiridae	Ommexechidae	Romaleidae	Acrididae	Notes and references
Gonopore present	0/1*	0	0	1	1	1	1	1	1	*see text.
Ejaculatory sac ventral to endophallus	-*/1	1	1	1	1	1	1	1	1	*See text.
Spermatophore sac dorsal to ventral endophallic sclerites	1	1	1	1	1	1	0	0	1*/0	*“transverse” (Song & Mariño-Pérez 2013).
Gonopore process present	?1*	1§	1§	1§	1**	1**	1**	1	1	**if the hypothesis of Eades (1961) is correct for all families with spermatophore sac situated dorsal to the endophallus; see Discussion; **Eades (1961); §Eades (2000).
Dorsal endophallic aedeagal sclerite present	0	0	0	0	0	0	0	0/1*	0	*most prevalent state = 1.
No of monomorphic character states fully congruent with Ixalidiidae n. fam.	14	9	9	10	10	9	8	6	9	

(Lentulidae) (Brown 1962: fig. 4; Otte 2014, fig. 15) and in *E. pusillum* (Uvarov, 1925) (Dirsh 1961: 396, fig. 21 (5); Otte 2014: fig. 17). They do not appear to be present in other families of Acridoidea, but it is possible they may have been overlooked.

The zygoma of cingulum was defined by Dirsh (1956: 228) as “a transverse dorsal part of the cingulum, connecting the apodemes and, in most cases, the cingulum itself with the apical valves of the penis”. It is shared by most Acridoidea and their sister group, the Pyrgomorphoidea. However, this character is an expression of a strongly sclerotized ectophallus, hence Cigliano (1989) stated that there is no zygoma in Tristiridae. However, the zygoma is present in all Ixalidiidae Hemp, Song & Ritchie n. fam., whether as a narrow transverse sclerite joining the cingular apodemes in *Ixalidium*, *Mazaea* and *Barombia*, or incorporated into a larger dorsal plate covering much of the endophallus in *Rowellacris* Ritchie & Hemp n. gen. In each case it connects ventrally to the arch of cingulum.

The rami of cingulum, which generally cover the sides of a part of the endophallus, are present in all the families in Table 13, except for the Pamphagodidae and Pyrgacrididae if the interpretation of Descamps (1968) is correct.

The arch sclerite in Acridoidea, originally named “bridge of anterior phallotreme sclerites” (Snodgrass 1935), was subsequently named “arch of dorsal valves” and “arch of aedeagus” by Roberts (1941: 241), who considered it “a development from the aedeagal valves or endophallic membrane rather than from the zygoma of the cingulum”. Both Dirsh (1956: 225) and Amédégnato (1976: 7-8, Plate II, Figs 12-15) subsequently described and illustrated the “arch of cingulum” as a sclerite of ectophallic origin connecting the cingulum and the endophallic sclerites. Amédégnato (op. cit.) stated that in groups with a well-developed aedeagus the arch could either fuse with the dorsal valves of endophallic origin or alternatively it could give rise to genuine “valves of cingulum”.

Eades (1962: 6-7) noted that “homologies of the arch, bridge and dorsal aedeagal sclerites have never been suggested except by speculation”, before speculating that in Dericorythinae Jacobson & Bianchi, 1905 (now Dericorythidae), which he considered to be intermediate between Ommexechidae and Romaleidae and the Acrididae, the arch had initially developed as a pair of sclerites arising from the phallotreme membrane adjoining the “primitive” single pair of (ventral) aedeagal sclerites and extending dorsad to fuse with the ectophallic membrane at the rear of the cingulum, giving rise to a dorsal pair of aedeagal valves in some cases and subsequently becoming fused into a single structure bridging the ventral sclerites. Eades (1962: 6-7) indicated his belief that the arch in Dericorythidae was homologous with that in Acrididae, but he later (Eades 2000:184) expressed the view that it is a pseudoarch “not homologous with the true arch found in Charilaidae [= Pamphagodidae] and Acrididae”. However, Song *et al.* (2018: 4) considered that the arch sclerite is homoplasious within the Acridoidea, having apparently evolved separately in Pamphagodidae and Acrididae.

Presence or absence of the arch sclerite is difficult to establish and requires dissection of the phallic complex (Song *et al.* 2018: 13). Uvarov & Dirsh (1961: 153) argued that the arch was absent in several genera of Acrididae, “appearing sometimes only as a slightly sclerotised part of the ectophallic membrane”. The uncertainty derives from the variability in the degree of sclerotization of the structure in different genera and the subjectivity of a presence / absence decision. Song (2004) demonstrated that in *Schistocerca* Stål, 1873 the arch sclerite develops during the adult stage, being largely undeveloped at fledging, and only reaching its full size before sexual maturity. He suggested that this may have led to *S. braziliensis*

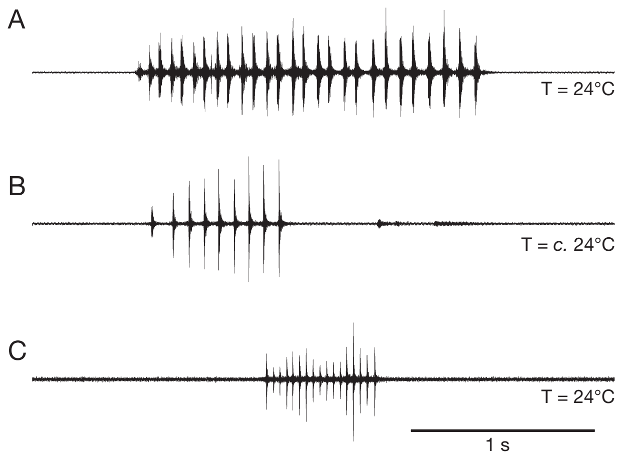

Fig. 20. — Oscillograms of single echemes of species of Ixalidiidae Hemp, Song & Ritchie n. fam.: **A**, *Rowellacris* Ritchie & Hemp n. gen. sp. (Lutindi, W Usambara); **B**, *Tangana asymmetrica* Ramme, 1929 (Nguru Mts); **C**, *Tangana* sp. (Tanzanian Coast, Zanzibar).

Dirsh, 1974 being defined on the basis of immature material (Dirsh 1974: 166).

Nonetheless, the presence of the arch of cingulum connecting the zygoma to the apical valves of the endophallus in most Acrididae and its absence in most Romaleidae has been considered of importance in establishing relationships (Amédégnato 1976, 1977; Eades 2000). In the absence of any other synapomorphy of the Acrididae, Song *et al.* (2018: 13) concluded that "the fact that we have recovered the monophyletic Acrididae strongly suggests that this obscure genital character [the arch of cingulum] may indeed be a synapomorphy for the family". In *Melanoplus rotundipennis* (Scudder, 1878) (Acrididae) Woller & Song (2017: 345, 351, 354) showed that the 'arch of aedeagus', arising from the dorsal valves and inserted into the lower region of the zygoma, provides through the zygoma a point of articulation and structural support for the aedeagus during mating.

Either a single arch sclerite or a pair of sclerites is present in all genera included within the family Ixalidiidae Hemp, Song & Ritchie n. fam. In the genus *Rowellacris* Ritchie & Hemp n. gen. the enlarged and expanded arch sclerite also appears to function as a stiffener and spacer that maintains the gap between the cingulum and the endophallus, otherwise usually connected only by membranes.

The presence in the aedeagus of sclerites of ectophallic origin or dorsal valves of the cingulum (Amédégnato 1976), together with an arch sclerite, was regarded by Song & Mariño-Pérez (2013) as an autapomorphy of the Acrididae, although cingular valves and an arch of ectophallic origin are also present in *Diponthus* (Romaleini, Pictet & Saussure, 1887) (Uvarov & Dirsh 1961; Amédégnato 1976: 8; Pocco *et al.* 2023). Eades (1962: 6-7) stated that in Romaleidae and Ommexechidae the arch was only present when a dorsal pair of aedeagal sclerites were also present.

In the present study of the members of the Ixalidiidae Hemp, Song & Ritchie n. fam. a bifurcated horn-like posterior medial outgrowth of the cingular arch, possibly representing incipient valves of cingulum (C. H. Rowell, personal communication, June 2020), has been found appressed to the dorsal surface of the posterior section of the endophallus in *Mazaea* (Fig. 18A, B). This structure was previously illustrated, but not commented on, in *Barombia* by Dirsh (1966, fig. 40) whose own dissected specimen has been photographed (Fig. 18C). Posterior medial dorsal projections of the zygoma in *Namatettix* Brown, 1970, *Atopotettix* Brown, 1970 (Brown 1970: 495, 505) and *Shelfordites* Karny, 1910 (Brown 1967: figs 1b,1c) (Lentulidae), that were considered by Brown as dorsal or cingular valves, may or may not be homologous with the structures found in *Mazaea* and *Barombia*.

The term "pseudoarch" was originally coined by Akbar (1966: 77) to describe the arch structure found in Pyrgomorphidae (specifically in *Poekilocerus pictus* Audinet-Serville, 1831). Akbar defined the pseudoarch as "a small transverse sclerite … developed in the distal part of the central membrane close to the base of the suprarami. It forms an inflection laterally, and carries dorsally a pair of valves of the cingulum". Akbar's drawings show that his pseudoarch was attached dorsally to the central membrane posterior to the zygoma rather than to the zygoma itself. In studies of the Tristiridae (Amédégnato 1977: 49; Cigliano 1989a, b) the term pseudoarch has been used to describe a sclerite, said to be of uncertain origin, attaching dorsally to the rear edge of the cingulum and ventrally to the endophallus in the same position as occurs with the arch of cingulum in Acrididae, but in the absence of a zygoma and dorsal valves of cingulum in the aedeagus. This arch structure may be absent, reduced or prominent (Cigliano 1989a) and is of significance in defining the subclades of a "*Tristira* generic group" (= tribe Tristirini) within the family. It is absent in those genera which lack an aedeagus (= without development of distal portion of endophallic sclerites, Cigliano 1989b), but well-developed in several genera, including *Moluchacris* Rehn, 1942, *Peplacris* Rehn, 1942 (Fig. 23A), *Punacris* Rehn, 1942, *Crites* Rehn, 1942, *Paracrites* Rehn, 1942, *Incacris* Rehn, 1942, and with incipient development in *Bufonacris* Walker, 1871 (Fig. 23E), *Tristira* Brunner von Wattenwyl, 1900 and *Circacris* Ronderos & Cigliano, 1989.

It is thus apparent that similar arch structures joining the cingulum to the aedeagus occur in different families of Acridomorpha, but there is no agreement as to their homologies or the appropriate terminology with which to describe them. A comparative morphological study of these arch structures would be a useful contribution to understanding the evolution of the genitalia in Acridomorpha.

