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Reconstruction of an extinct soundscape reveals ultrasonic communication in the Jurassic

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One sentence summary: Jurassic insects produced high-frequency songs, suggesting ultrasonic communication began long before the emergence of bats.

Summary paragraph:

A salient feature of biodiverse habitats is the acoustic landscape, which reveals key animal interactions and their ecologies. Very little is known about the acoustic landscape of long-gone environments, such as the Jurassic forests. The sounds made by dinosaurs and other charismatic vertebrates are not definitively known because their vocal organs rarely preserve well in fossils¹. Unlike tetrapod vocal cords, the sound-producing organs present in the sclerotised cuticle of some arthropods do fossilise well²⁻⁴. For example, the stridulatory structures (file, plectrum) can be observed and measured in the fossilised forewings of male katydids and allies. These fossils incorporate a fingerprint of the acoustic signals they generated⁴⁻⁷, offering a unique window into the soundscapes of the past. Call frequencies can be inferred from fossilised wings using phylogenetically informed predictions⁸, yet the reconstruction of wing vibrations and the songs' temporal patterns from fossil material remains elusive. Integrating phylogenetics, biomechanics, numerical simulations, and an AI-based approach, 20 ensiferan fossils (representing nine species) from a single location (Jiulongshan Formation, Inner Mongolia, China) were studied to recreate the acoustic landscape of the Middle Jurassic. These early singing insects produced pure-tone calls, an adaptation to avoid localization by eavesdropping predators. These species also exhibited rich diversity in their calling song frequencies and call repertoires, facilitated by specialised file morphologies and variation in wing size. While most species communicated using low frequencies, one species likely broadcast ultrasounds (>20 kHz). These findings support the hypothesis that ultrasonic communication in insects was established long before the emergence of bats, which appeared as fossil records in the Eocene. Analysis of mammalian hearing thresholds through time unveils potential undocumented coevolutionary pressures and constraints exerted by eavesdropping predators, prior to the evolution of echolocating bats. The arms race between ensiferan singing and auditory capabilities of early mammals likely constituted one of the key selective pressures driving Jurassic insect song diversity and the evolution of both mammalian and insect hearing systems.

Main

Sound is an important characteristic of the ecological landscape. From dense tropical forests to tundra and coral reefs, natural habitats are teeming with biologically generated acoustic signals, produced by animals for intra- and interspecific communication⁹. These soundscapes and their individual generators are easily heard and recorded by the present-day observer, but harder to establish for environments of the past. Undoubtedly, the forests, grasslands, and steppes of the

Cenozoic and Mesozoic were filled with acoustic signals emitted by a rich diversity of both invertebrates and vertebrates^{3,7,10}. While sound itself does not fossilise, we can infer the sounds of the past by either hypothesizing the ancestral sound-producing and hearing traits through ancestral state reconstruction based on the traits of extant group¹¹⁻¹³, or use the fossilised remains of sound-production and sound receiving organs to indirectly draw conclusions on the ancient soundscapes using predictions and biophysical models^{7,14}. However, this latter approach is often limited because key vocalization organs are membranous, cartilaginous, or otherwise soft tissue, and therefore rarely preserve. Examples of such fragile organs include the resonating air sacs in frogs, the larynx and vocal cords in mammals, the syrinx in birds, and the sound box in dinosaurs¹. Evidence of sound-producing soft tissue in the fossil record is rare and hardly extends beyond the Cenozoic^{1,3,15}. A notable exception is a Late Cretaceous avian syrinx (66-69 ma) belonging to a member of the Anseriformes (waterfowl), which was likely able to produce duck- or goose-like honking sounds¹⁶, and the larynx in a non-avian tetrapod, a pre-Cenozoic *Pinacosaurus*, which is believed to have produced loud booming calls as in many reptiles and birds¹. Other examples of fossilised acoustic structures are the osseous cranial crests of Late Cretaceous hadrosaurs (Ornithischia, Hadrosauridae) that are hypothesized to have functioned as resonance chambers for low-frequency social communication signals¹⁷.

In insects, acoustic communication is widespread and has evolved independently multiple times¹⁸ since probably the Early Permian^{3,7}. Crickets, katydids (bush-crickets), and their allies (Orthoptera, Ensifera) are dominant contributors to our planet's soundscapes, and have diversified since their emergence in the Late Carboniferous¹³. Most extant male katydids (*sensu lato*, here: Orthoptera, infraorder Tettigoniidea) produce loud calling songs by wing stridulation to attract distant females. The passing of a serrated wing vein (the stridulatory file) on one wing over a plectrum on the opposite wing produces sounds that are further enhanced

and radiated by specialised vibrating wing regions^{19,20}. The wings open and close rhythmically, but sound is mainly produced during the closing phase (Extended data, Figs. 1-4, Supplementary video 1). A single closing phase produces the most basic call unit, termed here a ‘syllable’.

In katydids, crickets, and grigs, the carrier frequency (f_c) of the mating calls matches the natural vibration of the wings^{21,22}. For example, to optimally produce a f_c of 5 kHz, the wings should resonate best at 5 kHz, and they should close with a velocity that drives the plectrum over the file engaging at a tooth strike rate of 5,000 teeth per second^{23,24} (Supplementary Video 1). Thus, as acoustic radiators, wings should be structured so that, when stimulated at their natural frequencies, they vibrate easily and therefore radiate acoustic energy at optimal amplitudes. Exploiting natural resonances allows loud sound production at low energetic cost^{25,26}. Resonances in ensiferan wings depend on wing size, dimensions of sub-structures involved, and other physical parameters^{8,25}. Many katydids generate pure-tone signals with highly resonant wings, while others create broadband songs with broadly tuned or non-resonant wings²⁷. The frequencies exploited across species range from ~1 to 150 kHz, with ca. 70% of known extant species using ultrasounds (i.e., sounds above the human hearing limit of ~20 kHz)⁸. The chitinous exoskeleton of crickets, katydids, and allies easily fossilises, and so do their sound-producing organs (the wings), which can be used to infer the nature of signals generated, as wing anatomy is a reliable predictor of acoustic features of their calls⁴⁻⁷. To investigate stridulatory sound production in Jurassic relict Ensifera, we can turn to their closest living relatives: the relict family Prophalangopsidae (e.g., *Tarragoilus diuturnus*, *Cyphoderris* spp., and *Prophalangopsis obscura*). These “living fossils” retain wing morphologies and stridulatory behaviours that are putatively deeply conserved, preserving key ancestral acoustic features. As a result, these insects provide a rare, functionally informed window into how early katydids—and their Jurassic ancestors—may have generated sound^{22,28}. Notably, the sound

generators of the living Prophalangopsidae (also known as grigs) look more like their Jurassic ancestors than the extant katydids (Figs. 1, 2d-i). There are approximately 100 described species of Prophalangopsidae, of which only nine extant species still exist in temperate habitats across China, India, Russia, the U.S.A., and Canada, while the remainder are known only from the fossil record²⁹.

Wing stridulation in the katydids' ancestors (stem-Ensifera) is known from the Late Permian and Middle Triassic^{2,30,31} and was already well-established and diversified by the Late Triassic and Middle Jurassic (174-163 ma)^{4,7}. It is known that, ~165 ma, *Archaboilus musicus*, a member of the extinct Haglidae (a family closely related to Prophalangopsidae and Tettigoniidae), produced calling songs by stridulation with low-frequency tones at ca. 5 kHz^{4,8,32}. In contrast, katydids (Tettigoniidae) are not known in the fossil record before the Cenozoic^{5,6}, although recent molecular data suggest that the Tettigoniidae originated in the Late Cretaceous¹³, but no fossils are available for that time. Two species of Tettigoniidae from the Middle Eocene (~55 ma) with intact stridulatory organs, *Pseudotettigonia amoena* and *P. leona*⁴⁻⁵, have enabled the inference of a f_c of 10.5 and 11 kHz, respectively, using phylogenetic comparative methods⁸, and one species of katydid in amber from the Eocene has allowed for the reconstruction of both acoustic signalling and hearing at 32 kHz³³. These examples demonstrate the use of several auditory channels by extinct insect species and the suitability of the Ensifera as a model for the reconstruction of the extinct soundscape.

