

**Response to “On the evolution of the tymbalian tymbal organ:
Comment on “Planthopper bugs use a fast, cyclic elastic recoil
mechanism for effective vibrational communication at small body size”
by Davranoglou et al. 2019”**

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Zusammenfassung: Kommunikation über Vibrationssignale in der Gruppe der Spitzkopfkadziden (Hemiptera: Fulgoromorpha) ist allgegenwärtig, doch war der zugrundeliegende Mechanismus bis zu einem kürzlich erschienenen Artikel von Davranoglou et al. (2019) unbekannt. In diesem Beitrag werden die funktionelle Morphologie, die Biomechanik des Verhaltens und die systematische Verbreitung eines weitverbreiteten Vibrationsmechanismus beschrieben, den die Autoren als Schnapporgan („snapping organ“) bezeichneten. Der Mechanismus dieses Schnapporgans unterscheidet sich prinzipiell von den einzigen vergleichbaren Vibrationsorganen innerhalb der Hemipteren, nämlich den Trommelorganen (Tymbal) der Singzikaden (Cicadidae, Cicadomorpha). Kurz nach der Veröffentlichung argumentierten Hoch et al. (2019), dass es „unnötig, wenn nicht sogar irreführend“ wäre, diesen Mechanismus als „snapping organ“ zu bezeichnen und führten aus, dass dieses vielmehr als tymbalähnliches Trommelorgan mit Schnappmechanismus („tymbalian tymbal organ with snapping mechanism“) bezeichnet werden sollte. Diese Bezeichnung bezieht sich auf die „Tymbalia“-Hypothese von Wessel et al. (2014), der zufolge alle bekannten abdominalen Vibrationsorgane der Hemiptera Modifikationen eines abdominalen Vibrationsorgans darstellen, das im letzten gemeinsamen Vorfahren der Fulgoromorpha, Cicadomorpha und Heteropteroidea vor 300 Mio. Jahren vorhanden war. In unserem Beitrag zeigen wir, dass die Kriterien, die Wessel et al. (2014) verwendeten, um das tymbalähnliche Trommelorgan zu definieren, auf fehlerhaften segmentalen Zuordnungen der Schlüsselmuskulaturen beruhen. Die „Tymbalia“-Hypothese muss daher neu evaluiert werden. Desweiteren zeigen wir, dass die von Davranoglou et al. (2019) verwendete Terminologie der Muskulatur dem Standard in diesem Forschungsgebiet entspricht und liefern morphologische Hinweise, die unsere Interpretation der Schnapporganmuskulatur als Muskulatur und nicht als Skolopoidalorgane unterstützen. Wir treten daher dafür ein, dass an der Unterscheidung zwischen den Schnapporganen der Fulgoromorpha und den Tymbalen bzw. tymbalähnlichen Organen der Cicadomorpha aus biomechanischen Gründen festgehalten werden sollte und halten es bestenfalls für verfrüht – und schlimmstenfalls für falsch –, das „snapping organ“ als „tymbalian tymbal organ“ zu bezeichnen, solange die „Tymbalia“-Hypothese nicht formal mit Hilfe kladistischer Methoden getestet worden ist.

Key words: snapping organ; tymbal; tergal plate; Tymbalia; Fulgoromorpha; Cicadomorpha.

1. Introduction

Davranoglou et al. (2019) recently described the functional morphology and biomechanics of a fast, cyclic elastic recoil mechanism used for vibrational communication by planthoppers (Hemiptera: Fulgoromorpha). This structure, which they called a “snapping organ“, spans the first two abdominal segments, and is located dorsally at the junction of the metathorax

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and abdomen. The mechanism was described in detail for a model species, *Agalmatium bilobum* (Fulgoromorpha: Issidae), but Davranoglou et al. (2019) identified similar structures with homologous musculature and innervation throughout the entire planthopper clade, with the exception of some Delphacidae and Derbidae, in which the snapping organ is highly modified. The snapping organ is defined by the presence of a Y-shaped cuticular lobe, the arms of which snap together suddenly following a slow contraction of the hypertrophied dorsal longitudinal muscles of the 1st abdominal segment (Idlm1-2). Contraction of Idlm1-2 cocks the system, storing elastic-potential energy that is transferred to the arms of the Y-lobe when a change in the conformational state of the system is triggered by contraction of the small dorsoventral muscles of the 2nd abdominal segment (Iledvm1-2; see below for discussion of the identification of these muscles). This action raises the abdominal mass, producing a rapidly decaying vibration that is communicated to the substrate through the legs. This is followed a short time later by a second vibrational transient as the abdomen is thrust downward by the sudden re-opening of the Y-lobe arms. This release of the elastic-potential energy now stored in the Y-lobe is triggered by relaxation of Iledvm1-2.

