

# Sexual selection and predation drive the repeated evolution of stridulation in Heteroptera and other arthropods

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## ABSTRACT

Acoustic and substrate-borne vibrations are among the most widely used signalling modalities in animals. Arthropods display a staggering diversity of vibroacoustic organs generating acoustic sound and/or substrate-borne vibrations, and are fundamental to our broader understanding of the evolution of animal signalling. The primary mechanism that arthropods use to generate vibroacoustic signals is stridulation, which involves the rubbing together of opposing body parts. Although stridulation is common, its behavioural context and evolutionary drivers are often hard to pinpoint, owing to limited synthesis of empirical observations on stridulatory species. This is exacerbated by the diversity of mechanisms involved and the sparsity of their description in the literature, which renders their documentation a challenging task. Here, we present the most comprehensive review to date on the systematic distribution and behavioural context of stridulation. We use the megadiverse heteropteran insects as a model, together with multiple arthropod outgroups (arachnids, myriapods, and selected pancrustaceans). We find that stridulatory vibroacoustic signalling has evolved independently at least 84 times and is present in roughly 20% of Heteroptera, representing a remarkable case of convergent evolution. By studying the behavioural context of stridulation across Heteroptera and 189 outgroup lineages, we find that predation pressure and sexual selection are the main behaviours associated with stridulation across arthropods, adding further evidence for their role as drivers of large-scale signalling and morphological innovation in animals. Remarkably, the absence of tympanal ears in most Heteroptera suggests that they typically cannot detect the acoustic component of their stridulatory signals. This demonstrates that the adoption of new signalling modalities is not always correlated with the ability to perceive those signals, especially when these signals are directed towards interspecific receivers in defensive contexts. Furthermore, by mapping their morphology and systematic distribution, we show that stridulatory organs tend to evolve in specific body parts, likely originating from cleaning motions and pre-copulatory displays that are common to most arthropods. By synthesising our understanding of stridulation and stridulatory organs across major arthropod groups, we create the necessary framework for future studies to explore their systematic and behavioural significance, their potential role in sensory evolution and innovation, and the biomechanics of this mode of signalling.

*Key words:* stridulitrum, plectrum, strigil, bioacoustics, Hemiptera, Orthoptera, Arachnida, Crustacea, Myriapoda, multimodal.

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## I. INTRODUCTION

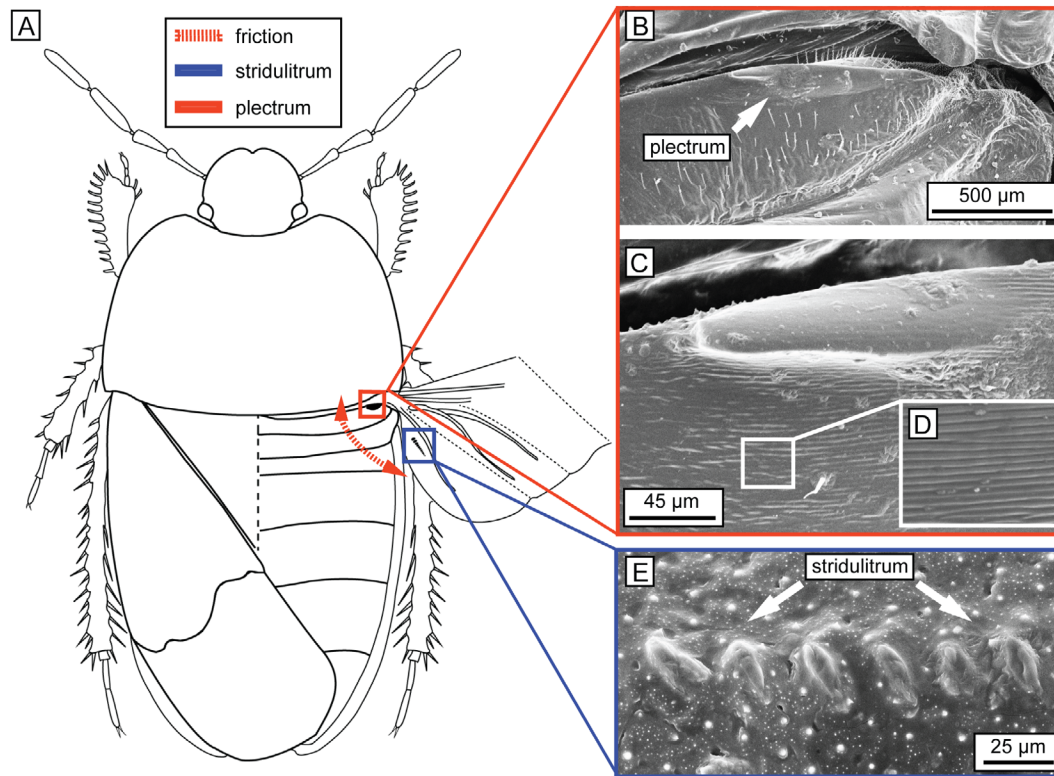
Sound production is one of the principal modes of signalling in animals (Hebets & Papaj, 2005; Ladich & Winkler, 2017; Ronald *et al.*, 2017) and has attracted scientific interest since the time of Aristotle (Weiss, 1929). Arthropods are champions of acoustic signalling, displaying an extraordinary diversity of sound-producing mechanisms that are used in a variety of behavioural contexts (Cocroft & Rodriguez, 2005; Čokl & Virant-Doberlet, 2003; Davranoglou *et al.*, 2020; Song *et al.*, 2020; Virant-Doberlet & Čokl, 2004). At least 200,000 arthropod species also communicate with substrate-borne vibrational signals that are inaudible to humans (Cocroft & Rodriguez, 2005; Hill & Wessel, 2016), in behavioural contexts that overlap with those used by sound-producing species. Some arthropods specialise in communicating exclusively *via* acoustic or vibrational signals, whereas others may generate combined vibroacoustic signals for bimodal or multimodal communication (Girard, Kasumovic & Elias, 2011; Hill, 2007; Robinson, 1969; Strauß & Lakes-Harlan, 2014; Strauß & Stumpner, 2014). As a result, arthropods serve as model organisms for research concerning the intricacies of vibroacoustic sensing and communication (Barth *et al.*, 1988; Brown *et al.*, 1996; Cresswell, 1998; Shaw, 1994; Strauß & Lakes-Harlan, 2014; Young & Bennet-Clark, 1995).

An outstanding problem in communication research is how small animals are able to overcome their limited muscle power to generate vibroacoustic signals that can be transmitted effectively and efficiently to receivers over large distances and through varying substrates (Bennet-Clark, 1998). A widespread solution to this problem is to use mechanisms that multiply the emitted song frequency and mechanical power of their vibroacoustic organs (Bennet-Clark, 1998; Davranoglou *et al.*, 2019a; Longo *et al.*, 2019). One of the simplest ways of achieving this morphologically is to use frequency multipliers in the form of stridulatory organs. Stridulation refers to any mechanism where opposing body parts are repeatedly struck or rubbed against each other to produce acoustic sound and/or substrate-borne vibrations (Figs 1 and 2C). The mechanism is simple in the sense that it consists of a movable component known as the plectrum (from ancient Greek *πλήκτρον*, meaning a musical pick) (Fig. 1B) that is struck against a stationary component termed the stridulitrum (from Latin, referring to the process of uttering or making a shrill noise) (Ashlock & Lattin, 1963; Čokl *et al.*, 2006; Masters, 1979) (Fig. 1E). As the plectrum is rubbed against the stridulitrum, the impact

of each tooth vibrates the exoskeleton and generates a vibroacoustic signal. Stridulatory signals exhibit remarkable diversity, as many contain multiple frequencies with complex harmonics (Akay, 2002), while others produce pure tones with low-energy harmonics (Montealegre-Z *et al.*, 2011; Montealegre-Z, 2009). The advantage of this mechanically uncomplicated motion is that it enables the production of song frequencies that would be impossible to achieve through cyclical muscle action alone (Haskell, 1957; Masters, 1980; Bennet-Clark, 1998; Čokl *et al.*, 2006).

Due to their morphological simplicity and energetic efficiency, stridulatory mechanisms are the prevailing vibroacoustic frequency multipliers in arthropods (Alexander, 1957a,b; Hrušková-Martišová, Pekár & Gromov, 2008; Marilyn, 1977; Masters, 1979), and have evolved occasionally in diverse vertebrates, from tenrecs (Mammalia: Tenrecidae) to manakins (Aves: Pipridae) (Bostwick & Prum, 2005; Cresswell, 1998; Gould, 1965). Although stridulation is the most common vibroacoustic mechanism, it is also one of the least well understood in terms of its evolutionary origins. It is widely assumed among specialists in arthropod bioacoustics and systematics that stridulatory organs have evolved many times independently, yet this has rarely been verified beyond species or genus level, except in recent work on the evolution of stridulation in Orthoptera (Song *et al.*, 2020). The staggering and largely uncatalogued diversity of stridulatory structures displayed by arthropod groups such as insects and arachnids makes mapping their systematic distribution and the number of times they evolved a challenging task.

Consequently, the behavioural contexts in which stridulatory signals are used have also remained largely unstudied (Alexander, 1957b; Lourenço & Cloudsley-Thompson, 1995), while current theoretical and empirical approaches do not explain how stridulation originated from simpler behavioural backgrounds, or why it has evolved repeatedly across animal phyla (Alexander, 1957b; Guinot-Dumortier & Dumortier, 1960; Kronstedt, 1973; Song *et al.*, 2020). Furthermore, the questions of whether stridulation represents a persistent strategy through evolutionary time, and whether it is associated with the development of hearing, remain poorly understood except in Orthoptera (Song *et al.*, 2020). For these reasons, even recent studies on the behavioural significance of stridulation in insects mention only a fraction of the known mechanisms, and make no inferences regarding their evolution (Low, Naranjo & Yack, 2021).

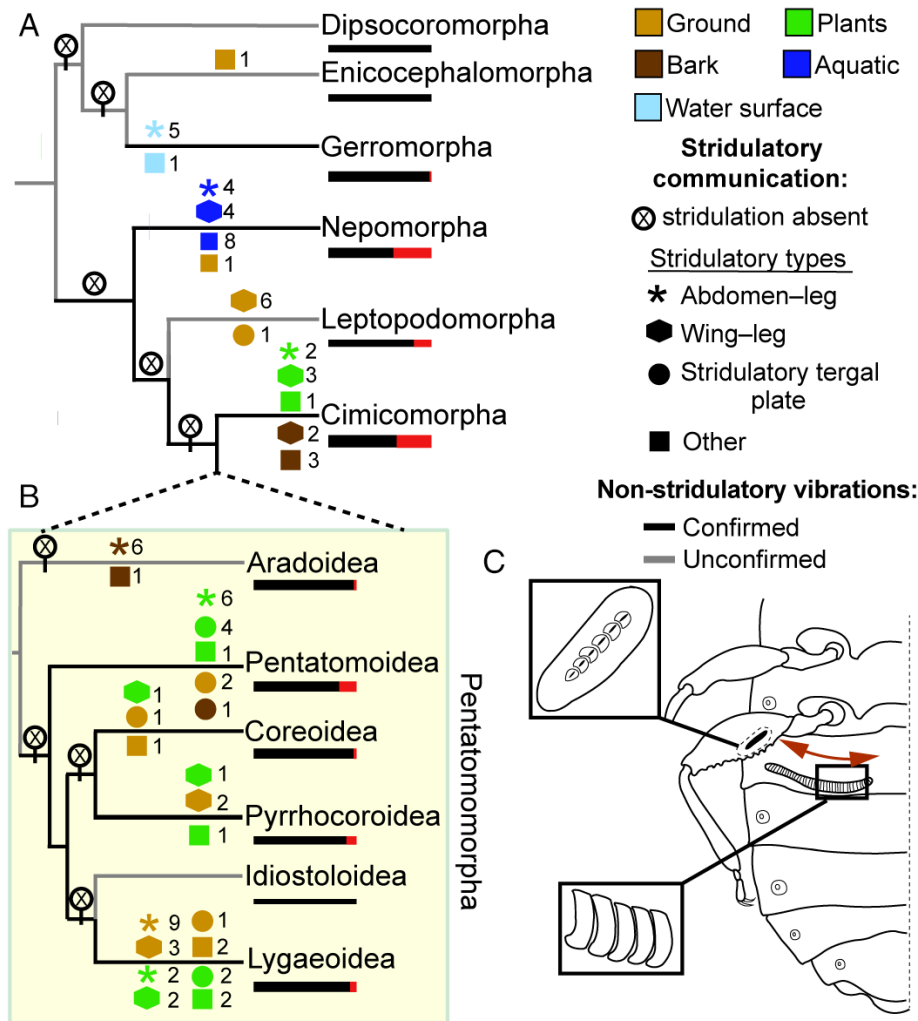


**Fig. 1.** An example of stridulation in the burrowing bug *Cydnus aterrimus* (Forster) (Heteroptera: Pentatomomorpha). (A) Dorsal view of bug, showing the location of the stridulatory mechanism, where the plectrum is on the first abdominal segment (red inset), and strikes against the stridulitrum, which is located on the ventral surface of the hind wing (blue inset). The dashed arrows indicate the friction between the two components. (B) Closeup of the first abdominal segment of *C. aterrimus*, white arrow indicating the location of the plectrum; original photograph, taken using scanning electron microscopy. (C) Magnified view of the plectrum. (D) Inset showing the plectral file. (E) Structure of the stridulitrum, which consists of a series of blunt teeth. Specimen collected from Rhodes, Greece, and examined using a JEOL Neoscope JCM-5000 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.

Heteroptera, or true bugs, provide a particularly good model system for studying the evolution of stridulation, for the following reasons: (i) they possess a very large number of distinct stridulatory mechanisms (Polhemus, 1994; Schaefer, Pupedis & Schaefer, 2015; Schuh & Weirauch, 2020); (ii) their phylogeny is well supported (Wang *et al.*, 2017), making it possible to map the evolutionary origins of these organs phylogenetically; (iii) they are well studied morphologically, which facilitates detailed inferences on the homologies of the respective components of their different stridulatory mechanisms; (iv) their perception of acoustic signals is confined to a single group (Nepomorpha), which allows factors affecting the origin of stridulation to be tested independently of the evolution of their ability to sense the acoustic component of a stridulatory call; and (v) they communicate using multimodal chemical (Davranoglou *et al.*, 2017) and vibrational (McBrien, Čokl & Millar, 2002; Miklas, Lasnier & Renou, 2003) displays, which makes it possible to examine the adaptive advantages of adding an acoustic component to their signals – even in those cases where conspecifics may be unable to perceive this (Gogala *et al.*, 1974). Indeed, chemical signals produced by specialised scent glands and vibrational signals produced through the tremulation

(i.e. body shaking or trembling) of an abdominal organ known as the tergal plate are thought to have originated at the root of Heteroptera (Davranoglou *et al.*, 2017; Gogala, 1984; Wang *et al.*, 2017). Vibrational signals may also be generated through derived appendage percussion (Koczor & Čokl, 2014), non-abdominal tremulation and wing buzzing (Kavčič *et al.*, 2013), so the stridulatory signals of Heteroptera have evolved against a broader backdrop of multimodal communication.

Herein we use Heteroptera as an informative case study to enhance our understanding of the evolutionary origins and adaptive value of stridulation more generally. To this end, we conduct the most extensive literature survey of stridulatory mechanisms to date, covering Heteroptera as well as several selected arthropod outgroups where stridulation is known, including arachnids. This enables us to document the phylogenetic distribution, evolutionary patterns, and behavioural significance of stridulation across arthropods with unprecedented precision. Our overarching aim is to use the data of our comprehensive literature survey to generate hypotheses that future phylogenetically controlled statistical studies could test using a narrower set of species, for which all of the relevant information is made available in the present work.



