On the morphology and possible function of two putative vibroacoustic mechanisms in derbid planthoppers (Hemiptera: Fulgoromorpha: Derbidae)

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Abstract

A mechanism involving interaction of the metathoracic wing and third abdominal segment of derbid planthoppers was first discovered over a century ago, and interpreted as a stridulatory organ for sound production. Although referred to occasionally in later taxonomic works, the detailed morphology, systematic distribution, and behavioural significance of this structure have remained unknown, and its proposed use in sound production has never been corroborated. Here we examine the distribution and morphology of the supposed stridulatory organ of Derbidae and the recently-described vibratory mechanism of planthoppers – the snapping organ, across 168 species covering the entire taxonomic spectrum of the family. We find that many derbids possess snapping organs morphologically similar to those of other planthoppers, and find no evidence for the presence of tymbal organs, which were previously thought to generate vibrational signals in derbids. We find the supposed stridulatory mechanism to be widespread in Derbidae, and conclude that it provides several systematically and taxonomically important characters. Nevertheless, its morphology appears unsuitable for the production of sound, and we instead speculate that the mechanism plays a role in spreading chemical secretions or wax. Finally, we observe wax production by tergal glands in derbid larvae, and illustrate their external morphology in adults.

Key words

snapping organ, stridulation, tergal glands, tymbal, Auchenorrhyncha, Fulgoroidea

Highlights

- Supposed stridulatory organs are widespread in Derbidae.
- Their morphology does not appear well adapted to producing sound.
- Many derbids possess snapping organs, but we found no tymbal-like organs.

- Tergal glands produce wax filaments in some derbid larvae.

1. Introduction

Hemiptera, or true bugs, exploit acoustic and substrate-borne vibrational communication more than any other insect Order (Cocroft & Rodriguez, 2005). Hemipterans are known to generate such vibrations in various ways, including: (i) stridulation, where a scraper (plectrum) and a file (stridulitrum) are moved against one another to generate sound (Čokl et al., 2006); (ii) buzzing (Kavčič et al., 2013), in which the wings are vibrated to generate sound; (iii) percussion, where the legs tap against a surface (Žunič et al., 2008); (iv) tremulation, where the body vibrates relative to the legs (Žunič et al., 2008; Kavčič et al., 2013); (v) tymbal buckling, which is a bistable mechanism involving a buckling membrane, usually with ribs that pop bent then straight (Young & Bennet-Clark, 1995); and (vi) abdominal snapping, in which the abdomen is jerked up and down using a newly-described mechanism involving the snapping shut then open of a Y-shaped cuticular lobe (Davranoglou et al., 2019a). The last of these mechanisms, known as a snapping organ (Davranoglou *et al.*, 2019a), is present throughout the planthoppers (Hemiptera: Fulgoromorpha), including within the family Delphacidae, in which the snapping organ appears to have been modified (Davranoglou *et al.*, 2019a) into a highly-specialised structure referred to previously as a drumming organ (Mitomi et al., 1984). The only other vibroacoustic mechanisms identified in planthoppers to date are a supposed stridulatory apparatus found within the family Derbidae (see Kirkaldy, 1907).

Derbids are among the most taxonomically diverse planthoppers, with *ca.* 1,700 described species occurring primarily in tropical and subtropical areas (Bartlett et al., 2014; Bourgoïn, 2019). Their morphology is similarly diverse. Defining traits of derbids include a small and tapered apical labial segment; a row of spines on the second hind tarsal segment; and parameres that greatly extend beyond the abdomen (Wilson, 2005; Bartlett et al., 2014). Peculiar modifications in some taxa include forward-facing expansions of the pronotum known as subantennal processes; greatly enlarged, sexually dimorphic antennae; and unique antennal appendages (Emeljanov, 1996; Bourgoïn & Yap, 2010; Bartlett et al., 2014). In terms of their habits, derbid larvae are considered mycophagous, and can be found in rotting logs and leaf litter (O'Brien & Wilson, 1985; Yang & Yeh, 1994; Howard et al., 2001; Gossner & Damken, 2018), whereas adults typically feed on monocot plants (often palms) and woody dicot plants (Wilson et al., 1994; Howard et al., 2001), often forming large aggregations under their leaves (Kirkaldy, 1907; O'Brien, 2002). Approximately 20 species are potential agricultural pests, and some may transmit phytoplasmas (Wilson, 2005; Brown et al., 2006; Halbert et al., 2014).

Within the Derbidae, substrate-borne vibrational signals have so far been recorded only from *Cedusa* spp., their origin having been speculatively attributed to as yet unknown tymbal organs (Tishechkin, 2003, 2008). On the other hand, Davranoglou et al. (2019a) recently reported the presence of a snapping organ in some Derbidae, so it is reasonable to suppose that derbids may instead produce substrate-borne vibrations using an abdominal snapping mechanism similar to that of other planthoppers. Acoustic signalling has not yet been experimentally demonstrated in planthoppers, but the eminent hemipterist F.A.G. Muir reported noise emanating from hundreds of individuals of the derbid *Muiria stridula* Kirkaldy, 1907, which were aggregating under a palm. Based on his observations of live animals, Muir identified the sound as being stridulatory in origin, and proposed a mechanism where a part of the metathoracic (hind) wing

is modified into a stridulitrum and strikes against a field of hairs on the abdomen, supposed to act as a plectrum. Since Muir's original observations and illustrations (reported in Kirkaldy, 1907), the supposed stridulitrum has occasionally been used in descriptive taxonomy and classification of derbids (e.g. Fennah, 1952; Emeljanov, 1996; Banaszkiewicz & Szwedo, 2005), albeit that its detailed morphology, systematic distribution, homologies, and function have remained unstudied. The abdominal hairs that Muir interpreted as functioning as a plectrum have been neglected by most subsequent studies, and their structure and distribution has remained undocumented. In addition, there have been no subsequent observations of acoustic signalling in derbids that would confirm Muir's observations, and the function of this unusual mechanism has not been examined in a behavioural context.

In order to gain a better understanding of the morphological basis of vibroacoustic or vibrational communication in derbids, we examined the external morphology of the pregenital abdominal segments and putative stridulatory structures of 168 species of Derbidae, covering almost all currently recognised subfamilies, tribes, and subtribes of the family. We also investigated the internal morphology of one species using synchrotron-based micro computed tomography (SR- μ CT). Our findings confirm the presence of a snapping organ in Derbidae, and present novel morphological information which may be important for reconstructing the systematics and taxonomy of Derbidae, and provide a new perspective on the functional morphology and behavioural significance of the supposed stridulatory mechanism of the group. Finally, we also show wax production from tergal glands in derbid larvae, and detail the external morphology of the tergal glands of adults for the first time.