It will be apparent from this description that the focus of Davranoglou et al. (2019) was on the functional morphology and biomechanics of the snapping organ, which differ fundamentally from the functional morphology and biomechanics of the only other comparably well-described hemipteran vibroacoustic organs: the tymbal organs of modern cicadas (Cicadomorpha: Cicadidae). Prior work on the mechanism of the tymbal organ was neatly summarised by Young & Bennet-Clark (1995): “the tymbal membrane forms a convex dome, which is set in a ring of sclerotised cuticle. Posteriorly on the tymbal, there is an irregularly shaped region of sclerotised cuticle, the tymbal plate, onto which the tymbal muscle attaches dorsally. Anteriorly, there are a number of long sclerotised ribs, which alternate with short ribs arranged in a line. When the tymbal muscle contracts, the tymbal buckles inwards along the line of short ribs in a stepwise manner; each step results in a sound pulse and is due to the buckling of one or more long ribs, beginning with the most posterior.” The tymbal organ itself acts as a resonator, and is coupled to a second resonator comprising the large abdominal air sac and the paired tympanal membranes on the anterior part of the abdomen, which together function as a Helmholtz resonator, rather like the air cavity of a guitar. Different forms of tymbal organs are found in other Cicadomorpha, but their mechanisms have not yet been described in detail.

With this biomechanical background in mind, Davranoglou et al.’s (2019) statement that the mechanism of the snapping organ of planthoppers differs fundamentally from the mechanism of the tymbal organ of cicadids ought to have been uncontroversial. We are therefore surprised that Hoch et al. (2019), who assume that the snapping organ of planthoppers is homologous with the tymbal organ of cicadids, conclude that it is “unnecessary, if not misleading” to introduce a new name for what they regard as “a particular configuration in a long and complex chain of evolutionary transformation”. Instead, Hoch et al. (2019) recommend using the rather less snappy name “tymbalian tymbal organ with a snapping mechanism”. This recommendation refers to the proposal by some of the same authors (Wessel et al. 2014) of the name “Tymbalia” for “the taxon comprising Cicadomorpha, Fulgoromorpha, and Heteropteroidea [and to be strictly correct, all descendants of the last common ancestor thereof], based on the possession of a tymbal apparatus as an autapomorphic [or correctly, synapomorphic] character”. Wessel et al.’s (2014) “Tymbalia” hypothesis (Fig. 1) echoes earlier work by Sweet (1996) who proposed that “tymbals may be an important synapomorphy relating the Coleorrhyncha to the Auchenorrhyncha

[i.e. Cicadomorpha and Fulgoromorpha] *and the Heteroptera*”, and by Senter (2008) who referred to the same taxa as “*the tymbaled superclade*”.

To call the vibrational organ of planthoppers a “*tymbalian tymbal organ with a snapping mechanism*” (Hoch et al. 2019) is to assert or assume homology of this organ with the tymbal organs of cicadids. This represents a logically stronger claim than referring to it merely as a “*snapping organ*” (Davranoglou et al. 2019), which makes no claim either way (Fig. 1). The onus is therefore upon Hoch et al. (2019) to demonstrate homology of the structure that we have described to the tymbal organs of cicadids. But do their claims bear scrutiny? As we explain below, there is no reason yet to reject outright the “Tymbalia” hypothesis that the tymbal organs of cicadids and the snapping organs of planthoppers both represent modifications of an abdominal vibrational organ that was already present in their last common ancestor (i.e. just as the wings of a hummingbird and the wings of an albatross each represent modifications of the functional wings that were present in the last common ancestor of modern birds). Equally, there is no reason yet to reject the alternative hypothesis that the tymbal organs of cicadids and the snapping organs of planthoppers represent independent origins of abdominal vibroacoustic organs, involving some of the same musculoskeletal elements (i.e. just as the wings of a bird and the wings of a bat represent modifications of the pentadactyl limb of tetrapods, but are independently evolved as wings). Until such time as these hypotheses have been tested formally using rigorous cladistic methodology, it would be premature to conclude either way. It would be equally premature – and perhaps false – to describe the snapping organ as a “tymbalian tymbal organ” as Hoch et al. (2019) would have us do. We respond to their more detailed comments on our work below.