**Fig. 2.** (A) Distribution of signalling modalities across heteropteran infraorders. (B) Square inset showing vibroacoustic signalling in Pentatomomorpha. Horizontal bars beneath each infraorder in (A) and (B) represent species number (thickest bars being most speciose), the red portion of each bar (when present) indicates the percentage of stridulating species (on a scale from 0 to 100%). The three dominant stridulatory mechanisms are represented by different symbols (see key on top right) with all remaining mechanisms identified by a square), their colour indicates the habitat type where signalling takes place (see Table S4). Numbers on the right side of each symbol indicate how many times a particular stridulatory mechanism evolved independently in the corresponding infraorder, based on its morphology and phylogenetic distribution (relaxed estimates, see Table 1). The encircled X symbol indicates that stridulation was absent at the root of each infraorder, and therefore all stridulatory mechanisms represent derived developments. Black branches of the phylogenetic tree indicate taxa where non-stridulatory vibrational signals have been experimentally confirmed; unconfirmed cases possess grey branches. Note that all non-stridulatory vibrational signals shown here are produced by abdominal tremulatory tergal plates, with the exception of the Gerromorpha, which use their legs (based on Davranoglou *et al.*, 2017). Phylogeny based on Wang *et al.* (2017). (C) An example of the frequently evolved abdomen–leg stridulatory mechanism in the genus *Pictinus* (Aradidae; adapted from Usinger & Matsuda, 1959), where the plectrum (top inset) strikes against an immobile stridulいたrum (bottom inset; direction of motion depicted in red arrow).

**II. METHODS**

Our first step was to document the presence or absence of stridulatory mechanisms across Heteroptera and the selected arthropod outgroups, which we treated as a top-level binary character. We used strict morphological criteria to identify structures as stridulatory mechanisms (see online supporting information, Appendix S1). Some structures that have been described as stridulatory either do not satisfy these criteria,

do not appear to be adapted for this function, or only one stridulatory component is known. However, they cannot be rejected outright as non-stridulatory, due to the absence of detailed morphological data, and are therefore identified as ambiguous in Tables 1 and 2 (ten cases in Heteroptera and three in the selected outgroups). When estimating how many times stridulatory structures evolved, we used both a strict and relaxed approach, which either includes or excludes ambiguous cases, respectively. The relaxed estimates do not



Table 1. List of all known heteropteran stridulatory mechanisms, with both conservative and relaxed estimates of the number of times they have evolved. If a structure is plesiomorphic and evolved once in a family, it is numbered only the first time it appears in the table. The presence of a tremulatory tergal plate (TTP) was determined from vibrational experiments, figures in the cited literature, or specimens directly examined by us.

Infraorder	Taxon	Vibrational signals	Acoustic signals	Times evolved
<b>Dipsocoromorpha</b>				
	<b>All families</b>	TTP (Sweet, 1996)	–	<b>Total: 0</b>
<b>Enicocephalomorpha</b>				
	<b>Aenictopecheidae</b>	TTP (Davranoglou <i>et al.</i> , 2017)	–	
	<b>Enicocephalidae</b>	TTP (Davranoglou <i>et al.</i> , 2017)	Coxal-prosternal mechanism ( <i>Heissaptera janaki</i> ) <sup>A</sup> (Štys & Baňar, 2006)	1
				<b>Total: 0–1</b>
<b>Gerromorpha</b>				
<b>Gerridae</b>				
	Gerrinae	Leg-based ripples (e.g. <i>Gerris remigis</i> ) (Wilcox, 1979)	–	
	Rhagadotarsinae	Leg-based ripples (e.g. <i>Rhagadotarsus</i> spp.) (Polhemus, 1990b)	–	
	Trepobatinae	Leg-based ripples ( <i>Cryptobatoidea brunneus</i> ) (Polhemus, 1990b, 1991)	Stridulitrum on metaacetabulum–pectrum on metatrochanter (half of <i>Metrobates</i> spp.) (Polhemus & Polhemus, 1993; Polhemus, 1994)	1
	Ptilomerinae	Leg-based ripples (?)	Abdominal stridulitrum on sternites 2–6–pectrum on metatrochanter ( <i>Stridulobates</i> ) (Zettel & Thirumalai, 2000)	1
<b>Veliidae</b>				
	Microveliinae	Leg-based ripples ( <i>Microvelia longipes</i> ) (Polhemus, 1990b)	–	
	Veliinae	Leg-based ripples (?)	Stridulitrum on connexival margin of segments 2–3–pectrum on basal surface of metafemur ( <i>Angilovelina y-alba</i> , <i>Stridulivelina</i> ) (Andersen, 1981; Zettel, 1996; Zettel & Thirumalai, 2000)	1
	Veliinae	Leg-based ripples (?)	Abdominal stridulitrum laterally on sternites 3–4–pectrum on metatrochanter ( <i>Paravelia stenoptera</i> ) (Polhemus & Polhemus, 1984)	1
	Rhagoveliinae	Leg-based ripples (?)	Abdominal stridulitrum on connexival margin of segments 2–3–pectrum on basal surface of metafemur ( <i>Chenevelia stridulans</i> ) (Zettel, 1996)	1
	Rhagoveliinae	Leg-based ripples (?)	Stridulitrum on connexival margin of segment 4–pectrum on metatrochanter ( <i>Rhagovelia lugubris</i> ) (Polhemus & Polhemus, 1988)	1
				<b>Total: 6</b>
<b>Nepomorpha</b>				
<b>Belostomatidae</b>				
	Belostomatinae	Surface waves generated by body pumping ( <i>Abedus</i> ) (Kraus, 1989)	–	
	Lethocerinae	TTP-based signals ( <i>Lethocerus</i> ) (Barber, 1971); surface waves generated by body pumping ( <i>Sphaerocoris</i> ) (Kraus, 1989)	–	
	<b>Corixidae</b>	–	Stridulitrum on lateral side of head (maxillary plate)–pectrum on inner surface of profemur (Aiken, 1985)	1

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Table 1. (Cont.)

Infraorder	Taxon	Vibrational signals	Acoustic signals	Times evolved
	<b>Micronectidae</b>	–	Generate signals up to 99 dB (Sueur <i>et al.</i> , 2011); stridulitrum on segment 8–plectrum on paramere (Jansson, 1989); <i>Austronecta</i> ; <i>Micronecta</i> , <i>Papuanecta</i> (Tinerella, 2008, 2013)	1
	<b>Diaprepocoridae</b>	–	–	–
	<b>Gelastocoridae</b>	–	Stridulitrum on dorsally oriented part of sternum 9–plectrum on dorsal surface of proctiger (broadly distributed in <i>Nerthra</i> ) (Polhemus & Lindskog, 1994)	1
	<b>Helotrephidae</b>			
	Helotrephini	–	Wing edge–metafemur stridulatory device (all genera excluding <i>Esakiella</i> ) (Polhemus, 1990a)	1
	Helotrephini	–	Rastrate patch on mesepisternum (stridulitrum)–finger-like process (plectrum) on prosternum ( <i>Helotrephes formosanus</i> and <i>H. semiglobosus</i> , possibly synonymous) <sup>A</sup> (Polhemus, 1994)	1
	Trephotomasinae	–	Wing edge–metafemur stridulatory device ( <i>Trephotomas compactus</i> ) (Papáček <i>et al.</i> , 1990)	1
	Limnotrephini	–	Thorax–thorax mechanism involving serrations on wing base (stridulitrum)–denticles on posterior margin of cephalonotum <sup>A</sup> (Polhemus, 1990a)	1
	<b>Naucoridae</b>			
	Limnocorinae	–	Stridulitrum on lateral margin of abdominal segments 2–3–plectrum on metafemur ( <i>Limnocoris</i> ) (Polhemus, 1994)	1
	Naucorinae	–	Acoustic signals known; proposed mechanism involves interaction between abdominal terga 1–2 or 5–6 ( <i>Ilyocoris cimicoides</i> ) (Aiken, 1985)	1
	<b>Nepidae</b>	–	Stridulitrum on acetabulum of procoxa–plectrum on procoxa (four spp. of New World <i>Ranatra</i> ) (Aiken, 1985; Polhemus, 1994; Torre Bueno, 1905)	1
	<b>Notonectidae</b>			
	Anisopinae	–	Stridulitrum on rostrum–plectrum on protibial comb ( <i>Anisops</i> , <i>Buenoa</i> ) (Aiken, 1985; Polhemus, 1994)	1
	Anisopinae	–	Stridulitrum on coxa–plectrum on femur ( <i>Buenoa</i> ) (Aiken, 1985; Polhemus, 1994)	1
	Anisopinae	–	stridulitrum below abdominal connexiva–plectrum on metafemur (males of <i>Anisops milloti</i> species group, <i>A. hancocki</i> and <i>A. psyche</i> ) (Polhemus, 1994)	2
	Anisopinae	–	Wing edge–metafemur stridulatory device (two different types within the females of <i>A. milotti</i> group) (Polhemus, 1994)	2
	Notonectinae	–	Stridulitrum below abdominal connexiva–plectrum on metafemur ( <i>Enithares</i> ) (Polhemus, 1994)	1
	Notonectinae	–	Wing edge–metafemur stridulatory device ( <i>Martarega</i> ) (Polhemus, 1994)	1

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Table 1. (Cont.)

Infraorder	Taxon	Vibrational signals	Acoustic signals	Times evolved
	<b>Pleidae</b> (Carpintero, 2014)	–	Acoustic signals known (Aiken, 1985); tentative stridulatory organ, consisting of a rastrate patch on mesepisternum (stridulitrum)–finger-like process (plectrum) on prosternum <sup>A</sup> (Wefelscheid, 1912)	
				<b>Total:</b> <b>15–18</b>
<b>Leptopodomorpha</b>	<b>Leptopodidae</b>	–	STP (present in entire family excluding primitive <i>Leotichius</i> ) (Pericart & Polhemus, 1990)	1
	<b>Saldidae</b>			
	Chiloxanthinae	TTP (Sweet, 1996)	–	
	Saldini	–	Wing edge–metafemur stridulatory device ( <i>Lampracanthia</i> ) (Polhemus, 1985)	1
	Saldooidini	–	Wing edge–metafemur stridulatory device ( <i>Chartoscirta</i> , <i>Ioscytus</i> , <i>Macrosaldula</i> , <i>Rupisalda</i> , <i>Saldoida</i> ) (Polhemus, 1985)	5
				<b>Total: 7</b>
<b>Cimicomorpha</b>	<b>Anthocoridae</b>	TTP(?) (Carpintero & Dellapé, 2012)	Stridulatory teeth in coxa and trochanter ( <i>Guayascoris</i> , <i>Nidicola</i> ) <sup>A</sup> (Carpintero & Dellapé, 2012)	1
	<b>Lasiophilidae</b>	TTP(?) (Carpintero, 2014)	Stridulatory organ of procoxa–protrochanter ( <i>Lasiophilus</i> ) <sup>A</sup> (Carpintero, 2014)	1
		–	Wing edge with stridulitrum (emboliar margin)–plectrum on mesotibia ( <i>Lasiocolpus</i> ) (Carpintero, 2014)	1
	<b>Miridae</b>			
	Bryocorinae	TTP-based vibrations ( <i>Macrolophus</i> ) (Gemeno <i>et al.</i> , 2015)	–	
	Cylapinae	–	Wing edge–metafemur stridulatory device ( <i>Euchilofulvius</i> , <i>Samoafulvius</i> ) (Gorczyca, 1998, 2004)	1
	Deraecorinae	–	Wing edge–metafemur stridulatory device ( <i>Obudua</i> ) (Akingbohngbe, 1979)	1
	Mirinae	Abdominal tapping signals ( <i>Lygus</i> ) (Koczor & Čokl, 2014)	–	
	Orthotylinae	–	Wing edge stridulatory device (e.g. <i>Renodaeus</i> species group) (Henry, 2015)	1
	Orthotylinae	–	Stridulitrum in sternites 2–3 – plectrum unknown but likely hind femur ( <i>Renodaeus</i> group of genera but not <i>Renodaeus</i> ) (Henry, 2015)	1
	Phylinae	–	Wing edge–metafemur stridulatory device [Hallodapini ( <i>Alloemimella</i> , part of <i>Hallodapus</i> , <i>Cleotomiris</i> and <i>Wygomiris</i> ; all <i>Laemocoris</i> , <i>Systellonotopsis</i> and <i>Trichophthalmocapsus</i> ) and <i>Clypomiris</i> (Leucophoropterini)] (Tamada <i>et al.</i> , 2020; Schuh, 1974, 1984; Yasunaga <i>et al.</i> , 2019)	1
	Phylinae	–	Stridulitrum on second abdominal sternum–plectrum unknown but likely hind femur ( <i>Arafuramiris</i> , <i>Waterhouseana</i> ; Leucophoropterini) (Schuh, 1984)	1
	<b>Reduviidae</b>	TTP-based vibrations ( <i>Rhynocoris iracundus</i> ) (Gogala, 1985)	Prosternal stridulitrum–labial plectrum (Cai <i>et al.</i> , 1994)	1

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Table 1. (Cont.)

Infraorder	Taxon	Vibrational signals	Acoustic signals	Times evolved
	<b>Tingidae</b>	Vibrational signals (TTP?) known in both adults and nymphs (Cocroft, 2001)	Acoustic signals known in <i>Corythucha ciliata</i> ; possible wing edge stridulitrum–abdominal plectrum <sup>A</sup> (Gogala, 1984)	1
				<b>Total: 8–11</b>
	<b><u>Pentatomomorpha</u></b>			
	<b><u>Aradoidea</u></b>			
	<b><u>Aradidae</u></b>			
	Mezirinae	–	Stridulitrum on abdominal sternum 3–pectrum on metafemur ( <i>Illibus</i> , <i>Pictinus</i> , <i>Psectrocoris</i> , <i>Stelgidocoris</i> ) (Usinger & Matsuda, 1959)	4
	Mezirinae	–	Stridulitrum on abdominal sternum 3–4–pectrum on metatibia ( <i>Artabanus</i> , <i>Rossius</i> ) (Usinger & Matsuda, 1959; Kormilev, 1971)	1
	Mezirinae	–	Stridulitrum on abdominal sternum 4–pectrum on metafemur ( <i>Strigocoris</i> ) (Usinger & Matsuda, 1959)	1
	Calisiinae	–	Stridulitrum on metapleuron–pectrum on metafemur ( <i>Aradacanthia</i> ) (Usinger & Matsuda, 1959)	1
	<b><u>Coreoidea</u></b>			
	<b><u>Alydidae</u></b>	TTP-based vibrations (Gogala, 1984; Numata <i>et al.</i> , 1989)	Wing edge–metafemur stridulatory device (Alydinae, in a group of related Nearctic genera) (Schaefer <i>et al.</i> , 2015); also <i>Alydus</i> and <i>Megalotomus</i> (Moulet, 1991)	1
	<b><u>Rhopalidae</u></b>	TTP-based vibrations (Gogala, 1984)	STP in <i>Jadera</i> (Zych <i>et al.</i> , 2012)	1
	<b><u>Coreidae</u></b>	TTP-based vibrations; tapping signals on wood (Gogala, 1984; Takács <i>et al.</i> , 2008)	Acoustic signals known (Gogala, 1984); stridulitrum on ventrolateral edge of pronotum–pectrum on lateral margin of fore wing (“CGPP” clade, i.e. <i>Centrocoris</i> , <i>Enoplops</i> , <i>Spathocera</i> , <i>Phyllomorpha</i> , <i>Prionotylus</i> and others) (Forthman, 2022; Moulet, 1991; Schaefer, 1962; Štys, 1961)	1
	<b><u>Stenocephalidae</u></b>	–	–	
	<b><u>Hyocephalidae</u></b>	–	–	
	<b><u>Pyrhoroidea</u></b>			
	<b><u>Largidae</u></b>	–	Wing edge–metafemur stridulatory device (Larginae: <i>Arrhaphe</i> ; absent in related genera) (Lattin, 1958)	1
	Physopeltinae	–	Procoxal stridulitrum–protrochanteral plectrum ( <i>Physopelta</i> ) <sup>A</sup> (Stehlik & Kment, 2012; Stehlik, 2013)	1
	Physopeltinae	–	Wing edge (and in some species supplemented lateral pronotal margin) stridulitrum–meso- and metafemoral plectrum ( <i>Delacampius</i> ) <sup>A</sup> (Stehlik & Jindra, 2006)	1
	<b><u>Pyrhacoridae</u></b>	Tremulatory signals known from adults and nymphs of <i>Pyrhacoris apterus</i> (Benediktov, 2007) (TTP)	Wing edge (and in some species supplemented lateral pronotal margin) stridulitrum–meso- and metafemoral plectrum ( <i>Dindymus</i> ) <sup>A</sup> (Stehlik, 2005)	1
	<b><u>Idiostoloidea</u></b>			
	<b><u>Idiostolidae</u></b>	–	–	
	<b><u>Henicocoridae</u></b>	–	–	
	<b><u>Lygaeoidea</u></b>			

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Table 1. (Cont.)

