Zoological Studies **61**:37 (2022)
doi:10.6620/ZS.2022.61-37

Zoological Studies

Open Access

Descriptive Morphology of Male and Female Genitalia of the Long-horned Grasshopper in the Tribe Aphractini (Orthoptera: Tettigoniidae), with a Key to the Genera

Alejandro Vera[1,*] and Paula Prelo[1]

[1]*Departamento de Biología, Facultad de Ciencias Básicas, Universidad Metropolitana de Ciencias de la Educación, Chile.*
**Correspondence: E-mail: alejandro.vera@umce.cl (Vera).*
E-mail: paulaprelo@gmail.com (Prelo)

Received 12 August 2020 / Accepted 4 May 2022 / Published 15 August 2022
Communicated by Benny K.K. Chan

The male and female genital morphologies of the tribe Aphractini are presented in this study. Four species are included: *Aphractus acuminatus*, *Paraphractus abbreviatus*, *Polycleptidella chilensis* and *Polycleptis scutellifera*. A dichotomous key to the genera is provided. The lengths between the female spermathecal duct and titillatory articulated processes are similar within species but differ between them. Therefore, we propose that the function of these organs could be associated with the sperm removal strategy.

Key words: Pseudophyllinae, Sexual selection, South America, Taxonomy.

BACKGROUND

The katydids of the tribe Aphractini (Beier 1962), constitute a small taxonomic group with four genera and seven species, all endemic to Chile and distributed between Illapel and Chiloé (Elgueta et al. 1999; Cigliano et al. 2021). Mugleston and collaborators (2018) in a phylogenetic study included 15 of the 19 tribes of Pseudophyllinae, identified as paraphyletic in clades of the Old World and New World, but did not include Aphractini in their analysis.

The genus *Polycleptis* Karsch 1891 includes four species: *P. gracilis* Beier 1962; *P. inermis* Karsch 1891; *P. rugulosa* Beier 1962 and *P. scutellifera* Karsch 1891. Males and females have been described for all but one, *P. gracilis*, for which no female has been described. The monotypic species *Aphractus acuminatus* Brunner von Wattenwyl 1895 and *Paraphractus abbreviatus* Brunner von Wattenwyl 1895 were described only with female holotypes, and for *Polycleptidella chilensis* Beier 1962 both female and male were described. The last taxonomic contribution was the redescription of *Aphractus acuminatus*, for which the eggs and the male genitalia were described (Vera 2010).

The titillator is a very differentiated structure in the male genitalia of Tettigoniidae and has been used to accurately identify species (Rentz 1985 1993 2001). However, the role it plays during mating has been controversial. The Tettigoniinae *Roeseliana roeselii roeselii* (Hagenbach 1822) has been studied in detail, identifying two titillator functions during copulation (Wulff et al. 2017). At an early stage of copulation, the titillator enters the female genital chamber and rhythmically stimulates specific regions on the dorsum of the female subgenital plate (Wulff et al. 2015), and the female nervous system has been experimentally shown to respond to stimulation (Wulff et al. 2018). Then, the titillator participated in the transfer of the spermatophore (Wulff and Lehmann 2016). Wulff and Lehmann (2020) extended this analysis to two other Tettigoniinae species with morphologically similar titillators. The response of the females was different: in *Pholidoptera littoralis*

Citation: Vera A, Prelo P. 2022. Descriptive morphology of male and female genitalia of the long-horned grasshopper in the tribe Aphractini (Orthoptera: Tettigoniidae), with a key to the genera. Zool Stud **61**:37. doi:10.6620/ZS.2022.61-37.

littoralis the titillator works as an anchor, mechanically positioning the female genital chamber.

Chamorro-Rengifo and Lopes-Andrade (2014) reviewed the nomenclature associated with the phallus in Tettigoniidae and homologized the contributions from Vahed et al. (2011) and Lehmann et al. (2017), creating a ranked classification system from zero to six to reflect titillator complexity. Zero was defined as the absence of processes in the titillator, and six as two pairs of titillators, longer sclerotized processes and conspicuous spines. However, these studies omitted Vera (2010), in which the titillator of *Aphractus* was described as presenting long articulated processes.

Vera (2010) suggested that *Aphractus* males may use the titillatory articulated processes to remove the previous sperm from the female spermatheca during mating. While this modified structure has not been described for other Tettigoniidae, the sperm removal strategy has been identified in the bush-cricket *Metaplastes ornatus* Ramme 1931; this species uses its subgenital plate to simulate an egg, causing evacuation of the spermatheca (Helversen and Helversen 1991). This study describes and compares Aphractini male and female genital morphologies for known genera belonging to this tribe. We identified diagnostic traits for both sexes in each taxa, and the male genitalia of *Paraphractus* are described for the first time. A taxonomic key is provided, showing a specific relationship between the spermathecal duct length of females and the titillatory articulated processes of males.

MATERIALS AND METHODS

Specimen collection

The specimens described were obtained by active collection during the night, following the audible song of males, and observing bushes and trees with a flashlight to find females. The specimens were kept alive until copulation was observed. This helped pair males and females from each species. After this, specimens were conserved in 90% ethanol. Additionally, dry and pinned insects were studied from the Entomological Collection of the Instituto de Entomología of the Universidad Metropolitana de Ciencias de la Educación, Santiago, Chile (IE-UMCE).

Studied material

Aphractus acuminatus 4 ♂, 6 ♀: CHILE, Cauquenes, Los Ruiles, 3-XII-2004 (1 ♂, 1 ♀ in etanol), 23-I-2004 (3 ♂, 5 ♀ in etanol), col A. Vera.