As the shift from low- to high-frequency signalling and the proportional hearing abilities in katydids appears broadly contemporaneous with the rise of bats³⁴⁻³⁶, it is tempting to interpret their ultrasonic communication as an adaptation to bat predation—especially following the evolution of laryngeal echolocation in bats ~50 Ma³³. Yet, this timing does not uniquely implicate bats: early bats were themselves sensitive to high frequencies, and bat stem lineages may have possessed some capacity for echolocation³⁷. Moreover, high-frequency hearing is

thought to have been present in nocturnal mammalian ancestors long before bat echolocation evolved^{12,38}. Taken together, these observations motivate three, not mutually exclusive, hypotheses for the origin of ultrasonic signalling in katydids: (i) ultrasonic communication evolved as a countermeasure to eavesdropping by echolocating bats (and potentially other high-frequency predators); (ii) ultrasonic traits arose prior the evolution of bats as a general anti-eavesdropping strategy against earlier predators with high-frequency sensitivity; and (iii) ultrasound evolved through acoustic niche partitioning, allowing signalling to escape masking and interference in increasingly noisy communities of sympatric callers³⁹.

To test these hypotheses, we used a combination of phylogenetic regressions and informed predictions of extant species, biomechanical experimentation on living forms, and numerical analysis, to reconstruct wing vibrations and acoustic signals of 20 fossil ensiferans from the Middle Jurassic (~165 ma; consisting of seven species within the Prophalangopsidae and two within Haglidae—an extinct family that existed from the Triassic to Cretaceous). All 20 fossil specimens offered exceptionally well-preserved stridulatory structures (see Fig. 1a-j, and extended data, Fig. 5) and originated from the Jiulongshan Formation of Daohugou village (Nei Mongol Autonomous Region, China). Because these species co-occurred in both time and place (157–165 Ma)⁴⁰, they form a true palaeo-acoustic assemblage—the oldest yet assembled. This provides the first “ensemble” framework for palaeo-acoustic inference and allows us to reconstruct a substantial portion of the Middle Jurassic soundscape at a level of detail not previously achieved.

The physical reality of living wings vs. the unknown physical reality of fossilised wings

1) Physical reality and acoustic mechanism of stridulatory wings in living forms

We examined living species from three subfamilies (Prophalangopsidae, Gryllidae, and Tettigoniidae) with well-characterised calling songs. Using micro-scanning Laser Doppler

Vibrometry (LDV), we measured wing resonance, damping, and vibrating areas, and captured wing mechanics with high-speed video (Supplementary Video 1) and motion detectors. As a proof of concept, using COMSOL multi-physics, we then built finite-element models of 2D wing geometries, treating both call features and resonances as unknowns (Supplementary Video 2). Two-dimensional models are necessary to apply a similar and consistent process to fossilised wings, which can be recovered in 2D for modelling. The numerical models match the physical reality of the living wings (Fig. 2a-i); we therefore validated the models. Hence, the same modelling approach used for living species could then be applied to fossilised wings, even though their physical reality is unknown.

Reconstruction of the fundamental syllable in living forms. A syllable is made of continuous oscillations produced by individual but continuous tooth-strikes. We used the method proposed by Montealegre-Z & Mason¹⁹, which recovers the basic oscillation of a single tooth strike from a real wing using LDV. Subsequently, a Matlab algorithm that uses a time vector, file teeth spacing, and the basic tooth-strike oscillation, was used to reconstruct the basic syllable amplitude envelope. The time and frequency components of this reconstructed syllable were compared with the original acoustic recordings (physical reality) of each living species. The reconstructed syllable matches the recorded pattern from singing males (Extended Data, Figs. 1-4), therefore we validated the model. Again, this concept was used to reconstruct the fundamental syllable from fossilised wings.

2) Vibrations and eigenfrequencies in fossilised wings

Understandably, the physical reality and acoustics of fossilised wings cannot be measured with LDV (Fig. 2j-l). We therefore extracted wing geometries from these fossils (Extended Data, Figs. 5) and created 2D models using Adobe Illustrator vector outlines, for further FEA, implementing all the structural parameters used for extant species (Supplementary Video 3).

Numerical simulations were conducted using the same approach described above for living insects. We used an eigenfrequency analysis to identify potential natural resonances of the vibrating area of the wings, based on the vibrating area observed in extant *Prophalangopsidae*²² (Fig. 2e), and accepted the model when the natural frequency was in the range predicted by the phylogenetically informed model (next section, see Fig. 1). While this limits our model to the presented taxa as other ensiferans have unique wing morphologies that can affect wing vibration mechanics⁴¹, it is sufficient for the species used in this study, and was used to allow us to simulate a vibration event in the wing membrane for syllable reconstruction (see Methodology).

Determination of song frequency in extant and fossil Ensifera

When comparing the stridulatory organs of extinct ensiferans (i.e. the forewings and the serrated file) with those of extant species, it becomes clear that the basic mechanism of song production in this group has not undergone significant changes since the late Triassic^{4,7} (Figs. 1a-j, 4a, b, Extended Data, Figs 1a, 2a, 3a, 4a). To infer song frequencies in Ensifera, we first reconstructed a robust phylogeny of Tettigoniidea based on 147 extant taxa and 1,077 single-copy orthologs generated using target enrichment⁴². We estimated divergence times based on this phylogenomic tree using a curated set of fossil calibrations. The resulting tree was trimmed down to 95 species for which calling songs and physical reality of wings were known. This tree was used for subsequent phylogenetic comparative methods. We generated ordinary least squares (OLS) and phylogenetic generalised least squares (PGLS) models to understand the relationship between file length and f_c (Fig. 1), building on existing models to develop an improved, phylogenetically informed approach to fossil song reconstruction³². Rather than predicting fossil f_c from file length simply using the PGLS model equation, we used a phylogenetically informed approach. We attached fossil taxa between two specified internal nodes in the phylogeny based on current taxonomy (Fig. 1) and computed the phylogenetic

covariance between the fossil species and all species in the extant dataset. This allowed us to adjust the PGLS model predictions based on possible phylogenetic positions of the fossils. This was conducted across paired nodes that contain the fossil taxa based on taxonomy, to provide a predicted range of f_c spanning the broadest possible phylogenetic positions.

The OLS model found a strong negative relationship between (log) file length and (log) f_c (Figure 1, estimate = -0.95, $t = -12.12$, $P < 0.001$). The PGLS model also found a strong negative relationship between (log) file length and (log) f_c , but with a slightly lower intercept and shallower slope (Figure 1, estimate = -0.91, $t = -12.07$, $P < 0.001$). Based on the PGLS model, we ran phylogenetically informed predictions of f_c for each fossil species based on the mean length of the stridulatory file of each species. These predictions provided estimates and error ranges for f_c (Extended data, Table 1). We concluded that the mean predicted f_c values were our most conservative estimates and compared them with the results from computational modelling for syllable reconstruction.

The results of these informed predictions indicate that Jurassic ensiferans already produced a great diversity of acoustic signals, from low frequencies around 5 kHz (e.g. *Bacharaboilus curvus*, *Novaboilus ovatus*, *Gurenia caii*) up to likely ultrasonic frequencies (*Sigmaboilus peregrinus*). These predictions overlapped well with the frequency estimates provided from numerical modelling (Extended data, Table 1, Fig. 3), strengthening the support of our approach and confirming the likely acoustic signals produced by each species.

Reconstruction of fundamental syllable from fossilised wings.

Since fossilised wings do not allow us to produce file/plectrum clicks and record their vibrations using LDV (Fig. 2h), we used the vibro-acoustic FEA models (Fig. 3) to recreate a

single click and its basic oscillation pattern. For the time-dependent numerical simulations, a stridulatory file was excited with a force of 1.3×10^{-3} to 2.5×10^{-3} N, as inferred from high-speed videos of stridulating species (see Supplementary video 1). This caused the wing to enter resonance and vibrate in real time in response to the applied force. The resulting simulated vibrations of the wing were used to construct the fundamental syllable associated with each species, and the syllable was analysed using FFT to confirm the vibration retained the expected f_c (see below and Fig. 4c).

These syllables represent the most basic and fundamental component of the call repertoire that can be recovered from fossilised wings. Other parts of the calls, like amplitude and frequency modulations and temporal patterns, are dictated by neural and behavioural variables⁴³ which do not fossilise, hence remain elusive in this analysis. Therefore, a Gaussian Process Regression (GPR) model was trained using the morphological and acoustic parameters of extant insect species to predict calling syllable rates of the fossilised insects. The model results demonstrated strong fit, low prediction error, and suitability for extrapolating to fossil species while maintaining biologically plausible uncertainty bounds. The predicted syllable rate was used to construct a hypothetical Jurassic soundscape (see Supplementary Video 4, and Audio 1).