Infraorder	Taxon	Vibrational signals	Acoustic signals	Times evolved
	<b>Artheneidae</b>	TTP-based vibrational signals (Gogala, 1984)	–	
	<b>Berytidae</b>	–	–	
	<b>Blissidae</b>	TTP-based vibrational signals (Minghetti <i>et al.</i> , 2020)	Stridulitrum on abdominal sternites 3–6–metatibial plectrum ( <i>Heteroblissus</i> ) (Ashlock & Lattin, 1963)	1
	<b>Colobathristidae</b>	TTP (Rengifo-Correa & Gonzáles, 2011)	Infraocular stridulitrum–plectrum on prefemur ( <i>Trichocentrus</i> ) (Coscarón & Dellapé, 2003)	1
	<b>Cryptorhamphidae</b>	–	–	
	<b>Cymidae</b>	–	–	
	<b>Geocoridae</b>			
	Australocorinae	TTP (Malipatil, 2012)	–	
	Pamphantinae	–	Wing edge–metafemur stridulatory device ( <i>Abpamphantus gibbosus</i> ; Cuban species of <i>Pamphantus</i> ) (Ashlock & Lattin, 1963; Rengifo-Correa <i>et al.</i> , 2014)	1
	Pamphantinae	–	Wing edge–metafemur stridulatory device ( <i>Epipolops stridulatus</i> ) (Rengifo-Correa <i>et al.</i> , 2014)	1
	Pamphantinae	–	Abdominal stridulitrum on sternum 3–plectrum on metafemur ( <i>Cymapamphantus</i> ) (Henry, 2013)	1
	Pamphantinae	–	Infraocular stridulitrum–plectrum on prefemur (Cattarini) (Henry, 2013)	1
	Pamphantinae: Indopamphantini	TTP? (Malipatil, 2017)	Absent (Malipatil, 2017)	
	<b>Heterogastridae</b>	–	–	
	<b>Lygaeidae</b>			
	Lygaeinae	TTP (Gogala, 2006)	–	
	Orsillinae	–	Wing edge–metafemur stridulatory device ( <i>Xyonyssius</i> , <i>Oceanides</i> , <i>Metarga</i> ) (Ashlock & Lattin, 1963)	1
	Ischnorrhynchinae	–	STP ( <i>Kleidocerys</i> ) (Gogala, 2006; Leston, 1957)	1
	<b>Malcidae</b>	–	–	
	<b>Meschiidae</b>	TTP (Malipatil, 2014)	–	
	<b>Ninidae</b>	–	–	
	<b>Oxycarenidae</b>	–	–	
	<b>Pachygrontidae</b>	–	–	
	<b>Piesmatidae</b>	–	STP ( <i>Piesma</i> spp.) (Jorigtoo <i>et al.</i> , 1998)	1
	<b>Rhyparochromidae</b>			
	Rhyparochrominae			
	Cleradini	–	Abdominal stridulitrum on sternites 3–4–plectrum on metafemur (Ashlock & Lattin, 1963; Malipatil, 1981; Malipatil & Blacket, 2011)	1
	Drymini	TTP (Pericart, 1998)	Abdominal stridulitrum on sternites 3–4–plectrum on metafemur ( <i>Grossander major</i> , <i>Retrodrymus abundans</i> , <i>Austrodrymus flindersi</i> ) (Malipatil, 1977)	1
	Lethaeini	TTP (Pericart, 1998)	–	
	Myodochini	–	Abdominal stridulitrum on sternites 2–4–plectrum on metafemur ( <i>Ashlockaria</i> ) (Ashlock & Lattin, 1963; Harrington, 1980)	1
	Myodochini	–	Abdominal stridulitrum on sternites 2–4–plectrum on metafemur ( <i>Afrovertanus</i> , <i>Erlacda</i> , <i>Pseudopamera</i> ) (Ashlock & Lattin, 1963; Harrington, 1980)	1

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Table 1. (Cont.)

Infraorder	Taxon	Vibrational signals	Acoustic signals	Times evolved
	Myodochini	–	Abdominal stridulitrum on sternites 3–4 – plectrum on metafemur ( <i>Eucosmetus albomarginatus</i> ) (Ashlock & Lattin, 1963; Harrington, 1980)	1
	Myodochini	–	Abdominal stridulitrum on sternites 2–4 – plectrum on metafemur ( <i>Froeschneria</i> , <i>Ligyrocoris</i> , <i>Slaterobius</i> ) (Ashlock & Lattin, 1963; Harrington, 1980)	1
	Myodochini	–	Abdominal stridulitrum on sternite 3 ( <i>Stridulocoris</i> )–plectrum on metafemur (Ashlock & Lattin, 1963; Harrington, 1980)	1
	Myodochini	–	Stridulitrum on lateral areas of prothorax–plectrum on prefemur ( <i>Pseudocnemodus canadensis</i> ) (Ashlock & Lattin, 1963; Harrington, 1980)	1
	Myodochini	–	Wing edge–metafemur stridulatory device ( <i>Villalobosothignus</i> ) (Dellapé, 2003)	1
	Ozophorini	TTP (Pericart, 1998)	Wing edge–metafemur stridulatory device ( <i>Balboa</i> , <i>Prosomoeus brunneus</i> , 3 species of <i>Primierus</i> , <i>Vertomannus</i> ) (Ashlock & Lattin, 1963; Ashlock & Slater, 1982)	1
	Ozophorini	–	Abdominal stridulitrum on sternites 2–4 – plectrum on metafemur ( <i>Lygofuscanellus</i> ) (Ashlock & Slater, 1982; Slater, 1999)	1
	Rhyparochromini	TTP (Pericart, 1998)	Abdominal stridulitrum on sternites 2–4 – plectrum on metafemur ( <i>Altomarus</i> , <i>Scudderocoris albomarginatus</i> ) (Ashlock & Lattin, 1963; Dellapé <i>et al.</i> , 2017)	1
	Udeocorini	TTP ( <i>Daerlac cephalotes</i> ) (Cassis & Symonds, 2012)	–	
	Plinthisinae	TTP (Pericart, 1998)	STP defines subfamily (Pericart, 1998). Modifications: double plectrum on terga 1 and 2 – double stridulitra on metathoracic wing veins (one on vein Cu, the other on Pcu); <i>Plinthisus hirsutus</i> group; <i>P. pulchellus</i> group; two wing stridulitra in <i>P. ericae</i> (Sweet & Slater, 2004)	1
	Plinthisinae	–	additional stridulitrum on propleuron – plectrum on prefemur ( <i>P. peninsularis</i> ) (Sweet & Slater, 2004)	1
	<b>Pentatomoidea</b>			
	<b>Acanthosomatidae</b>	Vibrational signals using TTP (Jordan, 1958)	–	
	<b>Aphylidae</b>	–	Absent (Grazia <i>et al.</i> , 2008)	
	<b>Canopidae</b>	–	STP (Grazia <i>et al.</i> , 2008)	1
	<b>Cydnidae</b>	Low-frequency vibrations concurrent with acoustic signalling (Gogala <i>et al.</i> , 1974)	STP (all subfamilies) (Gogala, 1984; Grazia <i>et al.</i> , 2008; Lawson & Chu, 1971; Lis & Heyna, 2001)	1
	Garsaurinae	TTP (?)	STP absent in <i>Garsauria</i> and <i>Nishocoris</i> (Grazia <i>et al.</i> , 2008; Lis & Heyna, 2001)	
	<b>Dinidoridae</b>	–	Absent (Grazia <i>et al.</i> , 2008)	
	<b>Lestoniidae</b>	–	Absent (Grazia <i>et al.</i> , 2008)	
	<b>Megaridiidae</b>	TTP	Absent (Grazia <i>et al.</i> , 2008)	

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Table 1. (Cont.)

Infraorder	Taxon	Vibrational signals	Acoustic signals	Times evolved
	<b>Pentatomidae</b>	Vibrational signals using TTP (Gogala, 2006)		
	Pentatominae (Mecideini; Diemeniini)	–	Abdominal stridulitrum on sternites 2–4–plectrum on metafemur (Leston, 1954)	1
	“Arrow-headed bugs”	–	Abdominal stridulitrum on sternite 3 (Štys, 2000)	1
	Discocephalinae	–	Abdominal stridulitrum on sternites 5–7–plectrum on metatibia ( <i>Caridophthalmus</i> ; <i>Uncinula tau</i> ) (McDonald, 1979)	1
	<b>Phloeidae</b>	–	Absent (Grazia <i>et al.</i> , 2008)	
	<b>Plataspidae</b>	TTP-based vibrational signals (Gogala, 2006)	Absent (Grazia <i>et al.</i> , 2008)	
	<b>Saileriolidae</b>	–	Absent (Grazia <i>et al.</i> , 2008)	
	<b>Scutelleridae</b>			
	Hoteinae, Odontotarsinae, Pachycorinae	–	Abdominal stridulitrum on sternites 5, 6 sometimes extending to 7–plectrum on metatibia (Leston, 1954)	3
	Pachycorinae, Scutellerinae (Sphaerocorini)	–	STP (Grazia <i>et al.</i> , 2008)	2
	Sphaerocorini (Scutellerinae)	–	Stridulitrum on posterior border of pygophore–plectrum on conjunctival sclerites (Leston, 1952)	1
	<b>Tessaratomidae</b>	–	STP (Grazia <i>et al.</i> , 2008)	1
	Oncomerinae	TTP (Leston, 1954)	Absent (Grazia <i>et al.</i> , 2008)	
	<b>Thaumastellidae</b>	–	STP (Grazia <i>et al.</i> , 2008; Jacobs, 1989; Štys, 1964)	1
	<b>Urostylididae</b>	–	STP (Grazia <i>et al.</i> , 2008)	1
				<b>Total:</b>
				<b>48–51</b>
	<b>Total number of independent appearances of heteropteran stridulatory mechanisms, minimum estimate (excluding ambiguous groups)</b>			<b>84</b>
	<b>Total number of independent appearances of heteropteran stridulatory mechanisms, maximum estimate (including ambiguous groups)</b>			<b>94</b>

STP = stridulatory tergal plate, i.e. a TTP that is equipped with a plectrum that is struck against a stridulitrum located on a hindwing vein. A dash (–) denotes that a certain structure or behaviour has not been reported in the literature.

<sup>A</sup>Denotes structures whose function as stridulatory mechanisms is ambiguous or doubtful.

include morphological characters that were initially misidentified as stridulatory but were later shown to have another function (e.g. Davranoglou *et al.*, 2019b). Like most previous authors, we assume that the presence of an apparent stridulatory mechanism indicates that a species is capable of producing vibroacoustic signals, even in the absence of behavioural observations to confirm this (see Appendix S1 for a justification for this assumption). Having compiled a list of all Heteroptera and arthropod outgroups known to possess an apparent stridulatory mechanism, we sub-classified these mechanisms into different stridulatory types, which we treated as representing distinct mechanistic character states. To do so, we adopted the terminology of Ashlock & Lattin (1963), where the mobile component of the stridulatory mechanism is termed the plectrum (typically a spine, tubercle, stiff hair, granule or a series thereof; occasionally also a

file), and the stationary component is termed the stridulitrum (usually, but not always, a file). We classified each stridulatory type based on the anatomical location of the plectrum and stridulitrum. Thus, a mechanism involving a wing plectrum striking against an abdominal stridulitrum is classified as a different stridulatory type from a mechanism involving a leg plectrum striking against a head stridulitrum. Differences in the segmental position of the plectrum or stridulitrum did not change our classification of stridulatory type (e.g. an abdomen–leg stridulatory mechanism was classified as such regardless of whether the stridulitrum was located on the second or third abdominal segment), but these differences were used to establish instances of parallel evolution of the same stridulatory type (see below). A compendium of all known types of heteropteran stridulatory organs is provided in Table 1, and its equivalent for our outgroups in Table 2.

Table 2. Summary of the distribution of stridulatory types in selected arthropods (Arachnida, Myriapoda, and selected Pancrustacea), with relaxed and conservative estimates of the number of times they have evolved, as well as the behavioural contexts in which stridulatory vibroacoustic signals are produced, when known. If a structure is plesiomorphic and evolved once in a family, it is numbered only the first time it appears in the table. Although the list is as comprehensive as possible, some stridulatory mechanisms may have been omitted due to the number of taxa examined.

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
<b>Arachnida</b>				
<b>Tetrapulmonata</b>				
<b>Pedipalpi</b>				
<b>Amblypygi</b>				
	<b>Phrynidae</b> [ <i>Acanthophrynus</i> , <i>Paraphrynus</i> (?)]	Chelicera–chelicera mechanism (using stridulatory setae)	Defence (Shear, 1970; Quintero <i>et al.</i> , 2010)	1
	<b>Phrynichidae</b> [ <i>Euphrynichus</i> (?), <i>Muscodamon</i> , <i>Phrynichus</i> (?)]	Chelicera–chelicera mechanism (using stridulatory setae)	Defence (Shear, 1970; Prendini <i>et al.</i> , 2005)	
				<b>Total: 1</b>
<b>Schizomida</b>				
	<b>Schizomidae</b> ( <i>Schizomus</i> , <i>Trithyreus</i> )	Chelicera–chelicera mechanism	– (Cokendolpher & Sites, 1988; Shimojana, 1981)	1
				<b>Total: 1</b>
<b>Thelyphonida</b>				
	<b>Thelyphonidae</b> ( <i>Mastigoproctus</i> )	Stridulitrum on chelicera–plectrum on pedipalp coxa	Defence (Barrales-Alcalá <i>et al.</i> , 2018)	1
				<b>Total: 1</b>
<b>Araneae</b>				
<b>Mygalomorphae</b>				
	<b>Barychelidae</b> ( <i>Aureocrypta</i> , <i>Idiommata</i> )	Stridulitrum on chelicera–plectrum on pedipalp coxa	– (Raven, 1994)	1
	<b>Dipluridae</b> (e.g. <i>Diplura</i> , <i>Trechona</i> )	Stridulitrum on chelicera–plectrum on pedipalp coxa	– (Pedroso <i>et al.</i> , 2019; Uetz & Stratton, 1982)	1
	<b>Hexathelidae</b> ( <i>Macrothelè</i> )	Setae on palpal trochanter–setae on trochanter of leg 1	– (Snazell & Allison, 1989)	1
	<b>Theraphosidae</b>			
	<i>Acanthoscurria</i> (Theraphosinae)	Setae on palpal trochanter–setae on trochanter of leg 1	Defence (?) (Bertani <i>et al.</i> , 2008; Pérez-Miles <i>et al.</i> , 2005)	1
	<i>Pamphobeteus</i> (Theraphosinae)	Setae on coxa and trochanter of leg 3–setae on coxa and trochanter of leg 4	Defence (Bertani <i>et al.</i> , 2008)	
	Theraphosinae	Palpal coxa stridulitrum–plectrum on coxa of leg 1; setae on coxa, trochanter and femur of legs 1–2; setae on pedipalpal coxa–trochanter and trochanter–setae on coxa and trochanter of leg 1	Defence (Bertani <i>et al.</i> , 2008; Marshall <i>et al.</i> , 1995; Perafán <i>et al.</i> , 2015; Raven, 1985)	1
	Some Ornithoctoninae; most Selenocosmiinae; all Thrigmopoeinae; <i>Harpactira</i> (Harpactirinae); many Aviculariinae and some Poecilotheriinae	Stridulitrum on chelicera–plectrum on pedipalp coxa	Defence (?) (Bertani <i>et al.</i> , 2008)	1
	Eumenophorinae	Setae on pedipalpal coxa–setae on coxa of leg 1, occasionally on coxa of leg 2 as well	Defence (Raven, 1985)	1
	Harpactirinae	Setae on chelicera–setae on pedipalpal trochanter; additional setae on chelicera in <i>Trichognatha</i>	– (Gallon, 2002)	1

