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Biomechanics of a Moth Scale at Ultrasonic Frequencies

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Abstract

The wings of moths and butterflies are densely covered in scales that exhibit intricate shapes and sculptured nanostructures. While certain butterfly scales create nanoscale photonic effects, moth scales show different nanostructures suggesting different functionality. Here we investigate moth scale vibrodynamics to understand their role in creating acoustic camouflage against bat echolocation, where scales on wings provide ultrasound absorber functionality. For this, individual scales can be considered as building blocks with adapted biomechanical properties at ultrasonic frequencies. The 3D nanostructure of a full *Bunaea alcinoe* moth forewing scale was characterised using confocal microscopy. Structurally, this scale is double layered and endowed with different perforation rates on the upper and lower laminae, which are interconnected by trabeculae pillars. From these observations a parameterized model of the scale's nanostructure was formed and its effective elastic stiffness matrix extracted. Macroscale numerical modelling of scale vibrodynamics showed close qualitative and quantitative agreement with scanning laser Doppler vibrometry measurement of this scale's oscillations, suggesting that the governing biomechanics have been captured accurately. Importantly, this scale of *Bunaea alcinoe* exhibits its first three resonances in the typical echolocation frequency range of bats, suggesting it has evolved as resonant absorber. Damping coefficients of the moth scale resonator and ultrasonic absorption of scaled wing were estimated using numerical modelling. The calculated absorption coefficient of 0.50 agrees with the published maximum acoustic effect of wing scaling. Understanding scale vibroacoustic behaviour helps create macroscopic structures with the capacity for broadband acoustic camouflage.

Significance

Ultrathin sound absorbers offer lightweight solutions from building acoustics to sonar cloaking. The scales on moth wings have evolved to reduce the echo returning to bats, and we investigate their resonant sound absorber functionality. Resonant absorbers are most efficient at resonance, and Laser Doppler vibrometry (LDV) revealed that an individual moth scale's three resonance modes indeed span the biosonar frequencies of bats. The porous anisotropic nanostructure of such scales was parameterized and its effective stiffness properties calculated. Modal analysis on a 3D model accurately predicts resonance modes and frequencies found by LDV, and confirms absorption performance matching measurements. Our ability to model the absorbers contributing to evolved biosonar camouflage has implications for developing bioinspired thin and lightweight resonant sound absorbers.

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Introduction

The nocturnal acoustic arms race between moths and echolocating bats has been ongoing for 65 million years. To defend themselves against the bats' biosonar (most relevant frequencies from 20 to 150 kHz, with wavelengths from 16.6 to 2.3 mm), different moth species have evolved a wealth of active and passive defence strategies. Several moth taxa have independently evolved ears that can detect the ultrasonic frequencies of the biosonar calls of an approaching bat (1), which allows them to respond with evasive flight behaviours (2). In addition, Arctiinae, Geometridae and some other moths produce loud ultrasound clicks when under attack, which can startle bats, alert them to the moths' toxicity or even jam the bats' biosonar (1, 3, 4). Recent findings suggest some other moth species mimic such aposematic ultrasound clicks (5, 6). The many non-toxic moth species without hearing capability, however, have to rely on passive acoustic camouflage to avoid capture by bats (7, 8).

Like in most flying insects, moth and butterfly wings consist of a solid thin chitinous membrane suspended between a network of stiffer wing veins. In contrast to most other insects however, both the upper and lower wing surface of moths and butterflies are covered with arrays of overlapping scales, which has given the order Lepidoptera its scientific name (Greek lepidos = scale; pteron = wing). The scales and wing membrane are part of the insect exoskeleton consisting of a sclerotised biomaterial matrix of mainly chitin and protein (9). A typical moth scale is anchored into a socket in the wing membrane with a narrow pedicel and widens into a flattened blade (10). Each scale itself is a highly sculptured porous structure, and scales show diverse morphologies even on a single wing (11). The highly sculptured scale structure implies sophisticated evolutionary adaptations, analogous to the highly organised nanoscale photonic structures for visual signalling (12, 13). Across moths, scale morphologies are diverse and hence provide a large candidate pool for biophysical adaptations. Previous studies have highlighted the role of moth scale morphology in creating multiple functions of moth wings such as aerodynamics, thermal regulation, and wettability (14-16). Additionally, moth wings have been hypothesised as the main organ bringing about acoustic camouflage. Micro-reverberation chamber testing revealed that scale-covered moth wings are more absorbent at frequencies from 40 to 60 kHz than wings with scales removed (8). There is, however, no explanation for how the moth wing, and more specifically its microstructure, creates this acoustic absorber functionality.