2. Material and Methods

2.1. Material

2.1.1. Specimens examined using stereomicroscopy

We examined dry-mounted specimens of 168 species under a stereomicroscope (Table S1), using material deposited in the Natural History Museum, London, UK (BMNH) and the Moravian Museum, Brno, Czech Republic (MMBC).

2.1.2. Specimens examined using other techniques

We also analysed the following species using the methods described in Sections 2.2. –2.5, based on material deposited at the BMNH, MMBC, the Oxford University Museum of Natural History, UK (OUMNH), as well as some specimens in the wild:

Adults

- 115 1. *Alara fumata* (Melichar, 1914). Male holotype, Indonesia, Java, Goenoeng Oengaran,
116 xii.1909, E. Jacobson leg. (coll. Melichar, MMBC).
- 117 2. *Cedusa* sp. Two males, Peru, Callanga (coll. Melichar, MMBC).
- 118 3. *Derbe* sp. One male, Ecuador, Pichincha, Nambillo Valley near Mindo, 1450 m, 15.viii.
119 1987, M. Cooper leg. (BMNH).
- 120 4. *Kaha* sp. One male, Philippines, Luzon, Los Banos, P. I. Baker leg. (coll. Melichar, MMBC).
- 121 5. *Malenia bosnica* (Horváth, 1907). One male, Bulgaria, gara Kresna railway station, Kresna
122 Gorge near Struma River, 230–300 m, 20–21.viii.1972, P. Lauterer leg. One female, Bulgaria,
123 Lilyanovo, towards Sandanski, Sandanska Bystrica valley, 13.vii.1971, P. Lauterer leg. (both
124 MMBC).
- 125 6. *Mysidia* sp. One male, Ecuador, Shushufindi, ii.1987, ex palms in forest, B. Pertnui leg.,
126 CIE A18814, sp. 235 (BMNH).
- 127 7. *Omolicna joi* Wilson, Halbert & Bextine, 2014. One male and one female, USA, Florida,
128 Highlands County, Venus, Archbold Biological Station, 27°10'53"N, 81°20'54"W, 45–69 m,
129 1–2.x.2016, scrub with *Sabal etonia* and *Serenoa repens*, I. Malenovský leg. (MMBC).
- 130 8. *Paraphenice mawae* Wilson, 1987. One male paratype, Tanzania, Chambezi, iv.1984, on
131 *Cocos nucifera*, M. Schuiling leg., C.I.E. AI5996 (BMNH).
- 132 9. *Proutista* sp. One male, Uganda, Unyoro, Bugoma “oserdo” 3700, vii. 1914, Kittenberger
133 leg. dd '19, C.A. Wiggins (OUMNH).
- 134 10. *Zoraida pterophoroides* (Westwood, 1851). One female, India, Assam, Khasia (coll.
135 Melichar, MMBC).
- 136 11. *Zoraida* sp. 1. One male, SUNII, Indonesia, Sulawesi, Toraut, viii.1985, S. Greenwood leg.
137 (OUMNH-2010-089).
- 138 12. *Zoraida* sp. 2. One female, same data label as above (OUMNH).

139 *Larvae*

- 140 1. *Pamendanga* sp. Fifth instar, Singapore, Zhenghua park, 21.x.2016, photographed by N.
141 Bay.
- 142 2. *Zoraida* sp. Fifth instar, Singapore, 14.ix.2014, photographed by N. Bay.

2.2. Photomicrography

The metathoracic wing and abdomen of *Proutista* sp. and *Derbe* sp. were imaged using a Leica M165c microscope with a Leica DFC490 camera, while stacked images were combined using Helicon Focus (Helicon Soft, Kharkiv, Ukraine). The slide-mounted metathoracic wings of *Alara fumata*, *Malenia bosnica* and *Omolicna joi* and a spread metathoracic wing of a dry-mounted specimen of *Zoraida pterophoroides* were imaged using a Keyence VHX-5000 digital microscope with VH-Z20T and VH-ZST objectives.

2.3. Macrophotography

The two derbid larvae, tentatively identified as *Zoraida* sp. and *Pamendanga* sp., were photographed in the wild by Nicky Bay (see Acknowledgments) using a Nikon D800 camera equipped with a Tamron 90mm F2.8 SP Di Macro Lens.

2.4. Scanning Electron Microscopy (SEM)

Two critical point-dried specimens of Zoraidinae (*Zoraida* sp. 1 & sp. 2) and a dry-mounted specimen of *Mysidia* sp. were examined in a JEOL Neoscope JCM-5000 (SEM, JEOL, Ltd) at 15 kV high vacuum, following coating for 150 s at 18 mA with gold/palladium (Quorum Technologies SC7620), giving a coating of 12.5 nm. Scanning electron micrographs of *Cedusa* sp., *Omolicna joi* and *Kaha* sp. were taken from dry-mounted specimens without coating by a Hitachi S-3700N environmental electron microscope at 15 kV high vacuum.

2.5. SR- μ CT

A specimen of a critical-point dried *Zoraida* sp.1 was scanned at the TOMCAT beamline, Swiss Light Source (SLS), Paul Scherrer Institut, Switzerland, at a beam energy of 15.99 keV with final pixel size of 1.625 μ m. Three-dimensional reconstruction was carried out using Amira 6.1 software (Mercury Systems). Image labelling and illustrations were generated in Adobe Illustrator CC/CS6 (Adobe Systems Incorporated, San Jose, California, USA).

2.6. Terminology

We follow the terminology of Dworakowska (1988) regarding metathoracic wing venation. Although we describe a posterobasal sclerotisation/pigmentation of the metathoracic wing membrane that Dworakowska (1988) identified as the posterior jugal vein (JP), we are

uncertain on whether it represents a true vein. This structure may in fact be a secondarily detached thoracic sclerite, in particular from the posterior notal wing process – a transformation which frequently occurs in other insects (e.g. Snodgrass, 1935; as a fourth axillary sclerite). According to the same author, the posterior anal (AP) and anterior jugal (JA) veins fuse basally in most Auchenorrhyncha. We indeed observe a close basal association of the two veins, but noting that their situation is unclear, we refer to them as AP and JA respectively.