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
<b>Araneomorphae</b> <b>Dysderoidea</b>	Theraphosidae undetermined	Chelicera–chelicera	– (Uetz & Stratton, 1982)	1
	<b>Segestriidae</b> e.g. <i>Ariadna</i> , <i>Citharoceps</i>	Carapace stridulitrum– plectrum on femur of leg 1	Defence (Giroti & Brescovit, 2015; Maddison, 1987)	1
<b>Scytodoidea and Lost Tracheae clade</b>		Cheliceral stridulitrum–palpal femur plectrum		1
	<b>Ochyroceratidae</b> <i>Ochyrocerata</i>	Pedical plectrum–unknown (abdominal stridulitrum?)	– (Baptista <i>et al.</i> , 2008)	1
	<i>Speocera</i>	Cheliceral stridulitrum–palpal femur plectrum	– (Brignoli, 1977)	
	<b>Sicariidae</b> ( <i>Loxosceles</i> , <i>Sicarius</i> )	Cheliceral stridulitrum–palpal femur plectrum	Courtship (Binford <i>et al.</i> , 2008; Cramer, 2015; Fischer <i>et al.</i> , 2009)	
	<b>Pholcidae</b> Several genera (both sexes, males or females only) Only females of certain genera; males have cheliceral stridulitrum–palpal femur plectrum or no mechanism at all	Cheliceral stridulitrum–palpal femur plectrum Stridulitrum on carapace–plectrum on abdomen	Courtship; disturbance (Huber, 1995) Courtship; disturbance (Huber, 1995)	1
<b>Diguetidae</b> (all species)	Cheliceral stridulitrum–palpal femur plectrum	Courtship, defence (Adams, 2014; Gertsch, 1958)		
	<b>Plectreuridae</b>	Cheliceral stridulitrum–palpal femur plectrum	– (Jocqué & Dippenaar-Schoeman, 2003)	
<b>Synspermiata</b> <b><i>incertae sedis</i></b>	<b>Telemidae</b> ( <i>Kinku</i> )	Stridulitrum on anteroventral surface of abdomen–plectrum on coxa 4	– (Dupérré & Tapia, 2015)	1
<b>Gradungulidae- Archoleptonetidae</b> <b>clade</b>	<b>Gradungulidae</b> (most species)	Cheliceral stridulitrum–palpal femur plectrum	– (Davies, 1993; Jocqué & Dippenaar-Schoeman, 2003)	
	<b>Archoleptonetidae</b> ( <i>Darkoneta</i> )	Plectrum on carapace–stridulitrum on dorsal surface of abdomen	– (Ledford <i>et al.</i> , 2011)	1
<b>CY Spigot clade</b>	<b>Austrochilidae</b> ( <i>Thaïda</i> )	Cheliceral stridulitrum–palpal femur plectrum	– (Griswold <i>et al.</i> , 2005)	
	<b>Leptonetidae</b> <i>Appaleptoneta</i> , <i>Chisoneta</i> , <i>Neoleptoneta</i> , <i>Ozarkia</i> , <i>Tayshaneta</i>	Cheliceral stridulitrum–plectrum on pedipalpal tibia (?)	– (Ledford <i>et al.</i> , 2011)	
<b>Palpimanoidea</b>	<b>Archaeidae</b> (most species)	Stridulitrum on chelicera–plectrum on pedipalpal tarsus; stridulitrum on petiole–plectrum on abdomen	– (Griswold <i>et al.</i> , 2005; Wood & Scharff, 2018)	1
	<b>Huttoniidae</b> ( <i>Huttonia</i> )	Cheliceral stridulitrum–palpal femur plectrum	– (Griswold <i>et al.</i> , 2005)	

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
	<b>Mechysmaucheniidae</b> ( <i>Mechysmauchenius</i> )	Cheliceral stridulitrum–palpal femur plectrum	– (Orster <i>et al.</i> , 2000)	
	<b>Palpimanidae</b> (e.g. <i>Palpimanus</i> )	Cheliceral stridulitrum–palpal femur plectrum	Defence; mating (Liznarová <i>et al.</i> , 2018; Uhl & Schmitt, 1996)	
<b>Araneoidea</b>				
	<b>Anapidae</b> <i>Micropholcomma</i>	Pedipalpal patella stridulitrum–femoral plectrum on leg 1	– (Rix & Harvey, 2010)	1
	Most Micropholcommatini	Cheliceral stridulitrum–pectrum on pedipalpal trochanter	– (Rix & Harvey, 2010)	1
	<b>Araneidae</b> ( <i>Microathena</i> )	Stridulitrum on book lung–pectrum on coxa of fourth leg	Defence (Hinton & Wilson, 1970; Scharff & Coddington, 1997)	1
	<b>Cyatholipidae</b>	Carapace stridulitrum–abdominal plectrum	– (Griswold, 1997)	1
	<b>Linyphiidae</b> Most genera	Stridulitrum on chelicera–pedipalp plectrum?	– (Scharff & Coddington, 1997; Uetz & Stratton, 1982)	1
	e.g. <i>Asthenargus</i> , <i>Semljicola</i>	Stridulitrum on book lung–pectrum on coxa of fourth leg	– (Jocqué, 2005; Miller, 2007)	1
	Undetermined	Palpal stridulitrum–pectrum on coxa 1	– (Jocqué, 2005)	1
	e.g. <i>Porhomma</i>	Stridulitrum on coxa 1–pectrum on trochanter 2	– (Uetz & Stratton, 1982)	1
	<b>Malkaridae</b> <i>Pararchaea</i>	Stridulitrum on chelicera–unknown (pedipalp plectrum?); plectrum on femur 1–stridulatory file on femur 2	– (Griswold <i>et al.</i> , 2005; Rix, 2005)	2
	<i>Chilenodes</i>	Stridulitrum on lateral spinneret–pectrum unknown	– (Agnarsson, 2004)	1
	<b>Mimetidae</b> ( <i>Ero</i> )	Stridulitrum on chelicera–unknown (pectrum on pedipalp?)	– (Lissner, 2018)	1
	<b>Mysmenidae</b> (Mysmenopsinae)	Plectrum on femur of leg 1 (males only)–stridulitrum unknown; plectrum on femur of leg 4 (both sexes)	– (Hormiga, 2015)	2
	<b>Physoglenidae</b> (most genera, with some secondary losses)	Carapace stridulitrum–abdominal plectrum	– (Dimitrov <i>et al.</i> , 2017; Forster <i>et al.</i> , 1990)	
	<i>Calcarsynotaxus</i>	Stridulitrum on posterior sternum, covering coxa 4–pectrum on petiole	– (Rix <i>et al.</i> , 2009)	1
	<b>Pimoidae</b> ( <i>Pimoida</i> )	Stridulitrum on chelicera–unknown (pedipalp plectrum?)	– (Scharff & Coddington, 1997)	
	<b>Tetragnathidae</b> <i>Metellina</i> , <i>Zygiometella</i>	Cheliceral stridulitrum–palpal femur plectrum	– (Jocqué, 2005; Özkütük <i>et al.</i> , 2017)	1
	Nanometinae	Stridulitrum on book lung–pectrum on coxa of fourth leg	– (Álvarez-Padilla & Hormiga, 2011)	1
	<i>Pinkfloydia</i>	Possible leg–leg mechanism: markings on legs 1 and 4	– (Dimitrov & Hormiga, 2011)	1

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
	<b>Theridiidae</b>			
	Synapomorphic (excluding Hadrotarsinae)	Stridulitrum on carapace–pectrum on abdomen	Competition; courtship (Agnarsson, 2004; Gwinner-Hanke, 1970)	1
	Certain Hadrotarsinae	Stridulitrum on lateral spinneret–pectrum unknown	– (Agnarsson, 2004)	1
<b>Former Deinopoidea</b>	<b>Uloboridae</b> ( <i>Polencia</i> , <i>Tangaroa</i> , <i>Waikera</i> )	Pedipalpal endite stridulitrum–palpal tarsus plectrum	– (Opell, 1979)	1
<b>Titanoecoidea</b>	<b>Phyxelididae</b> (most species)	Stridulitral scales on chelicera–pectral setae on pedipalp femur	Courtship (Griswold <i>et al.</i> , 2012)	1
	<b>Titanoecidae</b> (many species)	Stridulitral setae on chelicera–pectral granules on pedipalp femur	– (Almeida-Silva <i>et al.</i> , 2009, 2010)	1
<b>Zodarioidea</b>	<b>Zodariidae</b>			
	<i>Akyttara homunculus</i>	Carapace stridulitrum–abdominal plectrum	– (Jocqué, 2005)	1
	<i>Mallinella</i>	4–6 stridulatory organs: leg–leg mechanism: stridulitra on femora 1–2–3, corresponding plectra on femora 2–3–4	– (Jocqué, 2005)	6
<b>Marronoid clade</b>	<b>Amaurobiidae</b> ( <i>Anisacate</i> ; <i>Emmenomma</i> ; <i>Macrobus</i> ; <i>Rubrius</i> )	Stridulitrum on pedipalpal tarsus–pedipalpal tibial plectrum	– (Griswold <i>et al.</i> , 2005)	1
	<b>Hahniidae</b> <i>Antistea</i> , <i>Neoantistea</i>	Carapace stridulitrum–abdominal plectrum	Courtship (Galán-Sánchez & Alvarez-Padilla, 2017; Jocqué & Bosmans, 1982; Uetz & Stratton, 1982)	1
	<i>Hahnia</i>	Stridulitrum on chelicera–pectrum on pedipalp patella	– (Jocqué & Bosmans, 1982)	1
<b>Oval Calamistrum clade</b>	<b>Lycosidae</b>			
	<i>Pardosa</i>	Stridulitrum on book lung–pectrum on coxa of fourth leg	Courtship; competition (Kronstedt, 1973; Rypstra <i>et al.</i> , 2009)	1
	Occurs broadly in family	Stridulitrum on pedipalpal tarsus–pectrum on pedipalpal tibia	Courtship; competition (Fernández-Montraveta <i>et al.</i> , 2000; Sweger & Uetz, 2016)	1
<b>Dionycha part B</b>	<b>Corinnidae</b> ( <i>Olbus</i> )	Stridulitrum on abdomen–pectrum on femur 4; stridulitrum on femur 4–pectrum on femur 3	– (Jocqué, 2005)	2
	<i>Castianeira</i>	Carapace stridulitrum–abdominal plectrum	–	1
	<b>Salticidae</b> e.g. <i>Habronattus agilis</i> group, <i>H. dosseus</i> , <i>Saitis michaelsoni</i>	Carapace stridulitrum–abdominal plectrum	Courtship (Gwynne & Dadour, 1985; Elias <i>et al.</i> , 2003; Maddison & Stratton, 1988)	1

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
	e.g. <i>Menemerus</i> ; <i>Phiddipus mystaceus</i>	Stridulitrum on palpal tarsus–plectrum on palpal tibia	– (Gwynne & Dadour, 1985; Wesolowska, 1999)	1
	Certain Arachnomureae and Heliophaninae	Stridulitrum on carapace below eyes–plectrum on femur of leg 1	– (Maddison, 1987)	1
				<b>Total:</b> <b>57</b>
<b>Other Arachnida</b>				
<b>Opiliones</b>				
<b>Dyspnoi</b>				
	<b>Ischyropsalididae</b> ( <i>Ceratolasma</i> )	Stridulitrum on pedipalpal femur–plectrum on cheliceral segment 1	– (Gruber, 1978; Šilhavý, 1978)	1
	<b>Nemastomatidae</b> <i>Giljarovia</i> , <i>Mediostoma</i>	Stridulitrum on ocularium–plectrum on pedipalpal femur	– (Gruber, 1978; Šilhavý, 1978)	1
	<i>Histicostoma</i> , <i>Mediostoma</i>	Chelicera–chelicera mechanism (row of ridges on cheliceral segment 1)	– (Martens, 1978)	1
	<i>Nemastoma</i>	Stridulitrum on femur of leg 3–plectrum on femur of leg 2	– (Šilhavý, 1978)	1
<b>Laniatores</b>				
	<b>Cosmetidae</b> ( <i>Cynorta</i> , <i>Paecilaema</i> )	Stridulitrum on pedipalpal femur–plectrum on cheliceral segment 1	Defence (Townsend <i>et al.</i> , 2019)	1
	<b>Cryptogobiidae</b> ( <i>Bissulla</i> , <i>Pseudopachylus</i> , <i>Tibangara</i> )	Plectrum on base of pedipalpal femur (and apex of trochanter in <i>Bissulla</i> )–stridulitrum unknown (cheliceral base?)	– (Kury, 2014)	1
	<b>Epedanidae</b> ( <i>Bupares</i> )	Stridulitrum on pedipalpal femur–plectrum on cheliceral segment 1	– (Šilhavý, 1978)	1
	<b>Guasiniidae</b> ( <i>Guasiniá</i> )	Chelicera–chelicera mechanism: stridulatory granules and two large processes on chelicera	– (Pinto-da-Rocha & Kury, 2003)	1
	<b>Phalangodidae</b> ( <i>Minuides</i> )	Stridulitrum on ocularium–plectrum on tibia of leg 3	– (Šilhavý, 1978)	1
	<b>Samoidae</b> ( <i>Maracaynatum</i> )	Stridulitrum on segment 1 of chelicera–plectrum unknown	– (Colmenares & Tourinho, 2016)	1
	<b>Stygnopsidae</b> <i>Hoplobunus</i>	Unknown	Defence (Pomini <i>et al.</i> , 2010)	–
	<i>Panzosus</i>	Chelicera–chelicera mechanism (row of ridges on cheliceral segment 2)	– (Gruber, 1976; Martens, 1978)	1
	<b>Travuniidae</b> ( <i>Peltonychia</i> )	Chelicera–chelicera mechanism (row of ridges on cheliceral segment 1)	– (Martens, 1978)	1
	<b>Triaenonychidae</b> ( <i>Amatola</i> , <i>Biacumontia</i> , <i>Lawrencella</i> , <i>Lispomontia</i> )	Chelicera–chelicera mechanism (row of ridges on cheliceral segment 2)	– (Lawrence, 1937)	1
	<b>Zalmoxidae</b> ( <i>Minuides</i> )	Stridulitrum on ocularium–plectrum on tibia of leg 3	– (Šilhavý, 1978)	1

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
				<b>Total:</b> <b>14</b>
<b>Scorpiones</b>				
	<b>Bothriuridae</b> ( <i>Brachistosternus</i> ; <i>Timogenes</i> )	Tergum–tergum mechanism: granules on mesosomal terga 1–7; terga rub against each other	Defence (Acosta & Maury, 1990; Ochoa & Ojanguren Affilastro, 2007)	1
	<b>Buthidae</b> <i>Parabuthus</i>	Stridulitrum on mesosomal tergum 7 and metasomal terga 1–3–aculeus acts as plectrum	Defence (Alexander, 1957a; Prendini, 2004)	1
	Centruroidinae (several related genera)	Stridulitrum on sternum 3–pectrum on pecten	Defence (Esposito <i>et al.</i> , 2018; Lourenço & Cloudsley-Thompson, 1995)	1
	<b>Diplocentridae</b> ( <i>Oiclus</i> )	Fine hairs on coxa of leg 1–denticles of pedipalpal coxa	Defence (Acosta & Maury, 1990)	1
	<b>Scorpionidae</b> <i>Heterometrus</i>	Stiff setae on maxillary process of coxa of leg 1–tubercles on pedipalpal coxa	Defence (Alexander, 1957a, 1958)	0–1
	certain <i>Opisthophthalmus</i>	Stridulitrum on carapace–pectrum in the form of setae on chelicera; chelicera–chelicera mechanism, using specialised plate-like cuticle	Defence (Alexander, 1957a)	2
	<i>Pandinus</i>	Stiff setae on pedipalpal coxa–denticles on coxa of leg 1	Defence (Alexander, 1957a)	0–1
	<i>Scorpio</i>	Denticles on pedipalpal coxa–denticles on coxa of leg 1	Defence (Acosta & Maury, 1990; Constantinou & Cloudsley-Thompson, 1984)	0–1
				<b>Total:</b> <b>6–9</b>
<b>Solifugae</b>	(all species)	Chelicera–chelicera mechanism: two identical files on each chelicera (rubbed against each other)	Defence (Hrušková-Martišová <i>et al.</i> , 2008)	1
				<b>Total: 1</b>
<b>Myriapoda</b>				
<b>Chilopoda</b>				
	<b>Scolopendridae</b> ( <i>Alipes</i> , <i>Rhysida</i> )	Bending of ultimate legs	Defence (Cloudsley-Thompson, 1961a; Kronmüller & Lewis, 2015)	1
	<b>Scutigera</b> ( <i>Scutigera</i> )	Bending of ultimate legs	Defence (Dumortier, 1963)	1
<b>Diplopoda</b>				
<b>Sphaerotheriida</b>	<b>Arthrophaeridae</b> (most species)	Anterior telopod with stridulation ribs on male harp/female washboard–processes on inner margin of anal shield	Courtship (Moritz & Wesener, 2017; Wesener <i>et al.</i> , 2011)	1
				<b>Total: 3</b>