Endophallus

Amédégnato (1976, 1977) considered the sclerotised endophallus to be constituted in three sections, anterior, middle and posterior. The anterior part consists of the paired endophallic apodemes; the middle part is a pair of sclerites, in Acrididae called the *lateral plates* of Roberts (1941), which strengthen and support the walls of the ejaculatory and spermatophore sacs, while the posterior part (which may be present or absent) participates in the formation of an aedeagus, where this

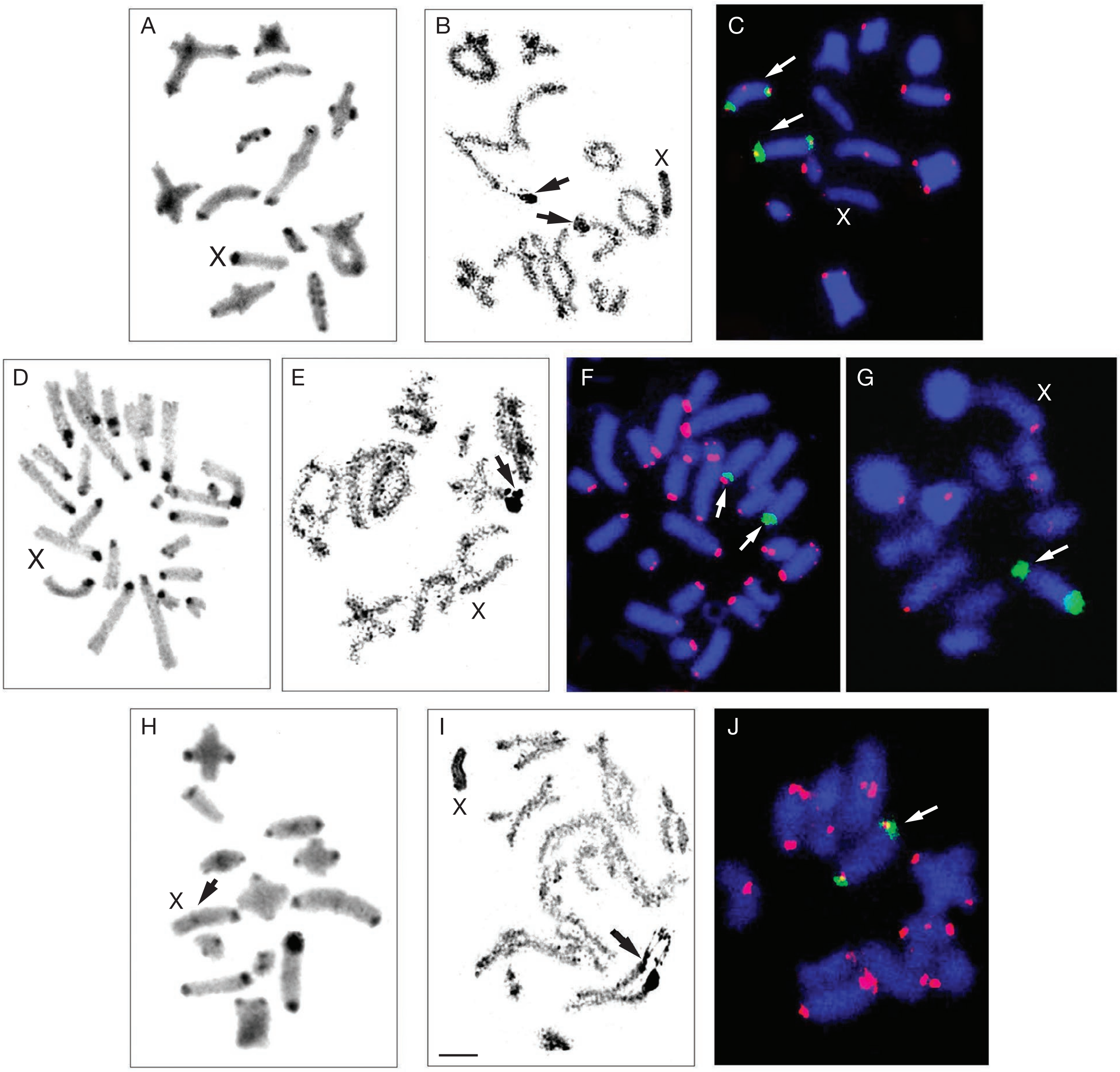

FIG. 21. — Examples of C-banding (**A**, **D**, **H**), active NOR visualized by silver staining (**B**, **E**, **I**), and fluorescence in situ hybridization (FISH) with both 18S rDNA (green) and telomeric DNA (red) probes (**C**, **F**, **G**, **J**) in male chromosomes of *Ixalidium sjostedti* (**A**-**C**), *Rowellacris usambarica* (**D**-**G**) and *Tangana asymmetrica* (Kimboza) (**H**-**J**); diakinesis/metaphase I (**A**-**C**, **E**, **G**, **H**-**J**) and spermatogonial metaphase (**D**, **F**); **black arrows** show NORs/NOR located in the medium-sized bivalents/bivalent (**B**, **E**, **I**), **white arrows** point the chromosomal location of rDNA clusters of one bivalent/pair; black arrowheads show interstitially located C-band on the sex chromosome (**H**). **X**, sex chromosome. Scale bar: 10 µm.

is present. Between the middle part and the posterior part of the endophallus there may be a fracture, creating a division. Possession of a divided endophallus groups the Ixalidiidae Hemp, Song & Ritchie n. fam. with the Pamphagodidae and Pamphagidae together with the Pyrgacrididae, Lithidiidae, some Tristiridae (Fig. 6) and some Lentulidae (see below). Other genera of Lentulidae (*Lentula* Stål, 1878, *Eremidium* Karsch, 1896) have an undivided endophallus (Dirsh 1956: 244), while in many Acrididae the endophallus is flexured, but without a break. Song & Mariño-Pérez (2013: table 3) considered the flexure as equivalent to a division, but that interpretation is not followed here, as explained below.

The presence of a divided endophallus with basal and apical pairs of sclerites articulated rather than completely disconnected, was considered by Song & Mariño-Pérez (2013: 253) to group the Tristiridae, Lentulidae, Pamphagidae, Ommexechidae, Romaleidae and Acrididae. However their character state "endophallus articulated" actually combined two distinct types of linkage between basal and apical sclerites of the endophallus. Firstly there may be a visible disjunction or fracture (Amédégnato 1976), forming a "hinge", as noted by Song & Mariño-Pérez (*op. cit.*) or, alternatively, there may be a spring-like thinning of the endophallus, the sigmoid flexure (Roberts 1941; Dirsh 1956, 1961), which may achieve the same function without creating a disjunction. This is the condition in many Romaleidae and Acrididae, including Ommatolampidinae, e.g. *Eujivarus* Bruner, 1911 and *Eugenacris* Descamps & Amedegnato, 1972 (Amédégnato 1976: figs 26, 28), Oedipodinae Walker, 1871, e.g. *Oedaleus* Fieber, 1853 and *Gastrimargus* Saussure, 1884 (Ritchie 1981, 1982), Acridinae (Popov *et al.* 2019) and Catantopinae (e.g. Rowell *et al.* 2018). Conflating these two forms of endophallic linkage in the character matrix may potentially obscure significant differences. In most members of the acridid subfamily Hemiacridinae, the endophallus is completely separated into basal and apical parts (Dirsh 1956: 155).

In Ixalidiidae Hemp, Song & Ritchie n. fam. the divided endophallus is hinged, with separate basal and apical parts, distinct but closely appressed anterior to the arch sclerite(s). The medial sclerites of the endophallus are dorso-ventrally flattened anteriorly and attenuated in *Mazaea* (Fig. 7H), *Barombia*, *Eubocoana* and *Ixalidium* continuous with the basal sclerites (Fig. 11D). In *Ixalidium* the conjoined medial sclerites are evidently flexible enough to allow the apical section of the endophallus to be folded upwards by as much as 30°, compressing the spermatophore sac. However, in *Rowellacris* Ritchie & Hemp n. gen. (Fig. 15H) and *Tangana* (Fig. 17T) the medial sclerites have been reduced almost completely, so that the hinge occurs between the anterior basal section (the endophallic apodemes) and the apical sclerites which, together with an ectophallic sheath, form the aedeagus.

The ejaculatory sac is normally ventral to the basal valves of the endophallus in the families of Acridoidea listed in Table 13, but the sac is apparently vestigial in *Rowellacris* Ritchie & Hemp n. gen., in which the ejaculatory duct is only minimally widened before becoming internalized within the fused basal valves of the endophallus. In *Tangana*, the ejaculatory duct also passes caudad within the fused basal valves of the endophallus to the dorsally-positioned spermatophore sac. However, there appears to be a small sac, appended to the ejaculatory duct well forward of its point of entry into the basal valves of the endophallus, which is not always preserved during dissection of the genitalia. This may represent the reduced ejaculatory sac.

The presence of a gonopore, defined as a constriction between the ejaculatory sac and the spermatophore sac (Snodgrass 1935), was regarded by Song & Mariño-Pérez (2013) as distinguishing the Acridoidea from all other superfamilies. However, in Ixalidiidae Hemp, Song & Ritchie n. fam., while the ejaculatory sac is constricted at its junction with the ejaculatory duct in *Ixalidium*, *Mazaea and Barombia*, in both *Rowellacris* Ritchie & Hemp n. gen. and *Tangana*, the presence of a gonopore is currently inferred rather than observed, due to the vestigial condition of the ejaculatory sac described above.

The gonopore processes are pointed postero-ventral protrusions of the endophallic apodemes (basal valves of the endophallus), constricting the gonopore in Acridoidea. Though initially regarded as absent in Pyrgomorphidae (Kevan *et al.* 1969: 185, 231), they were subsequently identified with the endophallic sclerites (Eades & Kevan 1974: 250). They were scored by Song & Mariño-Pérez (2013, table 3) in their character matrix as present only in the Acrididae and Romaleidae and absent from the Tristiridae and Ommexechidae, so that when morphological characters were superimposed onto their mitochondrial genome tree (*op. cit.*, fig. 5B) the presence of gonopore processes was shown as a synapomorphy of the Acrididae, Ommexechidae and Romaleidae, that had subsequently been secondarily lost in the Ommexechidae. However, Eades (1961: 162) had previously illustrated the presence of gonopore processes in the Ommexechinae, in contradiction to Dirsh (1956: 247), confirming the synapomorphy across all three families. According to the current paradigm in which the ventral endophallic sclerites of Pyrgomorphidae, Lentulidae and Tristiridae are considered to be homologous with the gonopore processes of Acrididae, gonopore processes must, by definition, be present in all those families, making this a synapomorphy that also includes Lentulidae and Tristiridae.