Wessel et al. (2014) used the term “tymbalian tymbal” to describe the vibroacoustic organs of all non-sternorrhynchan Hemiptera (Tymbalia), which they hypothesised were homologous. In this study, our definition of a tymbal is a strictly biomechanical one, describing an organ that uses paired buckling membranes, with or without buckling ribs, in order to generate vibroacoustic signals. This definition encompasses the primary vibrational organs of most Cicadomorpha, which are characterised morphologically by the presence of paired, buckling membranes on the lateral margin of tergum 1, which may or may not possess buckling ribs (Ossiannilsson, 1949). The snapping organ described by Davranoglou et al. (2019a), is mechanically and structurally distinct from cicadomorphan tymbals, and its external morphology consists of three main defining characters: 1) a ridge arising from the part of the first abdominal tergum which is fused to the thorax; 2) a Y-shaped lobe with two “arms” which snap together suddenly following contraction of the hypertrophied dorsal longitudinal muscles of the 1st abdominal segment (Idlm1-2); and 3) a membranous connector at the base of the Y-lobe which link it to tergum 2. We use these traits, along with their associated musculature, to identify the presence or absence of the snapping organ in Derbidae. We followed Bourgoïn (2019) for taxonomic nomenclature and classification. The derbid larvae on Fig. 10A, B were identified using the keys in Yang & Yeh (1994).

Abbreviations used in the figures: **AA**: Anterior Anal; **ajf**: anojugal fold; **AP**: Posterior Anal; **axc**: axillary cord; **C**: Costa; **CuA**: Anterior Cubitus; **CuP**: Posterior Cubitus; **cv**: cross-vein; **dm**: dense material; **gl**: tergal gland; **gr**: groove of tergal gland; **Idlm1**: group I dorsal longitudinal muscle of tergum 1; **JA**: Anterior Jugal; **JP**: Posterior Jugal; **l**: lumen; **lb**: Y-lobe of snapping organ; **lp**: loop of dense material; **MA**: Anterior Media; **MP**: Posterior Media; **mb**: membrane; **o**: ostiole of tergal gland; **rg**: ridge of snapping organ; **Pc**: Postcubitus; **plc**: plectrum; **po**: pore of stridulitrum; **R**: Radius; **ScA**: Anterior Subcosta; **ScP**: Posterior Subcosta; **sct**: scale-like tubercle; **set**: seta; **sp**: spiracle; **spn**: stridultral spine; **sst**: short seta; **std**: stridultral depression; **stl**: stridultral line; **str**: stridulitrum; **t**: tergum; **tc**: seta-bearing tubercle

3. Results

We first describe the condition found in Cedusinae and Cenchreini (Fulgoromorpha: Derbidae), in which all or most species lack the putative stridulatory mechanism, and which reflect a more generalised condition of the wings and abdomen, similar to non-derbid planthoppers. Subsequently, we examine the conditions in all other derbid subfamilies, describing the various modifications of the metathoracic wing and pregenital abdomen that have taken place. The descriptions are based on the species cited in the figures, unless explicitly stated otherwise.

218 3.1. Abdominal organs and metathoracic wing structures of Cedusinae

219 The first two abdominal segments of all examined tribes of Cedusinae display modifications
220 characteristic of a snapping organ (Davranoglou et al., 2019a). The first abdominal segment is
221 subdivided into two distinct units. The proximal portion of the first abdominal segment is strip-
222 like, followed by a broad membrane which is entirely deflated in the examined dry-mounted
223 specimens, obscuring the ridge which is present but not visible in Fig. 1A. A Y-lobe is present
224 (lb; Fig. 1A), its base being extremely elongate, with no visible external connector linking the
225 Y-lobe base to tergum 2 as was observed by Davranoglou et al. (2019a), although this structure
226 may have been missed here due to the observational method used (SEM), where the boundaries
227 between membranous structures may be unclear. The anterior arm of the Y-lobe is strongly
228 pronounced (Fig. 1A), separated from the posterior arm by a membrane (mb; Fig. 1A). The
229 posterior arm is much shorter, fusing to tergum 2 (Fig. 1A). Tergum 2 (t2) is narrow, poorly
230 sclerotized and separated from tergum 3 by a membrane in the anterolateral parts of its posterior
231 margin. In addition to possessing these features characteristic of a snapping organ, the first
232 three abdominal segments also display several other anatomical features of note: terga 1–2 are
233 surrounded by membranous cuticle, and the more sclerotized tergum 3 (t3) lacks distinct setae
234 on its surface (Fig. 1A); spiracle one is about two times larger than the remaining abdominal
235 spiracles.

236 The metathoracic wing lacks any structures that would indicate the presence of a stridulitrum
237 (Fig. 2A). The anterior jugal vein (JA) is present beneath the anojugal fold (ajf) and the
238 posterior jugal vein (JP) is indistinct except for a pigmentation along the jugal margin,
239 immediately above the axillary cord (axc; Fig. 2A).

240 3.2. Abdominal organs and metathoracic wing structures in part of Cenchreini (Derbinae)

241 Exoskeletal components defining a snapping organ such as a Y-lobe and ridge (rg) are present
242 in *Nesorhamma badia* (Muir, 1927) (Table S1) and *Omolicna joi* (Fig. 1B), very similar to
243 those of Cedusinae (Fig. 1A). Structural details of the first three abdominal segments could not
244 be observed in all specimens, but tergum 3 lacks distinct setae on its surface in most Cenchreini
245 (Table S1).

246 The metathoracic wing lacks any structure identifiable as a stridulitrum in most species (Fig.
247 2B; Table S1), JA is present and JP forms a pigmented area at the jugal margin (Fig. 2B), as in
248 Cedusinae (exceptions mentioned in section 3.3.1).

249

250 3.3. Abdominal organs and metathoracic wing structures in Derbidae (excluding Cedusinae,
251 Cenchreini and part of Derbini)

252 3.3.1. Metathoracic wing stridulitrum

253 The axillary cord in the jugal area of the metathoracic wing bears in its posterior margin a
254 thickened structure, which for consistency with earlier works, we refer to anatomically as a
255 stridulitrum (str; Figs. 3A, 5A–C, 6A, B, D). The stridulitrum is composed of multiple

transverse elevated areas termed stridultral lines (stl), each line succeeded by a deep stridultral depression (std; Figs. 3B, C, 4A, 5A, B). The number of stridultral lines per stridultrum ranges from 16 to 40, with smaller species generally having a higher number of stridultral lines (e.g. *Synavea* spp., 35–40 lines) than larger species (e.g. *Phenice* spp., 20 lines). The surface of both the stridultral lines and their depressions appears membranous and deflated in critical-point dried specimens (Fig. 3B), and is covered with a distinctive microsculpture, composed of thousands of small (<1 µm) pores (po; Fig. 3C, D). Given that the surface of the remainder of the axillary cord is covered by a different microsculpture (Fig. 3F), and that the stridultrum is morphologically continuous with the latter, it is likely that the stridultrum represents a modified part of the axillary cord.