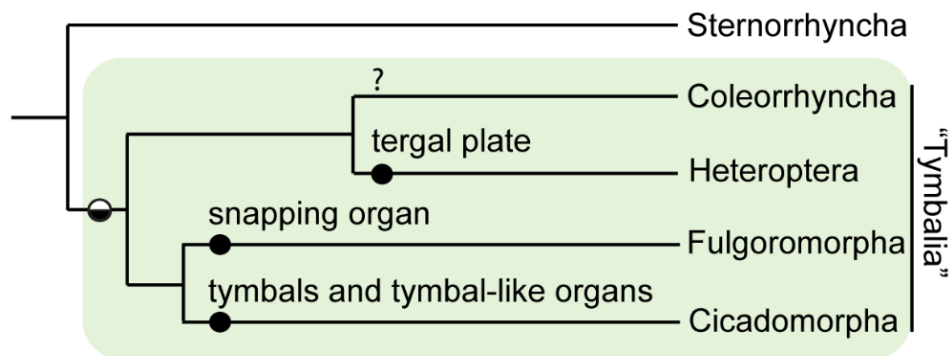


Figure 1. Systematic distribution of abdominal vibroacoustic organs in the Hemiptera, modified from Davranoglou et al. (2019). The clade within the green shaded area corresponds to the “Tymbalia” of Wessel et al. (2014), previously named the Euhemiptera. The half-filled circle denotes the ambiguous ancestral state of this clade: the main tenet of the “Tymbalia” hypothesis is that abdominal vibroacoustic organs were present as the ancestral state. Davranoglou et al. (2019) did not show this ambiguous ancestral state, but the present figure is intended to show that their presentation is compatible with either the presence or absence of abdominal vibroacoustic organs as the ancestral state. The question mark on the branch for Coleorrhyncha indicates that the detailed morphology of their vibroacoustic organs is not yet elucidated.

2. The criteria for identifying a “tymbalian tymbal organ” require re-evaluation

The monophyly of the taxon that Wessel et al. (2014) called the “Tymbalia” is not at issue here, although as Wessel et al. (2014) note, the name Euhemiptera has priority as a name for the same proposed clade. Nevertheless, as we discuss below, the identification of several of the key muscles that Wessel et al. (2014) used to homologise the “tymbalian tymbal organ” is highly questionable. Wessel et al.’s (2014) literature review, which Hoch et al. (2019) treat as authoritative, relied entirely on the anatomical interpretations of earlier authors. Our own research using state-of-the-art morphological techniques (Davranoglou et al. 2017, 2019) challenges the muscle identifications of Ossiannilsson (1949) and Weber (1928, 1930), upon which Wessel et al. (2014) based their conclusions. These new findings do not necessarily contradict the “Tymbalia” hypothesis, but they do cast serious doubt on the validity of the morphological criteria that Wessel et al. (2014) used to homologise the “tymbalian tymbal organ” across taxa, and they further reinforce our primary conclusion here that it would at best be premature to describe the snapping organ as a “*tymbalian tymbal organ with a snapping mechanism*”, as Hoch et al. (2019) recommend.

The first error in the muscle identifications of Wessel et al. (2014) was inherited from Ossiannilsson (1949), who frequently misidentified the ventral longitudinal muscle of the first abdominal segment as a metathoracic muscle, IIIvlm2 (Davranoglou et al. 2017). This error was repeated by Wessel et al. (2014), such that their metathoracic IIIvlm1 (confusingly, Ossiannilsson’s IIIvlm2) should in fact be identified as Iavlm following their convention of using an “a” to indicate a muscle of abdominal origin (Davranoglou et al. 2019). The second error in the muscle identifications of Wessel et al. (2014) also appears to have been inherited from Ossiannilsson (1949). By studying the innervation and location of the primary dorsoventral muscles of the vibrational organs of Fulgoromorpha, we demonstrated that Ossiannilsson’s (1949) assignment of these muscles to the first abdominal segment was erroneous, and that they instead belong to the second abdominal segment (see S1 Text in Davranoglou et al. 2019). Again, this error was repeated by Wessel et al. (2014), whose Iadvm1-2 should therefore be identified as IIadvm1-2, following their own naming conventions.