Paraphractus abbreviatus 4 ♂, 5 ♀: CHILE, Cauquenes, Los Ruiles, 5-XII-2005 (3 ♂, 2 ♀ in etanol), col A. Vera. Araucanía, Licán Ray, 1-II-2016 (1 ♂ in etanol), col A. Vera. Llanquihue, Frutillar Bajo, I-1965 (1 ♀), 7-II-1966 (1 ♀), col Silva IEUMCE. Chiloé, Cucao, 4-II-2001 (1 ♀), col A. Vera.

Polycleptis scutellifera 5 ♂, 5 ♀: CHILE, Talca, Vilches Alto, 1-V-2006 (5 ♂, 5 ♀ in etanol), col A. Vera.

Polycleptidella chilensis 5 ♂, 5 ♀: CHILE, Llanquihue, Anticura, 2-II-2009 (1 ♂, 2 ♀ in etanol), 19-II-2002 (2 ♂, 1 ♀ in etanol), col A. Vera. Chiloé, Cucao, 4-II-2001 (1 ♀), col A. Vera. Isla Redonda, 30-I-1987 (1 ♂), 1-II-1987 (1 ♂), col. Solervicens IEUMCE. Palena, Caleta Gonzalo, 4-II-2001(1 ♀), col Vera & Toledo.

Morphological methods

Morphology was studied using a Nikon stereomicroscope (10X eyepieces, 0.7X to 3X zoom lenses) with an integrated digital camera. Samples for SEM were coated with palladium-gold and images obtained with a Hitachi TM 3000 scanning electron microscope. For the study of genitalia, apical parts of the abdomen were removed and treated with 10% NaOH for 12 hours without heating. The morphological terminology of genitalia followed Ander (1970) and Chamorro-Rengifo and Lopes-Andrade (2014).

RESULTS

TAXONOMY

Family: Tettigoniidae Krauss, 1902
Subfamily: Pseudophyllinae Burmeister, 1838
Tribe: Aphractini Brunner von Wattenwyl, 1895

Morphology of the apical part of the abdomen

Male (Figs. 2A–L, 3A–B and 4A–F): Tergum X sclerotized. Epiproct with posterior margin variable. Cercus cylindrical, sclerotized and hirsute, with apical our sub-apical spine. Paraproct bilobulated. Subgenital plate trapezoidal and flat. Styles digitiform (absent in *Polycleptis*). Epiphallus conical. Titillator dorsally reversible. Titillator sclerites together at the middle line, keel-shaped, with sheet-shaped lateral apodeme. Titillatory processes articulated, stick-shaped and asymmetric apex, with variable apical spines (absent in *Polycleptidella*).

Female (Figs. 5A–H and 6A–D): Tergum X, epiproct, cercus and paraproct as in male, but less developed and without specializations such as

protuberances, spines and pronounced curvatures. Ovipositor ensiform, slightly sharp at the apex towards its dorsal margin. Subgenital plate transverse, trapezoidal, with variable marginal processes. Spermatheca is a flexible capsule, oval or spherical. Spermathecal duct of variable length. Accessory gland is a single duct folded towards the capsule.

Aphractus acuminatus Brunner von Wattenwyl, 1895

(Figs. 1A, 2A–C, 4A–B, 5A–B and 6A)

Male: Tergum X depressed in the midline. Epiproct as a prominent triangular sheet, with acute apex; 1.5 times as long as tergum X (Fig. 2B). Cercus cylindrical, slender, extended, sometimes with the distal half slightly dorsal, length 2.5–3.0 mm; apex rounded, with small subapical medial spine (Fig. 2A, B and C). Paraproct with elongated trapezoidal dorsal lobe; ventral lobe small, as sclerotized tubercle. Subgenital plate elongated, posterior margin narrow, triangular emarginated; style cylindrical, elongated, 0.3 as long as cercus, length equal or greater to the distance between them (Fig. 2A). Epiphallus with titillator sclerite (TS) apodemes rounded; middle keel ensiform, base with triangle not sclerotized, TS as long as middle keel (Fig. 4A). Articulated titillatory processes elongated, three times as long as the width of sclerite TS; apex acute, dorsal curved, with abundant subapical spines (Fig. 4B).

Female: Ovipositor length 12–15 mm; dorsal valvulae toothed on the first third; ventral valvulae with small basal process (Fig. 5B). Subgenital plate transverse, posterior margin truncated, with two marginal processes rounded and folded forward