Both the proximal and distal ends of the stridultrum are continuous with the axillary cord, and SR-µCT scans show a large lumen (l1) in cross sections of the organ (Fig. 4C, D). Given that the axillary cord transfers haemolymph towards the scutellum (Kukalová -Peck, 1983) it is plausible that haemolymph flows through this lumen. The stridultrum in cross-section is composed of optically dense material (dm; light colour in 4C) of uncertain origin, which is not fully attached to its external membrane (mb; Fig. 4C), possibly due to poor preservation. This dense material forms a loop (lp), its ventral portion being much thinner than its dorsal counterpart (Fig. 4C). The loop may possibly form a secondary lumen (labelled l2 in Fig. 4C). The outer surface of the stridultrum is strongly rugose, and the many fine stridultral lines are clearly visible in the SR-µCT scans (Fig. 4A).

The size and thickness of the stridultrum is highly variable across taxa. The stridultrum may be short (e.g. most Rhotanini; Table S1) or very long, occupying the entire length of the jugal lobe (Sikaianini, Zoraidini; Figs. 3A, 4A, 5B and 6C, D). It may be situated close (Otiocerini) or far (Rhotanini, Phenicini) from the wing base, depending on the size of the jugal lobe and the stridultrum (Table S1). The stridultrum may be very thin, appearing as a small, thickened strip of the axillary cord (some Otiocerinae; Table S1), moderately thick in others (e.g. Phenicini) or strongly expanded, occupying most of the jugal lobe (Kamendakini, Sikaianini, Zoraidini; Figs. 3A, 4A, 5B and 6C, D). The outer surface of the stridultrum is generally concave, although in Aquaeliciini, Neocyclokarini, Phenicini, Sikaianini, and Zoraidini, it is straight and slightly convex (Table S1).

The metathoracic wing of non-Cedusinae derbids also varies in terms of wing venation, the shape of the jugal area, and the morphology of the stridultrum. In the majority of derbids [part of Otiocerinae: Otiocerini, Kamendakini, most Rhotanini and some Cenchreini (Derbinae): *Dawnaria*, *Muirileguatia*, *Aethocauda*], the jugal area is very large and both JA and JP are present (Table S1). In others, primarily in the Otiocerinae [Phenicini, part of Rhotanini (*Alara*), all Sikaianini and Zoraidini] and part of Derbinae [Dawnarioidini (*Neodawnaria*), Derbini (*Dysimia*, *Symidia*)], the jugal area is reduced to a small quadrangular lobe which bears the stridultrum, and vein JA is absent (Fig. 5A, B). Among taxa possessing this metathoracic wing type, JP may be short and thick in some species (e.g. *Alara*, *Raizoda*; Fig. 5A), or long and slender in others (most species), depending on the size of the jugal lobe and consequently its distance from the axillary sclerites (Table S1).

There is no evidence of sexual dimorphism in the structure of the stridultrum in any of the examined species.

300 3.3.2. Structure of the first three abdominal segments

301 The first abdominal segment is very narrow, proximally fused to the metathorax, its distal part
 302 being membranous. At least in *Zoraida* sp. 1 and *Paraphenice mawae* (both Zoraidini), several
 303 components typical of a snapping organ are present: a pair of ridges distinctly fuse on the
 304 anterior arm of the Y-lobe, which is also present (Fig. 6A), and the principal muscle of the
 305 snapping organ (Idlm1) was also observed (Fig. 6B; please refer to the *Musculature* section
 306 below). The structure of the Y-lobe differs slightly from that of other planthoppers, in that it is
 307 dorsoventrally flattened and extremely narrow (Figs. 4A, B and 6A). Other morphological
 308 features of note, not obviously associated with the snapping organ, are the following:
 309 abdominal spiracle 1 is greatly enlarged (sp; Fig. 3A), at least 20 times larger than the
 310 remaining abdominal spiracles; segment 2 (t2) is very narrow, also largely membranous (Figs.
 311 4A, B and 6A); both segments 1 and 2 are strongly desiccated in most dried specimens and
 312 almost impossible to observe (Table S1).

313 Tergum 3 is greatly expanded laterally into a broad, spatulate plate, becoming much narrower
 314 medially (Fig. 6 C, D). The posterolateral margin of tergum 3 is distinctly raised, exposing a
 315 large membrane, which links it to tergum 4. The remaining segments are not as raised and the
 316 membrane is not visible. This conformation is present in all derbid taxa examined, except for
 317 Cedusinae, Cenchreini (part) and Derbini (part). In all taxa possessing a stridulitrum, a field of
 318 erect setae (set) is invariably present on tergum three, representing the structure that would
 319 constitute the plectrum (plc) of the supposed stridulatory mechanism (Figs. 3A, E, 4A and 6
 320 A–D; Table S1). The area covered by the setae, and their length and density are all variable:
 321 the setae may be long or short (some *Zoraida*; Table S1); they may form a dense field
 322 occupying the entirety of the first half of the abdomen (e.g. *Swezeyia*; Table S1), or confined
 323 to the posterior margin of tergum 3 (e.g. Rhotanini, some Zoraidini; Fig. 7C; Table S1). In
 324 others (e.g. *Phenice*), they may be concentrated in only a small area of tergum 3 (Table S1).
 325 The setae are usually densest towards the base of tergum 3, gradually narrowing into only a
 326 few rows of sparse setae towards the dorsal part of tergum 3 (Fig. 7C; Table S1). Among dried
 327 specimens, it is not unusual for the setae to be clumped together by the crystallised remnants
 328 of a presumably viscous secretion, or to be scraped off entirely (Table S1).

329 Distinctly raised tubercles (tc) form the bases for these setae (Figs. 3E, 7 A–C) and in at least
 330 one species two additional ultrastructures can be observed at high magnification: sparse, very
 331 short setae (sst) which insert in less raised tubercles, and conical, scale-like tubercles (sct)
 332 lining the posterior margin of tergum three (Fig. 7A, B). The remaining abdominal segments
 333 are typically glabrous (Fig. 3A).

334 We did not observe sexual dimorphism in the morphology of tergum 3 in any of the examined
 335 derbids.

336 *Musculature*: Largely not preserved in SR-μCT scans, although the main snapping organ
 337 muscle Idlm1 is distinct (Fig. 4B): this is the largest muscle of the pregenital abdomen, Origin
 338 – apodeme on metaphragma; Insertion – apodeme on antecosta of tergum two; Function –
 339 principal muscle of snapping organ mechanism (Davranoglou et al., 2019a).

