accompanying well data, in the Bengal basin has revealed that the Ganges–Brahmaputra delta started to grow rapidly ~40 Myr ago with an increase of sediment flux and development of significant prograding clastic depositional sequences. These sedimentation records are consistent with our view (based on the magmatism) that suggests an earlier rapid rise of eastern Tibet, from where thick piles of the lower sedimentary sequences in the Ganges–Brahmaputra delta and the Bengal fan could have been derived. A similar diachronous uplift history has been also proposed in the northern margin of the Tibetan plateau. On the basis of radiometric dating results of granites and gneisses, Arnaud et al. have argued that the basement unroofing and uplift in the eastern Kunlun Range occurred since ~35 Myr ago, and apparently preceded those in the western part of the Range.

Consequently, we suggest that the Tibetan plateau has undergone two main stages of rapid uplift caused by diachronous removal of thickened Asian lithosphere after the Indian indentation. Whereas the younger, and better-known, uplift began ~20 Myr ago in the western part of Tibet, the earlier event took place in the east, since ~40 Myr ago. Our observation can be reconciled with tectonic forcing models for the Cenozoic isotope evolution in the ocean and global climate change; these models put forward the effects of the rise and subsequent erosion and weathering of the Tibetan–Himalayan region. More specifically, it provides the first (to our knowledge) convincing time constraint that accommodates not only the rapid and steady increase in the seawater strontium isotope ratios beginning 40 Myr ago but also the onset of global cooling from the early Eocene.

We further propose that the late Palaeogene tectonic processes in eastern Tibet played an important role in initiating the Aila Shan–Red River shear zone, thus causing the continental extrusion and global climate change; these models put forward the effects of the rise and subsequent erosion and weathering of the Tibetan–Himalayan region. More specifically, it provides the first (to our knowledge) convincing time constraint that accommodates not only the rapid and steady increase in the seawater strontium isotope ratios beginning 40 Myr ago but also the onset of global cooling from the early Eocene.

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Evolutionary transition from stretch to hearing organs in ancient grasshoppers

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Ears of modern insects occur on a wide variety of body parts and are thought to have evolved from ubiquitous stretch or vibration receptors. This relationship, based on comparative anatomy and similarities in the embryological development of ears in divergent taxa, has led to the widespread assumption of homology of these structures in insects, although this has not been tested rigorously. Here we report on the hearing organs of a relatively ancient, atypomorphic bladder grasshopper (*Bullicras membracioides), which is capable of signalling acoustically over ~2 km. We show that, within single individuals of this species, serially repeated abdominal ears show functional continuity from simple to more complex forms. All 12 morphologically differentiated
organs respond to sound frequencies and intensities that are biologically significant, and mediate adaptive behavioural responses. By linking observations at the anatomical, physiological and behavioural level, our experiments provide evidence for the transition in function and selective advantage during the evolutionary development of this complex structure. It is possible that ancestral insects with only simple pleural receptors had auditory capability covering distances substantially greater than contemporary insects with tympanate ears.

Although they lack differentiated tympana, bladder grasshoppers (Pneumoridae, Orthoptera) possess hearing organs homologous to those found in locusts. Histological staining shows that this organ contains nearly 2,000 sensory units (Fig. 1a). Multicellular scolopidia, each consisting of a bipolar sensory neuron and several accessory cells, are attached to the pleural cuticle of the first abdominal segment (A1) by means of two bundles of very long attachment cells (1.4 mm in length compared with <100 μm in the tympanate hearing organs of modern grasshoppers). In addition, five pairs of smaller chordotonal organs form at the lateral body wall of abdominal segments A2–A6. Having only 11 scolopidia each, they attach by apical and basal cellular anchorages (Fig. 1b), with dendrites and attachment cells similar in length to those in A1.