Discussion

400 million years ago, insects already occupied all terrestrial habitats³¹ – long before their most notorious acoustically orienting predators, bats, who appeared in the Eocene (about 55 million years ago)^{34,37}. From pioneering work to recent days, it has been broadly accepted that the Orthoptera (grasshoppers, grigs, katydids and crickets) are perhaps the first lineage of insects to use sound for conspecific communication^{4,7,44}. Airborne signalling by wing stridulation in ancient ensiferans was already established by the middle/late Triassic⁷, and was

honed over time with the evolution of sound generators evolved to produce pure-tone sounds. In extant katydid species, pure-tone sound production is associated with narrowly tuned wing resonators, and with files with regularly spaced teeth. In some species, such as some modern-day *Typophyllum* spp.⁴⁵, *Peronura* spp. and *Melidia* spp.⁴⁶, the stridulatory files exhibit a distinctive and elaborate alignment of teeth, enabling tight control of the spectro-temporal composition of song (Extended data Fig. 6).

Here, we show that sophisticated stridulatory files with structural mechanical features to produce pure-tone calls (e.g. *Liassophyllum caii*, *Bacharaboilus curvus*, *Aboilus stratosus*, see also *Archaboilus musicus*⁴) or to enhance bimodal temporal/frequency alterations (e.g. *Archaboilus polyneurus*, *Allaboilus gigantus*, Fig. 4), were already present and well developed in the Jurassic. Mechanical frequency modulation was thus already used by ancient ensiferans in the Jurassic. The three specimens of *Archaboilus polyneurus* show a regularly consistent pattern of increasing and decreasing inter-tooth distances (Fig. 4), consistent with the production of such amplitude and frequency modulations, as seen in a present-day pterochrozine leaf-mimicking katydids⁴⁵ (see extended Data Fig. 6). Similarly, the four examined specimens of *Allaboilus gigantus* exhibit an elaborated stridulatory file, which clearly shows two regions with different tooth densities (a constant-density region and one with irregularly spaced ‘pegs’; Fig. 4), which would produce different temporal and song frequency patterns. Analogous bipartite morphology can be observed in the files of some extant katydid species, such as the genera *Horatosphaga*, *Acrometopa*, *Tenerasphaga*⁴⁶, and the cricket *Eneoptera guyanensis*⁴⁷. This reveals that as early as the Jurassic, ancient ensiferans had evolved mechanical and structural wing designs that enhanced their song repertoire and facilitated f_c diversification, and that these acoustic niches are still exploited today. What was the trigger of such early diversification?

The diversity of acoustic channels, and the pure-tone nature of these signals could have been driven by the need for acoustic niche partitioning in an increasingly noisy and species-rich environment, and also through the need to avoid the hearing range of eavesdropping predators (a form of evolutionary proactive anti-predator behaviour⁴⁸).

Males of living species of Prophalangopsidae produce low-frequency pure-tones, exhibit strong wing symmetry, long stridulatory files and some can produce sound during both wing opening and closing phases^{22,49} (see Extended data Fig. 1a-c). The earliest diverging lineage of Tettigoniidae also exhibits wing symmetry⁵⁰. Such wing symmetry is also found in the fossils studied here, implying that the ancestral condition for sound production involved the main amplitude components of the call produced during both the opening and closing phases of the wing stridulatory cycle. Five of the nine species studied here used low-frequency pure tones (5-7 kHz), and from previous work on *Archaboilus musicus*^{4,8,32} (using pure tones at ~5-6 kHz), it is evident that low-frequency pure-tones have been used as communication signals since Jurassic times, and still are in field crickets (Gryllidae) and in some Prophalangopsidae today. It is well known that pure-tones at around 5 kHz are less affected by spatial sound attenuation when signalling close to the ground, than higher frequencies⁵¹. Other species singing above 10 kHz (like *Aboilus stratosus*, *Novaboilus multifurcatus* or *Sigmaboilus peregrinus*; Fig. 4) could have started to find more favourable niches for sound transmission above ground, like understory vegetation or more arboreal perches, as we see today in *Cyphoderris*⁵² and *Paracyphoderris*⁵³, or even in many katydids using pure-tones above 10 kHz⁵⁴.

The evolution of hearing and singing

Driven by natural and sexual selection, insect ears evolved mainly for intraspecific communication and predator detection⁵⁵. In classical studies of insect hearing, it has been a chicken-and-egg question of what evolved first: the ability to sing or the ability to hear?⁴⁴.

Modern katydids (Tettigoniidae) are unique among arthropods for having evolved the three canonical steps of hearing as used by mammals. Their hearing system is endowed with outer, middle, and inner ear components⁵⁶. Frequency analysis is achieved in the inner ear by means of tonotopy (frequency mapping) and travelling waves^{56,57}. The inner ear is made of a sensory organ, the *crista acustica* (CA) which, in living species, hosts between 15 and 116 auditory sensilla⁵⁸ (Fig. 5c, d), and in a large number of species is enclosed in a fluid-filled cavity known as the auditory vesicle. In the extant Prophalangopsidae the inner ear structure is much simpler (Fig. 5ab).

The ability to produce sound by wing stridulation could have appeared before hearing as a defensive tool to deter terrestrial predators like reptiles⁵⁹ and insectivorous mammals, including gliding species⁶⁰. Many living katydids produce disturbance sounds to deter predators⁶¹. An interesting example where disturbance sounds are produced, but one's own ability to hear such signals is lacking, comes from the living Prophalangopsidae, *Cyphoderris monstrosa*, which produces broadband ultrasound (peaking at about 60 kHz) by tergo-tergal stridulation. Yet, male and female *Cyphoderris* spp., cannot hear these ultrasounds⁶², and therefore this defensive behaviour is hypothesised to deter insectivorous mammalian predators such as shrews⁶³. This exemplifies the possibility that sound production can evolve without ears, as well as the widespread presence of stridulatory organs in insects without ears²⁰. A primitive stridulatory organ in the forewing of early Ensifera could have been established by the Upper Permian in the family Oedischiidae⁶⁴, however the clearest evidence of a fully formed stridulum comes from the middle Triassic. Tympanal organs are known from this period as well⁶⁵ (Fig. 6). So, if a form of primitive stridulation emerged in the upper Permian, it is likely that sound production predated the ability to hear using tympanic membranes. However other studies have argued that based on the presence of tympanal organs in both major clades of the Ensifera (Grylloidea and Tettigonoidea), singing and hearing may have co-evolved in this group¹³. The

evolution of a single stridulatory file, with regularly spaced teeth is a clear departure or improvement from the relic condition of stridulation, with multiple randomly distributed teeth or pegs⁴. The adoption of a single stridulatory file with regularly spaced teeth, along the CuPb vein², was an important step for the evolution of more elaborate calls with narrower frequency bands. This file structure must then be accompanied by a corresponding single elastic plectrum (as opposed to multiple files and hard scraping regions⁴.

Certainly, singing in the presence of eavesdropping predators was dangerous, and one way to call safely was to narrow the bandwidth of the call. This is because pure tones are challenging to localise with the mammalian ear. In living mammals, the cochlea spectral differences that provide directional hearing cues are limited by a quality factor (Q_{-3}) of about 9–13. In many living katydids and all grigs, pure-tone songs exhibit $Q > 10$ (including the species shown here), implying that natural selection for pure-tone calls happened earlier in the insect-predator race. The cochlea of Jurassic mammals might have had a lower demand for pure-tone directional hearing, and thus lower Q resolution, making narrow-band calling an efficient strategy for early katydids to avoid eavesdropping predators. For eavesdropping strategies to remain functional, mammalian hearing resolution needed to improve, which gave rise to the earliest known acoustic arms-race. With short, uncoiled cochleae, these mammals had a limited frequency hearing range^{38,66} (Fig. 6a). Therefore, successfully selected eavesdroppers might have been those who coped with at least one of the two new strategies of the evolving prey. The hearing system in the ancient Ensifera should have gradually adapted to the musical but high-frequency tendency of conspecific calls (e.g., *S. peregrinus*), while continuing to function in detecting low-frequency sounds for environmental cues and predator detection. These combined pressures lead to the evolution of a more sophisticated frequency analysis organ - the insect cochlea⁵⁶.

The inner ear of extant Prophalangopsidae (e.g. *Cyphoderris* spp. and *Tarragoilus diuturnus*), considered “living fossils”, are vital to understand this process. The CA of *Cyphoderris* and *Tarragoilus* is very simple when compared to that of Tettigoniidae (Fig. 5). It has been recently shown that *Cyphoderris monstrosa* achieves frequency mapping via travelling waves on the tympanic membrane⁶⁷. In other words, the mechanoreceptors of a precursor CA in living Prophalangopsidae are neither completely isolated from the tympanic membrane nor enclosed in a fluid-filled vesicle, as in Tettigoniidae⁵⁶.