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
<b>Pancrustacea</b>				
<b>Eumalacostraca</b>				
<b>Peracarida</b>				
<b>Amphipoda</b>				
	<b>Aoridae</b> ( <i>Grandidierella</i> )	Rubbing of article 5–article 2 of gnathopod 1	– (Schmitz, 2002)	1
	<b>Ischyroceridae</b> ( <i>Erichthonius</i> )	Stridulitrum on ventral margin of coxal plate of gnathopod 2–unknown plectrum	– (Hiroyuki, 2009)	1
	<b>Melitidae</b> ( <i>Melitis</i> )	Coxal plate 5–unknown plectrum	– (Schmitz, 2002)	1
	<b>Photidae</b> ( <i>Photis</i> )	Modified surfaces on coxa of gnathopod 2 –coxa of pereopod 3 rubbing on each other	– (Jung <i>et al.</i> , 2017; Schmitz, 2002)	1
	<b>Talitridae</b> ( <i>Gazia samroiyodensis</i> )	Epimera 2–3 rubbing on each other	– (Azman <i>et al.</i> , 2014)	1
				<b>Total: 5</b>
<b>Isopoda</b>				
	<b>Armadillidae</b> ( <i>Armadillo</i> , <i>Cubaris</i> )	Stridulitrum on pereon epimeron–plectrum on propodus of pereopod 5	Defence; aggregation (?) (Cividini & Montesanto, 2018; Montesanto, 2018)	1
	<b>Sphaeromatidae</b> ( <i>Cymodoce</i> )	Tergum–tergum mechanism: file-like patches on thoracic terga	Aggression (Nakamachi <i>et al.</i> , 2015)	1
				<b>Total: 2</b>
<b>Decapoda</b>				
<b>Achelata</b>				
	<b>Palinuridae</b> ( <i>Linuparus</i> , <i>Palinurus</i> )	Stridulitrum on antennular plate–plectrum on last segment of antennal peduncle; rubbing together of abdominal segments	Aggression; defence (Bouwma & Herrkind, 2009; Schmitz, 2002)	1
				<b>Total: 1</b>
<b>Astacidea</b>				
	<b>Parastacidae</b> ( <i>Euastacus</i> )	Stridulitrum on tergal ridges–plectrum on tergal bristles	Defence (Sandeman & Wilkens, 1982)	1
				<b>Total: 1</b>
<b>Dendrobranchiata</b>				
	<b>Penaeidae</b> ( <i>Metapenaeopsis</i> , <i>Parapenaeus</i> )	Carapace–abdomen mechanism: ridges on posterior branchiostegite of carapace–anterior portion of first abdominal (pleon) segment	– (Schmitz, 2002)	1
				<b>Total: 1</b>
<b>Gebiidea</b>				
	<b>Thalassinidae</b> ( <i>Thalassinia</i> )	Pereiopod–carapace stridulation	– (Guinot-Dumortier & Dumortier, 1960)	1
	<b>Upogebiidae</b> ( <i>Upogebia</i> )	Pereiopod–pereiopod mechanism: stridulitrum on propodus of first pereiopod	– (Guinot-Dumortier & Dumortier, 1960)	1
				<b>Total: 2</b>
<b>Anomura</b>				
	<b>Coenobitidae</b> ( <i>Coenobita</i> )	Tubercles on dorsal surface of cheliped propodus	Defence (Imafuku & Ikeda, 1990; Reshmi & Bijukumar, 2010)	1

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
	<b>Diogenidae</b> ( <i>Ciliopagurus</i> )	Cheliped–cheliped mechanism: stridulitrum on propodus and dactylus of cheliped	Aggression; defence (Field <i>et al.</i> , 1987)	1
	<b>Pylochelidae</b> ( <i>Trizocheles</i> )	Tubercles on cheliped carpus–tubercles on propodium and carpus of second pereopod	– (Mclaughlin & Lemaitre, 2008)	1
				<b>Total: 3</b>
<b>Brachyura</b>				
<b>Heterotremata</b>				
<b>Calappoidea</b>				
	<b>Calappidae</b> <i>Acanthocarpus</i> , <i>Calappa</i> , <i>Matuta</i>	Plectrum on cheliped manus–stridulitrum on pterygostomial region	– (Guinot-Dumortier & Dumortier, 1960; Schmitz, 2002)	1
	<i>Mursia</i>	Stridulitrum on cheliped dactylus–pectrum on ischium of endopod of third maxilliped	– (Galil & Spiridonov, 1998; Guinot-Dumortier & Dumortier, 1960)	1
<b>Eriphioidea</b>				
	<b>Eriphiidae</b> ( <i>Globopilumnus</i> )	Leg–leg mechanism: granules on merus of cheliped and pereopods 2–4	– (Guinot-Dumortier & Dumortier, 1960)	1
	<b>Menippidae</b> ( <i>Mennipe</i> )	Stridulitrum on merus of cheliped–granules on orbital border	Defence (Guinot-Dumortier & Dumortier, 1960)	1
<b>Goneplacoidea</b>				
	<b>Goneplacidae</b> <i>Hexaplex</i> , <i>Hexapus</i> , <i>Lambdaphallus</i>	Stridulitrum on pterygostomial region–pectrum on cheliped dactyl	– (Guinot-Dumortier & Dumortier, 1960)	1
	<i>Ommatocarcinus</i>	Stridulitrum on pterygostomial region–pectrum on cheliped merus	– (Guinot-Dumortier & Dumortier, 1960)	1
	<i>Psopheticus</i>	Stridulitrum on suborbital protrusion–pectrum on cheliped merus	Defence (Guinot-Dumortier & Dumortier, 1960)	1
	<b>Euryplacidae</b> ( <i>Trizocarcinus</i> )	Plectrum on cheliped merus–stridulitrum on pterygostomial region	– (Guinot-Dumortier & Dumortier, 1960)	1
<b>Portunoidea</b>				
	<b>Portunidae</b> <i>Ovalipes</i>	Stridulitrum on pterygostomial region–pectrum on cheliped merus	– (Guinot-Dumortier & Dumortier, 1960)	1
	<i>Ovalipes</i>	Stridulitrum on propodus of cheliped–pectrum on second pereopod merus	Courtship (Buscaino <i>et al.</i> , 2015)	1
<b>Potamoidea</b>				
	<b>Potamonautidae</b> <i>Liberonantes latidactylus</i>	Setae on coxae of cheliped, pereopods 2 and 3–setae on branchiostegite	– (Guinot-Dumortier & Dumortier, 1960; Calman, 1908)	1
	<i>Sudanonantes</i> ( <i>S. africanus</i> , <i>S. aubryi</i> )	Setae on coxae of pereopods 2 and 3 (occasionally on cheliped too)–setae on branchiostegite	– (Guinot-Dumortier & Dumortier, 1960; Calman, 1908)	1
<b>Pseudozioidea</b>				
	<b>Pseudoziidae</b> ( <i>Euryozius</i> , <i>Pseudozius</i> )	Stridulitrum on pterygostomial region–pectrum on cheliped carpus	– (Guinot-Dumortier & Dumortier, 1960)	1

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
<b><u>Pseudothelphusoidea</u></b>				
	<b>Pseudothelphusidae</b> ( <i>Potamocarcinus</i> )	Stridulitrum on merus of third maxilliped–pectrum on propodus of second maxilliped	Defence (Lawrence <i>et al.</i> , 1973)	1
<b><u>Thoracotremata</u></b>				
<b><u>Grapsoidae</u></b>				
	<b>Gecarcinidae</b> ( <i>Gecarcinus</i> )	Stridulitrum on pterygostomial region–pectrum on cheliped propodus	Defence (Lawrence <i>et al.</i> , 1973)	1
	<b>Sesarmidae</b> ( <i>Perisesarma</i> , <i>Sesarma</i> )	Chela–chela mechanism (tubercles on cheliped dactyl and propodus)	Courtship; territoriality (Boon <i>et al.</i> , 2009)	1
	<b>Varunidae</b> ( <i>Acmaeopleura</i> , <i>Brachynotus</i> , <i>Chasmagnathus</i> , <i>Gaetice</i> , <i>Helice</i> , <i>Hemigrapsus</i> , <i>Metaplax</i> , <i>Tetragrapsus</i> )	Stridulitrum below eyes–pectrum on cheliped merus	Territoriality (Marilyn, 1977)	1
<b><u>Ocypodoidea</u></b>				
	<b>Dotillidae</b> <i>Dotilla</i>	Pereiopod–bristles on carapace	– (Guinot-Dumortier & Dumortier, 1960)	1
	<i>Ilyoplax</i>	Plectrum on carpus of cheliped–granules on infraorbital protuberance	– (Guinot-Dumortier & Dumortier, 1960)	1
	<b>Macrophthalmidae</b> ( <i>Macrophthalmus</i> )	Plectrum on merus of cheliped–granules on infraorbital protuberance	– (Guinot-Dumortier & Dumortier, 1960)	
	<b>Ocypodidae</b> <i>Ocypode</i>	Stridulitrum on propodus–pectrum on ischium of large cheliped; gastric mill stridulatory mechanism	Defence; territoriality (Guinot-Dumortier & Dumortier, 1960; Taylor <i>et al.</i> , 2019)	2
	<i>Uca</i>	Tubercles on propodus of large cheliped–granules on merus and carpus of first pereiopod	Courtship (Guinot-Dumortier & Dumortier, 1960; Salmon & Atsides, 1968)	1
				<b>Total:</b>
				<b>22</b>
<b><u>Hexapoda</u></b>				
<b><u>Palaeoptera</u></b>				
	<b>Odonata</b>			
	<b>Epiophlebiidae</b> ( <i>Epiophlebia</i> )	Stridulitrum on abdominal segments 3–6/7–pectrum on metafemur (present in larvae only)	Defence (Aiken, 1985; Carle, 2012)	1
				<b>Total: 1</b>
<b><u>Neoptera</u></b>				
<b><u>Dictyoptera</u></b>				
<b><u>Blattaria</u></b>				
	<b>Blaberidae</b>			
	<b>Epilamprinae</b> ( <i>Aptera fusca</i> )	Acoustic signals known; proposed mechanism involves interaction between abdominal terga <sup>A</sup>	Defence (Roth & Hartman, 1967)	1
				1

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
	<b>Oxyhaloinae</b> ( <i>Henschoutedenia</i> , <i>Jagrehnia</i> , <i>Oxyhaloa</i> , <i>Nauphoeta</i> , <i>Rhyparobia</i> )	Stridulitrum on costal margin of wing–pectrum on lateral margin of pronotum	Courtship; defence (Hartman & Roth, 1967; Roth & Hartman, 1967)	0–1
	<b>Panchlorinae</b> (many species of <i>Panchlora</i> )	Stridulitrum on costal margin of wing–pectrum on lateral margin of pronotum	– (Roth & Hartman, 1967)	
	<b>Blattidae</b>			
	<b>Archiblattinae</b> ( <i>Archiblatta</i> )	Stridulitrum (?) on hind wing–pectrum (?) on abdominal tergum 1 <sup>A</sup>	– (Dumortier, 1963; Roth & Hartman, 1967)	1
	<b>Polyzosteriinae</b> ( <i>Megazosteria patula</i> )	Interaction between stridulatory pegs on pro-, meso- and metathoracic terga	Defence (Rentz, 2017)	1
	<b>Ectobiidae</b>			
	<b>Nyctiborinae</b> ( <i>Megaloblatta</i> )	Stridulitrum on abdominal sternum 5–pectrum on abdominal sternum 6	Defence (Schal <i>et al.</i> , 1982)	1
				<b>Total: 3–6</b>
<b>Mantodea</b>				
	<b>Empusidae</b> (many genera, e.g. <i>Gongylus</i> , <i>Idolomantis</i> )	Stridulitrum on tegmen–pectrum on metafemur (sometimes on metacoxa)	Defence (Varley, 1939; Wood-Mason, 1878)	1
	<b>Hymenopodidae</b> <i>Hestiasula</i> <i>Pseudocreobotra</i>	Wings–(?) <sup>A</sup> Wing–abdomen mechanism (ridges on metathoracic wing–granules on abdomen?)	Defence (Shelford, 1903) Defence (Edmunds, 1972)	1 1
	<b>Mantidae</b> <i>Choeradodis</i>	Stridulitrum on lateral margin of pronotum–pectrum on fore femur	Defence (Ramsay, 1990; Robinson, 1969; Wieland, 2013)	1
	<i>Heterochaeta</i> , <i>Mantis</i> , <i>Stigmatoptera</i> , <i>Tenodera</i> <i>Sphodromantis</i> , <i>Rhombodera</i> , <i>Tamolanica</i>	Wing–abdomen mechanism: ridges on metathoracic wing–granules on abdomen (fine structure confirmed only for <i>Mantis</i> )	Defence (Heath, 1980; Hill, 2007; Wood-Mason, 1878)	
	<i>Hierodula</i> , <i>Sphodropoda</i>	Stridulitrum on tegmen–pectrum on metafemur	Defence (Varley, 1939; Wood-Mason, 1878)	
				<b>Total: 3–4</b>
<b>Hemiptera</b> <b>(non-Heteroptera)</b>				
<b>Sternorrhyncha</b>				
<b>Psylloidea</b>	(many families)	Stridulitrum on mesothorax–pectrum on axillary (?) (Liao <i>et al.</i> , 2019)	Courtship (Liao <i>et al.</i> , 2022)	1
<b>Auchenorrhyncha</b>				
	<b>Cicadidae</b> Many genera of Cicadinae and Tibicininae, e.g. <i>Babras</i> , <i>Calliopsida</i> , <i>Chonosia</i> , <i>Clidophleps</i> , <i>Onoralna</i> , <i>Plautilla</i> , <i>Tettigades</i> , <i>Tibicina</i> , <i>Subpsaltria</i> , <i>Zammaria</i>	Stridulitrum on mesonotum–pectrum on fore wing (Moulds, 2005)	Courtship (Luo & Wei, 2015)	2
	<i>Cyclochila</i>	Stridulitrum on pronotal collar–pectrum on fore wing base (Moulds, 2005)	– (Moulds, 2005)	1