Lepidoptera wing scales are usually less than 0.25 mm wide, and thus always smaller than one tenth of the smallest wavelength bats use for echolocation. Even the cross section thickness of the wing including upper and lower scale layers is always below the relevant wavelengths. Because wings are therefore ultrathin absorbers with subwavelength thickness, rigid porous absorption is inefficient, leaving the alternative of resonant absorber functionality (17). In resonant absorbers a resonant mass and spring system will provide maximum absorption at the frequency it is tuned to. Other resonant systems show maximum sound transmission at resonance (18). Both high absorbance and transmittance are viable strategies to reduce backscatter and hence detectability to bat biosonar. Since scales are the basic elements of moth wings, their vibrational response is essential in understanding the acoustic behaviour of entire moth wings and hence the acoustic camouflage effect in moth acoustic ecology and behaviour.

Moth wing scales show a hierarchical design, with a scale tiling pattern at the large scale, scale shape at the next and scale internal structure of nanometre order. As the first step to understanding this sophisticated natural structure, this paper focuses on exploring the vibrational behaviour of a single free-standing scale. Our prediction is that moth scales are resonant systems, and that their resonances are at biologically relevant frequencies used by bats for echolocation. We further provide an accurate numerical model of the dynamic behaviour of a scale, which captures the governing physical phenomena at work. Numerical modelling is used to show that the scale resonator can achieve high absorption coefficients at resonance.

Existing resonant absorbers are made of solid materials. In some designs a layer of porous material is added to achieve higher absorption coefficient or a broad band performance (19). The moth scale represents a new resonator design composed of resonating micro-perforated scales. Elucidating the acoustic mechanisms behind moth wing sound absorbance aims at developing bioinspired sound absorbing materials with a thickness below their functional wavelength for new applications in noise control, architectural acoustics and bio-inspired radar and sonar target concealment.

Results

Scale shape and structure

Scanning electron microscopy (SEM) of a *Bunaea alcinoe* wing (Fig. 1a, dorsal view) shows that neighbouring scales overlap both laterally and along their longitudinal axis. Scales have a leaf-like shape with the blade continuously widening from the basal socket, ending in a wide apical margin deeply incised forming several elongated extensions. Each scale possesses a top lamina and a bottom lamina connected by a framework of trabeculae forming the inter-trabecular sinus. Both laminae consist of parallel longitudinal ridges, and neighbouring longitudinal ridges are connected via series of cross ribs (Fig. 1b, e-h). This intricate arrangement makes scales highly porous with a large proportion of air-filled space.

One typical scale (Fig. 1d) was selected for detailed structural characterisation, vibrational analysis and dynamic modelling. We used confocal microscopy to obtain a high resolution 3D image of scale nanostructure (Fig. 1d-f). As a typical example of scales covering the dorsal aspect of the wing, this scale (Fig. 1d) is 295 µm long from its socket to the tip of the longest apical extension. The blade is roughly triangular with the greatest width at the base of the incisions being 189 µm, and a distance between the tips of the two lateral extensions of 214 µm. The longitudinal ribs (Fig. 1e) in the top lamina are 1.00±0.13 µm wide (mean±SD; n=5) and their distance is 2.59±0.11 µm. In the bottom lamina (Fig. 1f) they are 0.90±0.14 µm wide and spaced by 1.97±0.11 µm. Cross ribs in the top lamina are 0.29±0.03 µm wide and separated by 1.01±0.11 µm, and in the bottom lamina 0.25±0.03 µm wide and separated by 0.98±0.11 µm. As a result, both laminae are highly perforated with 31% of the top und 30% of the lower lamina area consisting of voids. For the area shown in Fig. 1e&f the scale is 3.18±0.6 µm thick between the peaks of the longitudinal ridges in upper and lower laminae.