Another fundamental component of the hearing system in living katydids is the acoustic trachea (or ear canal), which serves to augment gain and funnel sound to the tympanal organ and to enhance directional hearing sensitivity via a pressure-difference receiver system⁶⁸. Figure 5a shows the relic conditions of the acoustic trachea (bifurcated), which is not functional for sound transmission in the living Prophalangopsidae (*Cyphoderris* and *Tarragoilus*) but has been adapted as a sound guide in most living katydids (Fig. 5c). A bifurcated auditory trachea seems to be the plesiomorphic condition of a functional acoustic trachea (see Extended Data Fig. 7). Although the acoustic trachea is not preserved in fossilised Jurassic specimens, it is very likely that it was not specialised for sound transmission, as observed and measured in *Cyphoderris* and *Tarragoilus* (Fig. 5a), at least in species singing below 12 kHz. The most common form of acoustic trachea currently known in living katydid species is the exponential horn type, which serves to passively amplify sound waves and delay their propagation, favouring a more accurate sound source localisation in the form of a pressure difference receiver⁶⁸. The earliest record of this exponential-horn outer ear has recently been shown to have evolved in the Eocene³³ (Fig. 6), showing acoustic sensitivity between ~10 kHz and 89 kHz, which covers the frequency range of the male calling song and the echolocation calls of early bats.

These facts leave us with two hypotheses: 1) Jurassic ensiferans were able to detect a broad range of frequencies from low audio to moderate ultrasound, using the external surface of the

tympanic membrane, without the passive amplification function of the acoustic trachea, or 2) some species had started to evolve an ear canal with specialised geometries for broadband sound amplification, such as an exponential horn. The first hypothesis implies that species would have required a specialised CA able to analyse a broad range of frequencies, which is not the case in living but relic *Prophalangopsidae* (Fig. 5b), detecting frequencies below 13 kHz. The second hypothesis implies that species enhanced their directional hearing in the ultrasonic range, and improved predator detection of insectivorous mammals. The incorporation of high frequencies requires a more sophisticated sound-capturing system (e.g. ear canals, pinnae, and CA for frequency analysis, as shown in modern katydids, Fig. 5) than in extant grigs (*Prophalangopsidae*).

For now, we can only confirm that Jurassic ensiferans were communicating with a broad range of frequencies from low audio to moderate ultrasound. We show that ultrasonic communication was likely adopted by katydid ancestors during the Middle Jurassic, some 165 ma, the oldest record known for ultrasound communication in animals. In addition, these ancient ensiferans had already started to diversify in their acoustic signalling strategies, through changes in body size and stridulatory file morphology, producing pure-tone and high-pitch calls. Given that in extant katydids, the observed diversity in acoustic signalling strategies and the predominant use of pure-tone ultrasound are thought to have been driven by predator eavesdropping^{35,69}, it is likely that early mammals and non-mammalian ancestors were also listening in to the songs of ensiferans, driving early diversification of acoustic signalling strategies. This diversification could have also been driven by acoustic niche partitioning due to inter-specific competition. This, combined with evidence for ultrasound in Cretaceous moths⁷⁰, implies that bats emerged – nearly 100 million years after singing ensiferans – into a soundscape already busy with ultrasounds.

Methods

Micro-CT scanning of the hearing organs in living forms

Micro-Ct scanning and 3D segmentation follow established protocols^{63,71}.

Sound and wing motion recordings

Acoustic and wing motion recording are described in Woodrow et al.⁶³. Protocols for high-speed video are described in the supplementary methods.

Measurements of wing vibrations in living insects

This method is well established by the authors; and uses micro-scanning Laser Doppler Vibrometry^{22,24}.

Wing Geometry

To reconstruct the geometries of the forewings, illustrations of the wing venation were traced over scale-calibrated photographs of the fossil specimens in Adobe Illustrator v2023 (Adobe Inc., San Jose, California, United States). The lines were made to be vector based, and the forewing built as a .DXF file and imported into the xy plane of the numerical simulation software.

Wing Damping calculations

Wing damping in fossils was estimated using experimental data from living species. For small damping $\zeta < 1$, which means the decay is oscillatory. If $\zeta = 1$, the damping is critical and the displacement tends to zero in the shortest possible time. ζ varies from undamped ($\zeta = 0$), underdamped ($\zeta < 1$), through critically damped ($\zeta = 1$) to overdamped ($\zeta > 1$). ζ is a function of the Logarithmic decrement of the oscillation, therefore it is also a function of Q . We calculated both ways in several species (*Gryllus bimaculatus*, *Cyphoderris mostrosa*, *Tarragoilus diuturnus*, *Docidocercus sagittatus*, and *Panacanthus pallicornis*) with various calling

frequencies, using LDV, we calculated Q from the wing oscillation, or measuring the free decay or the oscillation produced by a single tooth strike (click), and found no differences (Extended data, Table 3). Thus, both ways are good indicators of ζ .

From the calculated numbers below, for left and right wings, ζ ranges from 0.03 to around 0.08, suggesting these Ensifera wings tend to be underdamped ($\zeta < 1$). We suggest fossil artificial oscillations decay around the values reported in Extended data table.

Finite Element Analysis (FEA)

The wing acoustic properties were simulated using the finite element simulation toolbox COMSOL Multiphysics, v. 6.1⁷². The mathematical models used the reconstructed wing geometry described in the section *Wing Geometry* above as the solution domain. The actively vibrating wing areas (wing membrane) were modelled using a linear shell formulation of COMSOL Multiphysics⁷², and were assumed to be isotropic and homogeneous. Wing membrane areas were selected based on the coherent active vibrating areas in the extant Prophalangopsidae including *Prophalangopsis obscura*²², *Cyphoderris monstrosa*²⁸, and the closest living relatives to the Ensifera of the Jurassic studied here, for example, *Tarragoilus diuturnus* (Fig. 2). This region of vibration is restricted to specific cells of the forewings, and thus we used the corresponding wing veins surrounding the outer-most margin of these cells to mark the edge of the vibrating areas, as learned from LDV experiments in *T. diuturnus* (Fig. 2) and *C. monstrosa*²⁸. In *P. obscura* and *T. diuturnus*, on the other hand, this vibration extends from the CuPb vein to the margins of the CuPa β and the CuPa α veins (Extended Data, Fig 5, Supplementary video 5)²². In *C. monstrosa*, this region extends from the CuPab vein to the margins of the CuPa and the CuPaa2 veins, and corresponds to the mirror, pre-mirror, and neck areas, with no contribution from the harps²⁸. As the forewings of extant Prophalangopsidae *P. obscura*, *Aboilomimus sichuanensis* and *T. diuturnus* are similar in geometry to those of the fossils studied here (Extended Fig. 5) and are estimated to have similar biophysical properties²²,

we used the wings of these species to determine the scope of the vibrating area. The geometry of the vibrating area is relevant here, and, contrary to early research^{73,74}, this area is not limited to a vein enclosure, such as the mirror of katydid wings, or the harp in crickets. The vibrating area in the Ensifera wings extends to other surrounding areas where vibration coherence is met^{8,24,28}.

The forewings of male Ensifera are substantially thicker than the hind wings; the values on thickness and elasticity are known from a few published papers on cricket⁷⁵ and locust⁷⁶ wings, and cannot be known from compression fossils. Thus, to estimate wing thickness, we used empirical measurements of Young's modulus (E) from the thickest part of the locust and cricket hind wings from references above (~9 GPa) and conducted a manual parameter sweep of membrane thickness until the resulting first natural frequency matched the frequency predicted by regression models of the stridulatory file length (see Eigenfrequency studies below). It should be noted, therefore, that variation in E is not considered in these reconstructions. This resulted in variation in wing membrane thickness within the range of 5.5-18 μm (Extended data, Table 2). As a proof of concept, the values were validated and used to recover wing vibration from extant species (*Tarragoilus diuturnus*, *Panacanthus pallicornis*, *Gryllus bimaculatus*), where the physical reality of wing vibration was previously known from Laser Doppler vibrometry experiments (see Fig. 2 in the main manuscript).

The veins on the wings were represented by a linear beam formulation and were also assumed to be isotropic and homogeneous. The veins were assigned the same elastic modulus of 9 GPa, and a thickness multiplier of 3 μm . This allowed us to consider that the veins are thicker than the wing membrane, but without having to specify the thickness of every vein individually. Based on fossil images and extant Prophalangopsidae, specialised veins do not appear to be present. Finally, the wing membrane and the veins were coupled using the Shell-Beam Connection feature of COMSOL Multiphysics, v. 6.1⁷². We highlight that further information

on the material properties of extant taxa will be crucial in refining these modelling-based approaches in the future. Our validation with extant taxa supports our current methodology. Extended data, Table 4 lists the material properties incorporated into the mathematical models for the wings.

The acoustic properties of the fossilised wings were investigated using an eigenfrequency study and by considering the problem in both the frequency and time domains. For all three problems, the solution to the variational form of the considered shell-beam formulation was obtained using the finite element method.

