

# Revision of the tusked bush-crickets (Tettigoniodea: Pseudophyllinae: *Dicranostomus*) with description of the hitherto unknown sexes

KLAUS-GERHARD HELLER<sup>1</sup>, MATTHIAS HELB<sup>2</sup>

<sup>1</sup> Grillenstieg 18, 39120 Magdeburg, Germany.

<sup>2</sup> Spessartstr. 101, 63457 Hanau, Germany.

Corresponding author: Klaus-Gerhard Heller ([heller.volleth@t-online.de](mailto:heller.volleth@t-online.de))

Academic editor: Ming Kai Tan | Received 17 December 2020 | Accepted 3 February 2021 | Published 3 June 2021

<http://zoobank.org/4BE14BC8-A200-42AA-BC49-6DE823F62085>

Citation: Heller K-G, Helb M (2021) Revision of the tusked bush-crickets (Tettigoniodea: Pseudophyllinae: *Dicranostomus*) with description of the hitherto unknown sexes. Journal of Orthoptera Research 30(1): 87–94. <https://doi.org/10.3897/jor.30.62170>

## Abstract

The genus *Dicranostomus* belongs to the very few Orthoptera with elongated mandibular processes, here called tusks. However, it is also one of the least studied genera from whose two species only one female and two males have been known so far. We present additional material from both species and sexes that confirms that the males have the relatively longest (2–2.8 times pronotal length) tusks of all Orthoptera. Surprisingly, the females of both species differ in this character: females of *D. monoceros* have tusks and those of *D. nitidus* do not. Based on a comparison with other species, we hypothesize that the species use holes that males can defend and use to monopolize the females.

## Keywords

Eucoconotini, mandible, Peru, South America, taxonomy, weapon

## Introduction

In many species of animals, males possess elaborate structures used mainly in intraspecific fights over access to females (Emlen 2008). Among mammals, well-known examples include antlers in deers, horns in bovines, and tusks in elephants. In many, but not all, of these species, the weapons are also found in a reduced version in females. In insects, impressive examples of such structures are observed, e.g., in Lucanidae (stag beetles; see Emlen 2008 for other species).

Such weapons are relatively rare among Orthoptera. There are some species where the mandibles are enlarged only in males (see review in Field and Deans 2001, Gorochov 2012), but only in very few species are these special structures found to be used (or, with good reasons, assumed to be used) in the context of antagonistic intraspecific contacts. Males with tusks are found in five species of the family Anostostomatidae [see Field and Deans 2001; in the New Zealand tusked wetas, a monophyletic group of three species in two genera (Trewick and Morgan-Richards 2004) and in two South African species, in *Libanasidus vittatus* (Kirby, 1899) and in *Libanasa capicola* (Péringuey, 1916)]. In the super-

family Tettigoniodea, there are two genera with tusks. Three species of the Neotropical genus *Listroscelis* Serville, 1831 (Listrocelidinae) have one asymmetrical tusk on the left mandible only (Fialho et al. 2014), while the two known species of the Neotropical genus *Dicranostomus* Dohrn, 1888 (Pseudophyllinae) have a tusk on both mandibles. *Dicranostomus nitidus* Brunner von Wattenwyl, 1895, so far known only from two males, has the relatively longest tusks of all Orthoptera, ranging from 2 to 2.7 times the pronotal length (Brunner von Wattenwyl 1895, Gurney 1950). The second species was, until recently, known from a single female that, interestingly, also bears tusks, but which are distinctly shorter than that of male *D. nitidus*. Having obtained some more specimens of this fascinating genus, including the missing sexes of both species, we herein revise the genus and provide a review of all available data.

## Methods

All specimens were dried, pinned, and photographed using a CANON EOS 1200D. Photos of cerci and mirrors were taken using a dissecting microscope (OLYMPUS SZ Binocular Stereo Zoom Microscope) and a digital camera (SONY Cyber-shot DSC-P120). The inter-tooth distances were measured as the mean between every eleven teeth (ten intervals), starting at the anal end, using ADOBE PHOTOSHOP Elements 6.

The specimens, collected between 2013 and 2018, were obtained from a trader with an export license ([http://gerfor.regionloreto.gob.pe/dublincore/biblioteca/descargar/4269/4500000100020\\_7.PDF](http://gerfor.regionloreto.gob.pe/dublincore/biblioteca/descargar/4269/4500000100020_7.PDF)).

*Depositories.*—

CH	Private collection of K.-G. Heller;
C_Helb	Private collection of M. Helb;
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
MZPW	Polish Academy of Science, Museum of the Institute of Zoology Warszawa, Poland.

## Results

### Taxonomy

Family Tettigoniidae Krauss, 1902

Subfamily Pseudophyllinae Burmeister, 1838

Tribe Eucoconotini Beier, 1960

#### Genus *Dicranostomus* Dohrn, 1888

*Type species: Dicranostomus monoceros* Dohrn, by original monotypy

*Redescription.*—[based on Dohrn 1888 (in Latin), Beier 1960 (in German)].