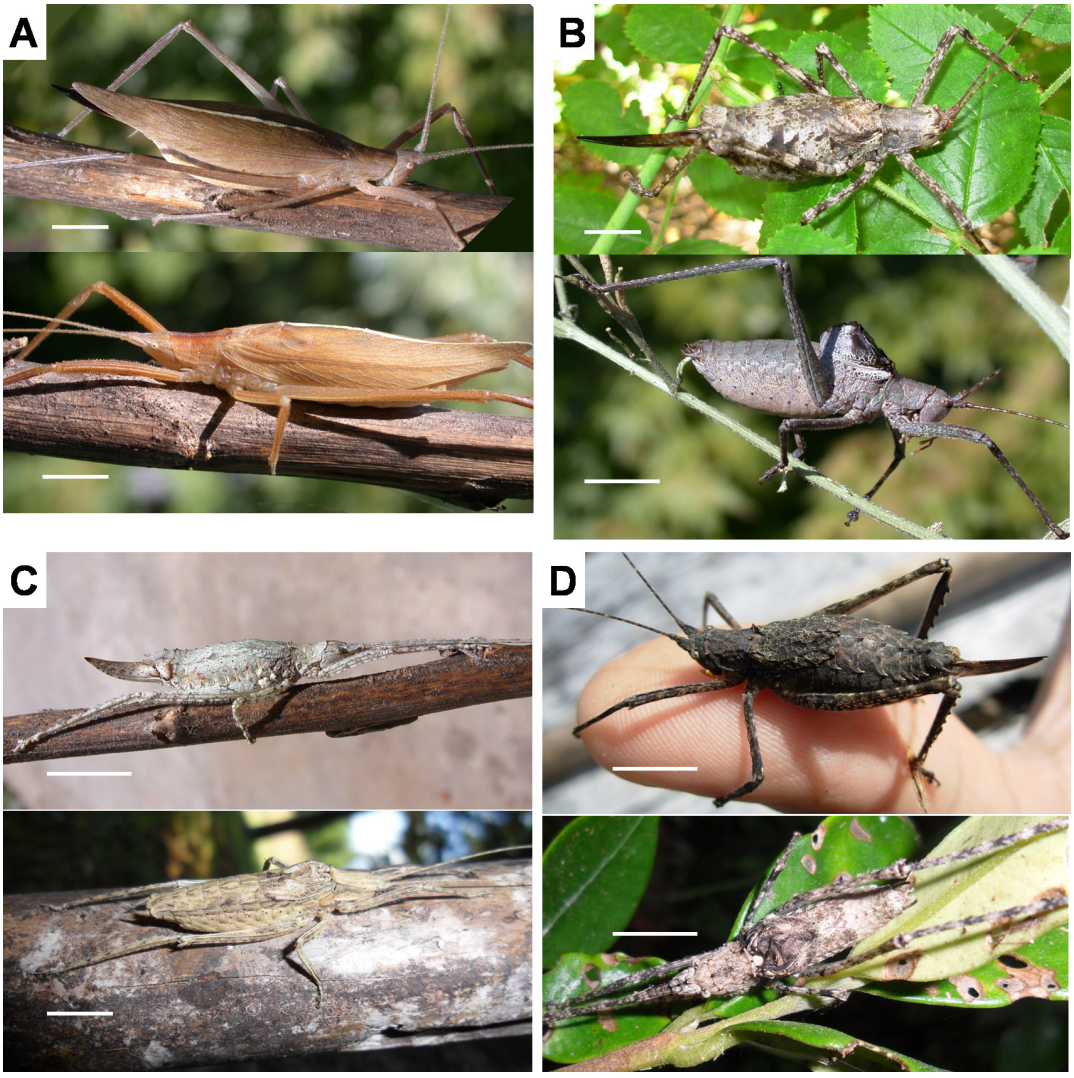

Fig. 1. Live habitus of Aphractini genera, females and males: A, *Aphractus acuminatus* (Los Ruiles); B, *Polycleptis scutellifera* (Vilches Alto); C, *Paraphractus abbreviatus* (♀ Los Ruiles, ♂ Licán Ray); D, *Polycleptidella chilensis* (Anticura). Scale bars = 10 mm.