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Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
	<i>Maroboduus</i>	Stridulitrum on hind wing costa-plectrum on anal vein of fore wing (Moulds, 2005)	– (Moulds, 2005)	1
	<i>Moana</i>	Stridulitrum on scutellum- plectrum on fore wing (Boulard, 1976)	– (Boulard, 1976)	1
	<i>Carineta</i>	Genital mechanism (Boulard, 1986)	– (Boulard, 1986)	1
				<b>Total: 7</b>
<b>Orthoptera</b>				
<b>Caelifera</b>				
<b>Acridoidea</b>				
	<b>Acrididae</b>			
	Many species of Acridinae (Truxalini), Catantopinae, Eremogryllinae, Gomphocerinae Many Oedipodinae	Stridulitrum on tegmen- plectrum on metafemur (type 1)	Courtship; territoriality (Lorier <i>et al.</i> , 2010; Otte, 1970; Uvarov, 1966)	1
	Many Oedipodinae	Stridulitrum on tegmen- plectrum on metafemur (type 2)	Courtship (Otte, 1970; Uvarov, 1966)	
	Gomphocerinae ( <i>Phonogaster</i> )	Stridulitrum on abdominal terga 3–5-plectrum on metafemur	– (Henry, 1942)	1
	Egnatiinae	Stridulitrum on abdominal terga 4–8-plectrum on metatibia	– (Henry, 1942)	1
	many Copiocerinae, certain Gomphocerinae (e.g. Aleuasini), Hemiacridinae, Oedipodinae	Stridulitrum on tegmen- plectrum on metatibia	Courtship; territoriality (Lorier <i>et al.</i> , 2002; Otte, 1970; Uvarov, 1966)	1
	<b>Ommexechidae</b>	Tegmen-metafemur	– (Song <i>et al.</i> , 2020)	1
	<b>Pamphagidae</b>			
	e.g. <i>Acinipe</i> , <i>Pamphagus</i>	Tegmen-wing	Courtship; defence (García <i>et al.</i> , 2014)	1
	(most species)	Krauss organ: stridulitrum on second abdominal tergum- plectrum on metafemur	Courtship; defence (Massa, 2012)	1
	Porthetinae	Stridulitrum on tegmen- plectrum on metatibia	Courtship; defence (Burt, 1946; Dirsh, 1961; Otte, 1970)	
	Tropidauchenini ( <i>Acrostira</i> , <i>Purpuraria</i> ); Pamphagini ( <i>Glaucia</i> ) (?)	Metanotum-basalar sclerite	Courtship (Johnsen, 1973; López <i>et al.</i> , 2008)	1
	Eurypteryphini ( <i>Eurypteryphes</i> )	Stridulitrum on tegmen- plectrum on mesotibia	Courtship (Korsakoff, 1941)	1
	Akicerinae (part)	Stridulitrum on hind wing- plectrum on mesotibia	– (Uvarov, 1943)	1
	<b>Pamphagodidae</b>	Tegmen-wing stridulation	– (Dirsh, 1961)	
	<b>Romaleidae</b>	Tegmen-wing stridulation	Courtship (Carbonell, 2007)	1
	(most species)			
<b>Pneumoroidea</b>				
	<b>Pneumoridae</b>			
	(all species)	Stridulitrum on third tergum- plectrum on metafemur	Courtship (Alexander & van Staaden, 1989; Smart, 1953; Van Staaden & Römer, 1997)	1

(Continues on next page)

Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
<b><u>Tanaoceroidea</u></b>	<b>Tanaoceridae</b> (all species)	Stridulitrum on third tergum– pectrum on metafemur	– (Dirsh, 1955)	
<b><u>Trigonopterygoidea</u></b>	<b>Xyronotidae- Trigonopterygidae</b> (all species)	Stridulitrum on third tergum– pectrum on metafemur	– (Dirsh, 1955)	
<b><u>Tridactyloidea</u></b>	<b>Tridactylidae</b> (most species)	Stridulitrum on fourth abdominal tergum–pectrum on underside of tegminal margin	– (Woo, 2020)	1
	<b>Cylindrachetidae</b> ( <i>Cylindraustralia</i> )	Mandibulo–maxillary mechanism	– (Günther, 1992)	1
<b><u>Ensifera</u></b>				
<b><u>Grylloidea</u></b>	<b>Gryllidae</b> (most species; lost many times independently)	Right-over-left tegmino– tegminal stridulation (Song <i>et al.</i> , 2020)	Courtship, defence, intraspecific competition (Alexander, 1961; Desutter- Grandcolas, 1998)	1–4
	<b>Mogoplistidae</b>	Ambidextrous tegmino– tegminal stridulation (Dambach & Gras, 1995)	Courtship (Dambach & Gras, 1995)	
	<b>Phalangopsidae</b> (most species; lost many times independently)	Left-over-right tegmino– tegminal stridulation (Gorochov, 2018; Nischk & Otte, 2000)	Courtship, intraspecific competition (Nischk & Otte, 2000)	
	<b>Trigonidiidae</b> (most species; secondarily lost many times)	Right-over-left tegmino– tegminal stridulation (Desutter-Grandcolas <i>et al.</i> , 2016)	Courtship (De Carvalho & Otte, 2006; Oliveira <i>et al.</i> , 2001)	
<b><u>Gryllotalpoidea</u></b>	<b>Gryllotalpidae</b>	Right-over-left/ambidextrous tegmino–tegminal stridulation (Hoffart <i>et al.</i> , 2002; Song <i>et al.</i> , 2020)	Courtship (Nickle & Carlyle, 1975)	
<b><u>Hagloidea</u></b>	<b>Prophalangopsidae</b>	Ambidextrous tegmino– tegminal stridulation (Song <i>et al.</i> , 2020)	Courtship, intraspecific competition, defence (Morris & Gwynne, 1978; Morris <i>et al.</i> , 2002)	
	<b>Prophalangopsidae</b> ( <i>Cyphoderris</i> , <i>Paracyphoderris</i> )	Stridulitrum on metanotum– pectrum on abdominal tergum I	Defence (Woodrow <i>et al.</i> , 2021)	1
<b><u>Schizodactyloidea</u></b>	<b>Schizodactylidae</b> <i>Schizodactylus</i> (brachypterous species); <i>Comicus</i>	Abdominal stridulitrum– femoral plectrum (Mason, 1961)	– (Mason, 1961)	1
	<i>Schizodactylus</i> (macropterous adults)	Fore wing stridulitrum–femoral pectrum (Mason, 1961)	– (Mason, 1961)	1
<b><u>Stenopelmatoidea</u></b>	<b>Anostomatidae</b> (all species)	Abdominal stridulitrum– femoral plectrum (Field, 1993)	Defence, intraspecific aggression, calling, courtship (Field, 1993)	

(Continues on next page)



Table 2. (Cont.)

Higher-level grouping	Taxon	Location	Behavioural context	Times evolved
	(Lutosinae: <i>Hemiandrus</i> )	Mandible–mandible mechanism (in addition to abdomen–femur mechanism) (Field, 1993)	Defence (Field, 1993)	1
	(Deinacridinae: <i>Hemideina</i> )	Abdominal stridulitrum–coxal plectrum (in addition to abdomen–femur mechanism) (Field, 1993)	Defence (Field, 1993)	1
	(Deinacridinae: <i>Deinacrida parva</i> , <i>D. rugosa</i> )	Tergal–tergal mechanism (in addition to abdomen–femur mechanism) (Field, 1993)	Defence (Field, 1993)	1
	<b>Gryllacrididae</b>	Abdominal stridulitrum–femoral plectrum (Field & Bailey, 1997)	Defence (Field & Bailey, 1997)	
	<b>Stenopelmatidae</b> (all or most species)	Abdomino–femoral mechanism (Weissman, 2001)	Defence (Weissman, 2001)	
<b><u>Tettigoniodea</u></b>	<b>Tettigoniidae</b> (most species, lost in some e.g. Phyllophorinae)	Left-over-right tegmino–tegminial stridulation (Song <i>et al.</i> , 2020)	Calling, mating, territoriality, defence (Kowalski <i>et al.</i> , 2014; Morris <i>et al.</i> , 1975; Nickle & Carlyle, 1975; Spooner, 1964)	
	Mecopodinae: <i>Saxava</i>	Mandibular–labral mechanism (Lloyd & Gurney, 1975)	Defence (Lloyd & Gurney, 1975)	1
	Conocephalinae: <i>Mygalopsis</i>	Abdominal stridulitrum–femoral plectrum (Sandow & Bailey, 1978)	Defence (Sandow & Bailey, 1978)	1
	Phyllophorinae	Stridulitrum on mesothoracic sternum–coxal plectrum (Lloyd, 1976)	Courtship, defence (Korsunovskaya <i>et al.</i> , 2020; Lloyd, 1976)	1
	Pseudophyllinae: <i>Pantecphylus</i>	Abdominal stridulitrum–hind wing plectrum (Heller, 1996)	Defence (Heller, 1996)	1
				<b>Total: 25–29</b>
<b><u>Phasmatodea</u></b>	<b>Phasmatidae</b> ( <i>Lobofemora</i> )	Stridulitrum on subcostal and radial wing veins–plectrum on tegmen	Defence (Bresseel & Constant, 2015)	1
	<b>Phylliidae</b> ( <i>Phyllium</i> )	Antenna–antenna mechanism: stridulitrum on antennal pedicel–plectrum on antennal pedicel (in larvae of both sexes; in adults only in females)	Courtship (?); defence (Friedemann <i>et al.</i> , 2012; Lelong, 1995)	1
	<b>Pseudophasmatidae</b> ( <i>Pterinoxylus</i> )	Stridulitrum on costal area of wing–plectrum on tergmen	Defence (Rehn, 1957; Robinson, 1968)	1
				<b>Total: 3</b>
<b><u>Stomatopoda</u></b>	<b>Nannosquillidae</b> ( <i>Coronis</i> )	Uropod–telson mechanism	– (Schmitz, 2002)	1
	<b>Squillidae</b> ( <i>Squilla</i> )	Uropod–telson mechanism	Defence (Kemp, 1913; Schmitz, 2002)	1
				<b>Total: 2</b>
<b><u>Sessilia</u></b>	<b>Balanidae</b> ( <i>Balanus</i> )	Scraping of appendages	– (Schmitz, 2002)	1
				<b>Total: 1</b>

The insect superorder Holometabola is not included in our pancrustacean outgroups due to its sheer size, the sparsity of the relevant literature, and the knowledge gaps in the lower-level phylogeny of many of the stridulating groups involved.

Having documented the taxonomic distribution of the different types of stridulatory mechanism, it was reasonably straightforward to establish their homology or otherwise with reference to morphology and phylogeny. When different species in the same lineage (genus, tribe, subfamily, or family) possessed distinct types of stridulatory mechanism (e.g. if species A used an abdomen–leg mechanism, whereas species B used a wing–leg mechanism), these were identified as being non-homologous. Likewise, where the same type of stridulatory mechanism was found in more than one species of a given lineage (genus, tribe, subfamily, or family), but differed in either: (1) its detailed anatomical position (e.g. located on a different appendage, a different segment on the leg or abdomen, or a different wing vein); or (2) its microstructure (e.g. when of different developmental origin, such as spines *versus* modified hairs), these were again identified as being non-homologous. To resolve the homology or otherwise of stridulatory mechanisms that could not be distinguished morphologically, we used parsimony as the ultimate criterion to infer the number of independent origins of the character state of stridulation in Heteroptera and other arthropod outgroups. This phylogenetic approach was essential when dealing with closely related taxa that possessed the same type of stridulatory mechanism (i.e. when it was not possible to establish homology based on morphological differences alone), except in those phylogenetic studies that had already coded stridulatory mechanisms in their character matrix and appropriately reported whether the mechanisms represented independent evolutionary events or not (e.g. Harrington, 1980; Polhemus, 1985; Song *et al.*, 2020).

We used published phylogenies to count the number of evolutionary steps required to explain the systematic distribution of stridulatory mechanisms, where we sought the maximally parsimonious explanation of the observed patterns, under the assumption that character gains and losses were equally likely to occur. We applied the criterion of parsimony by implementing the two algorithmic rules established by Maddison, Donoghue & Maddison (1984) for local outgroup reconstruction of ancestral character states. Working outward from a given ingroup, the first doublet rule states that if the first outgroup possesses the same character state as the first doublet (= two consecutive outgroups sharing the same state, possibly including the first outgroup) (Fig. S1A), then that is also the most parsimonious assignment for the ancestral state; conversely if the character states of the first outgroup and the first doublet differ, then the ancestral state is equivocal. When there are no doublets present, the alternating outgroup rule states that if the first and last outgroups share the same character state (Fig. S1B), then that is also the most parsimonious assignment for the ancestral character state; if not, then the ancestral character state is equivocal.

This morphological and phylogenetic approach to estimating the number of times that stridulatory organs have evolved convergently is likely to underestimate the number of independent origins, owing to the absence of detailed phylogenies for many taxa in which multiple species share morphologically similar stridulatory organs. We therefore expect that when the phylogeny of Heteroptera is more thoroughly resolved at the level of subfamilies, tribes, and genera, it will be found that the number of times that stridulatory organs have evolved convergently is higher than estimated herein. A detailed rationale for our estimates of the number of times that stridulation evolved in each of the examined groups can be found in Appendix S2.

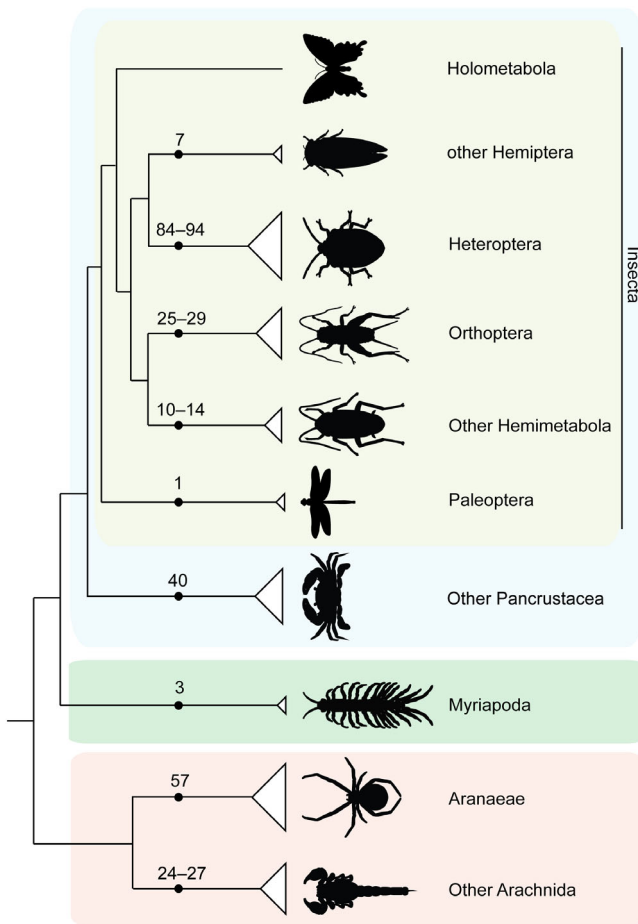
We should note that the estimates of independently evolved stridulatory mechanisms that we provide for both the Heteroptera (Table 1) and the selected outgroups (Table 2) should be treated as tentative. Although our report is comprehensive, there might be missing data, and in several cases, the phylogeny of a particular group or the homologies of certain stridulatory structures may have remained poorly understood. Our analysis is intended to provide the necessary framework for future phylogenetic, morphological, and bioacoustic studies, which will undoubtedly change the estimates provided here.

### III. RESULTS

#### (1) Evolution of stridulatory organs in Heteroptera and prevalence in other arthropods

Our survey of Heteroptera found that stridulatory organs have evolved independently between 84 and 94 times, based on strict and relaxed estimates, respectively (Fig. 2A, B; Table 1). This encompasses a great diversity of different stridulatory types, including modifications of the tremulatory tergal plate (TTP) that add stridulatory properties (to form a stridulatory tergal plate, STP) to its pre-existing vibrational mechanism. Heteroptera therefore represent an unrivalled example of parallel and convergent evolution of vibroacoustic signal generation among insects. For comparison, the present analysis shows that the other major insect group that widely uses vibroacoustic signalling, Orthoptera, have evolved stridulatory mechanisms at least 25 times independently [Fig. 3; Table 2, relying primarily on the analysis of Song *et al.* (2020) and our own findings, described in Appendix S2]. Only spiders (Araneae), in which vibroacoustic signalling is similarly prevalent, approach the diversity of stridulatory mechanisms seen in Heteroptera, having evolved these at least 57 times independently (Fig. 3; Table 2). Non-insect pancrustaceans have evolved stridulatory mechanisms at least 40 times independently (Fig. 3; Table 2), further demonstrating the prevalence of such organs across arthropods.