340

341 3.4. *Abdominal organs and metathoracic wing structures in the rest of Derbini*

342 3.4.1. *Metathoracic wing stridulitrum*

343 The metathoracic wing in part of *Derbina* (*Derbe*) and *Mysidiina* (*Mysidia*, *Pseudomysidia*) is
344 characterised by a smaller jugal lobe, the presence of JA and a modified stridulitrum (Figs. 5C,
345 8A–C; Table S1). The stridulitrum of most *Derbini* is extremely reduced and narrow, appearing
346 as a small, thickened flap of the axillary cord (Figs. 5C and 8A–C; Table S1). The typical
347 components of the stridulitrum which are otherwise found in most other derbids (stridulitral
348 lines and depressions) are not present, and the stridulitral surface is instead rather flat and
349 covered with short cuticular spines (spn; Fig. 8B, C).

350

351 3.4.2. *Structure of the first three abdominal segments*

352 The first two abdominal segments display the typical modifications of a snapping organ (in *D.*
353 *strigipennis* Westwood, 1840, Table S1): a ridge is present, dorsally obscuring the Y-lobe arms.
354 Tergum 2 is unmodified. Tergum 3 is not distinctly convex or broader than tergum 2, and
355 possesses a small field of sparse, short or long plectral hairs, at the narrow contact zone between
356 stridulitrum and plectrum in *Derbina* (*Derbe*) and at least some taxa of *Mysidiina* (*Dysimia*,
357 *Pseudomysidia*, *Symidia*; Table S1).

358

359 3.5. *Systematic distribution of the plectrum and stridulitrum*

360 The supposed stridulatory mechanism is common but not ubiquitous among derbids (Table
361 S1). It is absent in all examined taxa of *Cedusinae*. Among the *Derbinae*, it is lacking in most
362 *Cenchreini* that we examined (Fig. 2B), with the exceptions of *Aethocauda rubella* Williams,
363 1978, *Dawnaria atroterminata* (Distant, 1911) and *Muirileguatia fernandesi* (Muir, 1925)
364 (Table S1). The mechanism is absent or strongly reduced in most, but not all *Mysidiina*, and
365 part of *Dawnarioidini* [*Dawnarioides sordidulus* (Muir, 1918)] (Table S1). Within *Otiocerinae*,
366 it is absent from all examined *Nicertina* (Table S1).

367

368 3.6. *Interaction of the plectrum and stridulitrum*

369 The stridulitrum and plectrum are positioned in a way that maximises their contact when the
370 metathoracic wings move by a sudden jerk of the mesothoracic wings (Kirkaldy, 1907; Fig.
371 6C), which are functionally and morphologically connected to the metathoracic wings. The
372 stridulitrum in each species has a size that correlates with the width and position of the

plectrum, and the two structures can be seen in varying degrees of interaction in dry-mounted specimens (6A–D). In addition, in several taxa with smaller or more compact stridulitra (e.g. *Dawnaria*, *Derbe*), the plectrum is confined to the small area where the two structures can come into contact in a precise manner (Table S1). All taxa lacking a stridulitrum also lack a plectrum (Figs. 1A–B and 2A–B; Table S1), further supporting a functional correlation between the two structures.

The deflated appearance of the stridulitrum in dried specimens (Fig. 3B) suggests that in living specimens, the membranes may be more voluminous (possibly eversible?) and filled with haemolymph. The JP probably acts as a strengthening bar and adds structural support to the stridulitrum when it contacts the abdomen (Fig. 6C, D).

3.7. Systematic distribution of snapping organs in Derbidae

Snapping organs were found in all examined Cedusinae (Table S1; Fig. 1A), most Cenchreini (Table S1; Fig. 1B), some Derbina, Nicertina, Phenicini (Table S1) and Zoraidini (Fig. 4A, B). We were unable to observe the structure of the first two abdominal segments (which contain the snapping organ) in most dry-mounted species that we examined (Table S1), as their membranous nature caused them to shrivel significantly, obscuring any view of their morphology. However, the presence of the snapping organ in these major derbid tribes suggests that it is widespread in the family.

3.8. Tergal glands

We observed two pairs of large glands (gl) on the dorsolateral surface of tergum 6, and one pair on tergum 7 in *Zoraida* sp. 1 & sp. 2. The glands possess characteristic crescent-shaped grooves (gr; Fig. 9B–D), with a median slit-like ostiole (o; Fig. 9C, D). The internal structure of the glands could not be reconstructed in the SR-μCT scans. These glands are also present in the same locations in larval Zoraidini and exude long, thick filaments of wax (Fig. 10A, B). The larval glands form distinctly raised tubercles (Fig. 10A, B), whereas the adult counterparts are flattened (Fig. 9A–D).

The condition of the examined Zoraidini is not universal among derbids, as some Cedusinae, Cenchreini, Otiocerini and Rhotanini may possess only one gland on tergum 7, and *Basileocaphalus germanus* Yang & Wu, 1993 (Cenchreini) is unique in that tergites 5–7 each possess a single tergal gland (Yang & Yeh, 1994). Given that all known larval Zoraidini possess the same number of tergal wax glands (Yang & Yeh, 1994) with the adults of the two examined species (Fig. 9), it seems that at least in these taxa, the number of tergal glands does not change during the larva to adult transition.

410 4. Discussion

411 4.1. Vibrational communication in Cedusinae and other derbids

412 Tishechkin (2003) recorded vibrational signals from *Cedusa sarmatica* (Anufriev, 1966),
 413 which he attributed to tymbal organs yet to be identified. However, the published oscillograms
 414 of *C. sarmatica* (Tishechkin, 2003) as well as two other *Cedusa* spp. (Tishechkin, 2008) have
 415 a structure comprising a prolonged succession of syllables, sometimes paired, that is
 416 characteristic of other planthopper signals that have since been shown to be produced by the
 417 snapping organ (Davranoglou et al., 2019a). Our examination of the external morphology of
 418 the abdomen of Cedusinae failed to find any tymbal-like organ (i.e. any structure comprising
 419 buckling membranes with or without buckling ribs) (Fig. 1A), yet a snapping organ was
 420 invariably present in the first and second abdominal segments (Fig. 1A, Table S1). This
 421 suggests that in Cedusinae, at least, the snapping organ may be fully functional, and responsible
 422 for producing their recorded vibrations. Although there are, to our knowledge, no recordings
 423 of vibrational signals in any other derbid subfamily, the presence of components defining a
 424 snapping organ (ridge, Y-lobe) and its principal muscle, the hypertrophied Idlm1, in species of
 425 Cenchreini (Derbinae, Table S1) and Zoraidinae (Fig. 4B; Table S1), suggests that the snapping
 426 organ may be capable of generating vibrations in these subfamilies as well.