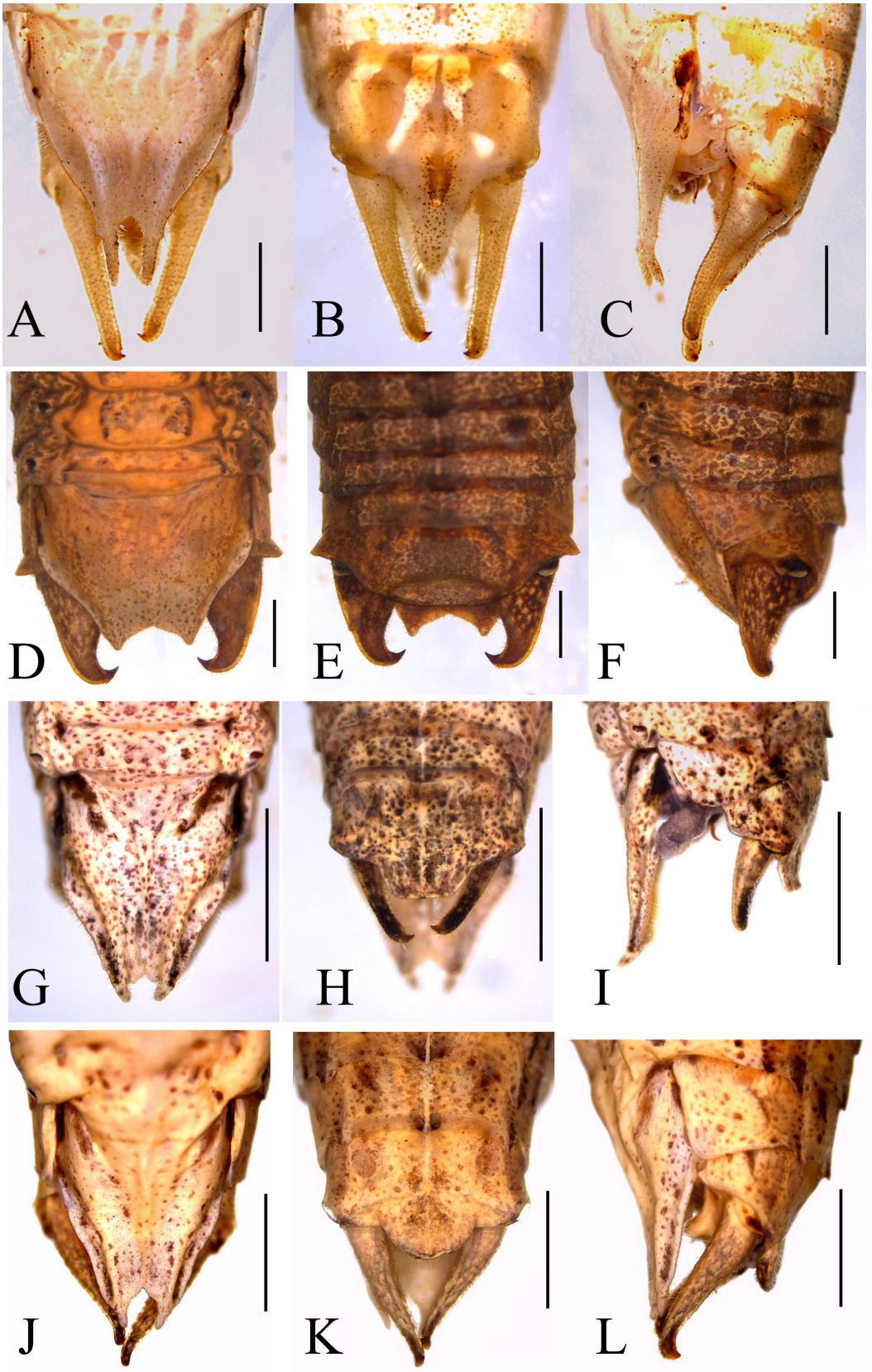

Fig. 2. Male abdominal apex. A, B, C, *Aphractus acuminatus*; D, E, F, *Polycleptis scutellifera*; G, H, I, *Polycleptidella chilensis*; J, K, L, *Paraphractus abbreviatus*. A, D, G, I ventral view; B, E, H, K dorsal view; C, F, I, K lateral view. Scale bars = 2 mm.

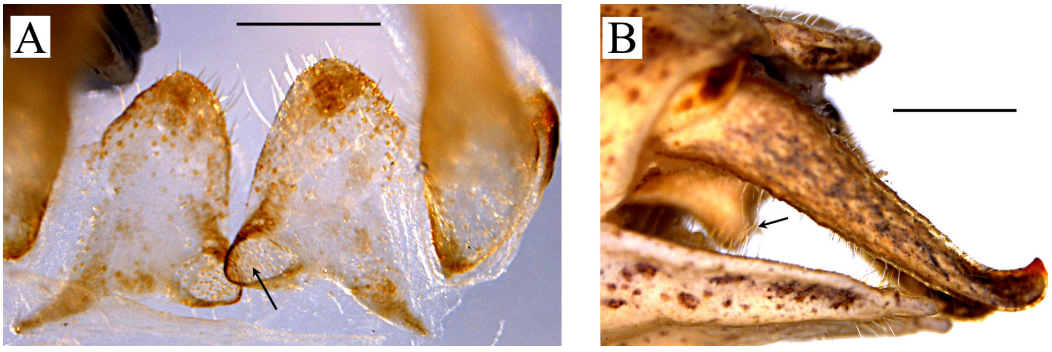

Fig. 3. *Paraphractus abbreviatus* male paraproct. A, ventral view; B, lateral view. Scale bars 1mm; arrows indicate ventral tubercle.