Prior to their synonymy with Lentulidae, the medial sclerites of the endophallus in Lithidiidae were also identified as enlarged gonopore processes (Eades 2000: 194). Table 13 therefore reflects this probable state. Given the apparent sister status of Ixalidiidae Hemp, Song & Ritchie n. fam. to Tristiridae in the phylogenetic tree derived from the mitochondrial genome (Fig. 1), it is likely that the medial sclerites of the endophallus in Ixalidiidae Hemp, Song & Ritchie n. fam. are also derived from enlarged gonopore processes and thus homologous with the ventral branch of the endophallus in Tristiridae.

Eades (2000: 185) describes additional small sclerites appended to the gonopore processes in Ommexechidae and some other acridoids which he termed antero-ventral flanges of the endophallic sclerite. In Tristiridae Cigliano (1989b: 56) noted that “a projection (gonopore process?) arises ventrally from the anterior region, the development of which is variable. This projection is barely hinted at in Elasmoderini and Atacamacridinae. In Tropidostethini it presents a greater development, joining the dorsal endophallic sclerite through a zone of lesser sclerification. In Tristirinae it is prominent”. If the original gonopore processes have become the ventral endophallic sclerites in Tristiridae, as proposed by Eades (1962), then perhaps these ventral projections of the gonopore processes (Fig. 23B) represent the antero-ventral flanges of Eades (2000). In Ixalidiidae Hemp, Song & Ritchie n. fam. these antero-ventral flanges of the endophallus are either absent or incipient (in a medial position in *Mazaea* and *Ixalidium* (Figs 7G; 10C).

The spermatophore sac is positioned distal to the ejaculatory sac in Acridoidea. It is placed dorsally in relation to the endophallus in Pamphagodidae, Pamphagidae, Pyrgacrididae, Lentulidae and in Ixalidiidae Hemp, Song & Ritchie n. fam. However, it is situated ventrally, below the endophallus, in Ommexechidae and Romaleidae. In Tristiridae the spermatophore sac is situated between the dorsal and ventral branches of the endophallic sclerites and therefore in a dorsal position relative to the ventral endophallic sclerites. Song & Mariño-Pérez (2013: 250) scored the spermatophore sac in Acrididae, uniquely, as “transverse” rather than ventral since part of the sac is situated above the flexure of the endophallus in

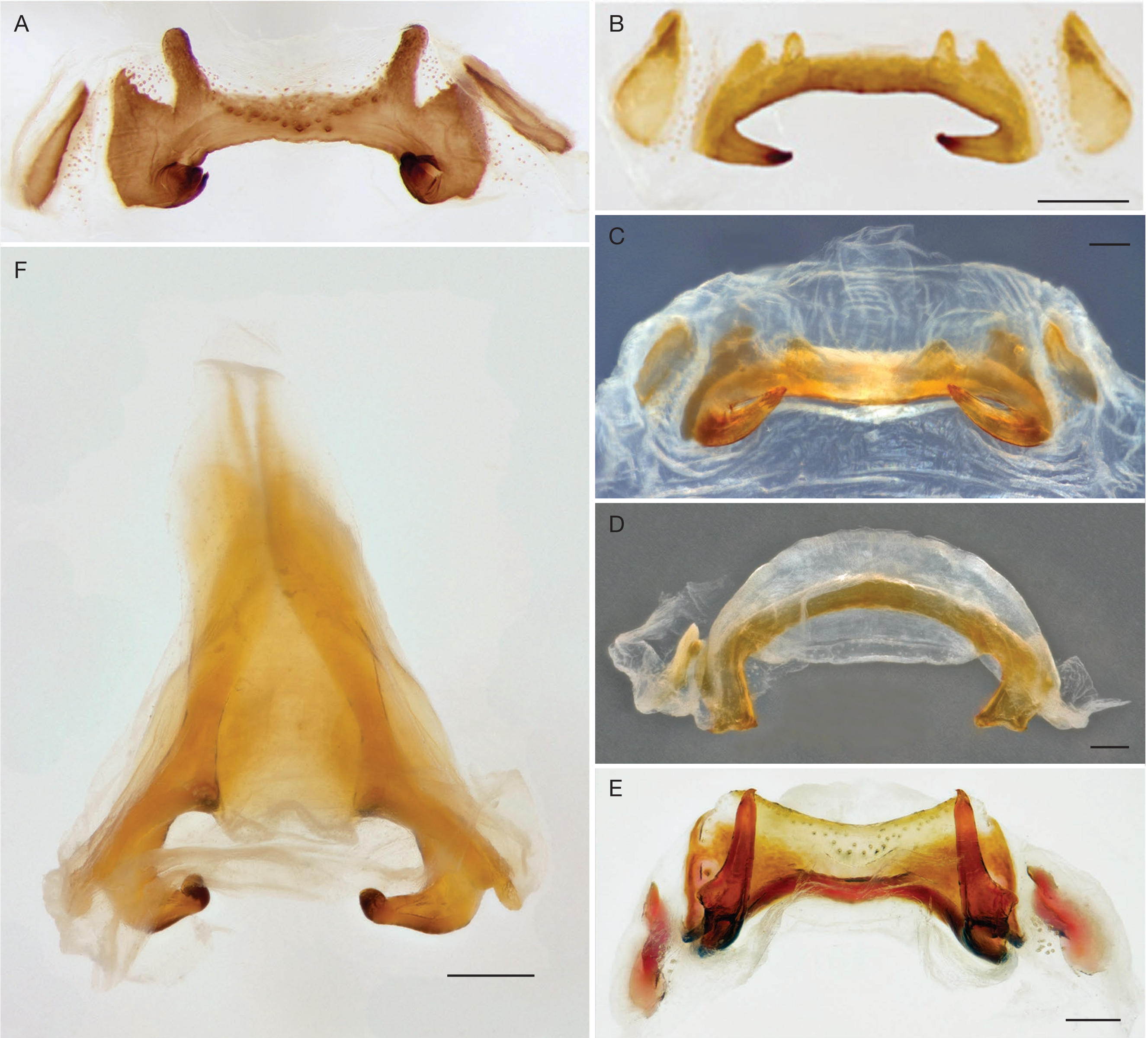

Fig. 22. — Epiphallus, dorsal view: **A**, **B**, Tristiridae Rehn, 1906: **A**, *Eremopachys bergi* Brancsik, 1901, Chile **B**, *Moluchacris cinerascens* (Philippi), Chile, after Song & Mariño-Pérez (2013, fig 4H); **C**-**F**, Ixalidiidae n. fam. Hemp, Song & Ritchie: **C**, *Mazaea granulosa*, Nigeria; **D**, *Rowellacris usambarica n. comb.*, Tanzania; **E**, *Ixalidium haematoscelis*, Kenya; **F**, *Tangana asymmetrica*, Tanzania. Scale bars: B, F, 0.5 mm; C-E, 0.2 mm; A, not to scale.

Acrididae. If it were regarded as ventral, this character state would be an uncontroverted synapomorphy of this terminal clade of the Acridoidea.

A revised character table for the Acridoidea

The basal families of the Acridoidea clade are the Pamphagidae and Pamphagodidae which are consistently recovered as sister clades (Leavitt *et al.* 2013; Song *et al.* 2015, 2020 and Fig. 1), Both families lack the bridge-shaped epiphallus bearing lophi that is shared by the Pyrgacrididae and the remaining eight families (including Ixalidiidae Hemp, Song & Ritchie n. fam.) of the core clade of Acridoidea. Accordingly, although they have been included in Table 13, they are not considered in depth in this study.

Table 13 uses a traffic light approach to indicate the congruence of character states between Ixalidiidae Hemp, Song & Ritchie n. fam. and the other acridoid families, with green for full congruence, amber for partial congruence and red for incongruence. Most of the characters defined by Song & Mariño-Pérez (2013) have been used, with some modification and augmentation, including the addition of characters of the male supra-anal plate (epiproct) and the female genitalia and the omission of a few characters which have identical character states for all families, or which appear to be inapplicable, unclear, or overly subjective. An extensive survey of relevant literature indicates that some of the male genitalic characters found to be monomorphic in the exemplar taxa studied by Song & Mariño-Pérez (2013) are in reality polymorphic at family level. In Table 13, out of a total of 24 genital characters analyzed, just 14 characters are found to be unambiguously monomorphic for the Ixalidiidae Hemp, Song & Ritchie n. fam. Among those, the largest number of monomorphic character states shared with another family is 10 with the Lentulidae and Pyrgacrididae, followed by nine with Pamphagodidae, Pamphagidae, Tristiridae and Acrididae, eight with Ommexechidae, and six with Romaleidae.

The interpretation of individual characters and their significance and application in some of the core families of Acridoidea are further examined in the Discussion section.

Bioacoustics

Up to now, in species of Ixalidiidae Hemp, Song & Ritchie n. fam., no sound producing organs or specialized modified structures have been found. Nevertheless, when kept in captivity, males of three species of *Rowellacris* Ritchie & Hemp n. gen. (*R. obscuripes* n. comb., *R. usambarica* n. comb., *R.* sp. (Lutindi W Usambara)) and two putative *Tangana species* (*T. asymmetrica*, *Tangana* sp. (coastal Tanzania and Kenya, Zanzibar)), as well as females (documented as *Tangana* sp. only), displayed the ability to generate relatively loud rhythmic sounds through drumming/tapping with their hind knees on the substrate. The observed echemes, consisting of 9-27 impacts with varying rates (12-16 Hz for *Rowellacris* Ritchie & Hemp n. gen. spp., *Tangana asymmetrica*, and 35-38 Hz for *Tangana* sp. (T = 23-27°C; Fig. 20), were produced at irregular intervals. Both legs were moved largely in phase. Females were observed to either respond to male signals or spontaneously produce similar signals.

Cytotaxonomy

All three examined genera, namely *Ixalidium*, *Rowellacris* Ritchie & Hemp n. gen., and *Tangana* (Fig. 23A-J), exhibited a diploid chromosome number of 2n = 25 in males and 2n = 26 in females, with a sex chromosome system of X0 in males and XX in females. The autosomes displayed a gradual reduction in size, while the sex chromosome (X) was acrocentric. During male spermatogonial mitosis and meiosis, C-positive blocks were consistently observed in the paracentromeric region of all chromosomes, with interstitial C heterochromatin bands present in the sex chromosome of *Tangana asymmetrica* (Fig. 21A, D, H).

Silver staining revealed the presence of two active nucleolar organizer regions (NORs) per haploid genome in *I. sjostedti* and one in *R. usambarica* n. comb. and *T. asymmetrica*. These NORs were situated in the paracentromeric region of two or one medium-sized bivalent, respectively (Fig. 21B, E, I). In addition, a substantial cluster of 18S rDNA was detected during mitotic metaphase or within bivalents from diakinesis to metaphase I, coinciding with the active NORs identified by Ag-NOR staining (Fig. 21C, F, G, J).