The 3D unit cell - structure

The nanoscale morphological analysis reveals the globally periodic structure of the scale, where an elementary unit, a structural cell comprising porous laminae and trabecular pillars, repeats in the 2D plane of the scale surface. Based on a transverse cross section (Fig. 2a) through the 3D iso-surface shown in Fig. 1g&h, a parameterized model of such a unit cell was developed (Fig. 2b). Both the top lamina and the bottom lamina are simplified as corrugated perforated plate structures. The corrugation is formed by juxtaposing a row of elliptical shells, which are then truncated by a cutting plane (Fig. 2a). Arrays of elliptical holes are then punctured in the troughs of the corrugation to mimic the perforation formed by the cross ribs. The trabeculae that link the upper and lower laminae are simplified as arrays of vertically positioned cylindrical pillars. 20 independent parameters are needed to describe the parameterized moth scale model (SI Appendix, Tbl. S1). Because the ridges are spaced more widely in the top compared to the bottom lamina, the unit cell includes two ridge periods in the top and three in the bottom lamina (Fig. 3a; SI Appendix, Tbl. S1). For comparison with butterfly scales, which in all documented cases have the lower lamina unperforated, a more 'butterfly-like' unit cell was created, where the lower lamina was not perforated but that was otherwise identical, increasing the mass of this 'butterfly-like' unit cell by 9.3% relative to the moth unit cell.

The 3D unit cell - effective stiffness matrix

Due to the periodic nature of the parameterized moth scale model, the single unit cell acts as the representative element of the whole scale structure (Fig. 3a). A set of boundary conditions (SI Appendix, Tbl. S2) is applied to introduce either a pure axial or a pure shear strain to the unit cell. Fig. 3b&c show the six surfaces where various displacement boundary conditions are applied. The stress distribution under such strains was calculated using finite element modelling. The stiffness matrix [1] was calculated based on the simulated stress distribution (Fig. 3d-i) (for details see Materials and Methods).

$$\text{Stiffness matrix } [c_{ij}] = \begin{bmatrix} 21.89 & 2.88 & 2.15 & 0 & 0 & 0 \\ 2.88 & 11.5 & 1.21 & 0 & 0 & 0 \\ 2.15 & 1.21 & 8.06 & 0 & 0 & 0 \\ 0 & 0 & 0 & 2.78 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1.13 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1.36 \end{bmatrix} \times GPa \qquad [1]$$

The ridges and the corrugated profile of laminae makes the scale material anisotropic in scale plane, with the stiffness in the ridge direction 1.75 times the value of the stiffness transverse to the ridge (Fig. 2b). The in-plane anisotropic nature of the nanostructure means that the scale shows different bending moduli along the ridge direction and the transverse direction. The perforated structure has a porosity of 57%. The perforated structure thus has an effective density of 43% of bulk chitin.

Scale vibrations at ultrasonic frequencies - modelling

The first three calculated resonances are at 28.4, 65.2 and 153.1 kHz respectively (Fig. 4d-f); ultrasonic frequencies overlapping with and spanning the majority of the entire bat biosonar range. The first vibration mode is a pitch vibration around the x-axis. The second mode is a twisting vibration around the middle longitudinal y-axis of the scale. The third mode is a yaw vibration of the scale constrained within the flat scale plane, rotating around the z-axis.