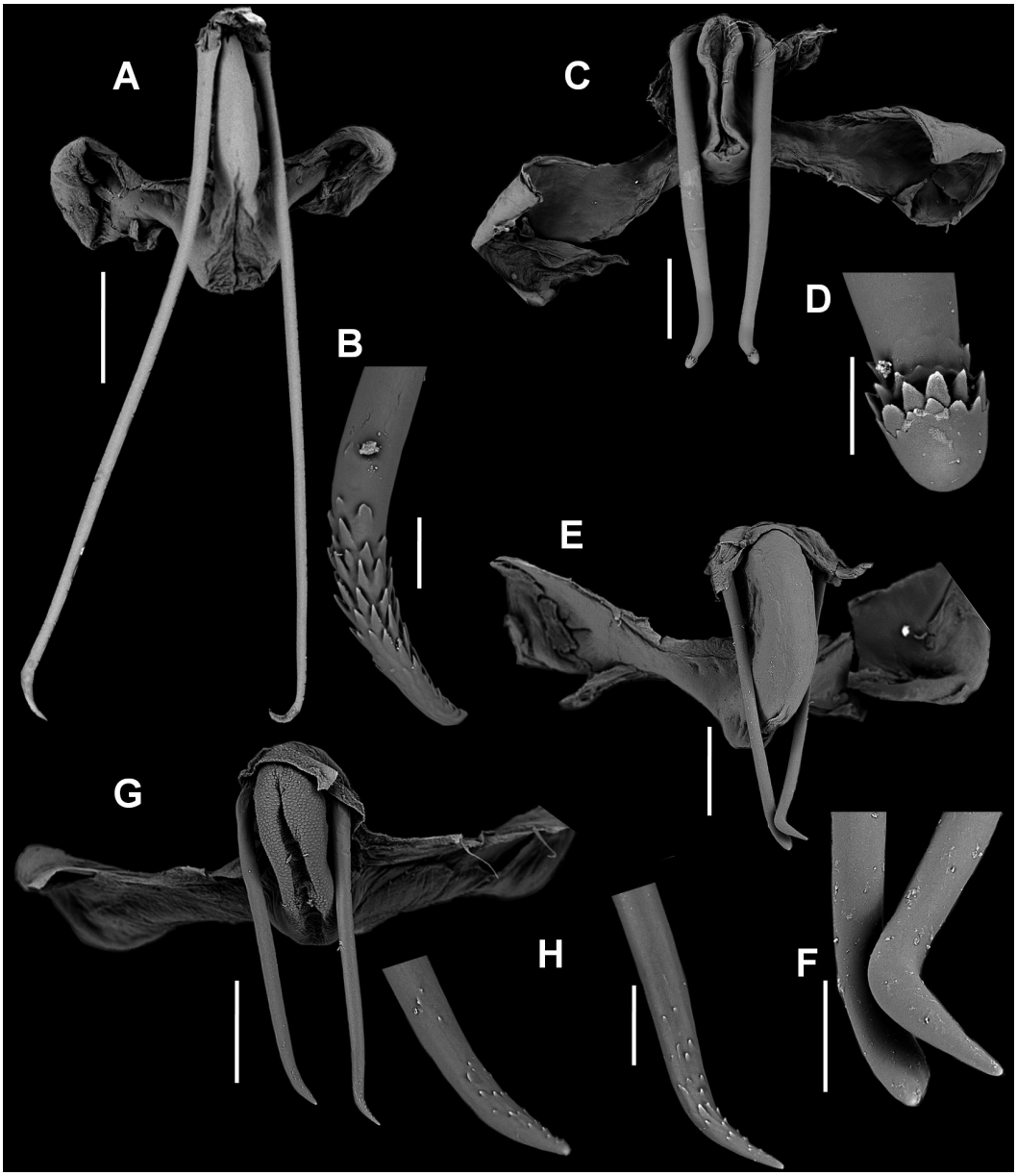

Fig. 4. Micrographs of male titillator and apex process. A, B, *Aphractus acuminatus*; C, D, *Polycleptis scutellifera*; E, F, *Polycleptidella chilensis*; G, H, *Paraphractus abbreviatus*. Scale bars: A, C = 500 µm; E, G = 250 µm; B, D, F, H = 50 µm.

(Fig. 5A). Sternites II–VI with two parallel and rectangular plates, sternite VII with divergent plates ("V"). Genital chamber with spermathecal pore in its posterior margin. Spermatheca with spherical capsule, diameter 1.5–3 mm; spermathecal duct wavy (Fig. 6A), length 2.47–3.64 mm.

***Polycleptis scutellifera* Karsch, 1891**

(Figs. 1B, 2D–F, 4C–D, 5C–D and 6B)

Male: Tergum X depressed. Epiproct posterior margin rounded and dorsally folded; 0.3 as long as tergum X (Fig. 2E). Cercus conical, wide, length 2.3–2.5 mm; strongly curved towards the middle line with its apex sclerotized in a conical spine (Fig. 2D, E and F). Paraproct dorsal lobe tongue-shaped, with round apex; ventral lobe small, as a sclerotized tubercle. Subgenital plate transverse, posterior margin wide, broadly emarginated; style absent (Fig. 2D). Epiphallus with titillator sclerites (TS) apodemes truncated; middle keel not sclerotized; middle keel smaller than TS length (Fig. 4C). Articulated titillatory processes smaller than the width of TS; apex rounded, laterally curved, with subapical spines rings (Fig. 4D).

