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: In ihrer kürzlich erschienenen Arbeit (Davranoglou et al. 2019) untersuchten die Autoren an lebenden Exemplaren von *Agalmatium bilobium* (Issidae) mit modernsten Methoden (microCT) die Interaktionen zwischen Muskulatur und bestimmten Anteilen des Exoskeletts zur Vibrationserzeugung und beschreiben deren biomechanische Grundlage. Auf der Basis des morphologischen Vergleichs mit Museumsmaterial von Vertretern der meisten Taxa der Fulgoromorpha (Spitzkopfzikaden) im Familienrang postulieren Davranoglou et al. (2019), ein „neues und bisher übersehenes" Organ entdeckt zu haben, das sie als „snapping organ" bezeichnen und als charakteristisch für die Fulgoromorpha (mit Ausnahme der Delphacidae) interpretieren. Wir sehen diese Ergebnisse aus folgenden Gründen kritisch:

1. In ihrer umfassenden Übersicht zu den vibrationserzeugenden Organen der Hemiptera stellten Wessel et al. (2014) die Hypothese auf, dass sich alle bisher bekannten Strukturen zur Schall- und Vibrationserzeugung auf ein Organ zurückführen lassen, das mit hoher Wahrscheinlichkeit bei der Stammart aller Hemipteren oberhalb der Sternorrhyncha vorhanden war, und eine Synapomorphie dieses Taxons, der sog. Tymbalia (Wessel et al. 2014), darstellt. Da aufgrund der morphologischen Disparität des Organs in den einzelnen Taxa die Homologieverhältnisse schwierig zu beurteilen sind, stellten Wessel et al. (2014) Kriterien für das „Tymbal der Tymbalia" auf. Das sogenannte „snapping organ" erfüllt alle Kriterien dieses Tymbal-Organes. Die Einführung eines neuen Begriffes für eine bestimmte Struktur in einer langen und komplexen Kette evolutionärer Transformationen ist daher unnötig, wenn nicht sogar irreführend. Wir empfehlen daher dringend, in zukünftigen Arbeiten den Begriff „tymbalian tymbal organ with a snapping mechanism" zu verwenden.
2. Die Grundannahme von Davranoglou et al. (2019), dass – im Gegensatz zum neu entdeckten „snapping organ" der Fulgoromorpha – allen Cicadomorpha ein „tymbal-ähnliches Organ" gemeinsam sei, ist zu stark vereinfacht und vernachlässigt die enorme Vielfalt der Ausprägungen des Tymbals bei Nicht-Singzikaden innerhalb der Cicadomorpha. In Anbetracht der verfügbaren Studien scheint es daher zweifelhaft, dass sich die vibrationserzeugenden Strukturen dreimal unabhängig voneinander entwickelt haben sollen, wie es die phylogenetische Interpretation bei Davranoglou et al. (2019: Abb. 3) suggeriert.

Key words: biotremology, Hemiptera, Fulgoromorpha, tymbal, snapping organ.

In their recent publication Davranoglou et al. (2019) studied the biomechanic basis of the vibration-producing structure in the abdomen of planthoppers (Hemiptera: Fulgoromorpha). Applying state-of-the-art technology the authors studied the interaction of muscles and parts of the exoskeleton in live specimens of *Agalmatium bilobum* (Fulgoromorpha: Issidae). From a morphological comparison obtained from preserved specimens representing all Fulgoromorphan taxa of family rank, they concluded that they had discovered a "new and previously

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overlooked" organ in planthoppers that they termed the "snapping organ". However, in biology proximate and ultimate causes must not be confused (see Mayr 1961), and the description of a "novel mechanism" is another story than to unravel its evolutionary origin.

In their comprehensive review of existing knowledge about vibration-producing organs in all subgroups of the Hemiptera, Wessel et al. (2014) hypothesized that all these organs are derivatives of the vibration-producing organ of the last common ancestor of the Hemipteran subgroups except Sternorrhyncha and proposed for this taxon the name Tymbalia. They postulated several criteria for this "tymbalian tymbal" organ, which are as follows:

"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 dlm + II a dlm + I a dvm + III vlm + II a vlm, see Fig. 20.5), working together in order to produce vibrations for communication purposes. In many taxa, we find that these muscles are combined with more or less specialized integumental parts (the 'tymbal plates') that transform the muscle actions into narrow band signals with harmonics, pure tones, or high-pitch pulses. These transformations occur by vibrating membranes or click mechanics or a combination of both. Vibrating or 'clicking' sclerites can be found at the lateral and/or dorsal parts of the first two abdominal segments. In some taxa, the signals may even be produced by the vibration/distortion of internal structures (apodemes) in combination with whole abdomen vibrations (see Gogala 2006). Abdominal vibrations (tremulation) may generally facilitate amplitude amplification in small species. In many taxa known to produce vibrational signals, there is as yet no knowledge about the precise mechanism (see Table A.1) and surprises are to be expected." (Wessel et al. 2014: 412).

The publication by Davranoglou et al. (2019) addresses just that desideratum and therefore is a valuable contribution to our understanding of the biomechanics of vibration-generating structures in one subgroup of the Tymbalia, and enhances the existing knowledge by analyzing how muscle action, organismic architecture and material properties can interact to produce sustained vibrations. These discoveries (pertaining to a proximate mechanism) without any doubt deserve recognition and merit.

To understand the ultimate cause, i.e., the evolutionary pathway that led to the currently observed diversity, it is mandatory to consider the phylogenetic frame within which the organismic transformations occurred.

The authors' basic assumption that all Cicadomorpha share the same "tymbal like organ" (as described for the Cicadidae by Young & Bennett-Clark 1995, i.e., a pair of tymbal plates buckling in and out producing clicks) is oversimplified as it neglects the enormous diversity in tymbalian tymbal structure across the non-cicadid subgroups of Cicadomorpha. The latter are a species-rich and enormously diverse taxon, about which our knowledge is still very patchy: in Cicadellidae alone, the largest family rank taxon comprising ca. 22,000 species, not only the exoskeletal parts but also the muscles involved show complex transformations in structure and function. Within Deltocephalinae and Aphrodinae, dorsoventral muscles that deliver the main energy for vibration production display a configuration that is similar to Cicadidae, the exoskeletal parts involved, however, are not simple lateral tymbal plates (cf. Young & Bennett-Clark 1995), but are located dorsally and constitute a complex pattern of membranous portions and sclerites (see Strübing & Schwarz-Mittelstädt 1986; Kuhelj et al. 2018 & unpublished data). In the Typhlocybinae, in contrast to all other Tymbalia, the ventrolongitudinal muscles (I a vlm) show extreme increase, while it appears that dorsoventral sclerites – as in other Tymbalia – transform the muscle actions in vibrational signals (Ossiannilsson 1949). In the Membracidae, Miles et al. (2017) have found "the set of muscles […] involved in the signaling of *U[mbonia] crassicornis* fit with the set proposed by Wessel et al. (2014) as being components of the tymbalian tymbal organ", but they could not identify specialized exoskeletal parts such as tymbal plates for transforming muscle action into vibrations.

Taking into account the existing information, however patchy, it must be at least considered doubtful that vibration producing structures evolved three times independently as indicated by the phylogenetic tree given by Davranoglou et al. (2019), Fig. 3.

On a more technical note, we want to express concern about the introduction of a new terminology for the musculature at this point: it is mistaken to speak of "external muscles", and it has to be confirmed whether all structures actually referred to as muscles really represent those or rather scolopidial organs. From the known "bauplan" and ongoing studies we expect to see at least three pairs of scolopidial organs in the section concerned (see Vondráček 1949, Bräunig 2018, Ehlers 2018, and Bräunig, Ehlers, Mühlethaler & Wessel unpublished data), which are not easily and certainly to distinguish in μCT scans.

It is obvious that much more information about structure and function of the diverse and disparate interplay of muscles and exoskeletal structures in the production of vibrations with a much larger taxon coverage is needed to identify homologies and to eventually reconstruct the ground pattern ("bauplan") of the tymbal organ in the ancestral species of the Tymbalia and the pathways of evolutionary transformation it underwent in different lineages. The so-called "snapping organ" matches all criteria for the tymbalian tymbal organ. Thus introducing a new name for a particular configuration in a long and complex chain of evolutionary transformation is unnecessary, if not misleading. We therefore strongly recommend to use in future work the term "tymbalian tymbal organ with a snapping mechanism".