The element size of the formed finite element mesh was determined based on a mesh sensitivity analysis carried out separately for each species. For this analysis, the mesh size was systematically refined to check for the mesh dependence of the solution. Based on this analysis, the mesh was given a maximum element size between 4-2 mm and a minimum element size of 0.5-0.2 mm. This mesh size also ensured that there were at least six finite elements per wavelength when the frequency is 1-30 kHz. While the speed of sound in the wing is not known, it is expected that in such a membranous structure as the fossil wings, it is around 1500 m/s. Extended data, Fig. 8a demonstrates the global mesh refinement carried out for the frequency domain solution of *Archaboilus polyneurus*. The maximum element size was reduced from 5 mm to 1.5 mm. As there was no significant difference in the solution after the element size was smaller than 2.5 mm, the maximum element size for this species was taken as 2.5 mm. A similar procedure was carried out for all the species.

Eigenfrequency Studies

The natural frequency and harmonics of the wings were calculated using COMSOL Multiphysics, v. 6.1. The discrete solution of the eigenfrequency study was obtained with the

finite element method, where the considered system of finite element equations was solved using the eigenfrequency solver ARPACK built in COMSOL Multiphysics, v. 6.1.

Frequency Domain Simulations

The system was excited by applying a fixed load to a vein within the actively vibrating wing area. The frequency range of the load was 1-30 kHz with a resolution of 0.5 kHz. The magnitude of the applied load was taken as 2.5e-5 N for all species. The magnitude was chosen based on the force applied during analogous experiments. Because the models are linear, however, the magnitude of the applied force is not of major significance for this study.

A fixed constraint was placed around the active wing area to ensure a stable solution. The problem was discretised using the finite element method as described above. Finally, the system of finite element equations was solved using the stationary solver MUMPS.

The solutions were obtained by recording the maximum displacement magnitude within the active membrane region at each frequency. The solution was then normalized with respect to the maximum displacement magnitude for each species.

Time Dependent Studies

To construct the fundamental syllable of the fossilised wings, numerical models were developed to simulate the wing vibrational response to an applied force on one of the veins within the active region of the wing. The model was set up using the coupled shell and beam formulations of COMSOL Multiphysics in the time domain. Using the edge load condition, a vein on the wing was excited with a force of magnitude 2.5e-5 N for all species. At each time step, the solution was obtained by the finite element method, as described in Veitch et al.⁶⁸. The time step was taken as

$$\Delta t = \frac{1}{128 \text{ kHz}} = 7.8125 \times 10^{-6} \text{ s},$$

and the simulation had a duration of 0.004 s. For the time discretization, the generalised alpha method was employed⁶⁸.

Phylogenomic analysis

DNA Extraction

To obtain high-molecular-weight genomic DNA (≥ 1 μ g per sample) for target enrichment and Illumina sequencing, we extracted DNA using the Gentra Puregene Tissue Kit (Qiagen) according to the manufacturer's protocol. DNA yield and purity were first assessed with a DeNovix spectrophotometer, then with the Qubit 2.0 fluorometer.

Target enrichment library preparation and sequencing

We generated hybrid capture (target-enrichment) sequence data following the general methodology of Shin et al.⁴². Briefly, genomic DNA was converted into Illumina-compatible libraries using an NEBNext® Ultra™ II FS DNA Library Prep Kit for Illumina, after which libraries were enriched using a custom OR-TE probe set⁴² developed for Orthoptera and synthesised for use with myBaits® Custom Hybridization Capture Kits for targeted DNA sequencing from Daicel Arbor Biosciences (Arbor Design ID D10583GRHP2). Enriched libraries were pooled and sequenced on an Illumina NovaSeq 6000 platform to generate paired-end reads.

Data processing, filtering, and phylogenomic analysis

We followed methods described in Shin et al.⁴² for raw read processing, contig assembly, orthology assignment, data cleaning, and alignment to create an input data for our phylogenomic analysis. We filtered alignments and removed initial transcriptomic biases using custom python scripts. To assess gene-level topological variation and identify problematic taxa, we inferred a gene tree for each filtered locus alignment in a maximum likelihood framework. We examined patterns of concordance and conflict among loci and identified sequences

exhibiting anomalous placement likely driven by missing data, alignment artifacts, or contamination using an established pipeline. We concatenated the final 1,077 locus alignments into a supermatrix and generated a best-fit partitioning scheme for our dataset. We inferred a maximum likelihood phylogeny and with nodal support valued assessed with 1,000 ultrafast bootstrap replicates. See Supplementary methods for fine details.

Divergence-time estimation using fossil calibrations

We estimated divergence times using MCMCtree (PAML v4.10.5)⁷⁷ within the MDGUI package of PhyloSuite v2⁷⁸ with a curated set of fossil calibrations selected on the basis of previous, well-supported Orthoptera phylogenies¹³ (Supplementary Table 1). These were justified following the logic laid out in Song et al.¹³ The fossils were conservatively used and only included if they had true synapomorphies linking the fossils to the proposed node. If a fossil could not confidently be placed as the crown, but was a stem, this calibration was placed back one deeper node. Two fossils, *Archepestodophylla* spp. and *Eomortoniellus handlirschi* were added to give further support to our more densely sampled katydid clade. Both are supported by synapomorphy in their original descriptions. To accommodate uncertainty associated with a sparse and uneven fossil record, we implemented soft time constraints using broad skew-t prior distributions parameterised in MCMCtreeR⁷⁹. Following Song et al.¹³ we used the Rhynie Chert (412 Ma) as a conservative soft maximum for the root (and selected deep nodes), assigning a distribution that allows non-zero probability of ancient ages without placing undue prior mass near the maximum. This approach provides a flexible but constrained compromise, consistent with broader insect chronology (e.g., even the oldest extant winged lineages such as Odonata are generally inferred to diversify well after ~412 Ma)⁸⁰. Dating analyses used a GTR substitution model on a concatenated supermatrix comprising 214 loci selected to be high-coverage and approximately evenly distributed across evolutionary rates. We used the Hessian approximation to estimate the gradient/Hessian and ran four independent

MCMC chains, each for 4,000,000 iterations (with burn-in removed prior to combining). Convergence and mixing were assessed in Tracer v1.7.2⁸¹ by evaluating trace stationarity and effective sample sizes (ESS); all chains achieved ESS > 200 for all parameters. Post-burn-in samples from converged chains were combined to obtain posterior means and credible intervals for node ages, producing a time-calibrated phylogeny suitable for downstream comparative and evolutionary analyses. Because acoustic data were available for only a subset of genomically sampled taxa, we first time-calibrated the phylogeny using the full taxon set to maximise dating robustness, and then pruned the tree to the acoustics-enabled subset for downstream phylogenetically informed analyses (Extended Figure 9).

Estimating fossil syllable-rate using Gaussian Process Regression

Syllable rates of fossil orthopteran insects were estimated using a probabilistic Gaussian Process Regression (GPR) framework trained on extant species⁸² (Extended Data, Fig. 8b, c). Four predictors were used: stridulatory file length, total tooth number, dominant frequency, and syllable duration. The target variable (syllable rate) was calculated at a standardised ambient temperature of 20 °C using published temperature–rate equations. Because syllable rate values are strictly positive and span an order of magnitude, the response variable was log-transformed prior to modelling.

A composite kernel combining a Matérn covariance function, a linear DotProduct component, and a WhiteKernel noise term was implemented to capture non-linear relationships while preserving extrapolative capacity. Kernel hyperparameters were optimised using Bayesian optimisation implemented via the Optuna framework⁸³ with cross-validation. Model performance was evaluated using conventional regression evaluation metrics.