To further probe the chromosomal structure, fluorescence in situ hybridization (FISH) using the (TTAGG)n probe (tDNA-FISH) was performed on spermatogonial mitoses and/or spermatocyte nuclei during meiosis, specifically at diakinesis and metaphase I. In all analyzed taxa, signals were consistently detected at the distal ends of each chromosome. Notably, the tDNA-FISH signals on chromosomes of *T. asymmetrica* appeared notably stronger compared to those observed in the other species of *Ixalidium* and *Rowellacris* Ritchie & Hemp n. gen. (Fig. 21J).

DISCUSSION

Bioacoustics

The findings of sound production in Ixalidiidae Hemp, Song & Ritchie n. fam. raise intriguing questions about the adaptive significance and communication purposes of this behaviour. The animals produced the sounds by drumming with their hind legs on the substrate, a form of sound production known as percussion (Baker & Chesmore 2020). Percussion is the generation of noises by the impact between parts of the body and the substrate, and it is widespread in the animal kingdom. Notably, it is relatively rare and/or poorly documented in Acridoidea, with detailed descriptions limited to Centroamerican proctolabine *Drymophilacris bimaculata* (Rehn, 1905) and the East African catantopine *Sauracris crypta* Popov, 1959 (Ritchie 1988) among acridids. Understanding the evolutionary and ecological factors influencing the development of such communication strategies in Ixalidiidae Hemp, Song & Ritchie n. fam. becomes crucial. The signals most likely contribute to the locatability of mating partners, although comprehensive studies on the informational content of these signals are currently lacking.

The purpose of percussion in Orthoptera appears to be primarily for the production of substrate vibrations rather than airborne sounds. Such signals are easily overlooked or unheard, as emphasized by Ingrisch & Rentz (2009), stating that "Many catantopines produce no audible sound, but some perform drumming actions on their host plants with the hind legs, thereby announcing the presence of a mate without the need for acoustical amplification" (Baker & Chesmore 2020).

The lack of specialized sound-producing organs in Ixalidiidae Hemp, Song & Ritchie n. fam. suggests a potentially unconventional route for acoustic communication within the family. The observed rhythmic patterns in sound production, along with the noted variability in rates among different species, open avenues for investigating the specificity and significance of these signals (Baker & Chesmore 2020). Consideration should be given to the environmental context, as suggested in the papers of Pollack *et al.* (2016) and Baker & Chesmore (2020), emphasizing the potential role of substrate characteristics in shaping the spectral patterns of these drumming signals. Pollack *et al.* (2016) assume that "drumming produces broadband "noisy" signals that are most often associated with heterogeneous substrates, where the filtering characteristics of the substrate are unpredictable". Under these conditions, only the temporal pattern of the sound may carry the intended information (Cocroft *et al.* 2014).

The potential role of female responses to male signals and the spontaneous sound production by females warrant further investigation. The study highlights the need for comprehensive research to decipher the specific information carried by these signals and their importance in mate attraction and communication within the Ixalidiidae Hemp, Song & Ritchie n. fam.

Cytogenetics

A comparative cytogenetic investigation of three genera of African Ixalidiidae Hemp, Song & Ritchie n. fam. offers novel insights into karyotype evolution among grasshoppers. The results showed that the male diploid chromosome number of one *Ixalidium*, two *Rowellacris* Ritchie & Hemp n. gen., and one *Tangana* species was 2n = 25 (24 + X0). Recent research by Husemann *et al.* (2022) confirmed the widely held belief that the karyotypes of Acrididae grasshoppers are very stable, with a male ancestral chromosome number of 2n = 23 (22 + X0), found in almost three-quarters of the over 1000 chromosome records studied across 339 genera. So far, a karyotype with 25 chromosomes has been found only in one species, *Oedipoda schochii* Brunner von Wattenwyl, 1884, collected in Turkey (Türkoglu & Koca 2002). Nevertheless, information regarding chromosome numbers in Tristiridae species, the closest family to Ixalidiidae Hemp, Song & Ritchie n. fam., remains limited. In this family, six South American species from the genera *Bufonacris*, *Elasmoderus*, *Elysiacris*, *Moluchacris*, *Peplacris*, and *Tripidostethus* have different numbers of male chromosomes, equaling 2n = 23, 2n = 21, and 2n = 19 (Mesa *et al.* 1982). Explanation of the presence of a chromosome number higher in Ixalidiidae Hemp, Song & Ritchie n. fam. (2n = 25) than ancestral or plesiomorphic (2n = 23) at present seems difficult, but it represents a cytogenetically distinct group.

To explore chromosomal markers and compare cytogenetic traits within African Acrididoidea, we conducted an exhaustive cytogenetic analysis employing both classical methods (C-banding technique, NOR Ag-staining) and molecular techniques (FISH using rDNA and tDNA). Recent studies on Acrididae grasshoppers have increasingly combined these methods for comparative mapping, yielding valuable insights into genome evolution in this taxonomic group (e.g., Jetybaev *et al.* 2012; Grzywacz *et al.* 2018, 2019).

This study presents, for the first time, chromosomal data for African Ixalidiidae Hemp, Song & Ritchie n. fam., revealing distinctions among species within *Ixalidium*, *Rowellacris* Ritchie & Hemp n. gen., and *Tangana*. We identified blocks of constitutive heterochromatin in the paracentromeric regions of autosomes and the X chromosome, with additional interstitial occurrences in the sex chromosome of *Tangana*. Our mapping of 18S rDNA genes in these species, which share the same chromosome number and are situated exclusively in the paracentromeric region, disclosed variations in the number of these genes between *Rowellacris* Ritchie & Hemp n. gen. and *Ixalidium*. In *I. sjostedti*, a single bivalent featured the rDNA cluster, while *Rowellacris* sp., *R. usambarica* n. comb., and *Tangana asymmetrica* displayed two bivalents. Physical mapping of rDNA sequences and heterochromatin in orthopterans provides valuable additional markers for deciphering chromosomal organization, distinguishing species or genera, and discerning phylogenetic relationships (e.g., Grzywacz *et al.* 2011, 2014; Warchałowska-Śliwa *et al.* 2011, 2013). The number and variability of major 18S rDNA can vary among closely related species and even within species among grasshoppers (e.g., Cabrero & Camacho 2008; Grzywacz *et al.* 2019) or tettigoniids (e.g., Warchałowska-Śliwa *et al.* 2013, 2021).

In all three genera examined in this study, our FISH analysis of 18S rDNA loci consistently corresponded with the active NORs identified via Ag-NOR staining. These NORs were consistently located in the paracentromeric region of the medium autosome, in agreement with prior research in other orthopterans (Grzywacz *et al.* 2014). Furthermore, the detection of (TTAGG)n repeats at the chromosome ends in the studied species aligns with previous findings in other Orthoptera, including certain grasshoppers and tettigoniids (Grzywacz *et al.* 2011; Jetybaev *et al.* 2012; Warchałowska-Śliwa *et al.* 2013).

Genital morphology in some core families of Acridoidea

Lentulidae

The only genitalic character defining the Lentulidae clade of the Acridoidea phylogenetic tree presented by Song & Mariño-Pérez (2013) was the possession of an undivided endophallus, based on dissection of a member of the type genus, *Lentula* Stål, 1878 (*op. cit:* 247) and figures representing *Lentula*, *Eremidium* and *Gymnidium* Karsch, 1896 in Dirsh (1956) which support this definition. However, a substantial number of genera currently included in the Lentulidae have a divided endophallus, including *Afrotettix* Brown, 1970, *Atopotettix* Brown, 1970, *Dirshidium* Brown, 1970 (Brown, 1970) and *Leatettix* Dirsh, 1956 (Shelforditinae) (Otte 2014a). Dirsh (1975: 140) erected the subfamily Shelforditinae for *Shelfordites* Karny, 1910 within his family Catantopidae, a family concept maintained by Li *et al.* (2011) but which has not been validated by recent synoptic phylogenetic studies (e.g. Song *et al.* 2018). Ritchie (1982a: 179) postulated a possible evolutionary sequence from the simple rod-like endophallus still found in *Lentula* or *Altiusambilla* Jago, 1981, via the attenuated ('flexured') endophallus of *Shelfordites* to the divided endophallus of *Leatettix*, *Calviniacris* Dirsh, 1956, *Uvarovidium* Dirsh, 1956 and *Afrotettix*, *Atopotettix* and *Dirshidium*, and ultimately the extreme condition of apical valve reduction found in *Eneremius* Saussure, 1888. He proposed redefining Dirsh's Shelforditinae (within the Lentulidae) as lacking a cingular arch and cingular valves and possessing an attenuated (flexured) or divided endophallus, cingular rami with lateral expansions and cingular apodemes which are elongated, parallel and close together. Otte (1995) incorrectly attributed the subfamily Shelforditinae to Ritchie (1982b), rather than to Dirsh (1975). This error has been repeated in several websites and papers (e.g. Cigliano *et al.* 2022; Matenaar *et al.* 2016). Matenaar *et al.* (2016) provided a partial phylogeny for the South African Lentulidae based on two mitochondrial genes, which indicates that the two currently recognised subfamilies Lentulinae and Shelforditinae are both paraphyletic and in need of taxonomic revision and molecular phylogenetic studies. They noted that *Devylderia* Sjöstedt, 1923 (currently Lentulinae) clusters with *Uvarovidium* and *Leatettix* (Shelforditinae). However, notwithstanding the misplacement of *Devylderia*, their dataset indicated two major radiations of species, corresponding to the two recognised subfamilies. Hemp *et al.* (2020) recovered the same two subfamily clades, showing the major Miocene radiation of Lentulinae into Eastern Africa.

Until recently the Lithidiidae were a small family of deserticolous grasshoppers from Namibia. They included *Lithidium* Uvarov, 1925, *Lithidiopsis* Dirsh, 1956, *Eneremius* and *Microtmethis* Karny, 1910 (the only winged genus), all of which (including the winged species *Microtmethis kuthyi* Karny, 1910) share with the Lentulidae the synapomorphy of complete absence of the tympanum (Dirsh 1961). The family was elevated from subfamily status within the Acrididae by Eades (2000) in a single paragraph of text largely based on one drawing of the genitalia of *Lithidium pusillum* (Uvarov, 1925) by Dirsh (1975: fig. 42), with a comment that the family has close affinities with Lentulidae and Pamphagidae. In Dirsh's Lithidiinae, the apical sclerites of the endophallus were thin and elongated, fully disconnected from the basal valves and covered by an ectophallic sheath (Dirsh 1961: 395-396). The divided endophallus was originally thought to separate them from Lentulidae which had previously been characterised as sharing a continuous, undivided endophallus (Dirsh 1956: 244). However, this character state is no longer present in many genera currently assigned to Lentulidae (see above). Otte (2014) synonymised *Lithidium* with *Eneremius* and transferred *Lithidiopsis* to the Lentulidae, on the grounds that it appeared related to *Leatettix* (Shelforditinae), although the molecular phylogeny presented here (Fig. 1) places *Lithidiopsis* close to *Lentula* (Lentulinae). Most recently Otte (2024) has finally synonymised Lithidiidae with Lentulidae, by transferring *Eneremius*. Otte (2024) excluded *Microtmethis* from Lentulidae on the grounds that it possesses forewings, unlike all Lentulidae. Its true phylogenetic position remains unknown. Otte (2014, 2014a, 2024) has provided greyscale images of the phallic complex for all genera, but these are not sufficiently sharply detailed to establish clear distinctions between genera in the absence of any accompanying commentary on comparative genital morphology. There is clearly a need for a wider molecular phylogenetic and morphotaxonomic study of all the genera currently assigned to the Lentulidae.