Stridulatory organs in Heteroptera have not only evolved repeatedly, but are also widespread, being present in



**Fig. 3.** The evolution of stridulation in selected arthropod lineages as recovered from our analysis. The nodes indicate the number of times that stridulatory mechanisms have evolved independently in each lineage (Tables 1 and 2). The size of the white triangles is correlated to the number of independent acquisitions of stridulatory mechanisms in each lineage: the larger the triangle, the more times stridulatory mechanisms have evolved in that group. No homology is assumed between the stridulatory mechanisms of different lineages. Phylogeny based on Giribet & Edgecombe (2019). Holometabola were not included in our analysis.

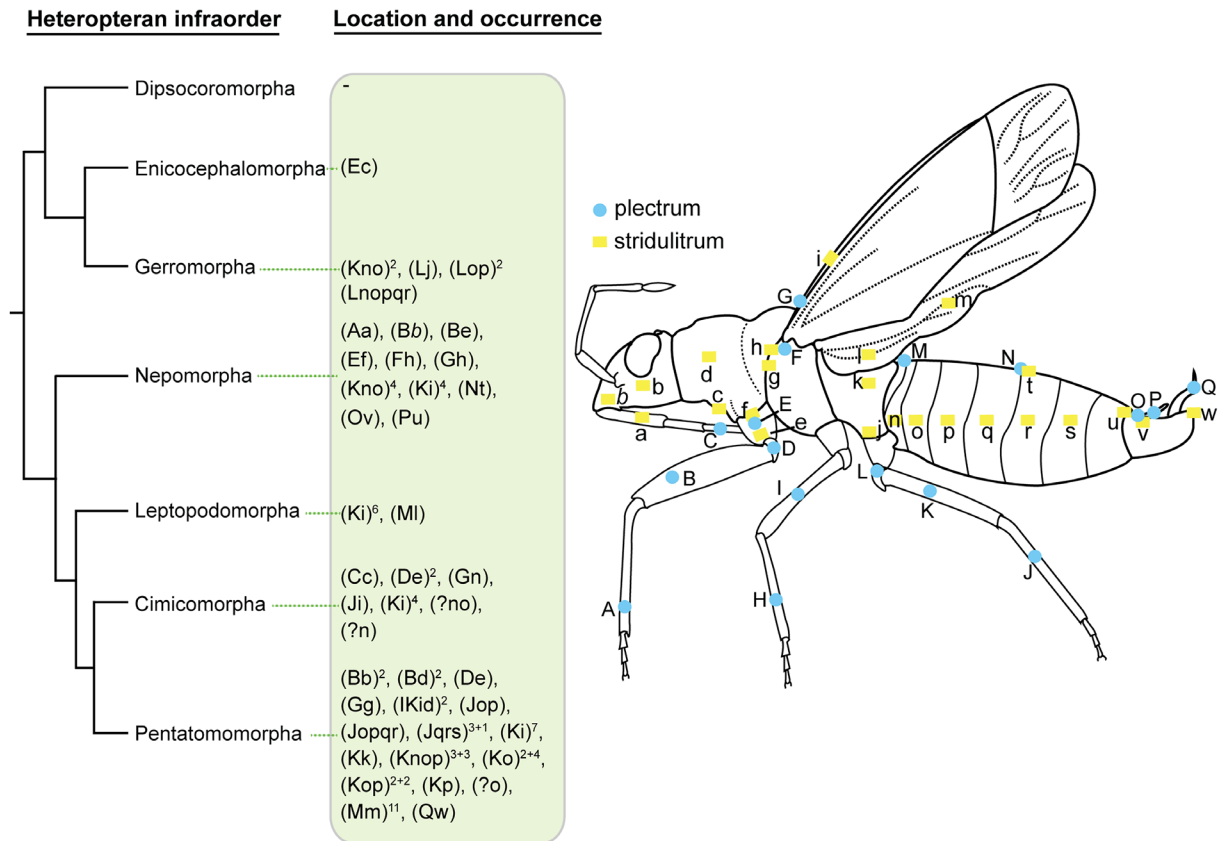
around 22% of approximately 40,000 extant species (Fig. 2A, B; Table S1). In most cases, stridulation is lineage specific, being present in only one or a few closely related species or genera (Table 1). Consequently, the number of times that stridulation evolves in a higher-level taxon may depend more on its species richness than its ecology. For example, the smallest heteropteran infraorders possess the least number of independent origins of stridulatory organs (if any), while the three most speciose ones have the most (Fig. 2A, B; Table S1), presumably due to the larger pool of lineages with the potential to evolve this trait. Based on their phylogenetic distribution, we conclude that stridulatory organs were invariably absent in the common ancestor of each heteropteran group (Fig. 2A, B). This is in contrast

to chemical and non-stridulatory vibrational signalling (e.g. tapping, buzzing, tremulation), each of which is thought to be present at the root of the order (Fig. 2A, B) (Carayon, 1971; Davranoglou *et al.*, 2017; Gogala, 1984; Schuh & Weirauch, 2020; Wheeler, Schuh & Bang, 1993). Thus, insects that already communicate by other means (i.e. chemicals, non-stridulatory vibrations) have repeatedly evolved stridulatory organs to produce more complex signals. Indeed, our results reveal a clear evolutionary tendency in Heteroptera and other arthropods towards the evolution of stridulatory organs, as multiple such mechanisms have evolved across distantly related groups over evolutionary time.

## (2) Stridulatory organs are more frequent in particular body parts and habitats

We identified up to 20 distinct types of heteropteran stridulatory mechanisms (15 if functionally ambiguous types are excluded), each involving modified surfaces on different body parts striking against each other (Fig. 4; Tables 1 and S2). This is a remarkably diverse set of mechanisms, as only 14 distinct types are known from the even more speciose Coleoptera (Wessel, 2006), although the occurrence of stridulatory mechanisms in the latter group may be under-reported. However, in Heteroptera, only three stridulatory types collectively account for 82% of all cases of convergent evolution of stridulatory mechanisms according to our conservative estimates (Table S3, Fig. 4), namely the abdomen–leg mechanism (legs rub against the abdomen; Fig. 2C), the wing edge–leg mechanism (legs rub against wing margin) and the STP (up-and-down shaking of the abdomen by a vibrational organ known as the TTP, which is equipped with a plectrum that strikes against a stridulitrum on the hind wing; Fig. 1). The arthropod outgroups that we analysed have also repeatedly evolved stridulatory mechanisms that overwhelmingly involve the same body parts (Table 2): stridulatory structures on the chelicerae dominate in Arachnida; the pterygostomial and infraorbital regions dominate in brachyuran crustaceans; and wing–leg mechanisms prevail in Orthoptera. The above examples demonstrate that the evolution of the morphological framework for arthropod vibroacoustic signalling can be biased towards the use of specific body parts, even when there are multiple solutions for how to generate acoustic and substrate-borne signals using stridulation. It is evident that the motions performed by certain body parts are especially prone to evolving into stridulatory mechanisms; we present a hypothesis on the behavioural background that leads to this morphological bias in Section IV.2.

Besides being prone to evolving in particular body parts, the evolution of stridulation may also be affected by the signalling medium. Stridulation appears to evolve overwhelmingly often in taxa inhabiting soil and leaf-litter, plants, and water, but less often in those living on the water surface or bark (both on and under it) (Fig. 2A, B; Table S4). This may indicate that either the physical properties of particular substrates increase the probability that stridulation will evolve, or that certain important biotic factors (e.g.



**Fig. 4.** Phylogenetic distribution of different combinations of plectra and stridulitra in Heteroptera. Heteropteran phylogeny and a generalised heteropteran, showing where the different types of plectra (blue circles) and stridulitra (yellow quadrangles) are located on the body, in what combinations they occur (letters in parentheses in green panel), and how many times they have evolved in each infraorder (superscript numbers). Capital letters next to the blue circles and lower case letters next to the yellow rectangles indicate a distinct combination of plectrum or stridulitrum respectively. Phylogeny based on Wang *et al.* (2017). Data from Table 1.

predation) are more prominent in particular habitats than others. The former may be the case for burrowing bugs (Cydnidae), where stridulation may provide a mechanical solution to signalling underground (Čokl *et al.*, 2006), and also for certain water striders (Gerridae) that are reported to produce signals of a different frequency band to the environmental noise produced in their torrential waterfall habitat (Zettel & Thirumalai, 2000).

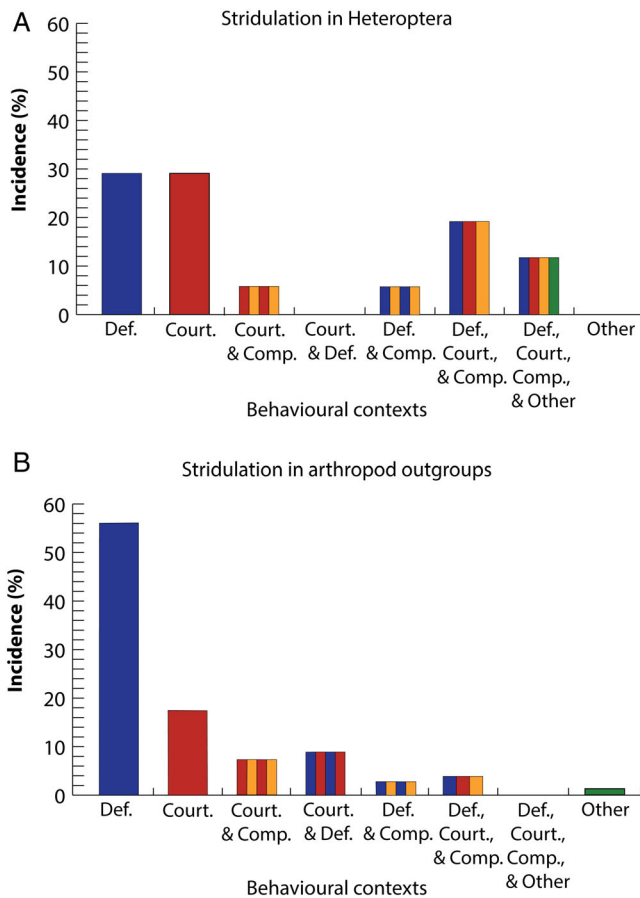
**(3) Behavioural context of stridulation**

The biological significance of stridulation is poorly documented; in 79% of stridulating heteropterans and in 52% of the arthropod outgroups, the behavioural context of stridulation is unknown (Tables S5 and S6). However, in arthropods where the behavioural significance of stridulation is known, we observe a strong association with sexual (courtship and mating) and defensive contexts (interactions with predators, disturbance/protest signals). In Heteroptera, roughly 30% of the described stridulatory behaviours are involved in defensive contexts only and 30% in sexual contexts only (Fig. 5A; Table S5). The remaining 40% of described

stridulatory behaviours combine both defensive and sexual contexts, occur together with competition, and/or are observed with other contexts such as aggregation, territoriality, or maternal care. The role of defence is even stronger in the arthropod outgroups: 55% of stridulation takes place only in defensive contexts, and 18% in courtship only; the remaining 27% combine sexual and defensive behaviours together and/or with other signalling contexts (Fig. 5B; Table S6).

Based on the above, we conclude that stridulation is most commonly used in defensive and sexual behaviours, either in isolation or in combination. The use of stridulation in other contexts is rarer and occurs almost exclusively in combination with sexual and/or defensive functions. However, we caution that the apparent extent of the use of stridulation in defensive contexts could reflect observational bias, as many cases of stridulation have been documented only when specimens were collected and handled by researchers (Field, Evans & Macmillan, 1987; Field, 1993; Field & Bailey, 1997; Leston, 1954, 1957). Targeted studies on the ethology of stridulating species are likely to reveal significant overlap between sexual, defensive, and other contexts of stridulation.





**Fig. 5.** The behavioural contexts in which stridulation has been recorded in Heteroptera (A) and in the examined arthropod outgroups (Arachnida, Myriapoda and selected Pancrustacea; B). Blue = defence/disturbance (Def.); red = courtship/mating (Court.); yellow = competition (Comp.); green = other behavioural context (Other). Data from Tables S5 and S6.

## IV. DISCUSSION

### (1) Sexual selection and predation explain the evolution of stridulation

Our comprehensive synthesis of the published literature reveals a clear link between stridulation and close-range defensive and sexual behaviours (Fig. 5; Tables S5 and S6). Most available ethological studies of Heteroptera show that stridulatory signals are used at close range in defensive, courtship, or mating behaviours (Gogala, 1984; Dodson & Marshall, 1984; Manrique & Lazzari, 1994; Schmidt, 1994; Zych *et al.*, 2012). These same functions are also common for other arthropods (e.g. Alexander, 1957*a*; Blair & Bilton, 2020; Bouwma & Herrnkind, 2009; Desutter-Grandcolas, 1998; Esposito *et al.*, 2018; Hrušková-Martišová *et al.*, 2008; Field, 1993; Kronmüller & Lewis, 2015; Low *et al.*, 2021; Lourenço & Cloudsley-Thompson, 1995; Field *et al.*, 1987; Masters, 1980; Polidori *et al.*, 2013; Pomini *et al.*, 2010; Woodrow

*et al.*, 2021) and vertebrates (Cresswell, 1998; Bostwick & Prum, 2005; Gans & Maderson, 1973; Gould, 1965). More rarely, stridulatory signals are used in other close-range behaviours, such as rivalry, aggregation, and triggering synchronous egg-hatching (Gogala *et al.*, 1974; Haskell, 1957; Jansson, 1972, 1989; Mukai *et al.*, 2014). The mechanical characteristics of stridulatory signals presumably explain why their vibrational component is used primarily for close-range interactions, as their high frequency (2–20 kHz) (Čokl *et al.*, 2006; Sueur, Mackie & Windmill, 2011; Yasunaga *et al.*, 2019) is unsuitable for long-distance substrate-borne transmission in the main arthropod signalling substrates (soil, plants and water; Fig. 2A, B, Table S4) (Bennet-Clark, 1998; Casas, Magal & Sueur, 2007; Čokl & Virant-Doberlet, 2003; Gogala, 1984, 2006; Lang, 1980; Michelsen *et al.*, 1982; Mortimer, 2017).

Stridulation is clearly an important signalling mechanism, as its repeated evolution across arthropods indicates strong selective pressures for its development. Stridulation is thought to be adaptive in defensive contexts by reducing predation risk in several ways, which are not mutually exclusive: (i) it can startle predators (Masters, 1979, 1980; Robinson, 1969); (ii) it can warn predators of undesirable qualities of the stridulating animal if an attack is realised, such as distasteful chemical secretions or painful stings (Ewing, 1984; Haskell, 1957; Masters, 1979; Kowalski *et al.*, 2014); (iii) it can be part of a deimatic display (Kowalski *et al.*, 2014; Low *et al.*, 2021; Umbers, Lehtonen & Mappes, 2015); (4) it can imitate the sounds of a dangerous or toxic animal (Masters, 1979; Sandow & Bailey, 1978); or (5) it can produce vibrations that cause physical discomfort when stridulating prey is in the mouth of a predator, due to overstimulation of tactile receptors (Masters, 1979, 1980; Senter, 2008; Song *et al.*, 2020); similar effects have been proposed for the presumably defensive buzzing of solitary bees (Larsen, Gleffe & Tengö, 1986). However, few of these hypotheses have been conclusively supported for the evolution of stridulation in arthropods (Alexander, 1957*a*; Masters, 1979, 1980; Rowe & Guilford, 1999; Sandow & Bailey, 1978; Stidham, 2020), due to the paucity of empirical studies. It is likely that stridulation is adaptive against different threats in different lineages of stridulating arthropods.