The validated model was applied to fossil taxa using reconstructed morphological and acoustic inputs. Posterior predictions were exponentiated to return values in physical units and

602 accompanied by uncertainty estimates derived from the GPR posterior distribution. Predicted
603 syllable rates were compared against biomechanical maxima derived from syllable duration to
604 ensure biological plausibility. See Supplementary methods for fine details.
605

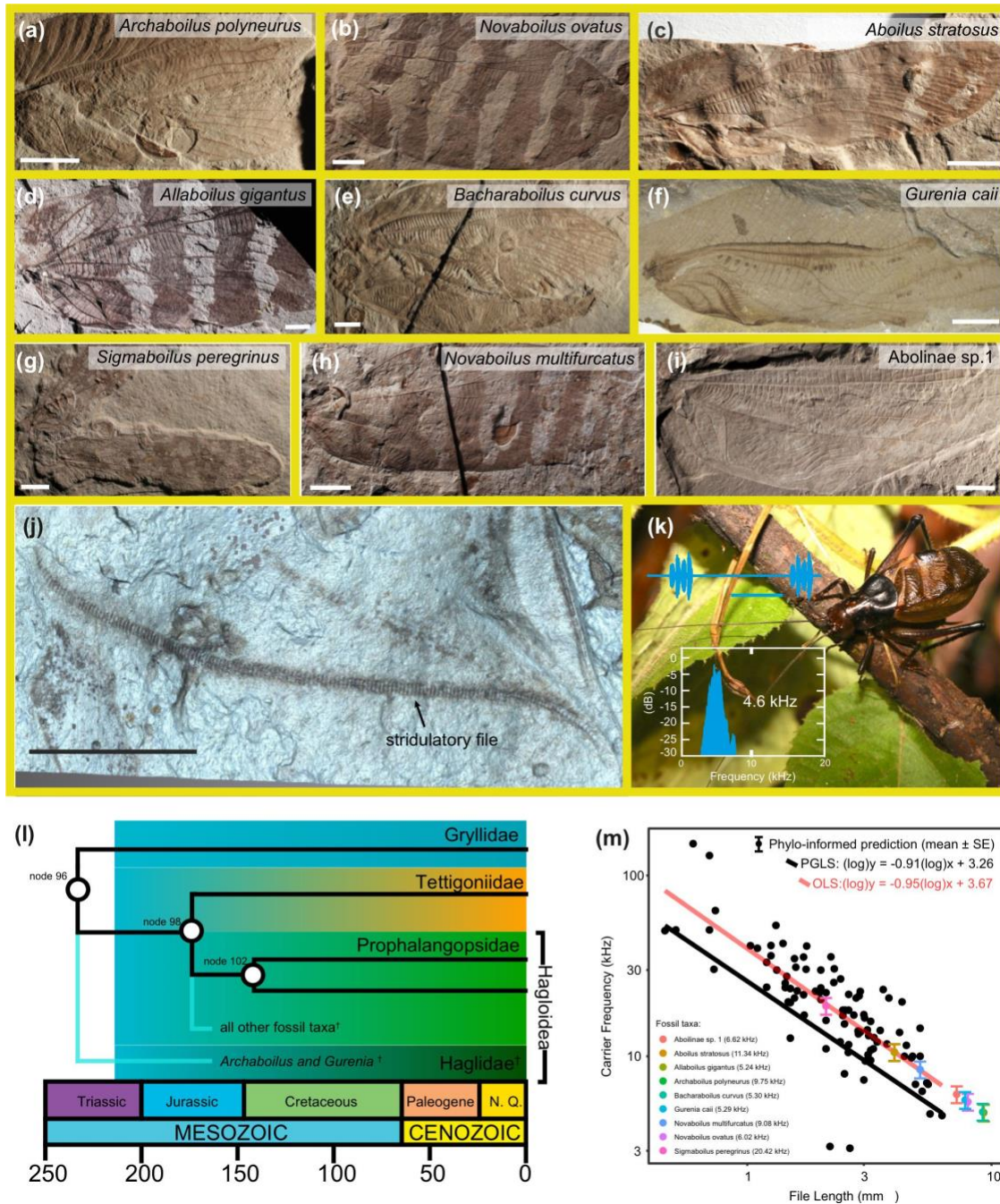


Fig 1. Fossilised wings and phylogenetically informed predictions of carrier frequency. (a-l) Examples of fossilised wings of the nine species presented in this study. (j) View of the stridulatory file of *Bacharaboilus curvus* (Prophalangopsidae). (k) *Tarragoilus diuturnus* (a living member of the Prophalangopsidae) displaying call oscillogram and acoustic spectral energy. (l) Broadest phylogenetic position of fossils used in this study, and indication of nodes between which taxa are positioned based on taxonomy. (m) Regression models and phylogenetically informed predictions of carrier frequency from file length for 95 extant ensiferans (black dots), and predictions for fossil taxa based on mean file lengths for each species (see symbols for each species). Red line indicates non-phylogenetically informed correlation (OLS model), while black line indicates the phylogenetically controlled PGLS model. Coloured points and error bars represent phylogenetically adjusted predictions from the PGLS model. Scales a-l=5.0mm; j=2mm; k=0.2s.

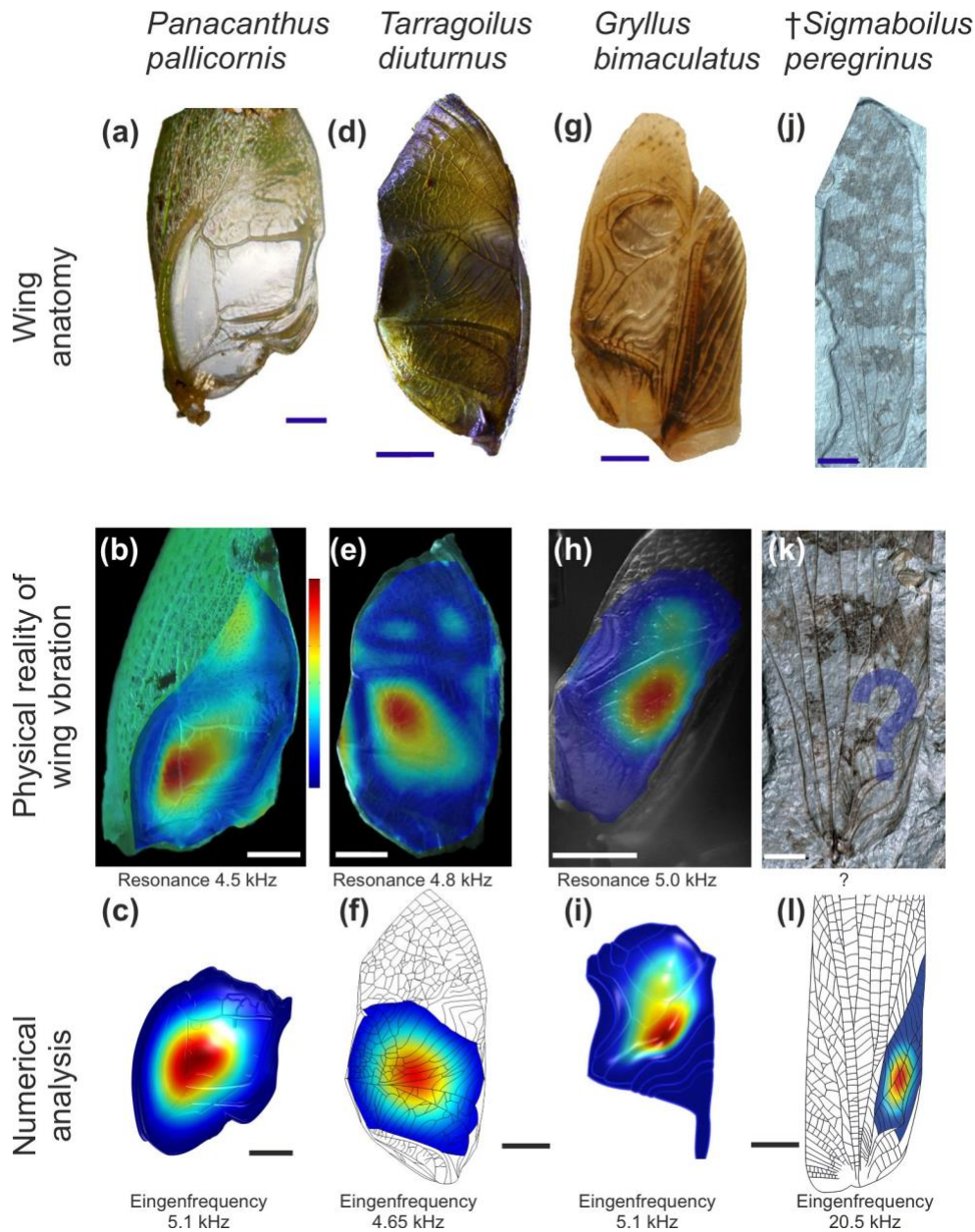


Fig 2. Validation of FEA models for extracting wing vibrations from fossilised wings, using living species as proof of concept. Morphology (a, d, g, j), LDV experimental data (b, e, h) and FEA results (c, f, i, l) of three extant and one extinct Ensifera. (a-c) *Panacanthus pallicornis* (LDV at 4.4 kHz, FEA at 5.0 kHz, songs 4.6-6.1 kHz, f at ~5 kHz). (d-f) *Tarragoilus diuturnus* (LDV at 4.4 kHz, FEA at 4.6 kHz, songs 4-5 kHz). (g-i) *Gryllus bimaculatus* (LDV at 4.9 kHz, FEA at 5.1 kHz, songs 4.8 kHz). (j-l) *Sigmaboilus peregrinus* (physical reality not possible to assess via LDV), FEA 20.50 kHz, f_c estimated at 20.42 kHz. Scale= 3mm.