Pyrgacrididae

The genital morphology of this family is still poorly understood and homologies with other families are unclear. It has been considered a transitional form between Pyrgomorphoidea and Acridoidea (Eades 2000), but this view is no longer tenable. The entries in Table 13 for this group are based on the descriptions of the morphology of *Pyrgacris relictus* Descamps, 1968 and *P. descampsi* Kevan, 1976 by Descamps (1968) and Hugel (2005) which sometimes conflict with character states reported by Song & Mariño-Pérez (2013: 248, fig. 3). It is not clear from published sources whether the basal and apical endophallic valves are fully disconnected or are hinged in *Pyrgacris*. An arch sclerite appears to be absent in this family, judging from the highly diagrammatic drawings by Descamps (1968), but he did not explicitly state this. In the current phylogenetic tree (Fig. 1) the Pyrgacrididae are a sister group basal to the remaining core families of the Acridoidea clade (excluding Lentulidae).

Tristiridae

The sister relationship between the Ixalidiidae Hemp, Song & Ritchie n. fam. and the Tristiridae clade revealed by analysis of the mitochondrial genome (Fig. 1) was unexpected. The Tristiridae are a small group of grasshoppers of small to medium size with an Andean/Patagonian distribution across southern and western parts of South America (Peru, Argentina and Chile). They have been divided into two subfamilies, the monotypic Atacamacridinae Carbonell & Mesa, 1972 and the Tristirinae with 16 genera and 24 species (Cigliano 1989b), with diverse external morphology and ranging from fully-winged, through brachypterous forms to apterous (Cigliano 1989b). The general habitus of some genera of Tristiridae (e.g. *Incacris*, *Paracrites*, *Moluchacris*, *Peplacris*, or *Tropidostethus*) is strongly convergent with that of the Ixalidiidae Hemp, Song & Ritchie n. fam., with the frons oblique and the fastigium of vertex strongly projecting (Fig. 19A, B). Even elements of the colour patterning, such as black lateral markings on the thoracic pleura and abdominal tergites may be closely similar.

The lower basal lobe of the hind femur may project beyond the upper lobe (Eades & Kevan 1974: 260), a feature characteristic of Pyrgomorphidae, or it may be as long as or shorter than the upper lobe, as shown by accurate drawings (Cigliano 1989b), sometimes varying even within a single genus. In Ixalidiidae Hemp, Song & Ritchie n. fam. the upper basal lobe of the hind femur is always longer than the lower. The external apical spine of the hind tibia is present in most Tristirinae, though lacking in *Incacris*, *Crites* and *Paracrites* and of variable occurrence in *Tebacris* and *Bufonacris*, sometimes varying within a single species or bilaterally within one individual. It is absent in the Atacamacridinae (Carbonell & Mesa 1972). All Tristiridae share a relatively simple female spermatheca with either a single apical ampulla only, or with an additional adjoining short appendix. Differences between the male genitalia of Tristiridae and those of Ixalidiidae Hemp, Song & Ritchie n. fam. are briefly summarised below.

Epiphallus (Fig. 22): In Tristiridae the ancorae are usually well developed (Fig. 22A, B), in contrast to their absence in most Ixalidiidae Hemp, Song & Ritchie n. fam. (Fig. 22C-F). However, in *Mazaea* (Ixalidiidae Hemp, Song & Ritchie n. fam.) incipient ancorae are present in the same location as those seen in some tristirids (Fig. 22C). There is no externo-lateral spur near the base of the lophi of Tristiridae as there is in most Ixalidiidae Hemp, Song & Ritchie n. fam. However, circular sensory pores in the medial area of the bridge, possibly campaniform or coeloconic sensilla, like those seen in Ixalidiidae Hemp, Song & Ritchie n. fam., can be observed in some tristirid species that have a wide bridge (*Tropidostethus*

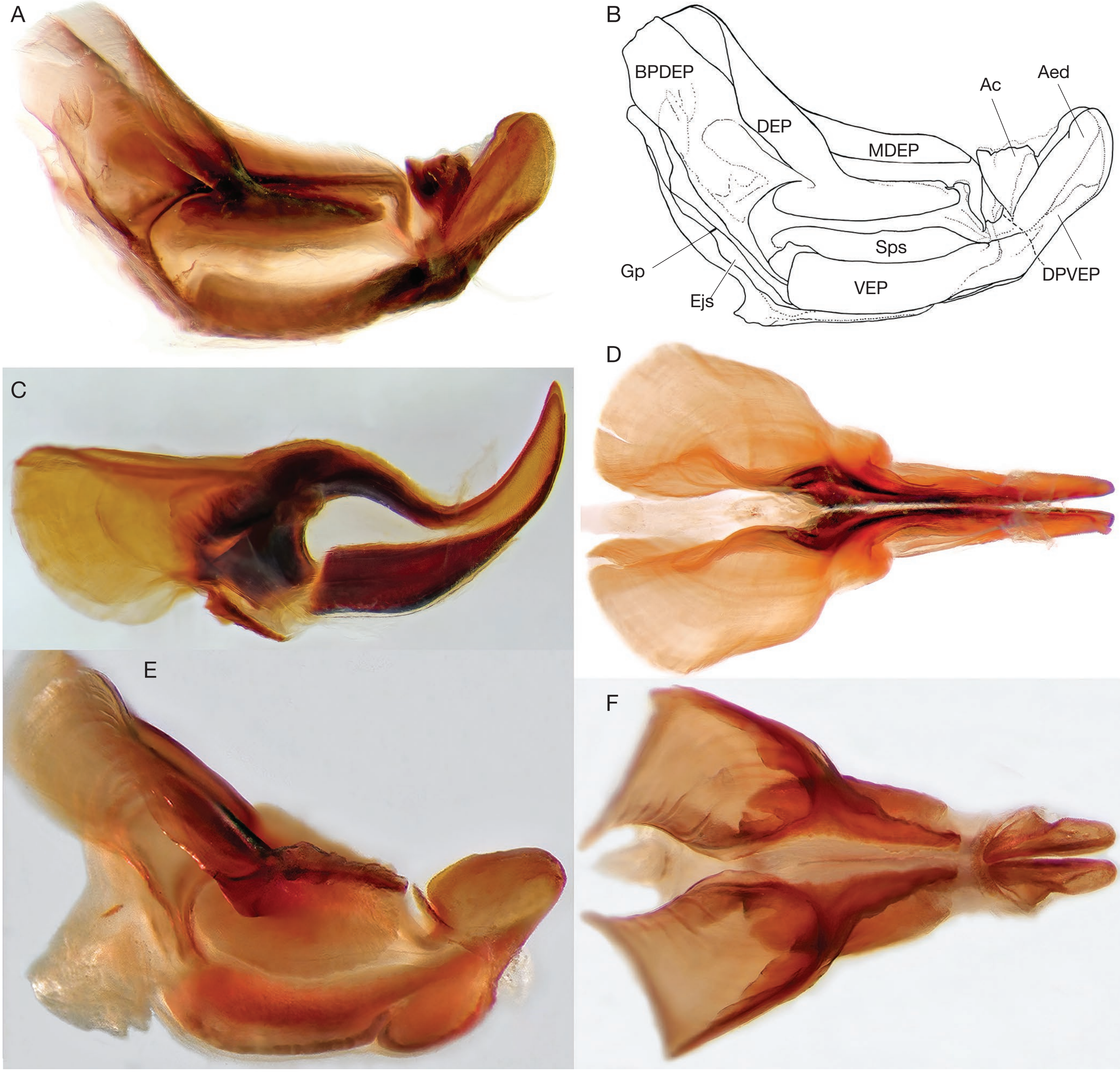

Fig. 23. — Endophallic sclerites, Tristiridae: **A**, **B**, *Peplacris recutita* Rehn, 1942; **C**, **D**, *Eremopachys bergi* Brancsik, 1901; **E**, **F**, *Bufonacris bruchii* Brancsik, 1901: **A**-**C**, **E**, lateral; **D**, **F**, dorsal. Abbreviations: **Ac**, arch sclerite; **Aed**, aedeagus; **BPDEP**, basal portion of dorsal endophallic sclerites; **DEP**, dorsal endophallic sclerites; **DDEP**, apical portion of dorsal endophallic sclerites; **DPVEP**, apical portion of ventral endophallic sclerites; **Ejs**, ejaculatory sac; **Gp**, gonopore process; **MPDEP**, medial portion of dorsal endophallic sclerites; **Sps**, spermatophore sac; **VEP**, ventral endophallic sclerites.

angusticollis (Blanchard, 1851), *Eremopachys bergi* Brancsik, 1901 (Fig. 22A), *Tebacris nigrisoma* Cigliano, 1989).

Ectophallus: In Tristirinae (the most diverse subfamily) the cingulum is usually sclerotized proximally and membranous caudally, with the development of a basal (dorsal) fold and usually of lateral sclerites. The apodemes of cingulum are proximally broad and plate-like, quite different in appearance to those observed in Ixalidiidae Hemp, Song & Ritchie n. fam. and considered by Kevan *et al.* (1969) as not homologous with the cingular apodemes of Acrididae. However, in the monotypic Atacamacridinae Cigliano (1989b) reported narrower apodemes of acridid type. The supplementary pair of delicate narrow apodemes of the cingulum and lateral spurs found in *Ixalidium* and *Mazaea* do not occur in Tristiridae. The rami of cingulum are of variable development and there is no evident development of a sclerotized zygoma (Cigliano, 1989).

Endophallus: The Tristiridae have been considered a monophyletic group of genera (Cigliano 1989a, b; Cigliano & Lange 2000) clearly distinguished morphologically from other families within the Acridoidea (Amédégnato 1977: 50; Cigliano 1989a: 379), by an autapomorphy of the endophallus, whereby the medial part of the endophallic sclerites is divided into dorsal and ventral branches (Fig. 23A-F).