Medium sized (body length 2.5–4.0 cm), yellowish-brown animals (habitus; Fig. 1). Head as broad as pronotum or broader. Frons shiny, smooth. Fastigium frontis elongated, curved or straight. Fastigium verticis compressed, narrow, with longitudinal furrow. Antennae very long, scapus unarmed. Male mandible at base with a very long, horizontally directed tusk (Fig. 2). Pronotum smooth or slightly granulated, with delicate anterior and medially deeply incised posterior sulcus; metazona flat, only slightly longer than mesozona, laterally no edges, humeral sinus very weak; side lobes longer than high, ventrally nearly straight

and finely edged, caudally weakly ascending, anterior edges even more broadly rounded than the also broadly rounded posterior edges. Openings of the tympanic organ in the fore tibia directing dorsally, slit-like. Auditory prothoracic spiracle quite small, just below the respiratory spiracle. Tegmina just surpassing abdomen, gradually becoming narrow, costal area with wide-meshed veins, Sc (subcosta) and R veins separated. The male mirror on both the left and right wing is translucent (Fig. 3). Teeth in stridulatory file regularly spaced (Fig. 4). Rs (radius sector) arising at the beginning of the apical quarter, media (M) and Sc stalked. Alae roundish, shorter than tegmina. Prosternum with two close spines between prothoracic legs. Mesosternal lobes pointed. Metafurcal pit deep. Middle coxae two-pronged. All femora ventrally armed. Inner genicular lobes of mid and hind femora with spine. Fore tibiae dorsally at the inner edge with a series of small humps. Mid tibiae dorsally with one to three spines internally. Supraanal plate triangular or rounded. Male cerci thick, nearly straight, with subapical spine and apical process (Fig. 5). Male subgenital plate distally narrowed, styli rod-like. Female subgenital plate transverse, slightly incised. Ovipositor short, relatively broad and slightly up-curved, at the upper edge very delicately crenulated (Fig. 6).

*Distribution.*—South America, Peru (Fig. 7).

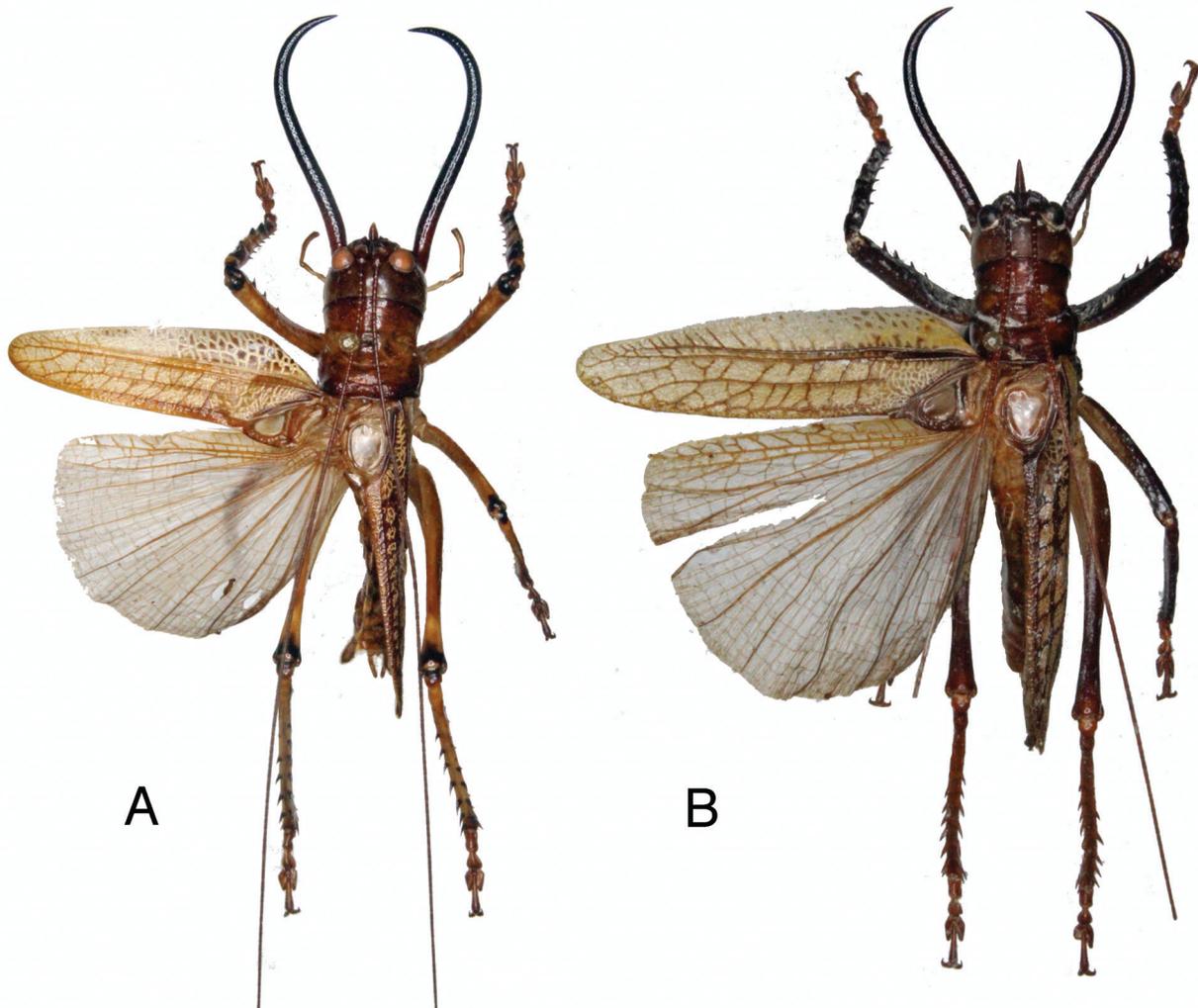


Fig. 1. Male habitus of A. *Dicranostomus monoceros* and B. *D. nitidus* (same scale for both figures).