In the more 'butterfly-like' unit cell, which differed from the moth scale only in that the perforation of the lower lamina was filled, the stiffness matrix changed to [2] and the resulting resonances shifted upwards substantially to 88.4 kHz, 150.9 kHz, and 406.0 kHz respectively.

$$\text{Stiffness matrix } [c_{ij}] = \begin{bmatrix} 23.71 & 4.61 & 2.14 & 0 & 0 & 0 \\ 4.61 & 13.78 & 1.41 & 0 & 0 & 0 \\ 2.14 & 1.41 & 6.59 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1.04 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1.09 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1.39 \end{bmatrix} 10^{10} Pa \qquad [2] \qquad [2]$$

Scale vibrations at ultrasonic frequencies – measurements

Using laser Doppler vibrometry (see Materials and Methods) the average vibrational spectra were measured, and three resonances were found at frequencies of 27.6, 90.8 and 152.3 kHz (Fig. 5). The deflection shapes of the resonances are shown in Fig. 4a-c. The average displacement amplitude at the resonance peaks is at the best 2.5 times the response at the non-resonance frequencies, showing that the scale vibrator has a broadband displacement response.

Scale damping coefficients and scaled wing absorption coefficients

A finite element model was built to simulate the ultrasonic absorption performance of a surface coated in an array of scales. Assuming Rayleigh damping, two damping parameters are used to capture the various damping mechanisms. These are found using a parameter search until the calculated displacement spectra best matched the measured spectra (Fig. 6a) (20). The resulting Rayleigh damping coefficients were $\alpha=1.51\times10^{4}$ and $\beta=8.30\times10^{-8}$, which are equivalent to a modal damping ratio of 4.5%.

With this experimentally extracted damping, the simulated transmission, reflection and absorption coefficients of a scaled wing were calculated from a finite element model (Fig. 6b). Modelling covers 20 kHz to 80 kHz, including the first resonance and representing the most relevant bat echolocation range. As expected, the absorption coefficient spectrum shows a peak at the first resonance frequency of the scale, with a maximum of 0.50 at 29 kHz. In contrast, the absorption peak disappears for a model just consisting of the wing membrane. Changing the material mass or stiffness shifts the peak, moving it potentially outside the pertinent echolocation frequencies.

Discussion and conclusion

This paper represents the first effort to numerically and experimentally characterize moth scale biomechanics and vibrational behaviour. Resonant functionality of scales could be adaptive in creating acoustic camouflage against bat echolocation. As predicted, both LDV and modelling confirmed resonant behaviour of the scale, and the first three resonances occurred within and fully included the relevant bat echolocation frequency range (20 to 150 kHz). In contrast, the modified 'butterfly-like' scale with solid lower lamina had much higher calculated resonance frequencies well outside the frequency range relevant for bat echolocation. This supports the notion that the moth's double-perforated scale nanostructure has evolved to create resonance frequencies in response to bat echolocation. The three resonance modes we found in our example scale have the potential to reduce echo strengths (backscatter) around the respective frequencies. Ultrasonic waves reaching a moth wing at one of these resonant frequencies should be transmitted (18) and/or absorbed (assuming resonant absorber; 17, 21) preferentially. This reduces the backscattered target strength and hence detectability to bat biosonar, affording an evolutionary advantage by reduced predation pressure.

A parameterized nano-structural model of a moth scale has been developed and used to extract effective material properties. A macroscopic dynamic finite element simulation of a moth scale using these effective scale properties has been able to replicate the experimental laser Doppler vibrometry well. Mode shapes found in the simulation (Fig. 4d-f) match those found by vibrational characterization (Fig. 4a-c); but note that the measured rotation axis is moved somewhat to the right of the scale's midline. Importantly, calculated first and third resonance frequencies differ by just 0.8 kHz (2.9%) and 1.2 kHz (1.0%) from the measured values. This match strongly suggests that the chosen modelling approach captures the most relevant governing biophysical parameters. Only the second resonance frequency differs more substantially (28%). The remaining deviations from calculated resonances might exist because: Firstly, the scale curvature has been simplified as spherical, while the true scale curvature profile is more complex. Secondly, the perforation rate was set as constant while it changes over different parts of the scale. Thirdly, the incident sound wave for laser Doppler vibrometry (LDV) was not normal to the scale surface (clear line of sight needed for laser), and the wave front was not perfectly flat (speaker close enough to reach adequate SPL exposure). In addition, the orientation of the principal axes of the effective anisotropic material stiffness matrix are fixed in the scale model. In the true scale, however, the material property primitive axes reorientate themselves normal to the development of the scale curvature. The very good overall model-experiment agreement in terms of the mode shapes and resonance frequencies suggests however, that these factors, which could be modelled in the future, play a secondary role.