Following the proposal of Eades (1962: 6) the dorsal branch of the endophallus in Tristiridae has been considered to represent the single pair of endophallic sclerites commonly occurring in the other families of Acridoidea (including Romaleidae and Acrididae), while the ventral endophallic sclerites have been identified as an extension of the gonopore processes. These ventral sclerites may remain relatively undeveloped, or they may extend caudally and be covered by an ectophallic sheath constituting the aedeagus, or both the dorsal and ventral sclerites may be extended caudally and be covered by an ectophallic sheath constituting the aedeagus (Fig. 23A-F).

Eades (*op. cit.*) suggested that the endophallus of Lentulidae and Pyrgomorphidae was formed in the same way, accompanied by the complete loss of the "true" endophallic sclerite found in Acrididae, thus explaining the dorsal position of the spermatophore sac in those families relative to the endophallus derived from the gonopore processes. After initially rejecting this hypothesis (Kevan *et al.* 1969: 186), Kevan later endorsed this interpretation for the Pyrgomorphidae (Eades & Kevan, 1974: 250) and subsequently Amédégnato (1977: 49) and Cigliano (1989b: 53) adopted it for the Tristiridae.

The location of the spermatophore sac between the dorsal and ventral branches of the endophallic sclerites places it in a dorsal position relative to the ventral endophallic sclerites. In terms of the character table developed by Song & Mariño-Pérez (2013) this is a character shared with the former Lithidiidae, Lentulidae and Ixalidiidae Hemp, Song & Ritchie n. fam. The dorsal (true) endophallic sclerites in Tristiridae are differentiated into a basal portion, the endophallic apodemes (homologous to those in *Ixalidium*), which may be laterally compressed or with a hemispheric apodeme in contact with the gonopore process (Fig. 23C, D). The middle portion of the dorsal endophallic sclerites forms the roof of the spermatophore sac.

If the ventral endophallic sclerites of the Tristiridae are a novel structure and not homologous with the endophallus in other families, then it is the dorsal sclerites that must be considered in relation to the division of the endophallus and the presence or absence of any articulation. In Table 13, Tristiridae are considered to be polymorphic for both these characters, the dorsal sclerites being undivided in some genera and divided in others (Fig. 23A-F). By contrast, the ventral sclerites of the tristirid endophallus are generally continuous between the basal and medial section, but may show a thinning or partial cleavage just posterior to the antero-ventral flanges of the gonopore processes in *Peplacris*, *Eremopachy*s (Fig. 23C) and *Tropidostethus*.

Based on dissection of the genitalia of *Moluchacris cinerascens* (Philippi, 1863), Song & Mariño-Pérez (2013) regarded Tristiridae as possessing a divided endophallus with an articulated break. In some genera of Tristiridae the dorsal endophallic sclerites have fractured, such that their middle section is not continuous with the aedeagus (Fig. 23A, B, E, F). However, in *Tropidostethus* and *Eremopachys* (Fig. 23C, D) the dorsal endophallic sclerites are continuous and without any fracture. In *Peplacris recutita* Rehn, 1942 and *Bufonacris bruchii* Brancsik, 1901 (Fig. 23A, B, E, F), there is a clear break in the dorsal sclerites, with the tip of the aedeagus being formed from a combination of the ventral endophallic sclerites (= gonopore processes) and a pair of apical dorsal sclerites which are separated from the medial portion of the dorsal endophallic sclerites, but contiguous with a pseudoarch that is attached by membrane to the posterior part of the cingulum. This apical section of the dorsal sclerites consists of a pair of sclerotised valves invested in a sheath of ectophallic origin. However, in *Eremopachys bergi* Brancsik, 1901 (Fig. 23C, D) there is no longer any sign of a break, and the dorsal valves appear to be entirely of endophallic origin.

The condition of the endophallus in Tristiridae, with its dorsal and ventral branches, appears at first sight radically different from the much simpler condition of the endophallus found in Ixalidiidae Hemp, Song & Ritchie n. fam. However, in *Ixalidium*, *Barombia* and *Mazaea* (Figs 7F; 9C; 10E, F; 11B, D) the posterior dorsal part of the endophallic apodemes projects a short distance rearwards over the spermatophore sac, while the paired medial sclerites of the endophallus emerge, not from this dorsal projection, but from the ventral surface of the endophallic apodemes further forward, in the position where the gonopore processes would emerge in Acrididae. It is at least conceivable that this short postero-dorsal extension of the endophallic apodemes may represent a late stage in a morphological trend leading to the loss of the dorsal branch of the endophallus found in Tristiridae.

Romaleidae

Romaleids may be fully-winged to apterous and are often brightly coloured. They have the prosternal process present, though sometimes reduced to a transverse ridge (Rehn & Grant 1959; Rowell 2012). Rehn & Grant (1959a) stated that ancorae of epiphallus were always present in Romaleinae (now Romaleidae) and that the female spermatheca was relatively simple, with a single apical ampulla (which they called the "preapical diverticulum"), always recurved (effectively S-shaped), sometimes with a secondary appendix ("apical diverticulum") adjoining the first curve of the main ampulla. The gonopore processes, ejaculatory sac and spermatophore sac are always present in Romaleidae.

According to Song *et al.* (2018: 13), citing Amédégnato (1977), Eades (2000) and Rowell (2013), Romaleidae can be morphologically distinguished from Acrididae by the presence of a pair of dorsal endophallic sclerites of the aedeagus and the absence of the arch of the cingulum (Roberts 1941; Rehn & Grant 1959a). These dorsal aedeagal sclerites are not homologous with the ectophallic cingular valves of Acrididae (Song *et al.* 2018). They are present in most, but not all Romaleidae (Rehn & Grant 1959b; Amédégnato 1976; Eades 2000; Song *et al.* 2018; Roberts 1941, fig. 55) but have not been found in other acridoid families, including the Ixalidiidae Hemp, Song & Ritchie n. fam. Based on recent mitogenome data (Song *et al.* 2015; 2018) the Ommexechidae, Romaleidae and Acrididae together consistently form a monophyletic group.

However the phylogenetic status of the Romaleidae remains unclear, requiring genomic sampling of a wider range of taxa for its resolution.

Ommexechidae

The genitalia of *Ommexecha servillei* were described and figured by Dirsh (1961, 1965), clearly indicating the presence of the zygoma, which Eades (1961: 162) nonetheless maintained was "not clearly defined". Ronderos (1978) also figured the zygoma for *O. brunneri* Bolívar, 1884. It was scored as present by Song & Mariño-Pérez (2013). Eades (1961: 162-163) regarded the gonopore process as present in *Aucacris* but later (Eades 2000) conceded it was "not well developed". *Ommexecha* species (Ommexechinae) have a tripartite epiphallus (Ronderos 1978) as does *Aucacris bullocki* Rehn, 1943 (Aucacrinae) (Ronderos 1973). However, in the subfamily Illapeliinae, represented by the unique species *Illapelia penai* Carbonell & Mesa, 1972, which is wingless and lacks a tympanum, the epiphallus appears (from drawings in Carbonell & Mesa 1972, figs 12, 18) to be in one piece rather than in three sections, bridge-shaped and with ancorae. The original drawings of the male genitalia (Carbonell & Mesa 1972) are not sufficiently detailed to relate *Illapelia* to other genera and families. The female spermatheca has a single duct with a terminal ampulla. Illapeliinae were originally placed within Acrididae but were moved to Tristiridae by Amédégnato (1977) and Kevan (1982), back to Acrididae (Cigliano 1989b) and then to Ommexechidae (Eades 2000). Critical study of the genital morphology and genomic analysis are required to finally confirm the true familial relationship of *Illapelia*.

Acrididae

Song *et al.* (2018: 13) found the currently recognised Acrididae to be a monophyletic group. They considered that all acridids could be morphologically distinguished from Romaleidae by the absence of dorsal aedeagal endophallic sclerites and the presence of the cingular arch, but they were unable to find any other obvious morphological synapomorphy that unites the subfamilies of the Acrididae. If the hypothesis of Eades (1961) is correct, then the Romaleidae, Ommexechidae and Acrididae have either lost, or their ancestral lineage never developed, the ventral endophallic sclerites derived from enlarged gonopore processes that constitute the endophallus in the more basal families of the Acridoidea clade. Instead they utilise only the dorsal endophallic sclerites seen in Tristiridae, leading to the ventral positioning of the spermatophore sac.

Biogeographical origins of Ixalidiidae Hemp, Song & Ritchie n. fam. and related families

Donato (2006) proposed that the Tristiridae originated during the late Oligocene-early Miocene period, in the Andean Subregion. Based on a divergence time estimate analysis of their genomic data, Song *et al.* (2018) postulated that the common ancestor of the South American endemic families (Tristiridae, Romaleidae, and Ommexechidae) and the Acrididae diverged from their African relatives (Pamphagidae, Pamphagodidae and Lentulidae) in the late Cretaceous period (100-65 Ma). However, based on the latest divergence time estimate analysis (Fig. 1) the split between the Tristiridae and Ixalidiidae Hemp, Song & Ritchie n. fam. seems likely to date from around the start of this period or just before (*c.* 105 Ma). This coincides with current modelling of the final separation of West Africa and South America (Seton *et al.* 2012; Fernie *et al.* 2018) which was complete by 90 Ma, although the Bight of Benin would already have formed before 110 Ma. A warm and increasingly humid equatorial belt is postulated to have developed across northern South America, West Central and northern Africa and Arabia during the late Aptian to early Albian periods (115 to 105 Ma) (Dou *et al.* 2023).

The divergence of the Acrididae from the Ommexechidae has previously been tentatively dated to the Paleocene of the Cenozoic period (59.3 Ma) with diversification in northern South America, giving rise to Marelliinae, Pauliniinae, Ommatolampidinae, Leptysminae, and Rhytidochrotinae (Song *et al.* 2018). The current divergence time estimate analysis (Fig. 1) suggests an even earlier date for this separation, before 80 ma. Since these acridoid families and acridid subfamilies are all endemic to South America, Song *et al.* (2018) considered that the Acrididae most probably originated in South America, with the common ancestor of the non-South American acridid subfamilies colonizing Africa in the late Paleocene (before 53 Ma), crossing oceanic barriers already in place by then (Song *et al.* 2015). Subsequently during the Cenozoic the Acrididae rapidly radiated throughout Africa, particularly in the newly developing grassland habitats, and colonized the Palearctic and Oriental regions, with several lineages subsequently recolonizing the Americas independently.

