direct evidence for such a ‘polluting’ mechanism might come from a correlation between maximum $^{40}Ar/^{36}Ar$ with radiogenic lead isotope ratios in MORBs[11].

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Singing and hearing in a Tertiary bushcricket

Communication organs are poorly represented in the fossil record, so their evolution is usually reconstructed by comparison of extant species using a phylogenetic approach. We have analysed some extremely well preserved stridulatory and hearing organs of the oldest known bushcrickets from the lowermost Tertiary sediments of Denmark (55 million years old). These fossils indicate that males sang with a broadband frequency spectrum, and it is likely that both sexes could hear ultrasound. The fossil wings have lower asymmetry than extant species, indicating that bushcrickets may have evolved from a bilaterally symmetrical ancestor.

Only a few, poorly preserved male forewings from fossil bushcrickets have previously been described[1]. Our specimens are from *Pseudotettigonia amoena*, which was a large bushcricket with a wing span of more than 120 mm that lived in subtropical Scandinavia during the Palaeogene[2]. They include 11 left and right male forewings and three forelegs with the ear.

The evolution of courtship behaviour, with males producing complex songs, has led to a strong left–right asymmetry of the forewings in extant male bushcrickets[3]. During singing, the left wing is always held on top of the right, and the ‘stridulatory file’, which is a dense row of cuticular teeth on the ventral surface of the left wing, is scratched over a raised vein on the right forewing. A thin membrane called the ‘mirror’, which is important for sound radiation and is surrounded by a frame of strong veins, is expressed more strongly on the right wing than on the left, and a complex of stout spines occurs exclusively on the dorsal surface of the right wing.

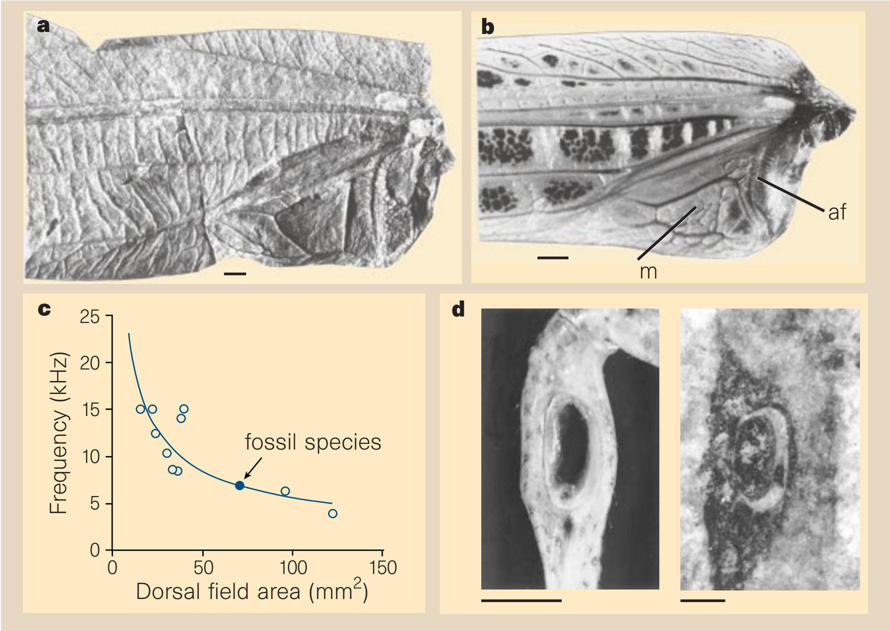

Figure 1 Comparison of the Lower Tertiary *Pseudotettigonia amoena* with a Recent Tettigoniidae. **a,** Dorsal view of *Pseudotettigonia* left forewing base (specimen HM 14M-3022) showing the stridulatory apparatus. **b,** Dorsal view of Recent *Decticus verrucivorus* left forewing base, showing the mirror (m) and the active file (af). Scale bars, 1 mm. **c,** Relation between dorsal field area and dominant frequency peak ($y = 93.886x^{-0.6151}$, $R^2 = 0.79$). Data include species from extant Tettigoniidae, Phaneropteridae and Ephippigeridae[4–6]. **d,** Tibial tympanum of fossil *Pseudotettigonia* (right, specimen HM 14M-C3272) compared with an anterior tympanum of Recent *Phaneroptera falcata* (left). Scale bars, 0.5 mm.

The fossil forewings of males show all these structures of their extant descendants (Fig. 1a,b) and are also asymmetrical. The stridulatory file is much more pronounced on the left wing, indicating that only the left file was used for sound production. The left mirror of *Pseudotettigonia* is larger than the right one, although the difference in size is less pronounced than in extant species. The spine complex occurs on the dorsal surface of both wings, in contrast to all living male bushcrickets. We interpret this condition as a primitive state in the development of wing asymmetry, and it is possible that *Pseudotettigonia* was able to fold the wings back in both left-over-right and right-over-left positions.

Comparative morphometric analysis of the dorsal fields of the fossil wings (the part of the wings that covers the body dorsally when the wings are closed) with data from Recent species[4–6] indicates that *Pseudotettigonia* produced a broadband frequency song with a dominant frequency peak at about 7 kHz (Fig. 1c) and an ultrasonic range, which was probably less pronounced than in extant species, as *Pseudotettigonia* had a comparatively small mirror area. The size of the mirror has increased during the evolution of the stridulatory structures, probably to increase the efficiency of ultrasound radiation[4,7]. In female bushcrickets, most of which are silent, the mirror is absent.

The ear in the foreleg of *Pseudotettigonia* resembles the structure of modern Phaneropterinae with open tympana[8] (Fig. 1d). Although the internal part of the hearing system is not preserved, we conclude from the modern arrangement of the different areas in the ear[9] that the hearing range was adapted to its own song frequencies, as it is in extant species. As the fossil bushcrickets could therefore presumably hear at least low ultrasound, they should also have been able to hear the echolocation calls of bats, which first occur in the fossil record at the same geological age[10].

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