Ultrasonic absorption modelling shows that the observed resonance behaviour of the single scale creates relevant ultrasonic absorption functionality of the scaled wing (assuming an array of scales). The absorption coefficient peak value of 0.50 is comparable with the empirical report on moth wing absorption (8, 22). The wing model is simplified as one layer formed by a rectangular grid of identical cover scales on a flat wing membrane. A real moth wing is composed of multiple layers of cover and base scales of different sizes, shapes and degrees of overlap. The ultrasonic absorption coefficient spectra of a real moth wing could therefore be higher than the numerical estimated value here. The different morphologies of scales suggest differing resonance frequencies. Such resonance variation of different scales may have evolved to cumulatively achieve more broadband acoustic absorption. Note that our current model does not include potential acoustic effects of the scale micro-perforation, which might further increase absorption.

The resonant moth scale absorber we investigated here has a morphology that differs substantially from existing resonant absorber designs. Moth scale resonators have the advantage of a small footprint, are easily assembled into densely overlapping arrays and resonator properties can be tuned via multiple parameter tuning. The parametric model of the moth wing structure paves the way to understanding and reconciling not only the acoustic but also the aerodynamic and thermal functionality of moth scales. Our model sheds light on new designs of biomimetic lightweight acoustic metamaterials that achieve specific acoustic absorption and transmission for applications in noise mitigation.

Material and methods

Specimens

Live *Bunaea alcinoe* (Cabbage tree emperor moth; Stoll, 1780) were obtained from wwb.co.uk as pupae on July 28th 2016. The pupae were housed in a temperature-controlled cabinet (Economic Deluxe, Snijders Scientific, Tilburg, Holland), where they were subject to a 12-hour night/day cycle in which temperature varied between 25°C and 30°C whilst humidity was maintained at a constant level of 70%. We checked daily for successful eclosion, which happened during the first week of August 2016. Intact specimens were euthanized and pinned in a natural position with the wings oriented horizontally to the dorsal plane. After being dried at room temperature for two weeks, scale specimens behind the bifurcation of the third vein on the front dorsal area of the right forewing were removed from the wing using a fine brush. Individual scales were then mounted in an upright position by clamping their stalk end using microsurgery tweezers (B5SA, Bondline Electronics Ltd, Wiltshere, UK) for scanning Doppler laser vibrometry (LDV, Polytec PSV-400, POLYTEC GmbH, Germany).

Scale microstructure

Nanostructure of individual *Bunaea alcinoe* moth scales was obtained using scanning electron microscopy (SEM, Zeiss Evo15 with Lab6 emitter, Germany) and confocal microscopy (CFM, Leica TCS SP5, Mannheim, Germany). For SEM, sections of wing were mounted on adhesive carbon tabs (EM Resolutions Ltd, UK) and coated with 5 nm of gold (Quorum Q150R ES, Quorum Technologies Ltd, UK). Scales were imaged in both high vacuum mode using a SE1 detector and variable pressure mode using a VPSE G3 detector. We used an electron high tension (EHT) of 15-20 kV with 50-100 pA probe and a magnification range from ×250 to ×10k.