We determined the neurophysiological function of both forms of abdominal chordotonal organ by recording extracellularly from nerve N1 of the respective ganglia. The male mating call is a resonant (Qmax = 4.1–4.6) call with a carrier frequency of 1.7 kHz, comprising a resonant sixth syllable (98 dB sound pressure level (SPL) at 1 m) and five lower-intensity (70 dB SPL) introductory syllables. We found that all abdominal chordotonal organs responded to acoustic stimulation within an intensity range that was biologically meaningful. Receptors in A1 have best frequencies of 4 kHz (Fig. 2), apparently mismatched to the 1.7 kHz carrier frequency of the male call. Despite this anomaly and the absence of an overt tympanum, the sensitivity of the A1 hearing organ at its best frequency is one of the highest recorded so far for insects (12.8 ± 4.89 dB SPL; n = 5) and, together with the intense calling sounds, accounts for the extraordinarily large communication distance. In contrast, the tuning of receptors in segments A2–A6 matches the species-specific male signal (1.5–2 kHz) but they are much less sensitive. Both individual tuning curves (Fig. 2) and mean threshold intensities (Fig. 3a) demonstrate increasing thresholds (58–77 dB SPL) from anterior to posterior segments. Nonetheless, the temporal song pattern of the male signal is detected in the spike discharge of all pleural chordotonal receptors and is faithfully represented when at suprathreshold intensity for a given segment (Fig. 3c; see A2 receptors).

It is the behaviour mediated by the serial chordotonal receptors, however, that establishes their role as functional hearing organs. First, we know from neurophysiological experiments with a biological microphone (that is, a small, portable set-up for recording action-potential activity of auditory neurons directly in the field) that females have an average neural sensitivity of 32 dB SPL to the male call, and hear males calling at a distance of 1–2 km. However, in behavioural playback experiments, females show no auditory response until stimulation intensity exceeds 60 dB SPL (Fig. 3a).

This in itself is not unusual as behavioural thresholds frequently exceed neurophysiological thresholds by such margins. More unusual is a conspicuous sexual asymmetry in both the active space and the degree of stereotypy of mate location calls. Whereas females hear the male call with their most sensitive hearing organ in A1 over distances up to 1.9 km, males hear the soft female response over a maximum of only 50 m. Sound pressure levels of 60 dB, as perceived by females, imply that males are 50–100 m distant. This distance approximates the active space of the female call for the male, indicating that females risk auditory exposure to nocturnal predators only when a potential mate is clearly within her acoustic transmission range. There would have been strong selection for chordotonal receptor mechanisms that discriminate between ‘advantageous’ and ‘disadvantageous’ airborne sound signals and such mechanisms should evolve to maximize the expected utility of the receiver’s response in this antiphonal duetting system.

Second, playback experiments show that this adaptive behavioural response is graded. In contrast to the stereotyped male call, the female response varies from one to eight syllables. Behavioural tests showed this to be a function of male call intensity; beyond the response threshold females add approximately one additional syllable for each 3-dB increase in male call intensity (Fig. 3b). We examined the neurophysiological basis for this behaviour by testing the differential responses of pleural chordo-
neural and behavioural14. That they are all true ears is further
removed the A1 organs bilaterally from previously responsive
the total absence of neural activity in the A1 afferent nerves of
organs and the female’s response would be subject to strong
directional selection.

We have shown that the serial receptors in A1–A6 of B. membracioides fulfill all three criteria for functional ears: morphological,
neutral and behavioural14. That they are all true ears is further
supported by results from ablation experiments in which we
removed the A1 organs bilaterally from previously responsive
females. Subsequent neurophysiological experiments confirmed
the total absence of neural activity in the A1 afferent nerves of
these individuals, but bilaterally operated females continued to
respond to male calls at distances from 8–16 m in playback experi-
ments. In addition, behavioural playback experiments to intact
animals provide more direct support for the role of A2–A6 in
mediating the adaptive female response. By using presentations
of pure tones of 1.7 kHz and 4 kHz, we found that females responded
almost invariably and exclusively to the lower frequency (96%
threshold and the behavioural response threshold (dashed line).

- **Figure 3** Chordotonal organs mediate adaptive behavioural responses to acoustic signals. **a**, Mean neurophysiological thresholds of organs A2–A6 of females (n = 10) to the male call. Note the close correspondence between the A2 threshold and the behavioural response threshold (dashed line). **b**, Behavioural response of females to playback of male calls that are between 0 and 12 dB above
response threshold. Females add approximately one syllable to their auditory
response for each 3-dB increase in SPL. **c**, Differential neurophysiological responses of pleural chordotonal organs in females to playbacks of a male call simulating sender–receiver distances of 8 and 30 m in the field. Scale bar, 500 ms.

- **Threshold to male call (dB SPL)**

  - **Segment**
    - A6
    - A5
    - A4
    - A3
    - A2

- **No. of syllables per response**

  - **Stimulus**
    - 8 m
    - 30 m