In a sexual context, the role of stridulation is less clear, and whether it conveys a particular quality of the signaller or serves simply as an advertisement remains to be determined. However, experimental and theoretical studies suggest that increased signalling complexity may be sexually adaptive (Ewing, 1984; Gerhardt, 1992). Multiple non-redundant signals may provide information on multiple qualities of the signaller (Chaine & Lyon, 2008; Stevens, 2013), whereas redundant multimodal signals are advantageous as they increase information transfer fidelity by acting as back-ups for each other (Ay, Flack & Krakauer, 2007; Stevens, 2013), are easier to detect by the receiver (Grafe & Wanger, 2007) and trigger faster behavioural responses in the receiver (Rowe & Guilford, 1999). In addition,

interactions between different signals during their transmission may be informative in themselves (Partan & Marler, 1999). In Heteroptera, most species are limited in the number of distinct types of vibrational signals they can produce, as their primary vibrational organ is the TTP, which generates simple abdominal vibration (Benediktov, 2007; Gogala, 1984; Moraes *et al.*, 2005; Kavčič *et al.*, 2013). However, many heteropteran species complement their tergal plate vibrations with appendage and abdominal tapping, body shaking and wing buzzing signals (Kavčič *et al.*, 2013; Takács *et al.*, 2008; Žunič *et al.*, 2008). We therefore suggest that stridulation is so successful as a vibroacoustic mechanism because it allows heteropterans and other arthropods to considerably expand their signalling repertoire with a minimal amount of morphological change.

Cuticle ultrastructure is highly malleable genetically (e.g. Finet *et al.*, 2022; Khila, Abouheif & Rowe, 2012), so its modification to create stridulatory surfaces may be simple developmentally (Alexander, 1958; Masters, 1979), compared to the drastic morphological reorganisation required for the evolution of complex vibroacoustic organs such as tymbals. Based on morphological data alone, it is evident that cuticle ultrastructure exhibits remarkable developmental plasticity, as it may be modified in different life stages (e.g. Guidotti & Barcellos, 2013), sexes (e.g. Khila *et al.*, 2012), species and higher-level groups (e.g. Galletti-Lima & Guadanucci, 2019; Hemala *et al.*, 2021), and in adaptive shifts to accommodate different life styles (Giglio *et al.*, 2003; Li *et al.*, 2021). Based on the above, the morphological plasticity of the arthropod cuticle may be the primary developmental factor underlying the repeated evolution of stridulation in arthropods.

Although our analysis shows a clear, large-scale pattern in the functions of stridulation (Fig. 5), stridulation is frequently used in several contexts by the same species (Tables S5 and S6). This raises the question of which was the context in which stridulation first evolved. Stridulatory vibroacoustic signals that were adaptive in a sexual context may have been secondarily co-opted into defensive behaviours or *vice versa*, but this evolutionary sequence is challenging to determine empirically on the basis of the available data. In species whose stridulatory organs are sexually dimorphic, it is most probable that they arose in a sexual context, or else that one sex faces greater predation risk than the other (Kowalski *et al.*, 2014). However, in most heteropterans, and in most other arthropods we have examined except Orthoptera, stridulatory organs are not sexually dimorphic, which may render a defensive rather than sexual function the more likely behavioural context for the origin of stridulation.

## (2) Likely behavioural contexts involved in the evolution of stridulation

Our findings on the systematic distribution and ethological contexts of stridulation provide new insights regarding the behavioural basis of its evolution. In Heteroptera, the three most common stridulatory mechanisms (abdomen–leg, wing edge–leg, STP; Fig. 2A, B, Tables S2, S3) have frequently

evolved in other insects as well (Aiken, 1985; Roth & Hartman, 1967; Wessel, 2006), meaning that certain areas of an animal's body are particularly prone to evolving into stridulatory organs. The cleaning/grooming motions performed by many insects, where the hind and mid legs scrape the abdomen, the wing edge, and themselves, may account for this morphological bias in the evolution of stridulation. These cleaning behaviours characterise the pre-mating and copulatory rituals of many insects (Jansson, 1972; Sweet, 1964), and they also take place in certain species when they are attacked by predators (L.-R. Davranoglou, personal observations). We suggest that these characteristic motions may form the behavioural background that is modified during the repeated evolution of abdomen–leg and wing edge–leg stridulatory mechanisms, and consequently, vibroacoustic signalling. These observations are consistent with our identification of sexual selection and predation as major drivers in the evolution of stridulation (Fig. 5).

Ethological observations provide additional support for our hypothesis, as these grooming behaviours frequently produce sound that is audible even to human listeners, in the absence of any modified cuticular surfaces (Jansson, 1972; Roth & Hartman, 1967; Uvarov, 1966). We propose that if the signals produced during these grooming behaviours are sexually or defensively adaptive, then sexual or natural selection may lead to further modifications of the morphological structures involved that will render them better suited for producing bimodal vibroacoustic signals, thereby leading to the evolution of stridulatory organs. This pattern likely applies to other arthropod groups as well. For example, masticatory and cleaning motions of the chelicerae are thought to underlie the evolution of stridulatory mechanisms in wind scorpions (Arachnida: Solifugae) (Bird, Wharton & Prendini, 2016; Cloudsley-Thompson, 1961b; Stidham, 2020); pre-mating motions and/or defensive movements likely formed the behavioural background for the evolution of stridulation in cockroaches (Roth & Hartman, 1967); and defensive or offensive strikes may have led to the development of the dominant scorpion stridulatory mechanisms (Alexander, 1958).

It is easier to pinpoint the behavioural context for the evolution of the STP, a mechanism that is broadly used in Heteroptera (Table 1) and Coleoptera (Wessel, 2006; referring to abdominal stridulatory mechanisms striking against their counterparts on the elytra or the hind wings). The STP comprises a plectrum on the abdomen and a stridulitrum typically situated on a wing vein (Lis & Heyna, 2001) (Table 1). The frequent interaction between the abdomen and the hind wing during wing tucking, tremulation (i.e. body-shaking or trembling to produce vibrations), and when attempting escape from the mouth of a predator, together with their morphological proximity, are the likely factors that underlie its frequent evolution. The morphology of the STP, which in Heteroptera combines tergal plate-based low-frequency vibrations with stridulatory signals generated by rubbing the latter against the wings (Gogala *et al.*, 1974), is congruent with hypotheses suggesting that fixed bimodal or multimodal displays tend to evolve using the same or adjacent structures



(Caldwell, 2014). However, we show that any opposing body parts can be modified to generate mechanical-based multimodal signals, as Heteroptera possess at least 15–20 different types of stridulatory mechanisms (Fig. 4, Tables 1 and S2).

### (3) Sensing of stridulation-based vibroacoustic signals

Whereas heteropterans primarily sense chemical signals using antennal olfactory receptors, they detect substrate-borne vibrations using Johnston's and subgenual organs on their antennae and legs respectively (Jeram & Čokl, 2006; Nishino, Mukai & Takanashi, 2016). Experimental evidence, although limited, suggests that most Heteroptera cannot perceive the acoustic component of their stridulatory signals, as their subgenual organs are sensitive only to substrate-borne vibrations (Čokl, 1983; Gogala *et al.*, 1974). Many heteropteran groups possess highly sensitive hair-like mechanoreceptors known as trichobothria (Drašlar, 1973; Schuh & Weirauch, 2020), yet their removal does not appear to affect vibration perception, and the species studied did not respond to the airborne component of their stridulatory signals (Gogala *et al.*, 1974). However, it cannot be excluded that trichobothria may allow at least some Heteroptera to detect nearfield airborne vibrations or air currents (Kavčič *et al.*, 2013). In addition, the majority of heteropterans lack tympana, the typical acoustic sensors of other insects (Strauß & Lakes-Harlan, 2014), with the exception of the aquatic and semiaquatic infraorder Nepomorpha (Parsons, 1964).

Their lack of acoustic sense organs means that most Heteroptera must only exploit the vibrational component of their vibroacoustic signal, or that in some cases their signals are directed towards other species (e.g. predators) capable of perceiving acoustic sound (Fig. 5). True acoustic communication is confined to the aquatic bugs (Nepomorpha), all of which are able to sense the acoustic component of the stridulatory signals they produce through tympana (Papáček, Štys & Tonner, 1990; Parsons, 1964), in conjunction with vibrational and chemical signals (Jansson, 1972, 1989; Parsons, 1964). However, the presence of tympana in Nepomorpha is not uniformly associated with the possession of stridulatory mechanisms, as the latter are present in only about 28% of all nepomorph species (Table S1). This suggests that tympanic organs in Nepomorpha may have evolved to detect cues or signals from other biotic or abiotic sources instead of stridulation, which may be particularly important for survival in their aquatic habitat. Overall, we can find no correlation between the use of acoustic signals and the development of tympanic organs in Heteroptera.

Caeliferan Orthoptera may have followed a similar trajectory, as it has been proposed that their tympana evolved either for evading predators or controlling flight manoeuvres, and only later became co-opted for communication (Song *et al.*, 2020). Interestingly, ensiferan Orthoptera have been proposed to have used stridulation initially for defensive purposes, without being able to perceive the signals they produced. However, at a later stage in their evolution, the

independent evolution of tympana led to the incorporation of stridulation into their mating ritual, and since then, the two structures have co-evolved (Song *et al.*, 2020). Considering the above, the incorporation of acoustic stridulatory signals into nepomorph and orthopteran communication may have evolved *via* sensory exploitation, a hypothesis which postulates that senders exploit pre-existing receiver biases by creating signals that match these biases (McClintock & Uetz, 1996). Evidently, more studies are needed to explain why Nepomorpha, among all other Heteroptera, have evolved (or ancestrally retained) tympanal ears.

The likely inability of most Heteroptera to detect the acoustic component of their stridulatory signals is important to our understanding of the origins of stridulation, as it demonstrates that the evolution of signals associated with acoustic energy is not always associated with, and does not necessarily lead to, the evolution of conspecific acoustic communication (i.e. acoustic signal generation and detection). Indeed, we show that use of a signalling modality can pre-date its perception by the species producing the signal, in the same way that some animals cannot perceive the acoustic component of their own defensive signals [e.g. hissing, stridulation and tail-rattling in snakes (Gans & Maderson, 1973), defensive ultrasounds in some moths (O'Reilly *et al.*, 2019)]. Consequently, the sensory evolution of Heteroptera is highly unusual compared to that of most other animals, including the arthropod outgroups examined here, as in most other cases a sense organ evolves in parallel with the emitted signalling modality (Shaw, 1994; Strauß & Lakes-Harlan, 2014).

This unusual aspect of heteropteran sensory evolution has important implications for our understanding of the selective pressures that drive the development of stridulation. Stridulatory acoustic signals may evolve for interspecific receivers, especially in a defensive context, which does not require their sensing by their own species. This is indeed the case in many groups of animals (e.g. aposematic millipedes and brittle stars), which are blind or have limited optic receptors respectively (Grober, 1988; Marek & Bond, 2009; Marek *et al.*, 2011). The above provides further support for the behavioural data we presented here (Fig. 5), and our hypothesis that predation is a major selective force for the evolution of stridulation in Heteroptera. Even so, the apparent 'deafness' of Heteroptera to the acoustic component of their signal is still unusual, as the examined outgroups, such as crustaceans and spiders (Araneae), which also employ stridulatory signals for their defence (Fig. 5B), possess mechanosensors that are highly sensitive to the signals they emit (Boon, Yeo & Todd, 2009; Breithaupt & Tautz, 1988; Gordon & Uetz, 2011; Horch & Salmon, 1969; Keil, 1997; Salmon & Atsaiades, 1968; Sweger & Uetz, 2016).

Alternatively, when the acoustic signals are used for conspecific communication, the receiver must be detecting them through other mechanical senses. Therefore, vibroacoustic mechanical signals may evolve to be detected in conspecifics by sensors adapted for other mechanical modes, here by substrate-borne vibration sensors (Čokl, 1983; Gogala *et al.*, 1974; Nishino *et al.*, 2016). This also confirms our

suggestion that sexual selection for increased courtship signal complexity is the other major driver in the evolution of stridulatory mechanisms.

#### (4) Is stridulation a persistent strategy through evolutionary time?

We have found that stridulation has evolved hundreds of times independently across arthropods, and we provide evidence that it serves as a valuable adaptive strategy, especially in defensive and sexual contexts (Fig. 5). However, a question that has never been addressed before is how long stridulatory organs persist in a lineage. In Heteroptera and the examined arthropod outgroups, stridulation is mainly confined to the tips of the phylogeny. Typically, stridulation is found to be present in a single species, genus, or cluster of closely related genera (Table 1) comprising only a small percentage of the total diversity of the group (Table S1). This may suggest that stridulation, although useful, provides only a short-term evolutionary solution, which is expected if it is part of an ongoing predator–prey or sexual arms race that requires rapid morphological and behavioural shifts. Indeed, even stridulatory structures necessary for mating can be lost within a few generations in the face of intense predation or parasitism (Zuk, Rotenberry & Tinghitella, 2006).

Within Heteroptera, there are a few notable exceptions where stridulatory organs are nearly ubiquitous and very ancient. These include assassin bugs (Reduviidae) [likely origin of mechanism 178 million years ago (Mya) (Hwang & Weirauch, 2012; Weirauch, 2008)], the Corixidae (about 170 Mya; Ye *et al.*, 2019, 2023), the Micronectidae (about 150 Mya; Ye *et al.*, 2019, 2023), and the cydnoid families (earliest fossil about 145 Mya, likely appeared much earlier; Yao, Cai & Ren, 2007). In these four groups, secondary losses of stridulatory mechanisms are extremely rare (Grazia, Schuh & Wheeler, 2008; Cai, Chou & Lu, 1994; Lis & Heyna, 2001), suggesting that stridulation plays a ubiquitous adaptive role in the lives of its bearers, and that there is therefore long-term selective pressure for its maintenance.

Likewise, among the arthropod outgroups that we have examined, the tegmino-tegminial mechanism of ensiferan Orthoptera dates back to the Carboniferous (about 300 Mya; Song *et al.*, 2020), and in many families of spiders, the ubiquitous presence of certain stridulatory organs also suggests an ancient retention; examples include the Dipluridae (90 Mya) and Hexathelidae (200 Mya; Opatova *et al.*, 2020). The detailed reasons why stridulatory mechanisms may persist for hundreds of millions of years in some taxa, but are short lived in other arthropods remain obscure. For example, the abovementioned groups do not share any particular behavioural, ecological, or morphological characteristics, with the possible exception of the assassin bugs and spiders, both of which are predators.

## V. CONCLUSIONS

(1) Our results bring together a large and scattered pool of literature into a manageable form that makes it easier

to explore the value of stridulatory organs as cladistic characters, and offers new targets for bioacoustic, biomechanical and behavioural experiments.

(2) We confirm that predation and sexual selection are the commonest behavioural contexts in which stridulation is used, suggesting that they represent the primary drivers for its evolution. The ethological and evolutionary patterns that we uncover provide the basis for formal hypothesis testing regarding the origins of stridulation, its prevalence and antiquity, and its effects on sensory evolution.

(3) Although multiple mechanical solutions exist for co-generating vibroacoustic signals, we suggest that a shared behavioural background has overwhelmingly predisposed certain structures to evolve into stridulatory organs over others across the examined arthropods.

(4) Our study challenges previous models which necessitate signal–sensor coevolution, and shows how animals can use complex signals but exploit only a subset of their properties, especially when they are directed towards interspecific receivers.

(5) We show that the precise function of most stridulatory mechanisms remains unknown, thereby setting a clear target for future research.

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## VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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### Appendix S1. Supplementary methods.

**Fig. S1.** Basic principles of the two-step parsimony rule of Maddison *et al.* (1984), using a hypothetical scenario of stridulatory evolution.

**Appendix S2.** Rationale for our estimates of the number of times that stridulation evolved in each of the examined groups.

**Table S1.** Taxonomic diversity of Heteroptera and percentage of stridulating species per infraorder.

**Table S2.** List of types of stridulatory mechanisms in Heteroptera.

**Table S3.** Number of times each type of stridulatory mechanism has evolved independently in Heteroptera.

**Table S4.** Habitat occupancy of stridulating Heteroptera.

**Table S5.** Behavioural context of stridulation-based vibroacoustic signals in Heteroptera, with percentages of the total incidence of each behaviour in all groups examined.

**Table S6.** Behavioural context of stridulation-based vibroacoustic signals in selected arthropod outgroups (Arachnida, Myriapoda, and selected Pancrustacea), with percentages of the total incidence of each behaviour in all groups examined.