427 It remains an open question whether the snapping organs of derbids and other planthoppers are
 428 homologous with the tymbal and tymbal-like organs of Cicadomorpha, as Hoch et al. (2019)
 429 have recently claimed, following Wessel et al.'s (2014) "Tymbalia" hypothesis. Here we
 430 adhere to a strictly biomechanical definition of each of these different vibroacoustic organ
 431 types. This makes sense because the mechanism of a snapping organ differs fundamentally
 432 from the mechanism of a tymbal organ, and Hoch et al.'s (2019) assertion of their homology
 433 is based simply on the involvement of a similar set of muscles in an otherwise different
 434 vibroacoustic mechanism located in the first two abdominal segments. Any conclusion
 435 regarding the homology or otherwise of these structures is premature in the absence of a formal
 436 cladistic analysis, particularly in light of the several errors in muscle segmental identification
 437 that are present in the work by Wessel et al. (2014) upon which Hoch et al. (2019) based their
 438 conclusions (Davranoglou et al., 2019b). In particular, previous research of ours (Davranoglou
 439 et al., 2017; Davranoglou et al., 2019a), used the innervation and exoskeletal structure of the
 440 abdomen to show that the segmental identity of several key muscles (Iadvml+2, IIIvlm) used
 441 in the definition of a "tymbalian tymbal organ" was incorrect in the study by Wessel et al.
 442 (2014). Furthermore, previous studies (Kramer, 1950; Snodgrass, 1933) were congruent with
 443 our interpretations on the segmental identity of auchenorrhynchan sterna (S1 Text in
 444 Davranoglou et al., 2019a), but not with those of Ossiannilsson (1949) and Weber (1928), on
 445 which Wessel et al. (2014) relied. The position of an element is one of the main criteria of
 446 homology (Remane, 1952; Patterson, 1982), and the aforementioned confusion over segmental
 447 identity between different hemipteran groups ought therefore to prompt a thorough re-
 448 evaluation of the muscle homologies proposed by Wessel et al. (2014).

450 4.2. Taxonomic and systematic implications

The internal phylogenetic relationships of Derbidae are poorly understood. The only comprehensive phylogenetic hypothesis is that of Emeljanov (1996), based on morphology. Although this served as a basis for the current classification of the family and remains a very influential work, it was not derived through cladistic methods, which would properly test the homology of the individual characters used by Emeljanov (1996) to define higher taxa, their monophyly, and sister-group relationships. As a result, we can make only limited inferences on the evolutionary implications of our findings.

The absence of a putative stridulitrum or plectrum in Cedusinae and part of Cenchreini (Fig. 2; Table S1) and the similarity in their metathoracic wing venation are treated here as possible symplesiomorphies shared with other planthoppers. Indeed, Cedusinae and part of Cenchreini may be closely related (Fennah, 1952) and the former have been considered the sister group to all other Derbidae (Emeljanov, 1996). This may suggest that the placement of Cenchreini within Derbinae or Otiocerinae as the sister group to Nicertina (Emeljanov, 1996) is artificial. The presence of a stridulitrum and plectrum in three genera (*Aethocauda*, *Dawnaria*, *Muirileguatia*) of Cenchreini (Table S1), which is similar to that of Otiocerinae, suggests that these taxa may be taxonomically misplaced. This being so, either the tribe as currently defined may be polyphyletic, or it may contain the same stridulatory structures as other derbids evolved independently, which in itself is a less parsimonious explanation.

Characters present in the remaining Derbidae, such as the external reduction of the snapping organ (covered almost entirely by the ridge; Fig. 6A, B), the further enlargement of abdominal spiracle one and the presence of the stridulitrum and plectrum could represent possible synapomorphies that unite all derbids excluding Cedusinae and Cenchreini. The significant reduction of the jugal area and its modification into an expanded quadrangular lobe in Sikaianini and Zoraidini (Figs. 3A, 4A, 5B, 6C, D) may indicate a close relationship between the two tribes, as suggested by Emeljanov (1996).

The unambiguous presence of the stridulitrum and plectrum in several taxa of Derbinae (Figs. 5C and 8A–C) contradicts Emeljanov (1996) and Banaszekiewicz & Szwed (2005), who key the subfamily as lacking this trait. At present, we cannot determine whether these supposed stridulatory structures of Derbini are homologous with those of other derbids. The morphology of the stridulitrum in some taxa (*Dysimia*, *Symidia*) is very similar to that of Otiocerinae (Table S1), while in *Derbe* spp. and some *Mysidia* spp. the stridulitrum is extremely small, narrow and has unique ultrastructure found in no other derbid group (Fig. 8A–C). Other Derbini (e.g. some *Mysidia* spp.) lack the mechanism altogether (Table S1). Given that Derbini are a well-defined group (Broomfield, 1985), these differences may stem from varying degrees of reduction of the stridulatory mechanism, or may otherwise be due to convergent evolution.

Our extensive microscopic examination of nearly 200 species revealed considerable variation in the components of the supposed stridulatory organ among different groups of derbids (Table S1). We are confident that detailed examination of both macro-and-microscopic features of the derbid stridulatory organ will reveal many taxonomically and systematically useful characters, and we recommend their use in future studies on this group of insects. It is likely that the unbalanced systematic distribution of many of these characters may challenge our current understanding of derbid subfamilies, tribes and subtribes. An in-depth phylogenetic analysis including the details of the supposed stridulatory mechanism and other morphological and molecular characters is needed.

496 *4.3. Evolution of supposed stridulatory organs in Derbidae*

497 Due to insufficient knowledge of derbid phylogeny, not much can be deduced regarding the
 498 evolutionary trajectory of derbid stridulatory organs. Based on our current work, we suggest
 499 the following preliminary conclusions: 1) In Cedusinae and part of Cenchreini, the
 500 metathoracic axillary cord is unmodified, presumably ancestrally and not as a result of
 501 secondary loss; 2) in most derbids except Cedusinae and Cenchreini, an area of the
 502 metathoracic axillary cord expands and becomes morphologically modified, forming the
 503 stridulitrum (this process perhaps taking place more than once); based on the current tribal
 504 classification, this supposed stridulatory organ was secondarily lost at least three times
 505 independently (Nicertina, part of Dawnarioidini and Mysidiina).

506

507 *4.4. Is the stridulatory mechanism actually involved in sound production?*

508 There is sufficient morphological (e.g. Fig. 6) and behavioural (Kirkaldy, 1907) evidence to
 509 conclude that a mechanical interaction between the stridulitrum and the plectral hairs takes
 510 place, but whether and how this could produce loud sound remains enigmatic. Although the
 511 stridulitrum is somewhat more rigid than the surrounding wing surface and receives structural
 512 support from the JP (Fig. 6C, D), it is still membranous, lacks sclerotisation in any part, and
 513 has a porous surface (Fig. 3C, D) unlike the typical file-like texture characterising most known
 514 stridulitra (e.g. Jansson, 1972; Čokl et al., 2006). Moreover, its assumed flexibility would make
 515 the stridulitrum unsuitable for generating the normal force and friction force necessary for
 516 stridulation involving a scraper and file. Concerning the supposed plectrum, its structure is also
 517 atypical compared to other known plectra. Setae forming part of a plectrum are not unknown,
 518 but they are usually much shorter, robust and strongly sclerotized (Jansson, 1972). The soft,
 519 easily removable plectral hairs of derbids (Table S1) do not appear to offer sufficient resistance
 520 against strikes by the stridulitrum – it is thus unlikely that they would produce appreciable
 521 sound in this way.