For confocal microscopy, a single target scale was immersed in mounting medium glycerol. It was sealed between two microscopy slides with nail polish (ethyl acetate and butyl acetate as main ingredients) as a sealing material. Auto-fluorescence of the scale material was strong enough to obtain clear confocal images without further labelling (23). The excitation and light emission frequency sweep spectra of the scale were characterized. The optimal confocal microscopic setting was determined by trial and error as: excitation wavelength=488 nm; emission band=495-720 nm; pinhole=60 nm; optical section thickness=0.46 µm; z step=80 nm. The 100× lens realized a pixel size of 30×30 nm, hence creating 3D voxels of 30×30×80 nm.

Modelling of the effective material property

The 3D data obtained from confocal microscopy were turned into a voxel space from which a 3D iso-surface model was created and saved in STL format using MATLAB (R2016a, The MathWorks, USA). This 3D model of the moth scale in STL format was then imported into a finite element methods software (COMSOL 5.2a, COMSOL Inc, Sweden) in order to identify and parameterize an idealized unit cell for modelling of the effective material properties. The effective material extraction process was greatly simplified due to the periodicity of the model since a single unit cell can be adopted as the representative element of the whole structure (Fig. 3a). Expanding the unit cell in three dimensions results in a 3D material possessing the symmetry of point group 2mm (Hermann-Mauguin point group notation), with a two-fold symmetry axis in the z-direction and two mirror planes in the x-z and y-z plane passing through the two-fold symmetry axis (Fig. 2b) (24). This 2mm symmetry leads to a 3D material with anisotropic elastic behaviour, which can be represented by the following constitutive equations:

$$[\boldsymbol{\sigma}] = [\boldsymbol{c}][\boldsymbol{\varepsilon}] \qquad [3]$$

$$\begin{bmatrix}\sigma_{xx}\\ \sigma_{yy}\\ \sigma_{zz}\\ \tau_{xy}\\ \tau_{yz}\\ \tau_{xz}\end{bmatrix}=\begin{bmatrix}c_{11} & c_{12} & c_{13} & & & \\ c_{12} & c_{22} & c_{23} & & \mathbf{0} & \\ c_{13} & c_{23} & c_{33} & & & \\ & & & c_{44} & 0 & 0\\ & \mathbf{0} & & 0 & c_{55} & 0\\ & & & 0 & 0 & c_{66}\end{bmatrix}\begin{bmatrix}\varepsilon_{xx}\\ \varepsilon_{yy}\\ \varepsilon_{zz}\\ \gamma_{xy}\\ \gamma_{yz}\\ \gamma_{xz}\end{bmatrix} \qquad [4]$$

where $[\boldsymbol{c}]$ is the stiffness matrix; σ_{xx}, σ_{yy} and σ_{zz} are the normal stress components; τ_{xy}, τ_{yz} and τ_{xz} are the shear stress components; ε_{xx}, ε_{yy} and ε_{zz} are the normal strain components; γ_{xy}, γ_{yz} and γ_{xz} are the shear strain components.

The non-zero values in the stiffness matrix are extracted from the finite element parameterized single unit cell model static stress-strain simulation (Fig. 3a), assuming the nanostructure is made of homogeneous chitin. Six boundary conditions (SI Appendix, Tbl. S2) were set: *u*, *v* and *w* represent displacement variables in the *x*-, *y*- and *z*-directions. *d*=0.01 µm represents an infinitesimal displacement to induce strain in the unit cell. Each boundary condition introduces either a pure axial strain or a shear strain in the unit cell, while the other five strain elements remain zeros. The strain vector $[\boldsymbol{\varepsilon}]$ in [4] thus has only one non-zero element. The stress distribution of the single unit cell element under such a boundary condition is then calculated (Fig. 3d-i) and the effective stress elements in the stress vector $[\boldsymbol{\sigma}]$ is calculated by averaging the simulated stress distribution on the respective boundaries. Similar method had been adopted in (25-27) to extract the effective elastic material property of a single layer perforation. The chitin's Young's modulus is 65 GPa and the density is 1300 kg/m^3 (28).