In Davranoglou et al. (2019), the same dorsoventral muscles of the second abdominal segment are labelled IIedvm1-2, where the “e” is an abbreviation of “external”. Rather than recognizing that the key scientific issue here is one of muscle segmental identity, Hoch et al. (2019) again take issue with our terminology, commenting that “*it is mistaken to speak of “external muscles”*”. In fact, use of the term “external muscles” has been standard in insect morphology since at least the foundational work of Snodgrass (1935), who wrote: “*With respect to the dorsal and ventral muscles the most general departure from the simple plan, in which the fibers all lie in a single plane against the body wall, consists of a differentiation of the fibers in each group into external muscles and internal muscles. Thus it is found in nearly all insects that the dorsal and ventral muscles comprise each two layers, there being, namely, internal dorsals (di) and external dorsals (de), and internal ventrals (vi) and external ventrals (ve). ... The lateral [i.e. dorsoventral] muscles are more subject to irregularities of position than are the dorsal and ventral muscles, but they likewise are often divided into internal laterals (Fig. 142, li) and external laterals (le).*” As this terminology has since been used consistently among insect morphologists (e.g. Albrecht 1953; Klug & Klass 2006; Klug & Bradler 2006), we see no error in using it to distinguish IIedvm1-2 from the distinct internal dorsoventral muscles of the same segment (IIidvm1-2).

Hoch et al. (2019) also hypothesised that some of the structures identified as dorsoventral muscles by Davranoglou et al. (2019) might be scolopidial organs, which they asserted are hard to distinguish from muscles in CT scans. Synchrotron-based μ CT (SR- μ CT) is in fact among the most accurate of all methods of morphological investigation (Friedrich et al. 2013), and its exceptional resolution has already allowed us to reconstruct the neuronal and muscular anatomy of another hemipteran abdomen in a previous study (Davranoglou et al. 2017). Of course, SR- μ CT tissue contrast depends on various factors, including sample preparation, sample preservation, and beam energy (Friedrich et al. 2013), and for this reason Davranoglou et al. (2019) also used a suite of other methods including laser confocal microscopy, manual dissection, and microtome sectioning (unpublished) to verify that the structures that they had identified using SR- μ CT were indeed muscles. This is particularly straightforward in this case, because ethanol-induced desiccation causes planthopper muscle fibres to split in a characteristic manner (Fig. 2A-E, white and black arrows) that is visible in both the 3D-volume rendered SR- μ CT reconstructions (Fig. 2A, C, D) and the original SR- μ CT tomograms (Fig. 2B, E). This clearly distinguishes these structures from neuronal tissue, which does not degrade similarly owing to the obvious absence of muscle fibres. Finally, the structures that we identified as dorsoventral muscles (Davranoglou et al. 2019) insert in identical positions (Fig. 2F, G) to known auchenorrhynchan dorsoventral muscles from previous studies (e.g. Ossiannilsson 1949, Mitomi 1984), leaving little doubt as to their identity.

It follows that Figure 20.5 of Wessel et al. (2014), which summarises the configuration and segmental identity of the muscles involved in their hypothesised “tymbalian tymbal organ”, is in error. Specifically, the muscles labelled therein as IIIv1m1 [which represents IIIv1m2 of Ossiannilsson (1949)] and Iadv1m are incorrectly identified as belonging to the metathorax and first abdominal segment, respectively, and should instead have been labelled Iav1m and IIadv1m. These muscles are of key importance to the argument of Wessel et al. (2014), who wrote “If we want to describe in short the “close similarity in the basic plan” (Pringle 1957: p. 154) of the tymbalian tymbal organs, we must refer first and foremost to a homologous set of muscles (I a d1m + II a d1m + I a dv1m + III v1m + II a v1m, see Fig. 20.5), working together in order to produce vibrations for communication purposes.” This confusion over muscle segmental identity is understandable, given that Wessel et al. (2014) did not examine muscle innervation, but it is obviously problematic in identifying muscle homology. Wessel et al. (2014) did not refer to the foundational works of Snodgrass (1933), Kramer (1950), and Wohlers & Bacon (1980), whose interpretations of abdominal segmentation and musculature in Auchenorrhyncha are congruent with our own (see S1 Text in Davranoglou *et al.* 2019), but not with those of Weber (1928) and Ossiannilsson (1949), upon which Wessel et al. (2014) relied. Wessel et al.’s (2014) criteria for identifying a “tymbalian tymbal organ” therefore require careful re-evaluation before they are used to draw any further conclusions regarding the homology or otherwise of the various hemipteran vibroacoustic organs.