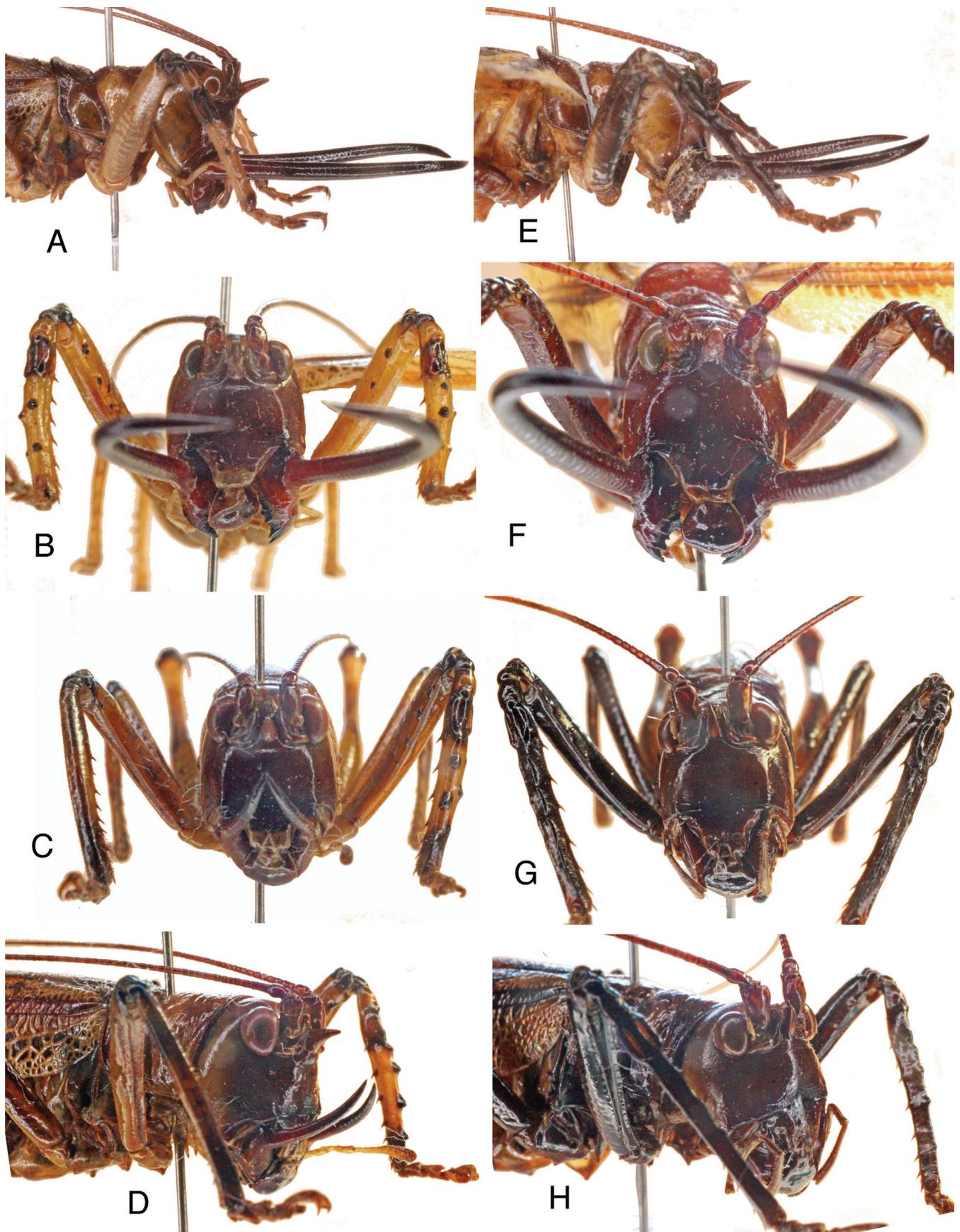


Fig. 2. Morphological details of *Dicranostomus monoceros* (A–D) and *D. nitidus* (E–H; same scale for corresponding figures). A, E. Male head lateral; B, F. Male head frontal; C, G. Female head frontal; D, H. Female head semilateral.

## Key to species (after Brunner von Wattenwyl 1895)

- 1 Pronotum weakly granulated. Knees and spines on legs black.....*D. monoceros*  
 – Pronotum smooth, glossy. Spines on legs and knees same color as leg.....*D. nitidus*

*Dicranostomus monoceros* Dohrn, 1888

Figs 1A, 2A–D, 3A, B, 4A, 5A, 6A

*Dicranostomus monoceros* Dohrn, 1888: 362

**Holotype.**—PERU • ♀; Cumbasi Peruviae ad Huallagam; [Cumbaza]; MZPW. [photos in Cigliano et al. 2021].

**Material examined.**—PERU • 2♂; San Martin Region, Prov. Rioja, Nueva Cajamarca; 10 Nov. 2016; local collector; C\_Helb8771-C\_Helb8772 • 1♀, 1♂; San Martin Region, Prov. Rioja, Nueva Cajamarca; Mar. 2018; local collector; C\_Helb8773-C\_Helb8774 • 2♂; San Martin Region, Prov. Rioja, confluente Altomayo river/Naranjos; 8 Mar. 2018 & 25 Apr. 2018; local collector; C\_Helb8775, ♂ C\_Helb8776.

**Remarks.**—Up to now, the species was known only by the female holotype. In one female (C\_Helb8773), the right foreleg is irregularly developed. Its tibia does not have a tympanic organ or dorsal black tubercles (Fig. 2).