Modelling scale vibrations at ultrasonic frequencies

To calculate the vibration of a single scale, a macroscale finite element model as shown in Fig. 4 was built in COMSOL. The polygonal outline of the scale is extracted from the confocal image as shown in Fig. 1d using the software ImageJ (1.46r, National Institutes of Health, USA). The polygon is then imported into COMSOL and the curved scale model is formed by penetrating the extruded outline polygon with a spherical surface. The radius of the spherical surface has been chosen as 700 µm, which is based on the SEM observation of the scale curvature morphology. Due to the size of the unit cell relative to the wavelength, the dynamics of the unit cell can be neglected in our finite element simulation and hence it is treated as a pure stiffness element. The effective material stiffness matrix is assigned to the single scale model and a modal analysis is conducted to obtain the resonances and the mode shapes of the single scale. When doing the modal analysis, the scale pedicel end is fully clamped, while all other edges are free. The scale was inserted in a socket structure in the wing membrane. The socket's structure and its mechanical degree of freedom, to the authors' knowledge, has not been reported. To simplify the experimental and numerical calculation study, a mechanically clamped boundary condition was used in this study.

Scanning Laser Doppler characterization of scale vibration

The vibrational behavior of the single scale was characterized using a laser Doppler vibrometer (LDV, Polytec PSV-400, POLYTEC GmbH, Germany). A micro scan lens PSV-A-CL-80 was used, who can focus the laser spot diameter to be as small as 10 µm.

The moth scale was mechanically clamped at one end using tweezers and mounted at a distance 13 cm from the lens. The vibration of the scale was excited by sound pressure from a custom-made speaker based on an electret film (HS-02-Film, Emfit Ltd., Finland), which was mounted at a distance of 7 cm and an angle of θ=40° below the specimen (SI Appendix, Fig. S1a). The speaker is located out of the optical path so that it would not block the path, the realized angle was as close as possible to normal incidence. We used a high voltage amplifier (PZD350, TREK Inc., Lockport, NY) with the speaker. The sound pressure level (SPL) at the sample position was calibrated using a calibration microphone (1/8" Microphone Type 4138, with Dual Microphone Supply Type 5935L as the amplifier; Brüel & Kjær, Denmark). The calibration was performed with the scale in place and the acoustic axis of the microphone aligned with that of the speaker. The scale and the microphone are on the same plane perpendicular to the laser beam path and maintain the same distance with the speaker. The SPL at 100 kHz was 59.0 dB SPL (SI Appendix, Fig. S1b). The vibrational spectrum from 20 to 180 kHz was obtained by amplitude averaging the displacement spectra of all the scanning points (Fig.4a-c). The scanning area is a fan shaped area defined on the blade part of the scale (Fig.4). The scanning point grid has a scanning step of 12 µm.

Modelling of scale damping coefficients and absorption coefficients of the scaled wing

Two models were built in COMSOL to explore the damping effect of the scale and the ultrasonic properties of the moth wing composed of such scales. The first model contained a single scale with one end fully clamped (SI Appendix, Fig. S2a). The scale was immersed an air chamber and had a 40 degree oblique angle with respect to the horizontal plane. Incident plane waves were assigned in the upper air chamber to mimic the waves generated by the speaker. The incident wave amplitude was based on the calibrated SPL spectrum (SI Appendix, Fig. S1b). Two perfect matched layers were added on the top and bottom of the model to absorb the reflected and transmitted waves so that the model mimicked an open space condition. A fan shaped area reflecting the LDV scanning are was defined on the scale. A frequency domain analysis was conducted with frequencies spanning from 20 kHz to 80 kHz, which focused on the first resonance and represents the most relevant bat biosonar range. The displacement spectra were calculated by performing a magnitude average on the scanning area following the frequency domain simulation.

A Rayleigh damping model was adopted to phenomenally describe damping in this model. The two Rayleigh damping coefficients, α and β were parameter swept in COMSOL and their values were determined when the calculated displacement spectra matched with the LDV detected spectra ($\alpha=1.51\times10^{4}$ and $\beta=8{,}30\times10^{-8}$).