Wessel et al. (2014) also attempted to homologue the muscles of “tymbalian” and “non-tymbalian” Hemiptera. For example, in their Figure 20.2, Wessel et al. (2014) highlight two pairs of dorsoventral muscles labelled Iadv1m-2 (but see above) in *Aphis fabae* (Sternorrhyncha) and *Platypleura capitata* (Auchenorrhyncha).

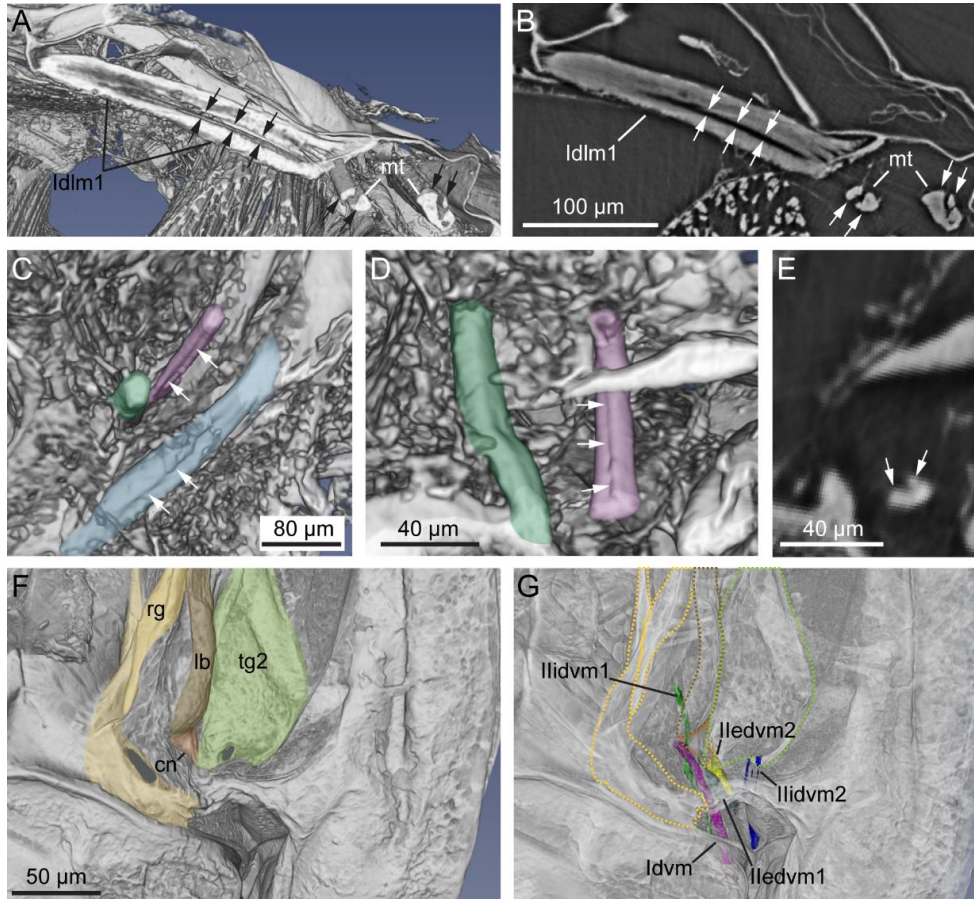


Figure 2. Effects of ethanol-induced desiccation as a guide to identifying muscle tissue in synchrotron-based μ CT-scans, using snapping organ musculature as an example. A) *Elasmoscelis* sp. (Lophopidae) volume-rendered reconstruction, showing the primary snapping organ muscle (Idlm1) and metathoracic muscles (mt), both of which exhibit distinct gaps (black arrows) due to the separation of muscle fibres; B) Same, SR- μ CT scan cross-section, where the effects of alcohol-induced desiccation are visible (white arrows); C) Same, false-coloured reconstruction of snapping organ dorsoventral muscles Iledvm1 (light blue), Iadvm (purple) and Iidvm1 (green) exhibiting distinct grooves due to the splitting of muscle fibres following ethanol-induced desiccation; D) Same, different view, with Iledvm1 not shown; E) Same, SR- μ CT scan cross-section, showing Iadvm1 splitting into two groups (white arrows); F) Volume-rendered, false-coloured reconstruction of *Phantia subquadrata* (Flatidae), showing the defining components of a snapping organ: a ridge (rg), a Y-lobe (lb; snapped shut), and a connector (cn) linking it to tergum 2 (tg2; green); G) Same, faded, to show the tergite insertions of the snapping organ dorsoventral muscles: Iadvm (purple); Iledvm1 (light blue); Iledvm2 (yellow); Iidvm1 (green) and Iidvm2 (dark blue).

The identification of the muscles in *Aphis* followed Weber (1928), but a later paper by the same author (Weber 1935) examining *Aleyrodes proletella* (Sternorrhyncha) demonstrated that sternorrhynchan abdominal dorsoventral musculature can be considerably more complex than suggested by his earlier work on *Aphis* (Weber 1928). Wessel et al. (2014) did not refer to the

later work by Weber (1935), and they did not explain how they were able to homologise these 2 pairs of muscles in Sternorrhyncha to any of the 6 or more pairs of dorsoventral muscles of the first and second abdominal segments of Auchenorrhyncha (see Ossiannilsson 1949; Davranoglou et al. 2019). In fact, the complex musculature of *Aleyrodes* is difficult to homologise with that of its fellow sternorrhynchan *Aphis* – let alone with that of a more distantly-related auchenorrhynchan (Fig. 1).