A few orthopteran lineages have been suggested to be relics of an early humid period when a continuous belt of forest existed across equatorial Africa. One such is the East African pseudophylline bush cricket genus *Pseudotomias* Hemp, 2016 and its near relative *Tomias* Karsch, 1890 with species in West and Central Africa. In that case the fully-winged East African population has been presumed to represent the centre of origin of a westward expansion (Hemp 2016). Hemp (2016) noted that many radiations of forest-dwelling Acridomorpha (and other Orthoptera) in East Africa are of relatively recent origin, including the apterous lentulid genus *Rhainopomma* Jago, 1981 (Schultz *et al.* 2007) and the micropterous coptacridine acridid genus *Parepistaurus* Karsch, 1896 (Hemp *et al.* 2015). Using divergence time estimate analysis, *Parepistaurus* has been shown to have spread westwards from East African coastal forests (Hemp *et al.* 2015), initially into the Eastern Arc mountains and thence into the more recently uplifted massifs of Kilimanjaro, Meru and Mt Kenya, during three successive humid periods at 2.7-2.5, 1.9-1.7 and 1.1-0.9Ma (Trauth *et al.* 2005). Speciation would then have been facilitated by habitat fragmentation during the ensuing drier periods. The alternative hypothesis, that the present-day distribution of *Parepistaurus* results from the fragmentation of a formerly widely distributed homogeneous ancestral species, is contradicted by the difference in age of the coastal and inland taxa (Hemp *et al.* 2015).

In the case of the Ixalidiidae Hemp, Song & Ritchie n. fam., the phylogenetic link with the South American Tristiridae, the basal position of the West African *Mazaea* in the ixalidiid clade (Fig. 1) and the consistently plesiomorphic characters of the genitalia of all the West African genera (elongated cingular apodemes, well-developed anterior ejaculatory sac) provide evidence for an initial eastward expansion of the family out of West Central Africa. Based on the divergence time estimate analysis for the Ixalidiidae Hemp, Song & Ritchie n. fam. (Fig. 1), it appears that the common ancestor of the East African lineage split off from the West African lineage (*Mazaea*) in the late Cretaceous, around 80 Ma. Subsequently the *Ixalidium* clade separated from the *Tangana* / *Rowellacris* Ritchie & Hemp n. gen. clade at the end of the Cretaceous, with the *Rowellacris* Ritchie & Hemp n. gen. and *Tangana* lineages separating during the first half of the Paleogene, before 50 Ma. Today, three well-differentiated genera (*Rowellacris* Ritchie & Hemp n. gen., *Tangana* and *Ixalidium*) survive in relict forest patches along the East African coast from southern Somalia to southern Tanzania and in submontane forests further inland. Each lineage has produced a scatter of closely-related species, distributed in isolated populations, with ranges sometimes overlapping between lineages. Given the range of morphological variation in coastal populations of *Tangana* (Fig. 17 and unpublished data), it seems possible that the group radiated first in the coastal forests and spread into the southern parts of the Eastern Arc mountains from there. Meanwhile its sister group *Rowellacris* Ritchie & Hemp n. gen. is represented by a range of related species occupying separate parts of the Eastern Arc Mountains, with two distinctive species in the East Usambaras, other species in the West Usambaras and one penetrating as far West as the South Pare Mountains. Only one *Rowellacris* Ritchie & Hemp n. gen. taxon, *R. obscuripes* n. comb. ranges from the eastern edge of the East Usambara mountains (Mlinga mountain) to the sub-coastal hills, with minor changes in male genitalia suggesting that this may have been a relatively recent colonization. Further molecular phylogenetic study of these taxa may provide clues as to the direction of spread of the *Rowellacris* Ritchie & Hemp n. gen. and *Tangana* lineages.

Ixalidium is the least humid-forest-dependent lineage of the family and has evidently followed a different course, with populations in the North and South Pare Mountains which have been able to colonise Mt Kilimanjaro and Mt Meru via intervening patches of woodland. Isolated populations occur on Kilibasi Hill, in riverine forest at Dwa Sisal Estate (an eastward extension of the Kibwezi Forest) and in the Chyulu Hills, a volcanic field dating from 1.4 Ma. Further north *I. bicoloripes* Uvarov, 1941 is known from the Emali Hills with the same or a related taxon on the nearby massif of Nzaui. The most northerly outlier of the genus occurs on the northern foot slope of Mt Kenya. In this instance it appears likely that the genus has spread out from the Pare mountains. A comparable distribution pattern is observed in other Orthoptera, such as the hexacentrine genus *Aerotegmina* Hemp, 2001. In this genus, morphologically more basal species are confined to the Taita Hills and the South Pare Mountains, whereas the more derived *A. kilimandjarica* Hemp, 2001 exhibits a broader distribution, extending to geologically younger volcanic formations from Mt. Kilimanjaro and Mt. Meru to Mt. Kenya in the north (Grzywacz *et al.* 2021). Similarly, within the lentulid genus *Rhainopomma* Jago, 1981, the most basal species in the phylogenetic tree is found in the Taita Hills, representing the sister taxon to species from the South Pare Mountains. The latter lineage subsequently gave rise to all other known species of *Rhainopomma* (Hemp *et al.* 2020).

CONCLUSIONS

Two East African genera in the Ixalidiidae Hemp, Song & Ritchie n. fam., *Rowellacris* Ritchie & Hemp n. gen. and *Tangana*, have been found to communicate through percussion, a behaviour involving their hind legs drumming on the substrate. Notably, in *Tangana*, females also exhibit this drumming behaviour. This form of communication is rare among Orthoptera and within the Ixalidiidae Hemp, Song & Ritchie n. fam. it is likely a synapomorphy of these two genera, which share a common ancestor. However, to test this hypothesis, representatives of the West African genus *Mazaea* should be studied in the laboratory.

We have shown that species of the East African genera of Ixalidiidae Hemp, Song & Ritchie n. fam. so far sampled are characterized by a karyotype of 2n♂ = 25 (X0), in marked contrast to the South American Tristiridae in which it is never more than 2n♂ = 21. It would be desirable to sample species of the West Central African genera of Ixalidiidae Hemp, Song & Ritchie n. fam. (*Barombia* and *Mazaea*) to determine whether the increase in chromosome number from the typical acridoid complement of 2n = 23 (X0) had occurred before or after the family spread into Eastern Africa.

The current mitochondrial genomic evidence (Fig. 1) places Ixalidiidae Hemp, Song & Ritchie n. fam. unambiguously as a sister group of the Tristiridae and the two families together as a sister clade basal to the combined Ommexechidae, Acrididae and Romaleidae. However, there is no single morphological character which defines the new family Ixalidiidae Hemp, Song & Ritchie n. fam. and separates it from all others. This lack of distinctiveness, in the context of the confusing range of morphological convergence and polymorphism among the Acrididae and related families, may partly explain how genera which have been known to science for well over 100 years have not previously been perceived as requiring their own subfamily or family status. Nonetheless, the absence of wings and tegmina with the retention of a tympanum, together with possession of a divided epiproct, a bridge-shaped epiphallus with pointed lophi, a divided endophallus, an arch sclerite (either single or paired) and a dorsal spermatophore sac are a combination of characters common to all members of the family and apparently not found together in other families. Mapping these genitalic and other morphological characters onto the latest phylogenetic tree might help to clarify relationships among the families of Acridoidea and the evolutionary history of the Ixalidiidae Hemp, Song & Ritchie n. fam.

Based on geological evidence for the timing of the final separation of South America and Africa (Fernie *et al.* 2018) and previous divergence time estimate analysis for the South American and African acridoid faunas (Song *et al.* 2018) we conclude that a common ancestor of the Tristiridae and the Ixalidiidae Hemp, Song & Ritchie n. fam. may have existed in Atlantica around the start of the late Cretaceous epoch, circa 100 Ma.

This paper has used the previously described species of Ixalidiidae Hemp, Song & Ritchie n. fam. as exemplar taxa to demonstrate the molecular phylogeny and morphological characters of the new family. In future we aim to investigate in greater detail the phylogeny of the different populations of each of the three East African lineages.

Acknowledgements

It is a pleasure to acknowledge the constant advice and encouragement of Dr Hugh Rowell over the long gestation of this study. We are also grateful for the kind loan of insect specimens and provision of related information by Dr Hugh Rowell (Coll. CHR), Dr Laure Desutter-Grandcolas, Muséum national d'Histoire naturelle (MNHN), Paris, Ms Birgit Jaenicke, Museum für Naturkunde (MfN), Berlin, Prof Dr Axel Hochkirch, University of Trier (Coll. AH) and Dr Jeanne A. Yetchom-Fondjo, Leibniz-Institut zur Analyse des Biodiversitätswandels, Hamburg. We are also grateful to Mario Elgueta from the Museo Nacional de Historia Natural in Santiago, Chile, for providing the *Elasmoderus lutescens* specimens for molecular analysis. In particular we are grateful to Dr Ben Price and Dr Beulah Garner, Natural History Museum, London (NHMUK) for access to the Orthoptera collection of the Museum (incorporating the former research collection of the Natural Resources Institute, University of Greenwich) and to the imaging and other facilities of the NHM Life Sciences Department. We thank the Texas A&M High-Performance Research Computing facility for enabling data analyses. HS was supported by the National Science Foundation (grant number DEB-1937815) and the United States Department of Agriculture (Hatch Grant TEX0-2-6584).

We gratefully acknowledge grants from the Deutsche Forschungsgemeinschaft. Part of this research received support from the Synthesys Project (http://www.synthesys.info/), financed by the European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area Programme", which enabled C. Hemp to visit various entomological collections across Europe. We also thank the Commission for Science and Technology, Tanzania, and the Tanzania Wildlife Research Institute, Tanzania, for granting research permits in Tanzania.

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Submitted on 4 August 2024;
accepted on 26 March 2025;
published on 3 October 2025.

APPENDIX

Appendix 1. — Vouchers for taxa of Acridoidea included in the molecular phylogeny (Figure 1) by family, subfamily, genus and species.