A second model (SI Appendix, Fig. S2b) was built to calculate the absorption coefficient of the scaled array and Rayleigh damping was added to the material. The leaf-shaped scale (length=295 µm, width=189 µm, thickness=3.86 µm) was attached on a 3 µm thick wing membrane made of chitin. The scale had a 25 degree insertion angle with the wing membrane. Periodic boundary conditions were assigned to the vertical unit cell walls to expand such a unit cell to a 2D array. The transmission coefficient R_{Π}, reflection coefficient T_{Π} and absorption coefficient α of the scale array were calculated by the following formulae (29):

$$R_{\Pi} = \frac{|p_r|^2}{|p_i|^2} \qquad [5]$$

$$T_{\Pi} = \frac{|p_t|^2}{|p_i|^2} \qquad [6]$$

$$\alpha = 1 - R_{\Pi} - T_{\Pi} \qquad [7]$$

where p_{ra}=the reflected acoustic pressure; p_i=the incident acoustic pressure; p_t=the transmitted acoustic pressure. The numerators and denominators in the above equations were calculated by doing average over the two planes located above and below the scale (SI Appendix, Fig. S2). For comparison, the absorption coefficients of a single layer of wing membrane was also calculated.

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Figure legends

Fig. 1. Scale arrangement and structure, (a) to (c): SEM images of *Bunaea alcinoe* scales; (a) partly disrupted tiling of scales; (b) perforated top lamina of a scale; (c) cross-section of a fractured scale revealing the inter-trabecular sinus between the two laminae. (d) to (f): Confocal microscopy of the scale; (d) individual scale used for further analysis; 20× magnification; white square indicates observation area of (e) top lamina and (f) bottom lamina; 100× magnification. (g) and (h): Iso-surface 3D visualisations of a mid-section shown in the yellow square in (d) of the individual scale; (g) the top lamina and (h) bottom lamina with longitudinal ridges and cross ribs. In (h) the lower lamina faces upwards, oriented with the basal socket of the scale to the back and the apical ridge facing towards the front.

Fig. 2. Schematic showing (a) how the 3D model of the scale was parameterized and (b) the implemented 3D model containing 2×10 unit cells.

Fig. 3. The moth scale model: (a) the parameterized single unit; (b) and (c) showing the different boundary conditions. Note that each boundary includes all the facets on the same plane. (d) to (i): Simulation results of stress distribution and deformation (solid line frame shows the original shape) in the single unit under different boundary conditions (SI Appendix, table S2). The unit cell undergoes a pure (d) ε_{xx} , (e) ε_{yy} , (f) ε_{zz} , (g) γ_{xy} , (h) γ_{yz} and (i) γ_{xz} strain.

Fig. 4. Modelled and measured resonances of the moth scale. (a) to (c): Scanning laser Doppler vibrometry results of the first three resonances of the scale. The resonance frequencies being: (a) 27.6 kHz; (b) 90.8 kHz and (c) 152.3 kHz. (d) to (f): Simulation of mode shape of a single scale with curvature radius of 700 µm. The colour profile shows the normalised z-component (the out of scale plane displacement of the vibrating scale), (d) rotational vibration around x-axis, pivoting at the clamped edge, at frequency 28.4 kHz; (e) twisting vibration around y-axis at 65.2 kHz; and (f) rotational vibration around z-axis, at 153.1 kHz. Grey outline of scale indicates rest position for comparison. Colour bar indicates displacement amplitude.

Fig. 5. Mechanical responses of a scale. The vibrational spectrum was calculated by averaging amplitude spectra over all scanning points. The inset shows scale shape and the scanning area.

Fig. 6. (a) Calculated displacement spectra vs. the measured displacement spectra from 20 kHz to 80 kHz. The calculated spectra were under the damping ratio of 4.5%. (b). Calculated reflection, transmission and absorption coefficients of the moth scaled wing. The absorption coefficient of a single wing membrane layer was also plotted for comparison.