We expressly do not blame the authors for overstating the significance of their work – "attention" and "visibility" have become the currency that drives the economy of the scientific market. The promise of visibility and attention draws from overstatements and "buys" acceptance in high-ranked journals, then publications in those "buys" large-scale funding, and the latter "buys" reputation and, alas, academic positions. We shall see more "new" and "spectacular", "previously overlooked" facts in the future. We should be aware, however, that to fully understand the natural world, many mosaic stones are necessary. Not all of them need to be termed milestones.

References

Bräunig P. (2018): Complex arrays of chordotonal receptors in the first two abdominal segments of froghoppers, leafhoppers, and planthoppers. – In: Mazzoni V (ed.) (2018): 2nd International Symposium on Biotremology, Abstract Book. S. Michele all'Adige: Fondazione Mach, p 23. Available from: https://eventi.fmach.it/biotremology2018/Book-of-Abstracts

Davranoglou L-R, Cicirello A, Taylor GK, Mortimer B. (2019): Planthopper bugs use a fast, cyclic elastic recoil mechanism for effective vibrational communication at small body size. – PLoS Biology 17: e3000155; https://doi.org/10.1371/journal.pbio.3000155.

Ehlers S. (2018): Leafhoppers got ears! The abdominal chordotonal organ of leafhoppers – a new type of vibration receiver in the Hemiptera (Hemiptera: Tymbalia: Cicadomorpha: Cicadellidae). – In Mazzoni V (ed.) (2018): 2nd International Symposium on Biotremology, Abstract Book. S. Michele all'Adige: Fondazione Mach, p 58. Available from: https://eventi.fmach.it/biotremology2018/Book-of-Abstracts.

Gogala M. (2006): Vibratory signals produced by Heteroptera - Pentatomorpha and Cimicomorpha. – In: Drosopoulos S, Claridge MF (eds): Insect sounds and communication: physiology, behaviour, ecology and evolution. Taylor & Francis, New York; pp 275–295.

Kuhelj A, Škorjanc A, Vittori M, Žnidaršič N, Hoch H, Wessel A, Virant-Doberlet M. (2018): Vibrational signal production in *Aphrodes makarovi*. – In: Mazzoni V (ed.) (2018): 2nd International Symposium on Biotremology, Abstract Book. S. Michele all'Adige: Fondazione Mach, p 24. Available from: https://eventi.fmach.it/biotremology2018/Book-of-Abstracts.

Mayr E. (1961): Cause and effect in biology. – Science 134: 1501–1506. https://doi.org/10.1126/science.134.3489.1501.

Miles CI, Allison BE, Losinger MJ, Su QT, Miles RN. (2017): Motor and mechanical bases of the courtship call of the male treehopper, *Umbonia crassicornis*. Journal of Experimental Biology 220(10): 1915–1924. doi: 10.1242/jeb.147819.

Pringle JWS. (1957): The structure and evolution of the organs of sound-production in cicadas. Proceedings of the Linnean Society of London 167: 144–159.

Ossiannilsson F. (1949): Insect drummers. A study on the morphology and function of the soundproducing organ of Swedish Homoptera Auchenorrhyncha with notes on their sound production. – Opuscula entomologica. Supplementum X: 1–146.

Strübing H, Schwarz-Mittelstaedt G. (1986): The vibratory membranes in the genus *Euscelis*. – In: Drosopoulos S, (ed.) (1986): Proceedings of 2nd International Congress Concerning the Rhynchota fauna of the Balkan and adjacent regions. Microlimni, Greece; pp. 49–52.

Vondráček K. (1949): Příspěvek k poznání zvukového ústrojí u samců křísů / Contribution to the knowledge of the sound-producing apparatus in the males of the leafhoppers (Homoptera-Auchenorrhyncha). – Acta Academiae Scientiarum Naturalium Moravo-Silesiacae 21: 1–36.

Wessel A, Mühlethaler R, Hartung V, Kuštor V, Gogala M. (2014): The Tymbal – Evolution of a complex vibration-producing organ in the Tymbalia (Hemiptera excl. Sternorrhyncha). – In: Cocroft RB, Gogala M, Hill PSM, Wessel A (eds.) (2014). Studying Vibrational Communication. Animal Signals and Communication 3. Berlin, Springer, pp. 395–444.

Young D, Bennet-Clark H. (1995): The role of the tymbal in cicada sound production. – Journal of Experimental Biology 198: 1001–1019.

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