To summarise, our findings challenge the validity of the criteria that Wessel et al. (2014) used to define the “tymbalian tymbal organ”, and demonstrate that the homologies of the musculature defining hemipteran vibroacoustic organs are far from resolved – just as Wessel et al. (2014) themselves cautioned. We are therefore unwilling to follow Hoch et al. (2019) in assuming homology of the snapping organs of Fulgoromorpha with the tymbal organs of Cicadomorpha and the tergal plates of Heteroptera (i.e. specialised terga of abdominal segments 1-2, used to generate vibrations), pending more detailed examination of the abdominal morphology of a broad range of Hemiptera. Our upcoming work (Davranoglou et al. in preparation) re-examines the homologies of the relevant abdominal musculature across Auchenorrhyncha, and will expand on the summary information that we have presented here. We do not wish to pre-judge the outcome of this analysis, but until the “Tymbalia” hypothesis is tested formally using cladistic methods of ancestral state reconstruction, we must respectfully disagree with Hoch et al.’s (2019) comment that “*it must be at least considered doubtful that vibration producing structures evolved three times independently*” in Cicadomorpha, Fulgoromorpha, and Heteropteroidea. We stress that what appears to be the most parsimonious explanation of a given evolutionary pattern does not always reflect actual evolutionary events. Notable examples include the stridulatory wings of crickets and allies, and the jumping mechanisms of Cicadomorpha and Fulgoromorpha – each of which are thought to have evolved independently (Desutter-Grandcolas et al. 2017; Ogawa & Yoshizawa 2017).

3. Recommended terminology

Even if the vibroacoustic organs of Cicadomorpha, Fulgoromorpha, and Heteropteroidea do turn out to be derived from a vibroacoustic organ that was already present in their last common ancestor – and for the avoidance of doubt, we reiterate that Davranoglou et al. (2019) makes no claim either way (see Fig. 1) – it is self-evident that we will still require a clear, agreed functional terminology to make sense of the diversity of hemipteran vibroacoustic mechanisms. We routinely describe the forelimb of a bird as a “wing”; not as a “pentadactyl limb with a feather mechanism”, though both descriptions are factually correct. In the same way, it is neither unnecessary nor misleading, as Hoch et al. (2019) claim, to describe the vibroacoustic mechanism of planthoppers as a snapping organ, in contradistinction to the tymbal organ of a cicadid. The former involves the snapping instability of a single pair of Y-shaped lobes; the latter involves the buckling instability of convex membranes and multiple curved ridges. These are fundamentally different mechanisms, and they each merit their own terminology.