**Redescription.**—General characters as genus.

**Male.** Fastigium frontis elongated horizontally (Fig. 2), mandibles each with one long (2.1–2.8 times as long as pronotum) process (tusk) (Figs 1, 2; Table 1). Pronotum weakly granulated. Fore and mid femora ventrally with 3 spines, hind femora with 4 spines at anterior edge. Fore tibiae dorsally with 2–3 large, black, blunt spine-like tubercles at the anterior and two small tubercles at the posterior edge, ventrally with ca. 6 spines on both sides, mid tibia dorsally with 1–2 spines on posterior edge, ventrally with ca. 6 spines on both sides, hind tibia with ca. 8 spines on all edges, the dorsal larger than the ventral spines. Mirror cell in left tegmen triangular with broadly rounded distal tip, on right tegmen larger, subquadratical (Fig. 3). Stridulatory file on lower side of left tegmen with ca. 130 regularly spaced teeth (inter-tooth interval 20–23 µm; Fig. 4; n=1 file). Supraanal plate transverse, distally rounded. Subgenital plate elongated, with ca. 1 mm long styli. Cerci with internal subapical spine and blunt apical process directed very slightly inwards.

**Female.** General characters as genus and male. Mandibles each with one long (0.8–0.9 times as long as pronotum), slightly upcurved process (tusk). Subgenital plate transverse, at the end straightly cut and distally slightly notched in the middle.

**Coloration.** Head with tusks and pronotum chestnut (tusks becoming darker towards the tips); legs yellowish, but knees, tympanic organ and tubercles in the fore tibia and larger spines in all legs black. Tegmina as in *D. nitidus* (see below). In some animals, the anterior and central lower parts of the paranota are brighter and more yellowish than the other parts.

**Measurements.**—See Table 1.

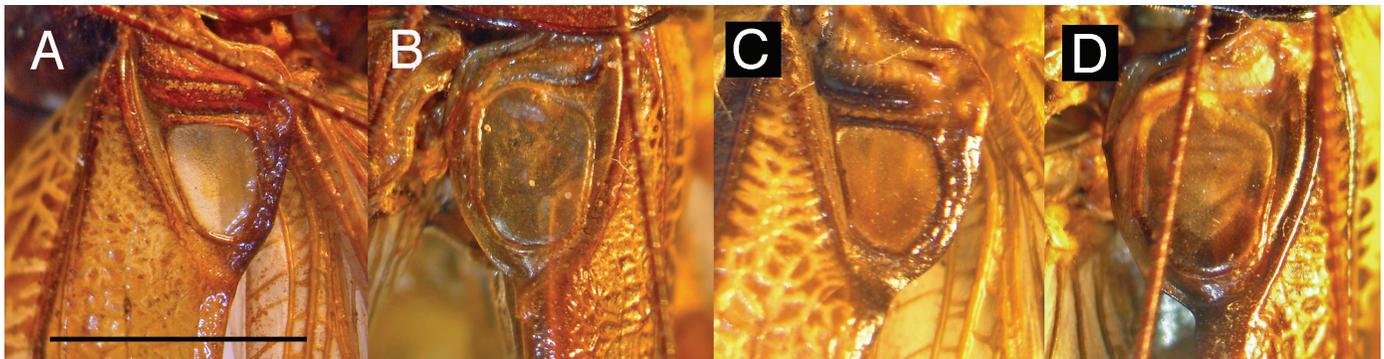


Fig. 3. Mirror cells of *Dicranostomus monoceros* (A, B) and *D. nitidus* (C, D). A, C. Left tegmen; B, D. Right tegmen. Scale bar: 5 mm.

Table 1. Measurements of males and females of both species of *Dicranostomus* (\*data from Beier 1960).

Species	Specimen #	Sex	Measurements (in mm)								
			body	body + tusk	pronotum	fore femur	hind femur	tegmen	antenna	tusk	ovipositor
<i>D. monoceros</i>	type*	♀	28		6.5	10.5	19	27	-	6	15
	C_Helb8773	♀	32	35	6.5	10.5	16.5	23	120	5.5	15.5
	C_Helb8771	♂	27	41	6	10	14.5	20	95	16	
	C_Helb8772	♂	32	44	7	11	16	21.5	95	15	
	C_Helb8774	♂	29	44	6	10.5	15.5	22	95	16.5	
	C_Helb8775	♂	27	40	6.5	10.5	16	21	-	16.5	
	C_Helb8776	♂	28.5	40	6.5		15.5	21	80	17	
<i>D. nitidus</i>	type*	♂	30		7	11.5	20	22	-	14	
	Gurney 1950	♂	35	58	7.5	12	19	26	-	20	
	CH4220	♂	38	53	7.5	12	20.5	27	-	18	
	C_Helb8769	♂	36	47	7.5	12	19.5	26	72	13.5	
	C_Helb8770	♀	33	-	7.5	12	20	28.5	100		17.5
	C_Helb8777	♂	36	49	7.5	13	19	27.5	68	17	