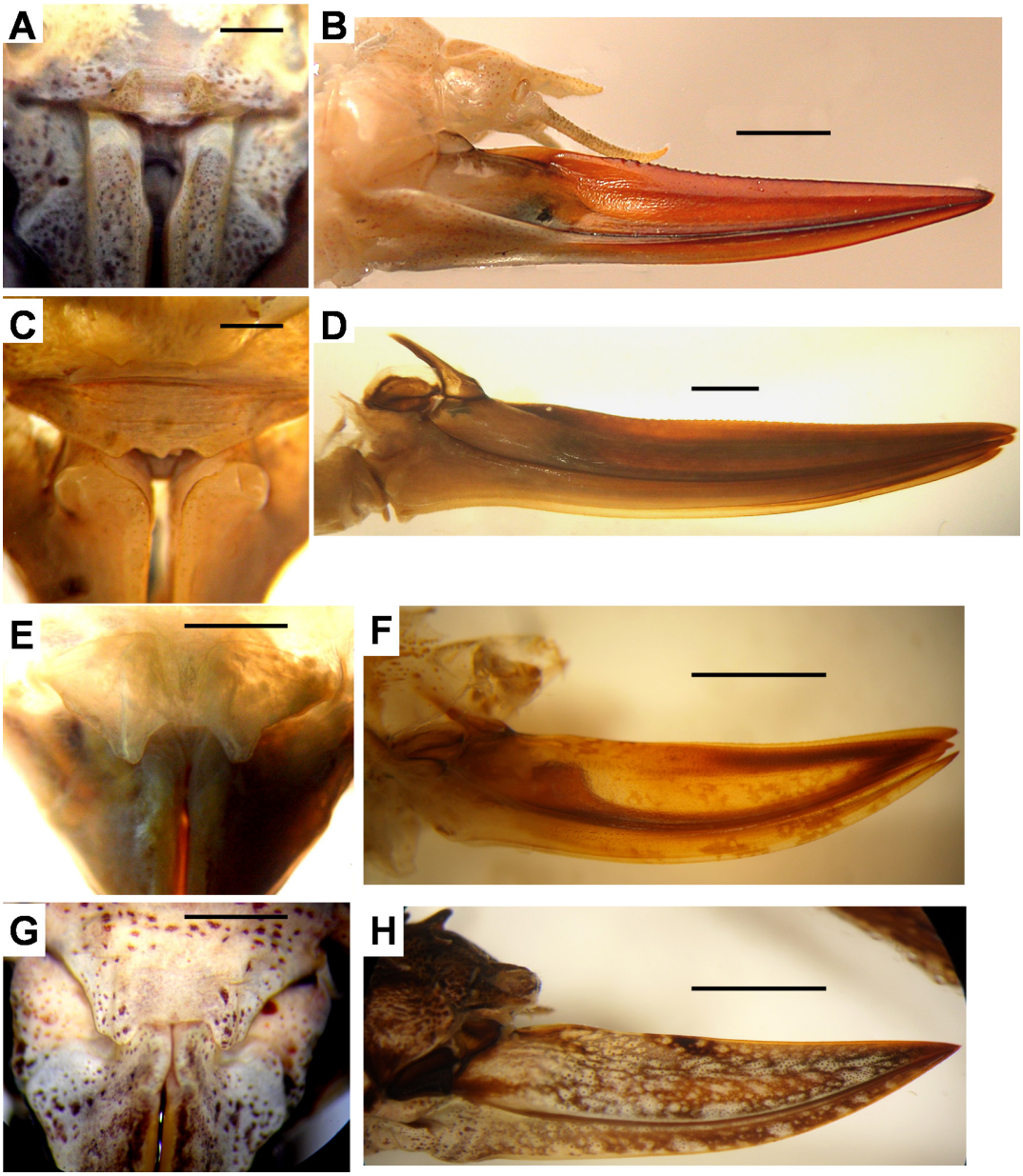

Fig. 5. Female abdomen. A, C, E, G, ventral view of subgenital plate, scale bar = 1 mm; B, D, F, G, lateral view of subgenital plate and ovipositor, scale bar: 3 mm. A, B, *Aphractus acuminatus*; C, D, *Polycleptis scutellifera*; E, F, *Paraphractus abbreviatus*; G, H, *Polycleptidella chilensis*.

Female: Ovipositor length 18–21 mm; dorsal valvulae with small tooth on the second third; ventral valvulae with prominent basal process (Fig. 5D). Subgenital plate transverse, posterior margin with medial triangle and two lateral tubercles (Fig. 5C). Sternites II–VII with a transverse and rectangular plate, sternite VII with two posterior tubercles. Genital chamber with spermathecal pore in its anterior fold. Spermatheca with spherical capsule, diameter 1.8–2.5 mm; spermathecal duct straight (Fig. 6B), length 1.88–2.17 mm.

Paraphractus abbreviatus Brunner von Wattenwyl, 1895

(Figs. 1C, 2J–L, 3A–B, 4G–H 5E–F and 6C)

Male: Tergum X convex. Epiproct posterior margin rounded or acute, as long as tergum X (Fig. 2K). Cercus cylindrical, apex laterally flat, with dorsal apical spine, length 1.5–2.0 mm (Figs. 2J–L, 3B). Paraproct dorsal lobe with triangular-tongue shape; ventral lobe as a prominent cylindrical process (Fig. 3A, B). Subgenital plate elongated, posterior margin narrow, triangular emarginated; style small, cylindrical, length equal to the distance between them (Fig. 2J). Epiphallus with TS apodemes truncated; middle keel not sclerotized, with sclerotized scale-like microstructures; middle keel smaller than TS length (Fig. 4G). Articulated titillatory processes smaller than width of TS; apex acute, dorsal curved, with few dorsal subapical spines (Fig. 4H).

Female: Ovipositor length 8–11 mm; dorsal valvulae not toothed (Fig. 5F); ventral valvulae with small basal process. Subgenital plate transverse, trapezoidal, divided in two obvious sclerites, posterior margin with U-shape emargination and prominent vertices; between them the margin of the ventral valvulae fits (Fig. 5E). Sternites II–VII not sclerotized. Genital chamber with spermathecal pore in its posterior margin. Spermatheca with spherical capsule, diameter 1.3–2.0 mm; spermathecal duct small (Fig. 6C), straight, length 0.16–0.58 mm.

Polycleptidella chilensis Beier, 1962

(Figs. 1D, 2G–I, 4E–F, 5G–H and 6D)

Male: Tergum X convex. Epiproct with posterior margin truncated or bilobed, as long as tergum X (Fig. 2H). Cercus cylindrical, lightly dorsally curved, apex with small subapical medial spine length 1.3–1.8 mm (Figs. 2J–L, 3B). Paraproct with dorsal lobe thick rectangular; ventral lobe as small tubercle. Subgenital plate elongate, posterior margin narrow, triangular emarginated or truncated; style small, length equal to the distance between them (Fig. 2G). Epiphallus with TS apodemes rounded; middle keel sclerotized, smooth; middle keel smaller than TS length (Fig. 4E). Articulated titillatory processes smaller than width of TS; apex acute, dorsally curved, without subapical spines (Fig. 4F).

Female: Ovipositor length 8–12 mm; dorsal valvulae not toothed (Fig. 5H); ventral valvulae with small basal process. Subgenital plate transverse, trapezoidal, posterior margin with quadrangular emargination, and two digitiform processes, between them the margin of the ventral valvulae fits (Fig. 5G). Sternites II–VII not sclerotized. Genital chamber with spermathecal pore in the middle. Spermatheca with oval capsule, diameter 1.8–2.5 mm; spermathecal duct small (Fig. 6D), straight, length 1.2–1.47 mm.