	Family	Subfamily	Genus	Species	Voucher Number	mtDNA	18S	28S
Acridoidea	Acrididae	Acridinae	*Acrida*	*willemsei*	OR059	NC_011303	KM853177	KM853512
Acridoidea	Acrididae	Calliptaminae	*Calliptamus*	*italicus*	OR193	NC_011305	KM853193	KM853497
Acridoidea	Acrididae	Catantopinae	*Coenona*	*brevipedalis*	TAMUIC-IGC-003853	PP943135	PP932370	PP932378
Acridoidea	Acrididae	Catantopinae	*Serpusia*	*opacula*	TAMUIC-IGC-003856	PP943136	PP932371	PP932379
Acridoidea	Acrididae	Catantopinae	*Xenocatantops*	*brachycerus*	OR236	NC_021609	MG888296	MG888303
Acridoidea	Acrididae	Copiocerinae	*Copiocera*	sp.	OR333	MG993384	KM853250	KM853440
Acridoidea	Acrididae	Coptacrinae	*Eucoptacra*	*cauta*	OR509	MG993445	KM853324	KM853368
Acridoidea	Acrididae	Cyrtacanthacridinae	*Cyrtacanthacris*	*tatarica*	OR181	MG993444	KM853184	KM853506
Acridoidea	Acrididae	Euryphyminae	*Euryphymus*	sp.	OR314	MG993388, MG993422, MG993436	KM853243	KM853447
Acridoidea	Acrididae	Eyprepocnemidinae	*Eyprepocnemis*	*plorans*	OR309	MG993386, MG993418, MG993424, MG993425, MG993427, MG993433, MG993437, MG993450	KM853239	KM853451
Acridoidea	Acrididae	Gomphocerinae	*Prorocorypha*	*snowi*	OR214	MG993438, MG993452, MG993453	KM853199	KM853491
Acridoidea	Acrididae	Hemiacridinae	*Leptacris*	*kraussii*	OR304	MG993429	KM853238	KM853452
Acridoidea	Acrididae	Leptysminae	*Stenacris*	*vitreipennis*	OR342	MN935544, MN935513, MN935578, MN935533, MN935523, MN935597, MN935555, MN935566, MN935609, MN935619, MN935630, MN935641	KM853255	KM853435
Acridoidea	Acrididae	Marelliinae	*Marellia*	*remipes*	OR344	MG993387, MG993423, MG993442, MG993447	KM853256	KM853434
Acridoidea	Acrididae	Melanoplinae	*Melanoplus*	*bivittatus*	OR245	MG993426	KM853211	KM853479
Acridoidea	Acrididae	Oedipodinae	*Locusta*	*migratoria*	OR191	NC_001712	KM853191	KM853499
Acridoidea	Acrididae	Ommatolampidinae	*Ommatolampis*	*quadrimaculata*	OR364	MG993443	KM853267	KM853423
Acridoidea	Acrididae	Oxyinae	*Oxya*	*chinensis*	OR315	NC_010219	KM853244	KM853446
Acridoidea	Acrididae	Pauliniinae	*Paulinia*	*acuminata*	OR345	MG993401, MG993416, MG993419, MG993430, MG993431, MG993446	KM853257	KM853433
Acridoidea	Acrididae	Proctolabinae	*Coscineuta*	sp.	OR249	MG993441	KM853212	KM853478
Acridoidea	Acrididae	Rhytidochrotinae	*Paropaon*	sp.	OR337	MG993393, MG993397, MG993421, MG993428, MG993449	KM853253	KM853437
Acridoidea	Acrididae	Spathosterninae	*Spathosternum*	*nigrotaeniatum*	OR224	MG993439	KM853203	KM853487
Acridoidea	Dericorythidae	Dericorythinae	*Dericorys*	*annulata*	NC_046555	NC_046555	N/A	N/A
Acridoidea	Ixalidiidae n. fam.		*Ixalidium*	*haematoscelis*	IXsp002	PP943126	PP932372	PP932394
Acridoidea	Ixalidiidae n. fam.		*Ixalidium*	*sjostedti*	Ixsj016	PP943125	PP932373	PP932395
Acridoidea	Ixalidiidae n. fam.		*Mazaea*	*cf granulosa*	TAMUIC-IGC-003854	PP943131	PP932366	PP932399
Acridoidea	Ixalidiidae n. fam.		*Rowellacris* n. gen.	*cf obscuripes*	TAMUIC-IGC-003734	PP943133	PP932369	PP932396
Acridoidea	Ixalidiidae n. fam.		*Rowellacris* n. gen.	*usambarica*	TAMUIC-IGC-003847	PP943134	PP932368	PP932397
Acridoidea	Ixalidiidae n. fam.		*Tangana*	*cf asymmetrica*	Tan002	PP943137	PP932367	PP932398
Acridoidea	Lentulidae	Lentulinae	*Bacteracris*	sp.	TAMUIC-IGC-002615		PP932356	PP932391
Acridoidea	Lentulidae	Lentulinae	*Lentula*	*callani*	OR295	NC_020774	KM853234	KM853456
Acridoidea	Lentulidae	Lentulinae	*Usambilla*	*sagonai*	TAMUIC-IGC-002676		PP932357	PP932393
Acridoidea	Lentulidae	Lentulinae	*Zulutettix*	*tarranti*	TAMUIC-IGC-002670		PP932376	PP932392
Acridoidea	Lentulidae	Lithidiinae	*Lithidiopsis*	*carinatus*	OR316	NC_020775	KM853245	KM853445
Acridoidea	Ommexechidae	Aucaridinae	*Aucacris*	*bullocki*	OR580	PP943130	PP932351	PP932382
Acridoidea	Ommexechidae	Ommexechinae	*Graea*	*horrida*	OR579	MN994068, MN994066, MN994062, MN994064, MN994060, MN994058, MN994056, MN994054, MN994050, MN994052	PP932352	PP932400

Apprendix 1. — Continuation.

	Family	Subfamily	Genus	Species	Voucher Number	mtDNA	18S	28S
Acridoidea	Ommexechidae	Ommexechinae	*Ommexecha*	*virens*	OR367	NC_020778	KM853269	KM853421
Acridoidea	Ommexechidae	Ommexechinae	*Spathalium*	*audouini*	OR581	PP943132	PP932354	PP932380
Acridoidea	Ommexechidae	Ommexechinae	*Tetrixocephalus*	*willemsei*	OR577	PP943129	PP932353	PP932381
Acridoidea	Pamphagidae	Porthetinae	*Hoplolopha*	*asina*	OR288		PP932365	PP932402
Acridoidea	Pamphagidae	Prionotropisinae	*Prionotropis*	*hystrix*	OR151	JX913764	KM853180	KM853509
Acridoidea	Pamphagidae	Thrinchinae	*Filchnerella*	*beicki*		NC_024923	N/A	N/A
Acridoidea	Pamphagidae	Thrinchinae	*Haplotropis*	*brunneriana*		NC_064211	N/A	N/A
Acridoidea	Pamphagidae	Thrinchinae	*Thrinchus*	*schrenkii*		NC_014610	N/A	N/A
Acridoidea	Pamphagogidae		*Hemicharilaus*	*monomorphus*	OR540	JX913773	KM853337	KM853355
Acridoidea	Pyrgacridae	Pyrgacridinae	*Pyrgacris*	*descampsi*	OR317	NC_020776	KM853246	KM853444
Acridoidea	Romaleidae	Romaleinae	*Xyleus*	*modestus*	OR265	NC_014490	KM853221	KM853469
Acridoidea	Romaleidae	Romaleinae	*Chromacris*	*trogon*	TAMUIC-IGC-004271		PP932355	PP932401
Acridoidea	Romaleidae	Romaleinae	*Romalea*	*microptera*	OR1000	MG993392, MG993394, MG993454, MG993455, MG993456, MG993457	MG888294	MG888343
Acridoidea	Tristiridae	Atacamacridinae	*Atacamacris*	*diminuta*	OR202		PP932350	PP932383
Acridoidea	Tristiridae	Tristirinae	*Bufonacris*	*bruchi*	OR205	MN974272	PP932359	PP932384
Acridoidea	Tristiridae	Tristirinae	*Punacris*	*peruviana*	OR206		PP932358	PP932390
Acridoidea	Tristiridae	Tristirinae	*Tristira*	*magellanica*	OR204	NC_020773	KM853197	KM853493
Acridoidea	Tristiridae	Tristirinae	*Tropidostethus*	*angusticollis*	OR203	MN994067, MN994065, MN994061, MN994063, MN994059, MN994057, MN994055, MN994053, MN994049, MN994048, MN994047, MN994051	PP932364	PP932388
Acridoidea	Tristridae	Tristirinae	*Circacris*	*auris*	HS32		PP932361	PP932385
Acridoidea	Tristridae	Tristirinae	*Elasmoderus*	*lutescens*	OR532	PP943127	PP932360	PP932386
Acridoidea	Tristridae	Tristirinae	*Eremopachys*	*bergi*	HS34		PP932362	PP932387
Acridoidea	Tristridae	Tristirinae	*Peplacris*	*recutita*	OR572	PP943128	PP932363	PP932389
Pneumoroidea	Pneumoridae		*Bullacris*	*membracioides*	TAMUIC-IGC-002428		PP932375	PP932404
Pneumoroidea	Pneumoridae		*Physemacris*	*variolosa*	OR293	NC_014491	KM853233	KM853457
Pyrgomorphoidea	Pyrgomorphidae	Orthacridinae	*Colemania*	*sphenarioides*	OR286	MK531234-54	MK370970	MK370950
Pyrgomorphoidea	Pyrgomorphidae	Orthacridinae	*Ichthyotettix*	*mexicanus*	OR1376	MK531214-33	MK370974	MK370954
Pyrgomorphoidea	Pyrgomorphidae	Orthacridinae	*Psedna*	*nana*	OR528	MK514100	MK370982	MK370962
Pyrgomorphoidea	Pyrgomorphidae	Orthacridinae	*Sphenacris*	*crassicornis*	OR1334	MK514099	MK370984	MK370964
Pyrgomorphoidea	Pyrgomorphidae	Pyrgomorphinae	*Tanita*	sp.	OR283	MK514110	MK370987	MK370967
Pyrgomorphoidea	Pyrgomorphoidea	Pyrgomorphidae	*Atractomorpha*	*sinensis*	OR282	NC011824	PP932377	PP932403
Pyrgomorphoidea	Pyrgomorphoidea	Pyrgomorphidae	*Chrotogonus*	*hemipterus*	OR284	MK514108	MK370969	MK370949
Pyrgomorphoidea	Pyrgomorphoidea	Pyrgomorphidae	*Monistria*	*discrepans*	OR527	MK514105	MK370976	MK370956
Pyrgomorphoidea	Pyrgomorphoidea	Pyrgomorphidae	*Phymateus*	*morbillosus*	OR273	MK514103	MK370978	MK370958
Pyrgomorphoidea	Pyrgomorphoidea	Pyrgomorphidae	*Poekilocerus*	*buffonius*	OR152	MK514102	MK370980	MK370960
Pyrgomorphoidea	Pyrgomorphoidea	Pyrgomorphidae	*Sphenarium*	*purpurascens*	OR1328	MK514107	MK370985	MK370966
Tanaoceroidea	Tanaoceridae		*Tanaocerus*	*koebelei*	OR559	NC_020777	KM853342	KM853350
Trigonopterygoidea	Trigonopterygidae	Trigonopteryginae	*Systella*	*rafflesii*		MT011447, MT011493, MT011539, MT011587, MT011632, MT011721, MT011762, MT011807, MT011851, MT011897	N/A	N/A
Trigonopterygoidea	Trigonopterygidae	Trigonopteryginae	*Trigonopteryx*	*hopei*	OR290	JX913767	KM853232	KM853458
Trigonopterygoidea	Xyronotidae		*Xyronotus*	*aztecus*	OR1175	MN935547, MN935516, MN935580, MN935536, MN935526, MN935600, MN935558, MN935569, MN935611, MN935622, MN935633, MN935644	PP932374	PP932405