522

523 *4.5. A role in chemical communication?*

524 In light of these observations, we suggest that the stridulitrum and plectrum may serve in the
 525 spreading of a chemical secretion (e.g. a pheromone) rather than in the production of sound,
 526 although this hypothesis should be treated as speculative in the absence of observations on live
 527 derbids. We base our hypothesis on a remarkably similar mechanism which exists in the
 528 tephritid fly *Bactrocera cucurbitae* (Coquillett, 1849) and its relatives (Kuba & Sokei, 1988),
 529 which was also initially thought to be a stridulatory organ (Monro, 1953; Kanmiya, 1988). In
 530 *Bactrocera*, the anal vein of the male mesothoracic wing is characterised by distinct
 531 microtrichia, opposed by long, erect hairs on the posterior margin of tergum 3, in a position
 532 identical to that of the derbid plectrum. When the male fly signals to females, it collects a
 533 chemical secretion from its anus with its hind legs, spreads it on the modified area of the

metathoracic wing, and then rapidly strikes the latter against the tergal hairs, creating a “pheromone cloud” (Kuba & Sokei, 1988). Our observation of clumped plectral hairs, covered by crystallised secretions in several dried derbids (Fig. 6D; Table S1), was also found in male tephritids (Kanmiya, 1988). This supports our speculative hypothesis that the organ may actually play a role in chemical signalling, although we cannot exclude the possibility that the “crystals” in derbids are in fact minute wax particles (see Section 4.6 below).

A role of wing-flicking in pheromone dissemination has been suggested in crickets as well (Heinzel & Dambach, 1987; Kämper & Dambach, 1979), and might even have been a behavioural-preadaptation necessary for the evolution of infrasound stridulation in these insects. Other morphological features of derbids, such as elaborate, sexually dimorphic antennae and antennal appendages (Emeljanov, 1996; Bourgoïn & Yap, 2010; Bartlett et al., 2014) may also indicate the presence of chemical signalling in this family, which remains unconfirmed from all Auchenorrhyncha. If our hypothesis is confirmed by future experimental studies, it may suggest that derbids use bimodal signalling, involving chemical signals produced by certain as yet undiscovered glands, perhaps distributed by the mechanical interaction of the plectrum and stridulitrum, and vibrational signals produced using the abdominal snapping organ.

4.6. Possible dissemination of wax and the role of tergal glands

Another possible function of the derbid metathoracic wing-abdomen mechanism is the production and dissemination of wax, which sometimes covers the bodies of derbid planthoppers. Support for this hypothesis stems from the porous surface of the stridulitrum which resembles the wax glands found on the abdomen of some non-derbid planthoppers, particularly the Cixiidae (Holzinger 2002; Holzinger et al., 2002). This similarity may be superficial, however, as the pores of the stridulitrum are much smaller ($<1\ \mu\text{m}$) compared to the abdominal wax glands of Cixiidae and Flatidae (*ca.* $2\ \mu\text{m}$; Sforza et al., 1999; Holzinger, 2002; Lucchi & Mazzoni, 2004), their shape is more irregular, and they seem to be less deeply impressed on the cuticle, implying that there is no underlying secretory unit. It is thus unlikely that the stridulitrum itself secretes wax, although this does not exclude it from being involved in its dissemination from another source. On the other hand, there is no apparent correlation between the possession of the stridulatory mechanism and wax – among *ca.* 55 species photographed in the wild, the abdomen and stridulitra of only six species were at least partly covered by wax (Bay, 2019). Species with reduced or absent stridulitra (e.g. *Cedusa*, *Mysidia*, *Nicertina*) may or may not be covered with wax, and the stridulitrum of Derbinae – a group frequently covered by wax – lacks the distinctive porous ultrastructure and bears no resemblance to a wax gland.

Although certain authors (e.g. Hamilton, 2011) claim that derbids lack abdominal wax glands altogether, photographs of derbid larvae exuding obvious wax filaments secreted from the tergal glands (Fig. 10A, B) contradict this notion. The few wax filaments of larval derbids are peculiar, since in some other planthoppers, extensive fields of wax glands exude hundreds or thousands of wax filaments that may coat the entire animal (e.g. Hamilton, 2011). Their morphology is also distinctive, since in other planthoppers, the wax gland pores are much smaller, form extensive honeycomb-like aggregations and are often provided with distinct secretory tubules (e.g. Sforza et al., 1999; Holzinger, 2002; Lucchi & Mazzoni, 2004). The function of tergal wax filaments in planthopper larvae remains unknown, with untested

hypotheses suggesting roles in cleaning, crypsis and defence (Hamilton, 2011). It is unclear whether tergal glands remain functional in adult derbids, which are generally covered with a powder-like layer of wax (if at all), instead of long filaments (Bay, 2019). It is thus possible that other, as yet unknown glands are responsible for wax production in adult derbids.

5. Conclusions

In the present study, we documented the detailed morphology and systematic distribution of two supposed vibroacoustic mechanisms of Derbidae for the first time. We find that snapping organs (Davranoglou et al., 2019a) are present in many derbids (Table S1), and propose that these may be responsible for the vibrational signals of Cedusini that were previously attributed to unknown tymbal organs (Tishechkin, 2003). This being so, we expect that the various other derbids possessing a snapping organ mechanism (Table S1) will also turn out to have the capacity for generating substrate-borne vibrations. Regarding the supposed stridulatory mechanism of Muir (Kirkaldy, 1907), we offer novel morphological information on the anatomy of the stridulitrum and plectrum that will be of use to derbid systematics and taxonomy, and challenge the long-held view that this structure functions as a stridulatory organ. Instead, we speculate that the stridulitrum and plectrum may make contact mechanically for the purposes of spreading a chemical secretion. However, the precise function of these structures remains ambiguous in the absence of detailed behavioural observations, and experimental work using live animals will be needed to elucidate the behavioural function of the enigmatic derbid metathoracic wing-abdomen mechanism and to test our hypotheses. If the organ is indeed a stridulatory mechanism as originally proposed, then its mechanism may be unique from a biomechanical and bioacoustic perspective. If our alternative, speculative hypothesis that the organ is used in chemical communication is experimentally confirmed, then it will be the first known instance of any auchenorrhynchan using this signalling modality, potentially paving the way for the design of pheromone traps for pest species in several areas of the world (Brown et al. 2006; Wilson, 2005).