Key for Aphractini genera based on abdominal terminalia

1. Tergum X with prominent epiproct in triangular sheet. Male with cylindrical cercus, extended, rounded apex, with small subapical spine; long articulated titillatory processes (larger than the width of TS); style long, equal or greater to the distance between them. Female subgenital plate with marginal processes rounded and

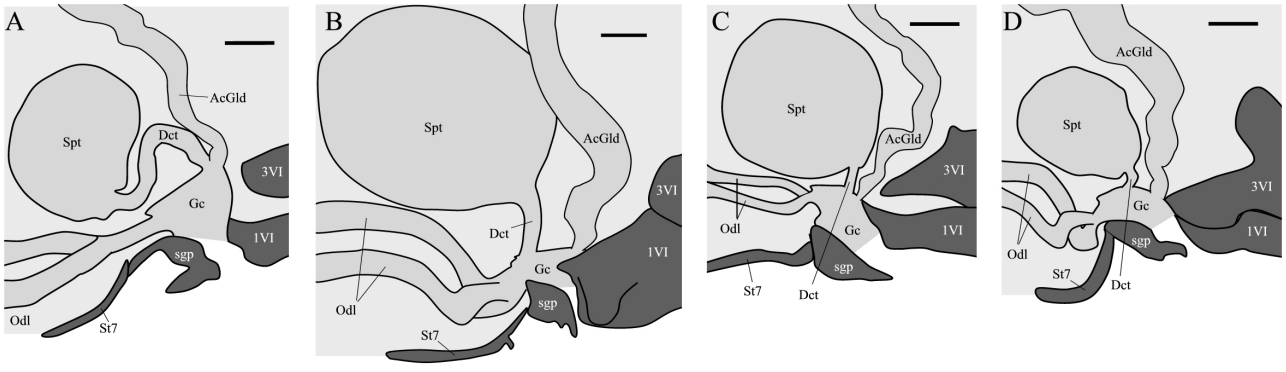

Fig. 6. Lateral view of the female spermathecal. A, *Aphractus acuminatus*; B, *Polycleptis scutellifera*; C, *Paraphractus abbreviatus*; D, *Polycleptidella chilensis*. AcGld, accessory gland; Dct, duct of the spermatheca; GC, genital chamber; Odl, lateral oviduct; Sgp, subgenital plate; Spt, spermatheca; St, abdominal sternite; VI, ovipositor blade. Scale bars = 1 mm.

folded forward ..... *Aphractus acuminatus*

- Tergum X without prominent epiproct in triangular sheet. Male with cylindrical or conical cercus, curved differently, apex different than above; short titillatory articulated processes (smaller than the width of TS); style smaller than distance between them. Female subgenital plate without marginal processes or present but not folded 2

2. Medially curved cercus with acute large spine-shaped apex. Male subgenital plate without style; articulated titillatory processes with round apex and subapical spine rings. Female with prominent basal process in ventral valve; ovipositor more than seven times the length of the subgenital plate ..... *Polycleptis* ssp.

- Cercus lightly dorsally curved, with small apical spine. Male subgenital plate with digitiform styles; articulated titillatory processes with acute apex. Female without prominent basal process in ventral valve; ovipositor less than seven times the length of the subgenital plate 3

3. Male epiproct rounded or acute; cercus apex laterally flat, with dorsal apical spine; paraproct ventral lobule as a prominent cylindrical process; articulated titillatory processes with few dorsal subapical spines. Female subgenital plate with divergent U-shape emargination in its posterior margin .... *Paraphractus abbreviatus*

- Male epiproct truncated; cylindric cercus apex, with small medial apical spine; paraproct ventral lobule small; articulated titillatory processes without subapical spines. Female subgenital plate with quadrangular emargination in its posterior margin, and with two digitiform processes ..... *Polycleptidella chilensis*

DISCUSSION

Our results from the male genitalia showed that the titillator is sclerotized in TS and *ti* components. The epiphallus can extend while the ectophallus is rolled back and vice versa (Vera 2010); this mechanism was confirmed in the four species studied. We propose that the first copulation movement could grant access to the articulated titillatory processes to the spermathecal pore. If the sperm removal strategy were to occur, the length between the articulated titillatory processes and spermathecal duct should be similar. Our results showed similar lengths in male and female components in each species (Table 1). In the females of the four species the values did lengths spermathecal duct not overlap, while in males it only occurred between *Paraphractus* and *Polycleptidella*; these species presented the smallest titillatory processes and spermatic ducts. Furthermore, except for *Paraphractus*, the titillatory processes presented subapical spines opposite to the apex in all species.

Our findings suggest a direct relationship between the lengths of the male-female components. This could be an important mechanism of mechanical incompatibility during genital coupling, if we consider the Lock-and-key reproductive isolation hypothesis (Masly 2012). However, the meaning of this pattern must be supported by experimental evidence studying copulatory behavior (Wulff and Lehmann 2020). Thus, Aphractini could be a good model for the study of these morphofunctional and reproductive isolation hypotheses.

From the perspective of taxonomy, the male

Table 1. Female spermathecal duct and male titillator process lengths in Aphractini species

Species	Female coding	Spermathecal duct length (mm)	Male coding	Titillator right process length (mm)	Titillator left process length (mm)
Paraphractus abbreviatus	26	0.16	21	0.75	0.74
	25	0.17	30	0.77	0.76
	22	0.48	20	0.80	0.80
	23	0.56	29	1.03	1.00
	34	0.58			
Polycleptidella chilensis	35	1.20	28	0.83	0.83
	11	1.30	24	0.84	0.92
	38	1.30	37	0.85	0.90
	32	1.32	27	0.90	0.90
	10	1.47	36	0.94	0.91
Polycleptis scutellifera	6	1.88	12	1.87	1.88
	9	2.10	15	2.00	2.03
	7	2.16	14	2.16	2.16
	5	2.17	39	2.30	2.30
	8	2.17	13	2.36	2.36
Aphractus acuminatus	2	2.47	18	2.83	2.83
	3	2.75	17	3.00	2.96
	4	3.00	31	3.05	3.00
	1	3.00	19	3.06	3.00
	33	3.64	16	3.23	3.45

phallus and the female genital camera allow specific discrimination; in addition to external abdominal morphology in the four species studied.