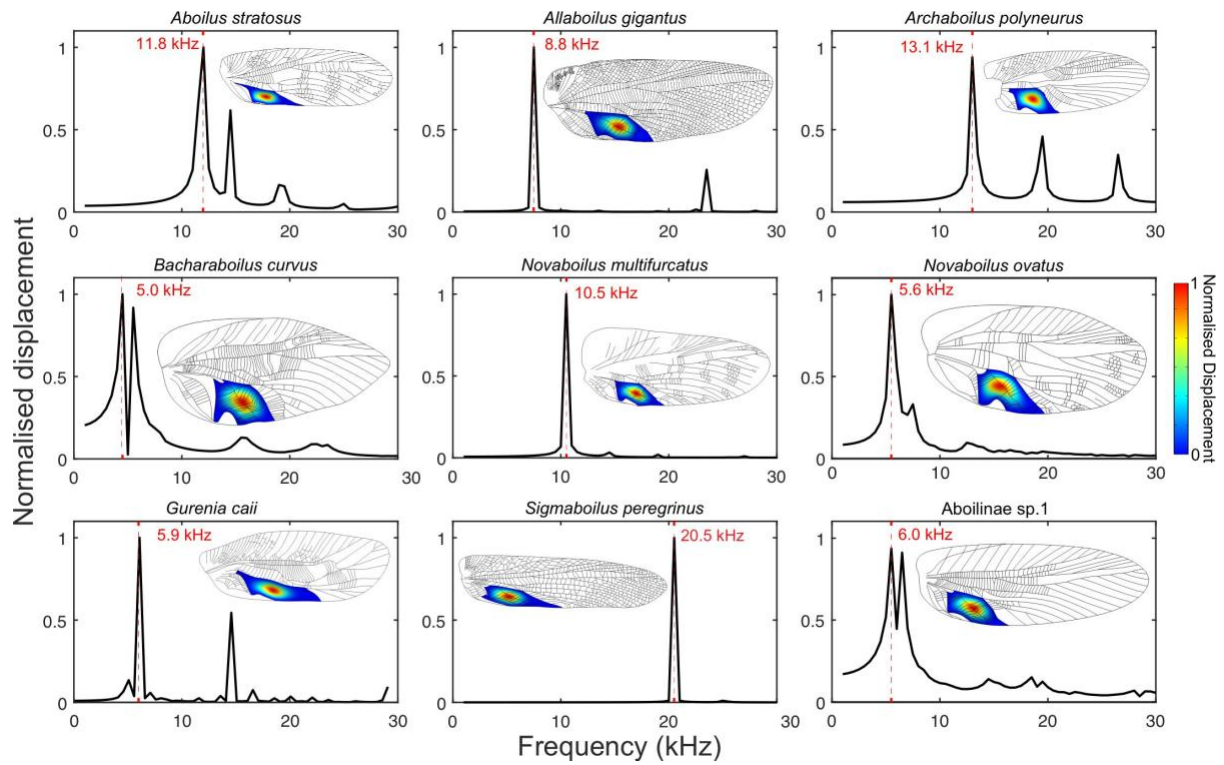


Fig 3. Reconstruction of main vibration of the stridulatory wing cells based on FEA models of nine fossil wing geometries. Deflection maps indicate relative minimum (blue) and maximum (red) deflection of the involved wing cells (see colour scale). The quality factor Q (peak width at -3 dB) is measured from the fundamental frequency (dashed red line).

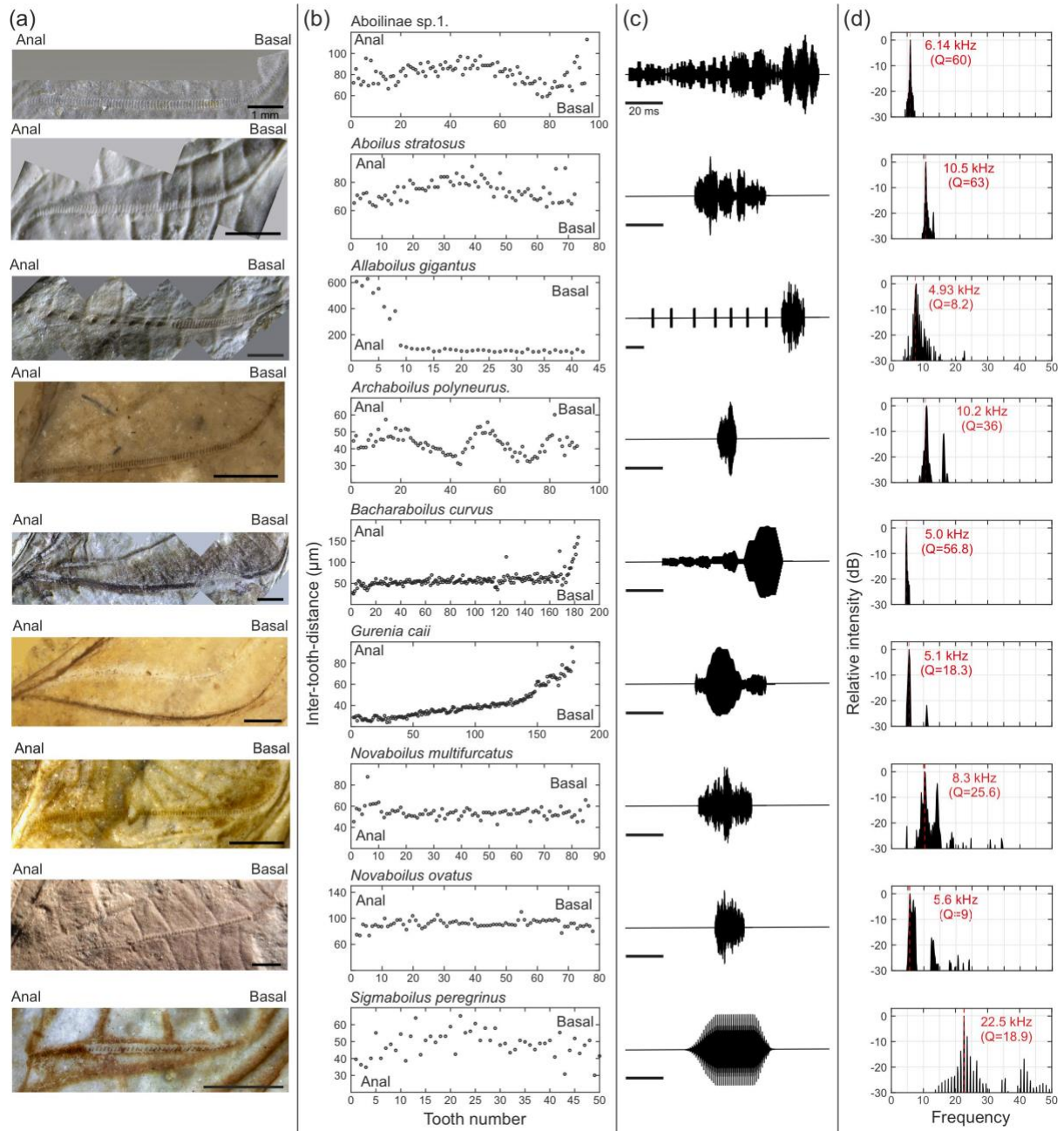


Fig.4. Reconstruction of the basic sound unit (syllable) of Jurassic ensiferan calls from stridulatory file morphology and model predicted carrier frequency. a) A fossilized stridulatory file of each of the nine species. Orientation: top is proximal, left is anal. Scale bars = 1 mm. b) Inter-tooth distances for each file fossil file in a). Teeth number starts from first teeth on anal part of file. c) Reconstruction of one syllable, based on tooth distribution, f_c , and numerical models (see also Fig. 3). Oscillations are calculated as produced during the closing movement of the wings, i.e. the scraper would move from left to right in a) and b). Scale bars = 20 ms. d) FFT analysis of the reconstructed syllable. f_c shown in red.