***Dicranostomus nitidus* Brunner von Wattenwyl, 1895**

Figs 1B, 2E–H, 3C, D, 4B, 5B, 6B

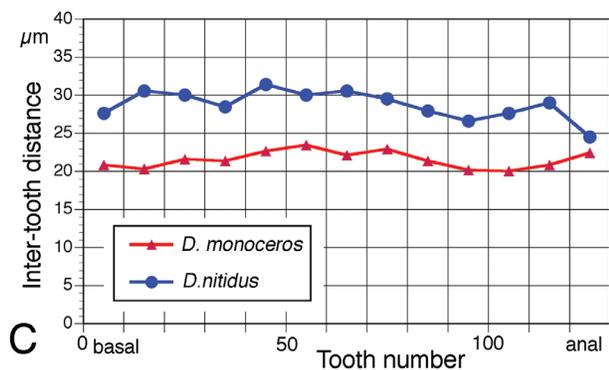
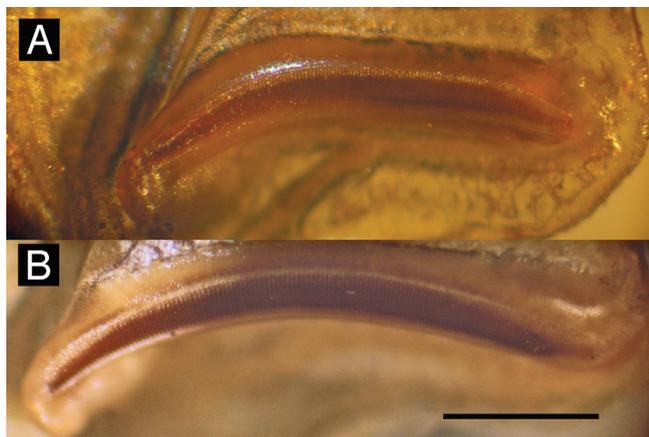
*Dicranostomus nitidus* Brunner von Wattenwyl, 1895: 180*Holotype*.—PERU • no details; ISNB. [photos in Cigliano et al. 2021].*Published record*.—PERU • 1♂; Department of Huanuco, Fundo Sinchono, 37 miles east of Tingo Maria on the road to Pucallpa; 1700 m a.s.l.; 5 Aug. 1947; Jose Schunke leg.; (Gurney 1950).*Material examined*.—PERU • 1♂; Oxapampa; Feb.–Apr. 1984; Rainer Marx leg.; CH4220 • 1♂, 1♀; Prov. Huanuco, Huanuco Road, between Huanuco and Tingo Maria, Malqui [Macora?] town, fog area [sic]; Aug. 2013; local collector; C\_Helb8769–C\_Helb8770 • 1♂; San Martin Region, Prov. Rioja, Nueva Cajamarca; Mar. 2018; local collector [assumed exchange of labels—see list for localities of *monoceros*]; C\_Helb8777*Remark*.—The species was known only by the male holotype and another male, described by Gurney (1950).*Reescription*.—General characters as genus.**Male.** Fastigium frontis elongated horizontally (Fig. 2), mandibles each with one long (1.8–2.7 times as long as pronotum) process (tusk) (Figs 1, 2, Table 1). Pronotum smooth. Fore and mid femora ventrally with 3–4 spines, hind femora with 4–6 spines at anterior edge. All tibiae ventrally with several spines on both sides; however, hind tibia ventrally only with few spines at tip of poste-

Fig. 4. Stridulatory files in *Dicranostomus*. A. *D. monoceros* (C\_Helb8775); B. *D. nitidus* (CH4225); C. Inter-tooth distances (specimens as in A, B). Scale bars: 1 mm (A, B).

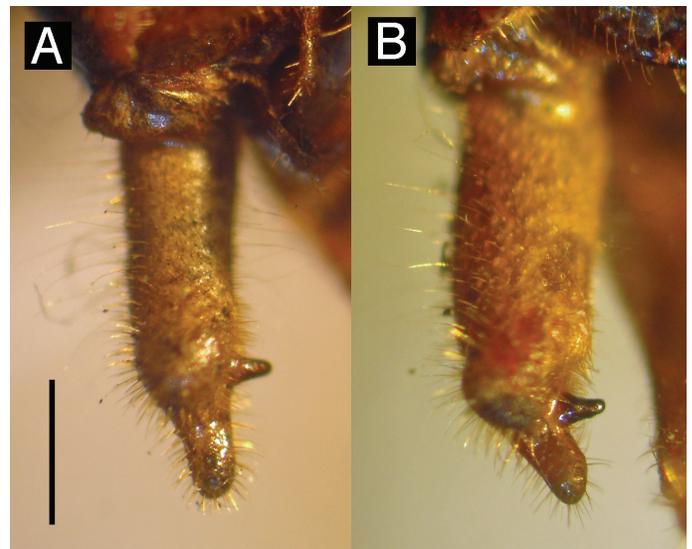


Fig. 5. Male cerci of A. *Dicranostomus monoceros* and B. *D. nitidus*. Scale 1 mm.



Fig. 6. Ovipositor of A. *Dicranostomus monoceros* and B. *D. nitidus* (same scale for both figures).



Fig. 7. Distribution map of *Dicranostomus* (all known localities; map based on SimpleMappr (Shorthouse 2010)).

rior edge. Fore tibiae dorsally with 4–5 blunt spine-like tubercles at the anterior edge, ventrally with ca. 6 spines on both sides, midtibia dorsally with 1–2 spines on posterior edge, ventrally with ca. 6 spines on both sides, hind tibia with ca. 8 spines on each edge, the dorsal larger than the ventral spines; however, ventrally only with few spines at tip of posterior edge. Mirror cells in both tegmina subquadratical; in the right larger than in the left (Fig. 3). Stridulatory file on lower side of left tegmen with ca. 130 regularly spaced teeth (inter-tooth interval 24–32  $\mu\text{m}$  = tooth density ca. 30  $\text{mm}^{-1}$ ; Fig. 4;  $n=1$  file), Supraanal plate transverse, distally rounded, or broadly cut off. Subgenital plate elongated, with ca. 1 mm long styli. Cerci with internal subapical spine and blunt apical process, directed inwards at an angle of about 40 degrees (Fig. 5).

**Female.** General characters as genus and male. Fastigium frontis elongated vertically (Fig. 2), mandibles without process (tusk). Subgenital plate transverse, at the distal end slightly and triangularly elongated and slightly incised in the middle.