CONCLUSIONS

Based on the genital morphology of four Aphractini genera, it was possible to discriminate all studied taxa; with diagnostic characters found in each species. The classic structures such as cercus, epiproct, paraprocts, subgenital plate and ovipositor are also good enough to diagnose the Aphractini species. The two articulated titillator processes were present in all species and had differences between them in apex shape and length. For each species, the spermathecal duct and articulated processes were similar in length, suggesting an interaction during mating.

Acknowledgments: We would like to thank Mario Elgueta (National Museum of Natural History, Chile) and Jaime Solervicens (IE-UMCE) for the access to the facilities to study specimens in the entomological collections. To Susana Toledo for her help in increasing the numbers of specimens. To Mario Elgueta, Cristian Villagra (IE-UMCE) and Patricia Henríquez-Piskulich for their valuable comments on this work. SEM images were funded by the DIUMCE MYS I-12-15 project.

Authors' contributions: Alejandro Vera and Paula Prelo contributed equally to this work.

Competing interests: Alejandro Vera and Paula Prelo have no conflict of interests.

Availability of data and materials: All the studied material is deposited in either museums or public institutions.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Ander K. 1970. Orthoptera Saltatoria. *In*: Tuxen SL (Ed) Taxonomist's glossary of genitalia in insects. Munksgaard, Copenhagen, pp. 61–71.

Beier M. 1962. Orthoptera: Tettigoniidae (Pseudophylliinae). Das Tierreich **73:**1–468.

Brunner Von Wattenwyl C. 1895. Monographie der Pseudophylliden. Verhandlungen der k. k. Zoologish-botanischen Gesellschaft in Wien, 40, 87–124, pls. 3–5.

Chamorro-Rengifo J, Lopes-Andrade C. 2014. The phallus in Tettigoniidae (Insecta: Orthoptera: Ensifera): revision of morphology and terminology, and discussion on its taxonomic importance and evolution. Zootaxa **3815(2):**151–199. doi:10.11646/zootaxa.3815.2.1.

Cigliano MM, Braun H, Eades DC, Otte D. 2021. Orthoptera Species File. Version 5.0/5.0. Available at: http://Orthoptera.SpeciesFile.org. Accessed 3 Aug. 2021.

Elgueta M, Camousseight A, Carbonell C. 1999. Catálogo de Orthoptera (Insecta) de Chile. Publicación Ocasional, Museo Nacional de Historia Natural-Chile **54:**5–60.

Helversen D von, Helversen O von. 1991. Pre-mating sperm removal in the bush cricket *Metaplastes ornatus* Ramme 1931 (Orthoptera, Tettigonioidea, Phaneropteridae). Beav Ecol Sociobiol **28:**391–396. doi:10.1007/BF00164120.

Lehmann GUC, Gilbert JDJ, Vahed K, Lehmann AW. 2017. Male genital titillators and the intensity of post-copulatory sexual selection across bushcrickets. Behav Ecol **28:**1198–1205. doi:10.1093/beheco/arx094.

Masly JP. 2012. 170 Years of "Lock-and-Key": Genital morphology and reproductive isolation. International Journal of Evolutionary Biology **2021:**1–10. doi:10.1155/2012/247352.

Mugleston JD, Naegle M, Song H, Whiting MF. 2018. A comprehensive phylogeny of Tettigoniidae (Orthoptera: Ensifera) reveals extensive ecomorph convergence and widespread taxonomic incongruence. Insect Systematics and Diversity **2(4-5):**1–27. doi:10.1093/isd/ixy010.

Rentz DCF. 1985. A monograph of the Tettigoniidae of Australia: Volume 1: The Tettigoniinae. Melbourne, Australia: CSIRO.

Rentz DCF. 1993. A monograph of the Tettigoniidae of Australia: Volume 2: The Austrosaginae, Phasmodinae and Zaprochilinae. Melbourne, Australia: CSIRO.

Rentz DCF. 2001. A monograph of the Tettigoniidae of Australia: Volume 3: The Listroscelidinae, Tympanophorinae, Meconematinae and Microtettigoniinae. Melbourne, Australia: CSIRO.

Vahed K, Lehmann AW, Gilbert JD, Lehmann GUC. 2011. Increased copulation duration before ejaculate transfer is associated with larger spermatophores, and male genital titillators, across bushcricket taxa. J Evol Biol **24:**1960–1968. doi:10.1111/j.1420-9101.2011.02325.x.

Vera A. 2010. Estudio taxonómico del género monotípico *Aphractus* (Orthoptera: Tettigoniidae, Pseudophyllinae). Revista de la Sociedad Entomológica de Argentina **69(3-4):**253–260.

Wulff NC, Lehmann GUC. 2016. Function of male genital titillators in mating and spermatophore transfer in the tettigoniid bushcricket *Metrioptera roeselii*. Biol J Linn Soc **117:**206–216. doi:10.1111/bij.12661.

Wulff NC, Lehmann GUC. 2020. Sexual selection on bushcricket genitalia operates in a mosaic pattern. Ecol Evol **10(5):**2320–2338. doi:10.1002/ece3.6025.

Wulff NC, Lehmann AW, Hipsley CA, Lehmann GUC. 2015. Copulatory courtship by bushcricket genital titillators: functional morphology, μCT scanning for 3D reconstruction and female sense structures. Arthropod Struct Dev **44:**388–397. doi:10.1016/j.asd.2015.05.001.

Wulff NC, van de Kamp T, dos Santos Rolo T, Baumbach T, Lehmann GUC. 2017. Copulatory courtship by internal genitalia in bushcrickets. Sci Rep **7:**42345. doi:10.1038/srep42345.

Wulff NC, Schöneich S, Lehmann G. 2018. Female perception of copulatory courtship by male titillators in a bushcricket. Proc R Soc B **285(1884):**20181235. doi:10.1098/rspb.2018.1235.