We agree with Hoch et al.’s (2019) comment that there is considerable variation in the types of vibroacoustic organs present in Cicadomorpha. In fact, the systematic distribution, morphology, and homology of these structures is the subject of an upcoming study of ours (Davranoglou et al. in preparation). However, there is little disagreement in the literature that most Cicadomorpha possess tymbal or tymbal-like organs, defined with reference to their

musculature and to the form of their exoskeletal components (Ossiannilsson 1949). The term tymbal-like is certainly useful here (Wessel et al. 2014; Davranoglou et al. 2019; cf. Hoch et al. 2019), because it points to the observed morphological similarity between the tymbal organs of cicadids and the vibracoustic organs of non-cicadid Cicadomorpha, whilst simultaneously highlighting the fact that their biomechanics are likely to differ in light of their key structural differences. For example, Deltocephalinae and Typhlocybinae possess vibrational mechanisms that have diverged greatly from those of other Cicadomorpha. Even so, there is little doubt that these mechanisms originate from a more generalised tymbal or tymbal-like condition (Ossiannilsson 1949). We cannot yet say the same of the snapping organs of Fulgoromorpha, but nor do we rule out this out as a possibility.

4. Conclusions

Here and in our previous work (Davranoglou et al. 2017, 2019), we have shown that the muscle homologies that Wessel et al. (2014) used to identify a “tymbalian tymbal organ” relied on misinterpretations by previous authors. To stand the test of time, the defining criteria of the “tymbalian tymbal organ” will need to be re-evaluated, and the “Tymbalia” hypothesis tested formally using cladistic methodology. Until then, it would be premature – and perhaps incorrect – to conclude as Hoch et al. (2019) would have us do, that the snapping organs of Fulgoromorpha are homologous with the tymbal and tymbal-like organs of Cicadomorpha, and with the tergal organs of Heteropteroidea. We firmly believe that a multidisciplinary approach, combining functional morphology, behavioural biomechanics, developmental biology, and phylogenetic systematics will be necessary to elucidate the origins of hemipteran vibroacoustic organs – key aspects of which we have studied in our own work both past (Davranoglou et al. 2017, 2019) and current (Davranoglou et al. in preparation). We have chosen not to engage with Hoch et al.’s (2019) discussion of “visibility” and “attention” as the “currency” of the “scientific market”, because we do not recognise their comments as having anything to say about our own research ethics.

5. Summary

Vibrational communication is ubiquitous in planthoppers (Hemiptera: Fulgoromorpha), but its mechanism remained unknown until a recent paper by Davranoglou et al. (2019) describing the functional morphology, behavioural biomechanics, and systematic distribution of a widespread vibrational mechanism that they termed a “snapping organ”. The mechanism of the snapping organ differs fundamentally from the only comparably well-known vibroacoustic organs of Hemiptera – the tymbal organs of cicadids (Cicadomorpha). Shortly after, Hoch et al. (2019) argued that it was “unnecessary, if not misleading” to call the mechanism a snapping organ, which they asserted should instead be identified as a “tymbalian tymbal organ with snapping mechanism”. This identification refers to the “Tymbalia” hypothesis of Wessel et al. (2014), who proposed that the known abdominal vibroacoustic organs of Hemiptera represent modifications of an abdominal vibrational organ hypothesised to have been present in the last common ancestor of Fulgoromorpha, Cicadomorpha, and Heteropteroidea over 300mya. Here, we demonstrate that the criteria that Wessel *et al.* (2014) used to define the tymbalian tymbal organ are based on segmental misidentifications of the key muscles. The “Tymbalia” hypothesis is therefore in need of re-evaluation. We further demonstrate that the muscle ter-

minology used by Davranoglou et al. (2019) is standard in the field, and provide morphological evidence that supports our identification of all of the snapping organ muscles as muscles, and not as scolopidial organs. We suggest that the distinctions between the snapping organs of Fulgoromorpha and the tymbals and tymbal-like organs of Cicadomorpha should be maintained on biomechanical grounds, and conclude that it would be at best premature – and at worst false – to describe the snapping organ as a “tymbalian tymbal organ” until the “Tymbalia” hypothesis has been tested formally using cladistic methods.

6. Author contributions

L.-R.D. analysed data, prepared figures, co-wrote this paper, and was first author of the original paper commented on by Hoch et al. (2019); A.C. was a co-author of the original paper; B.M. was the senior author of the original paper; G.T. co-wrote this paper, and was co-author of the original paper. All authors commented on and approved the final draft of this paper.

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