**Coloration.** “Head, thorax and legs chestnut, the tibiae darker, the mandibular appendages practically black, palpi pale. .... tegmen with veins brown, cellules and membrane yellowish, much brighter toward base in costal area; wing with veins pale brown, membrane slightly fuscous” (Gurney 1950). However, other specimens (C\_Helb8769, C\_Helb8777) not chestnut, but more olive-brown with pro- and metazona of pronotum darker than mesozona or pronotum uniform.

*Measurements.*—See Table 1.

## Discussion

The genus *Dicranostomus* belongs to the tribe Eucocconotini, which is part of the supertribe Pleminiiti Brunner von Wattenwyl, 1895 (Braun 2015) (or the subfamily Pleminiinae; Gorochov 2012). Within this tribe, the genus is most similar to *Gnathoclita* Haan, 1843 (see Gorochov 2012), with both genera having the “dorsal surface of anterior tibiae granular or with distinctive tubercles” (Cadena-Castañeda and Monzón-Sierra 2014). According to the key provided by these authors, males of the two genera are easily separable by their mouth parts: *Dicranostomus* males have tusks and *Gnathoclita* males have enlarged mandibles. The females, however, differ only in the presence of dorsal spine(s) on the middle tibia in *Dicranostomus*. Only *D. monoceros* females have tusks like their males. Possibly, both genera can also be separated by the presence of an elongated (either horizontally or vertically) fastigium frontis in *Dicranostomus*. Such a structure is not described nor figured for any *Gnathoclita* (*s.str.*; *sensu* Gorochov 2018) species [see *G. izerskyi* Gorochov, 2018, *G. peruviana* Carl, 1921 (Gorochov

2014), *G. laevifrons* Beier, 1960, *G. sodalis* Brunner von Wattenwyl, 1895, and *G. vorax* (Stoll, 1813) (Beier 1960)], although data for females are sparse.

*Dicranostomus* and *Gnathoclita* are also similar in the shape of their mirrors (compare Fig. 4 to figs 20, 21, 27, 28 in Gorochov 2018, and to fig. 7D in Hugel 2019) and—to a limited extent—in their stridulatory files. In tooth number, *Dicranostomus* (130 teeth) is situated between the two known *Gnathoclita* species (*G. vorax* c.101 teeth (Hugel 2019), *G. sodalis* 217 teeth (Montealegre-Z and Morris 1999)). The inter-tooth distances in both species (*G. vorax* 30  $\mu\text{m}$ ; *G. sodalis* 10  $\mu\text{m}$ ) correlate negatively with the carrier frequencies of their resonant songs (*G. vorax*, 8.8 kHz; *G. sodalis*, 16 kHz). From these data, it can be assumed that *Dicranostomus* males also sing in this audio range (but perhaps with each species at a different peak frequency) and that they can be located with unaided ears.

Unfortunately, no data are available concerning the function of the most distinctive structure of *Dicranostomus*: the tusks. These tusks are the longest found among Orthoptera in comparison to the male body size (measured relative to pronotal length) and are clearly longer than in the well-known tusked wetas (Table 2). In *Dicranostomus*, the tusks do not show any indication of being stridulatory structures, as documented for some wetas (Field 2001). However, although there are no observations of the use of the tusks, there are three lines of evidence that all point in the same direction. In his review about animal weapons, Emlen (2008) writes in the context of resource-defense or female-defense mating systems: “In a surprising diversity of taxa, these critical resources were burrows or tunnels where females lay eggs, and the especially defensible nature of burrows may have played an important role in favoring the evolutionary enlargement of weapons in these cases.” In line with these conclusions, the three New Zealand orthopteran species with long tusks (see Table 1) all inhabit burrows in the ground or holes in trees (see Treweek and Morgan-Richards 2014 for a review). The tusked king cricket *Libanasisidus vittatus* digs holes every night but may sometimes return to previously used holes (Bateman and Toms 1998). Also supporting these ideas, new behavioral observations in the genus *Gnathoclita*, sister to *Dicranostomus* (e.g., Gorochov 2012), have shown that *G. vorax* also inhabits the hollow dead stems of plants, with the males displaying “a form of mate guarding” (Hugel 2019). Thus, in our opinion, it is a plausible hypothesis that *Dicranostomus* inhabits holes, probably in plant material, and that the males defend these safe places against rivals using their tusks. Holes in plants are also used by other acoustically active species like frogs (e.g., the tree hole frog *Metaphrynella sundana*; Lardner & bin Lakim 2002). In *Disceratus* Scudder, 1869, a related genus, its low acoustically determined population density is used as an argument against male to male combat (Braun 2016). Thus, other reasons for

**Table 2.** Absolute and relative (compared to pronotum) tusk length in Orthoptera.

Species	Specimen(s)	Sex	Length (in mm) of			Tusk length / pronotum length	Source
			pronotum	hind femur	Tusk (range)		
<i>D. monoceros</i>	mean	♂	6.4	15.5	16.2 (15.17)	2.5	this paper
	mean	♀	6.5	17.8	5.8 (5–6)	0.9	this paper
<i>D. nitidus</i>	mean	♂	7.4	19.6	17.1 (18–27)	2.2	this paper
	holotype	♂	15	38.0	26.0	1.7	Johns 1997
<i>Motuweta isolata</i>	paratype	♂	10	28.0	9.0	0.9	Johns 1997
	mean	♂	12.5	33.0	17.5	1.4	Johns 1997
	mean	♂	7.7	24.0	6.4 (3–12)	0.8	Gibbs 2002
<i>Motuweta riparia</i>	mean	♂	7.7	24.0	6.4 (3–12)	0.8	Gibbs 2002
<i>Anisoura nicobarica</i>	holotype	♀	4.6	10.6	0.0		Ander 1933
	syn. <i>monstrosa</i>	♂			6.0	c. 1.3	Salmon 1950
<i>Libanasisidus vittatus</i>	mean	♂	9	21.5	7.5 (7–8)	0.8	Péringuey 1916
<i>Libanasa capicola</i>	holotype	♂		17.0	7.0	0.8	from figure; Péringuey 1916