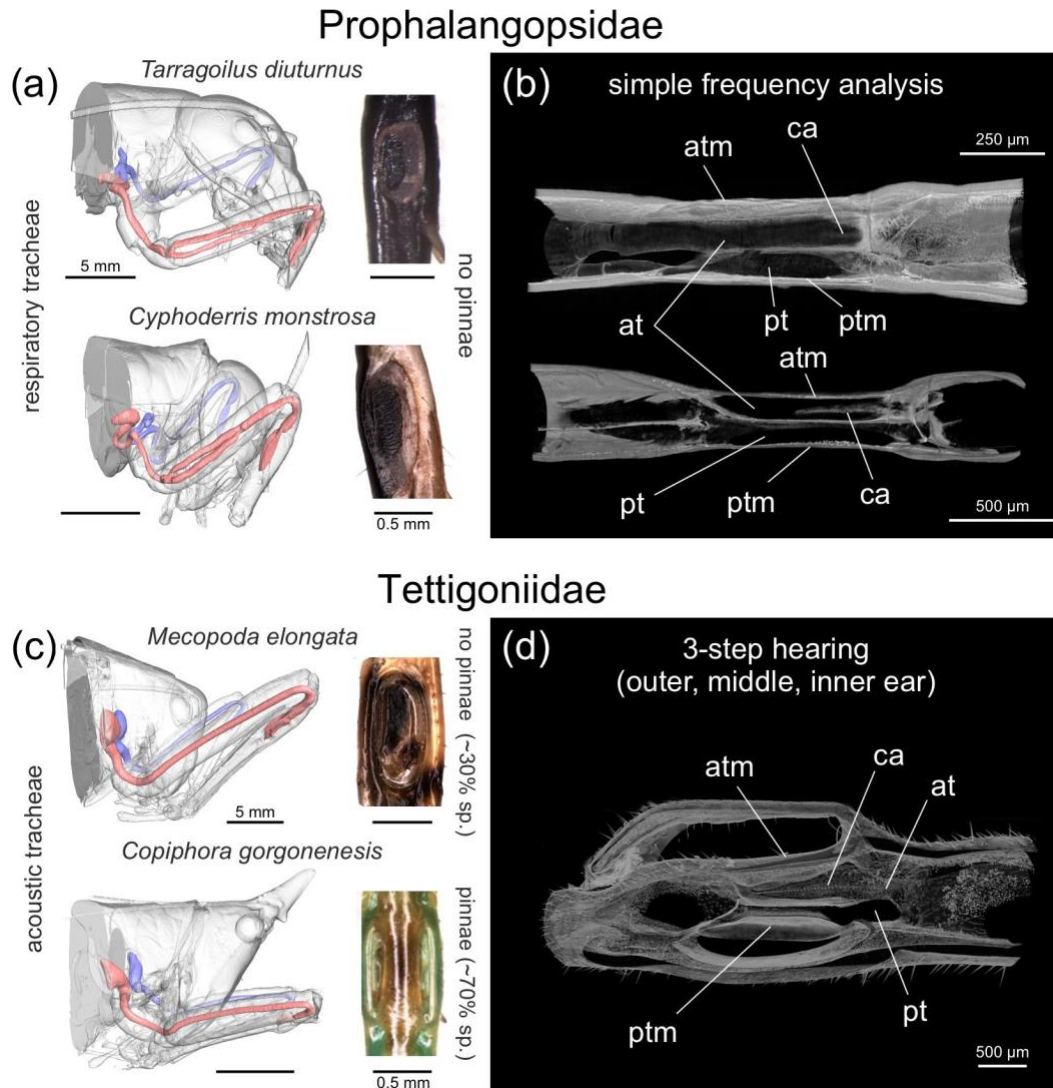


Fig. 5. The hearing system of extant grigs (Prophalangopsidae) and katydids (Tettigoniidae). (a) The bifurcated trachea in the forelegs of *T. diuturnus* and *C. monstrosa*, unspecialised for the transmission and capture of sound. (b) The simplified inner ear of the species in (a), showing a plesiomorphic version of a *crista acustica*, performing frequency analysis aided by the tympana. (c) The acoustic trachea, or ear canal, in extant katydids, displaying the common forms of tympana: naked or exposed (*M. elongata*), and covered by auditory pinnae (*C. gorgonensis*). (d) longitudinal section of a *C. gorgonensis* ear, showing the elaborated inner ear (or insect 'cochlea'), specialised for frequency analysis using frequency mapping and travelling waves. atm: anterior tympanic membrane; at: anterior tracheal branch of the acoustic trachea; ca: *crista acustica*; ptm: posterior tympanic membrane; pt: posterior tracheal branch. Scale for ears in (a, c): 0.5 mm; scale for tracheae in (a, c): 5 mm.

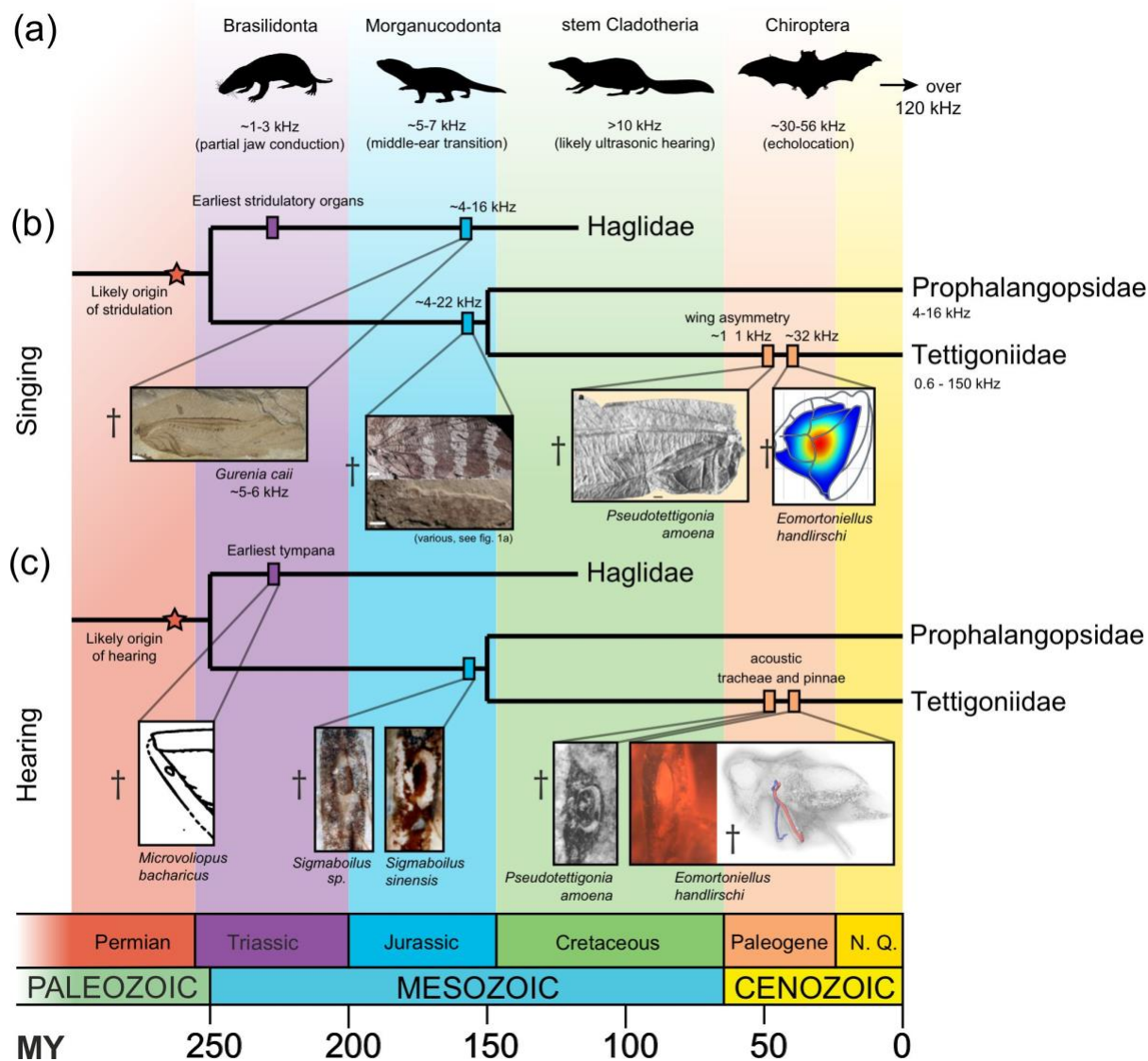


Fig. 6. Proposed scenario for the evolution of singing and hearing in grigs (Prophalangopsidae) and katydids (Tettigoniidae). (a) The evolution of auditory sensitivity in mammals and non-mammalian ancestors. (b) Evolutionary map of sound production by stridulation in Tettigoniidae. (c) Evolutionary scenario for hearing in Tettigoniidae. (*) Hearing organs adapted from: *M. bacharicus*: Gorochov⁶⁵. *A. hani*: Gu et al.⁸⁴. *Sigmaboilus* spp.: Xu et al.⁷. *P. amoena*: Rust et al.⁶. *E. handlirschi*: Woodrow et al.³³ (†). Wings adapted from: *P. amoena*: Rust et al.⁶. *E. handlirschi*: Woodrow et al.³³. N. Q. = Neogene and Quaternary.

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