

Choristers of the Jurassic

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The production of acoustic signals is among the most important behaviors in animal communication, because sending and receiving messages using sound is essential for the survival and success of almost all kinds of animals. However, the reconstruction of the evolutionary history of acoustic performance is a major challenge. Using phylogenetic methods based on data from living animals is the most prevalent approach for reconstructing the past, because the fossil record of morphological traits permitting the analysis of acoustic communication is rather poor (1). In PNAS, Gu et al. (2) present an elegant reconstruction of musical calls of an extinct Middle Jurassic katydid based on remarkably well-preserved fossil wings collected from 165-million-year-old sediments in China. Befittingly, they named the species *Archaboilus musicus*, for its capability to produce musical songs. *A. musicus* is a member of the extinct family Haglidae, a group basal to extant katydids that has a diverse fossil record spanning the Late Triassic to the Early Cretaceous.

Charles Darwin suggested that katydids, also called bushcrickets, are ideal candidates for the study of sexual selection (3, 4). Since then these insects have been intensively examined for their acoustic communication systems, in which singing males attract sexually receptive females (5). In living katydids as well as in a Tertiary species (6), the production of complex, species-specific songs has led to a pronounced left–right asymmetry of the forewings in males (Fig. 1). During singing, the left wing with a toothed vein called a “stridulatory file” is scratched across a raised vein, the “scraper” or “plectrum,” on the right forewing. A delicate membrane, the “mirror,” amplifies and radiates the sound and indeed has the appearance of a speaker cone in a loudspeaker system.

Most living katydids produce noisy, broadband songs spanning a huge range of frequency bands. In contrast, the wings of *A. musicus* are bilaterally symmetrical, with toothed stridulatory files on both wings. Furthermore, the preservation of the fossils is so exquisite that Gu et al. (2) are able to show an increase in tooth spacing toward the basal end of the files. Such an arrangement ensured a constant strike rate of the plectrum skipping from tooth to tooth and the radiation of a constant carrier frequency by the resonating wings. A phylogenetic regression model derived from extant species (7)



Fig. 1. Forewings of an extant great green bushcricket, showing the characteristic singing apparatus of most living katydids. The prominent dark vein on the left wing is the active toothed stridulatory file; the corresponding vein on the right forewing is vestigial. The active file is scratched across a raised vein, the scraper, on the right forewing. A large translucent wing cell close to the basis of the right forewing with a strengthened frame, the mirror, radiates the sound. As described in PNAS (2), Jurassic relatives of extant katydids showed symmetrical wings with active stridulatory files on both wings, enabling these animals to produce musical pure-tone calls at low frequencies.

made it possible for the authors to reconstruct a carrier frequency of 6.4 kHz and a pulse duration of a continuous spectrum sweep of 16 ms for the fossil species. Thus, *A. musicus* produced musical pure-tone calls at low frequencies; in other words, in comparison with living katydids, *A. musicus* was a baritone attracting females over long distances. As Gu et al. (2) point out, the symmetrical singing apparatus optimized the efficiency and power of sound radiation because the wings worked in concert.

Calling with low-frequency pure tones is common among extant katydids living on the ground, suggesting that the mating songs of *A. musicus* were well adapted for communication in the sparse forest vegetation dominated by coniferous trees and giant ferns characterizing the landscape of China 165 million years ago. Living katydid males prefer serenading females at night, a behavior that is especially well known from tropical forests today, and a nocturnal singing activity is also likely for *A. musicus*. Of course, singing in the dark is fraught with risk: not only are the females captivated by calling males, but there are always eavesdropping predators for which a katydid is a welcome morsel of food. In addition, parasitoids

such as wasps and flies are attracted by the songs. Today the main predators are bats and other mammals, as well as birds. In the nocturnal acoustic world of *A. musicus*, the enemies may have been amphibians, reptiles, early mammals, and other arthropods (8, 9). Whether the acoustic coevolution of predator (listener)–prey (singer) interactions promoted the development of sophisticated singing and hearing systems is a matter for future research.

In a phylogenetic context, the study of Gu et al. (2) shows that musical song production by resonance stridulation with symmetric wings as in *A. musicus* is an ancient condition. It preceded the specialized broadband calls of living katydids but is also seen in other primitive fossil and extant groups—such as grigs (Prophalangopsidae)—that are related to *A. musicus*. However, the production of resonant songs by Jurassic Haglidae suggests that there was a precursor with even more primitive wing stridulation. Strong candidates for such a primitive noise production system are the extinct Titanoptera, a fascinating group of orthopterans only known from the Triassic of Australia and Central Asia (9). These giant raptorial insects could reach up to 40 cm in wingspan. Most probably they produced sound by rubbing several stridulatory files on the forewings together, and large cells modified for sound radiation presumably generated noisy, deep calls, as in large frogs. The fossil record of even more primitive sound production involving wing activity is ambiguous.

The work of Gu et al. (2) beautifully shows the great potential of paleoacoustic studies for evolutionary analyses and the paleoecological reconstructions of past ecosystems. Their results considerably enrich our imagination of Jurassic ecosystems, which is usually dominated by the popular dinosaurs. However, whereas these roaring pop stars have left the stage, the background vocals of insect “choristers” are still there. Of course, the relevance of such studies depends largely on exceptionally preserved fossil material. Unfortunately, a good fossil record with high-quality preservation of vocal orthopteran insects is restricted to selected fossil

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deposits. A major reason for this deficiency is simply the fact that many orthopterans are excellent swimmers (10), which especially in smaller lakes and ponds keeps them from drowning and being covered by sediment, a necessary

prerequisite for becoming a fossil. In addition, in another major resource of fossil insects, fossilized resin or amber, they are underrepresented or only known by their youngsters because the adults were usually too large and too strong—when

they were trapped in resin they jumped away and sometimes left only an isolated disrupted leg behind. Nevertheless, the example of Gu et al. (2) raises our hopes of finding more outstanding fossil material for paleoacoustic studies.

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