the tusks should not be excluded. Completely unknown, however, is the function of the female tusks in *D. monoceros*. Females of *D. nitidus* do not possess tusks, but they have a strongly elongated fastigium frontis, as found in both sexes of *D. monoceros* and in *D. nitidus* males. Gwynne (2001) speculated on the probability of female-to-female interactions in *D. monoceros*, and certainly the access, possession, and defense of holes may be important for females as well. Unfortunately, data to confirm or deny this are missing.

## Acknowledgements

We are grateful to Holger Braun, Sigfrid Ingris, Ming Kai Tan, and an anonymous referee for helpful comments on the manuscript. The Orthopterists' Society provided free publication of this paper. Duplication of information presented in Cigliano et al. 2021 on request of the main editor.

## References

- Ander K (1933) Über *Anisoura nicobarica* m., eine bemerkenswerte Laubheuschrecke aus der Familie Gryllacrididae (Orth. Saltatoria). *Konowia*, 12: 217–230. [https://www.zobodat.at/pdf/KON\\_12\\_0217-0230.pdf](https://www.zobodat.at/pdf/KON_12_0217-0230.pdf)
- Bateman PW, Toms RB (1998) Mating, mate guarding and male-male relative strength assessment in an African king cricket (Orthoptera: Mimnermidae). *Transactions of the American Entomological Society* 124: 69–75. <https://www.jstor.org/stable/25078654>
- Beier M (1960) Orthoptera Tettigoniidae (Pseudophyllinae II). In: Mertens R, Hennig W, Wermuth H (Eds) *Das Tierreich*. 74. Walter de Gruyter & Co, Berlin, 396 pp.
- Braun H (2015) On the family-group ranks of katydids (Orthoptera, Tettigoniidae). *Zootaxa* 3956: 149–150. <https://doi.org/10.11646/zootaxa.3956.1.10>
- Braun H (2016) Notes on the tropical Andean genus *Disceratus* (Orthoptera, Tettigoniidae, Pseudophyllinae), the probable male of *D. nubiliger*, and its calling song. *Journal of Orthoptera Research* 25: 1–15. <https://doi.org/10.1665/034.025.0102>
- Brunnervon Wattenwyl C (1895) Monographie der Pseudophylliden. Kaiserlich-Königliche Zoologisch-Botanischen Gesellschaft, Vienna, 282 pp. [https://www.zobodat.at/pdf/MON-E-ORTH\\_0007\\_0001-0282.pdf](https://www.zobodat.at/pdf/MON-E-ORTH_0007_0001-0282.pdf)
- Burmeister H (1838) *Handbuch der Entomologie*, Zweiter Band. Besondere Entomologie. Zweite Abtheilung Kaukerfe, Gymnognatha. Erste Hälfte; vulgo Orthoptera. T.C.F. Enslin, Berlin, 457–756.
- Cadena-Castañeda OJ, Monzón-Sierra J (2014) A new species of the genus *Onychopygia* Beier (Orthoptera: Tettigoniidae: Pseudophyllinae) from Guatemala. *Insecta Mundi* 0329: 1–8. <https://journals.flvc.org/mundi/article/view/82728/79636>
- Carl J (1921) Phasgonurides nouveaux du Muséum de Genève. *Revue Suisse de Zoologie* 28: 301–309. <https://www.biodiversitylibrary.org/page/10708169>
- Cigliano MM, Braun H, Eades CD, Otte D (2021) Orthoptera Species File. Version 5.0/5.0. [01/01/2021] <http://Orthoptera.SpeciesFile.org>
- Dohrn H (1888) Ueber einige merkwürdige Pseudophylliden. *Stettiner Entomologische Zeitung* 49: 353–362. [https://www.zobodat.at/pdf/Entomologische-Zeitung-Stettin\\_49\\_0353-0362.pdf](https://www.zobodat.at/pdf/Entomologische-Zeitung-Stettin_49_0353-0362.pdf)
- Emlen DJ (2008) The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics* 39: 387–413. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173502>
- Fialho VS, Chamorro-Rengifo J, Lopes-Andrade C, Yotoko KSC (2014) Systematics of spiny predatory katydids (Tettigoniidae: Listrosclidinae) from the Brazilian Atlantic Forest based on morphology and molecular data. *PLoS ONE* 9: e103758. <https://doi.org/10.1371/journal.pone.0103758>
- Field LH (2001) Stridulatory mechanisms and associated behaviour in New Zealand wetas. In: Field LH (Ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI, Wallingford, 271–295. <https://doi.org/10.1079/9780851994086.0271>
- Field LH, Deans AN (2001) Sexual Selection and Secondary Sexual Characters of Wetas and King Crickets. In: Field L (Ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI, Wallingford, 179–204. <https://doi.org/10.1079/9780851994086.0179>
- Gibbs GW (2002) A new species of tusked weta from the Raukumara Range, North Island, New Zealand (Orthoptera: Anostostomatidae: *Motuweta*). *New Zealand Journal of Zoology* 29: 293–301. <https://doi.org/10.1080/03014223.2002.9518313>