5. Author contributions

L.-R.D. conceived and designed the study, collected and interpreted the data, performed the analysis, prepared figures, and wrote the paper. B.M and G.K.T collected the SR- μ CT data with L.-R.D., and contributed to their analysis. I.M. contributed to the collection of other morphological data with L.-R.D., including photomicrography and scanning electron microscopy, and contributed to data interpretation and analysis. All authors contributed to critical revision of the draft manuscript, and gave final approval of the version to be published.

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Figure Legends

Fig. 1. External morphology of the snapping organ and pregenital abdomen of Cedusinae and Cenchreini (SEM, false-coloured). A: Abdomen of *Cedusa* sp. (Cedusinae), male, dorso-caudal view, lb, Y-lobe of snapping organ; mb, membrane; t, tergum; B: Abdomen of *Omolicna joi* (Cenchreini), female, dorso-caudal view, rg, ridge of snapping organ.

Fig. 2. Metathoracic wing morphology of Cedusinae and Cenchreini (slide-mounted, dorsal view). A: *Malenia bosnica* (Cedusinae), AA, Anterior Anal; ajf, anojugal fold; AP, Posterior Anal; axc, axillary cord; C, Costa; CuA, Anterior Cubitus; CuP, Posterior Cubitus; JA, Anterior Jugal; JP, Posterior Jugal; MA, Anterior Media; MP, Posterior Media; Pc, Postcubitus; R, Radius; ScA, Anterior Subcosta; ScP, Posterior Subcosta; B: *Omolicna joi* (Cenchreini).

Fig. 3. Morphology and ultrastructure of stridulatory mechanism in *Zoraida* sp.1 (SEM). A: Dorso-caudal view of mechanism, white dashed line indicates outline of spiracle 1, axc, axillary cord; plc, plectrum; sp, spiracle; str, stridulitrum; B: Hind wing stridulitrum, std, stridultral depression; stl, stridultral line; C: Higher magnification view of stridulitrum; D:

Enlarged view of white inset of previous panel, showing the porous surface of the stridulitrum, po, pore of stridulitrum; E: Surface of plectrum (tergum three) (note that hairs are artificially appressed in CPD-treated specimens), set, seta; tc, seta-bearing tubercle; F: Enlarged view of white inset in panel A, demonstrating the ultrastructure of the axillary cord.

Fig. 4. SR- μ CT, volume-rendered 3D reconstruction of stridulatory mechanism in *Zoraida* sp.2. A: Dorsolateral view of metathoracic wing and proximal pregenital segments, dashed lines indicating planes of section of SR- μ CT tomograms in panels C and D, lb, Y-lobe of snapping organ; set, setae, std, stridultral depression; stl, stridultral line; str, stridulitrum; t, tergum; B: Lateral view of thorax and pregenital segments, Idlm1 (coloured green), group I dorsal longitudinal muscle of tergum 1; C: cross-section of stridulitrum, illustrating its internal morphology, dm, dense material; l, lumen; lp, loop of dense material; mb, membrane; D: Same, more anterior section.

Fig. 5. Main variations of metathoracic wing stridulitrum (dorsal view). A: *Alara fumata* (Otiocerinae: Rhotanini), slide mounted, AA, Anterior Anal; AP, Posterior Anal; C, Costa; CuA, Anterior Cubitus; CuP, Posterior Cubitus; cv, cross-vein; JP, Posterior Jugal; MA, Anterior Media; MP, Posterior Media; Pc, Postcubitus; R, Radius; ScA, Anterior Subcosta; ScP, Posterior Subcosta; str, stridulitrum; B: *Zoraida pterophoroides* (Otiocerinae: Zoraidini), wax visible immediately above stridulitrum, dashed line indicates outline of MP (obscured by mesothoracic wing); C: *Derbe* sp. (Derbinae: Derbini), dashed line indicates outline of JP, JA, Anterior Jugal.

Fig. 6. Different views of stridulitrum-plectrum interactions at various stages of contraction (dry-pinned specimens). A: *Paraphenice mawae*, dorsal view, with snapping organ Y-lobe arms snapped shut, lb, Y-lobe of snapping organ; plc, plectrum; rg, ridge of snapping organ; str, stridulitrum; t, tergum; B: same, higher magnification of stridulitrum-plectrum, set, setae; C: *Proutista* sp., lateral view, yellow inset marking position of the stridulatory mechanism; D: Same, higher magnification view of yellow inset in previous panel, the stridulitrum making contact with the plectrum, JA, Posterior Jugal.

Fig. 7. Surface ultrastructure of plectrum (tergum 3) in two derbid species (SEM; hairs artificially appressed in CPD-treated specimens). A: *Zoraida* sp.1 (Otiocerinae: Zoraidinae) posterior view of posterior margin of tergum 3, set, seta; sst, short seta; tc, seta-bearing tubercle; B: Enlarged view of white inset of previous panel, sct, scale-like tubercle; C: *Kaha* sp. (Otiocerinae: Otiocerini), lateral view of tergum three, t, tergum.

Fig. 8. External morphology and ultrastructure of stridulitrum of *Mysidia* sp. (SEM). A: Metathoracic wing, dorsal view, str, stridulitrum; B: Higher magnification of stridulitrum; C: Surface ultrastructure of stridulitrum, which is covered in spines, spn, spines.

Fig. 9. External morphology of derbid tergal glands (SEM). A: *Zoraida* sp.1 (Otiocerinae: Zoraidinae), abdomen, caudal view, demonstrating the position of tergal glands, gl, tergal gland; t, tergum; B: Same, enlarged view of white inset in previous panel; C: Same, higher magnification view of tergal gland, illustrating its detailed morphology, gr, groove of tergal gland; o, ostiole of tergal gland; D: *Zoraida* sp.2, tergal gland, demonstrating interspecific variation in the morphology of this structure.

Fig. 10. Wax filaments produced by abdominal tergal glands in larval derbids. A: *Zoraida* sp., white arrows indicating position of abdominal tergal glands; B: *Pamendanga* sp. Reproduced by kind permission of the photographer Nicky Bay.

Table Legend

Table S1. Distribution of stridulatory mechanisms and snapping organs in derbid planthoppers. All observations were made on dry-mounted specimens, using light stereomicroscopy. Hyphen (-) denotes that the said structure could not be observed in the particular specimen. The absence or presence of a certain structure is specifically stated. Abbreviations for depositories: Natural History Museum of London (BMNH); Moravian Museum of Brno (MMBC).

A **B**