- Gorochov AV (2012) Systematics of the American katydids (Orthoptera: Tettigoniidae). Communication 1. Proceedings of the Zoological Institute of the Russian Academy of Sciences, 316: 3–21. [https://www.zin.ru/journals/trudyzin/doc/vol\\_316\\_1/TZ\\_316\\_1\\_Gorochov.pdf](https://www.zin.ru/journals/trudyzin/doc/vol_316_1/TZ_316_1_Gorochov.pdf)
- Gorochov AV (2014) Systematics of the American katydids (Orthoptera: Tettigoniidae). Communication 3. Proceedings of the Zoological Institute RAS Vol. 318: 109–147. [https://acrenap.com/wp-content/uploads/2020/01/tz\\_318\\_2\\_gorochov.pdf](https://acrenap.com/wp-content/uploads/2020/01/tz_318_2_gorochov.pdf)
- Gorochov AV (2018) Systematics of the American katydids (Orthoptera: Tettigoniidae). Communication 8. Proceedings of the Zoological Institute RAS Vol. 322: 398–456. <https://doi.org/10.31610/trudyzin/2018.322.4.398>
- Gurney AB (1950) On *Dicranostomus*, a remarkable Peruvian genus of katydids; and notes on other insects having elongate mandibles (Orthoptera: Tettigoniidae). *Annals of the Entomological Society of America* 43: 546–554. <https://doi.org/10.1093/aesa/43.4.546>
- Gwynne DT (2001) *Katydids and Bush-Crickets*. Cornell University, Ithaca, 317 pp.
- Haan W de (1843) Bijdragen tot de kennis der Orthoptera. In: Temminck CJ (Ed.) *Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche Overzeesche Bezittingen, de Leden der Natuurkundige Commissie in Indië en andere Schrijvers* 19/20: 165–228.
- Hugel S (2019) *Panoploscelis scudderi* Beier, 1950 and *Gnathoclitia vorax* (Stoll, 1813): two katydids with unusual acoustic, reproductive and defense behaviors (Orthoptera, Pseudophyllinae). *Zoosystema* 40: 327–340. <https://doi.org/10.5252/zoosystema2019v41a17>
- Johns PM (1998) The Gondwanaland weta: family Anostostomatidae (formerly in Stenopelmatidae, Henicidae or Mimnermidae): nomenclatural problems, world checklist, new genera and species. *Journal of Orthoptera Research* 6: 125–138. <https://doi.org/10.2307/3503546>
- Kirby WF (1899) Notes on a collection of Gryllidae, Stenopelmatidae, Gryllacridae, and Hetrodidae formed by Mr. W.L. Distant in the Transvaal and other South- and East-African localities. *Annals and Magazine of Natural History* 3: 475–480. <https://doi.org/10.1080/00222939908678153>
- Krauss HA (1902) Die Namen der ältesten Dermapteren- (Orthopteren-) Gattungen und ihre Verwendung für Familien- und Unterfamilien-Benennungen auf Grund der jetzigen Nomenclaturregeln. *Zoologischer Anzeiger* 25: 530–543.
- Lardner B, bin Lakim M (2002) Tree-hole frogs exploit resonance effects. *Nature* 420: e475. <https://doi.org/10.1038/420475a>
- Montealegre-Z F, Morris GK (1999) Songs and systematics of some Tettigoniidae from Columbia and Ecuador I. Pseudophyllinae (Orthoptera). *Journal of Orthoptera Research* 8: 163–236. <https://doi.org/10.2307/3503439>
- Péringuey L (1916) Descriptions of new or little-known Orthoptera in the collection of the South African Museum. *Annals of the South African Museum* 15: 401–452. [pl. 42.] <https://doi.org/10.5962/bhl.part.22199>
- Salmon JT (1950) A revision of the New Zealand wetas – Anostostominae (Orthoptera, Stenopelmatidae). *Dominion Museum Records in Entomology, New Zealand* 1: 121–177. <http://www.bugz.org.nz/WebForms/ResultDetails.aspx?CurrentDoc=E3878A90-CE05-401A-A30A-D75D1B60D9AD&CurrentPage=57&searchType=1&StArtChar=>
- Scudder SH (1869) Entomological notes II: Notes on Orthoptera collected by Prof. James Orton on either side of the Andes of Equatorial South America. *Proceedings of the Boston Society of Natural History* 12: 330–345. <https://www.biodiversitylibrary.org/page/9493972>

- Shorthouse DP (2010) SimpleMapp, an online tool to produce publication-quality point maps. <http://www.simplemapp.net/> [accessed 05 October 2020]
- Stoll C (1813) *Natuurlijke en naar het leven nauwkeurig gekleurde afbeeldingen en beschrijvingen der spoken, wandelende bladen, zabel-springhanen, krekels, trek-springhanen en kakkerlakken*. J.C. Sepp & Sohn, Amsterdam, 344 pp. [Dutch and French] <https://doi.org/10.5962/bhl.title.169412>
- Trewick S, Morgan-Richards M (2004) Phylogenetics of New Zealand's tree, giant and tusked weta (Orthoptera: Anostomatidae): evidence from mitochondrial DNA. *Journal of Orthoptera Research* 13: 185–196. [https://doi.org/10.1665/1082-6467\(2004\)013\[0185:PONZ TG\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2004)013[0185:PONZ TG]2.0.CO;2)
- Trewick S, Morgan-Richards M (2014) *New Zealand Wildlife*. Publisher Penguin Books, Auckland, 240 pp.