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EXCEPTIONALLY PRESERVED FOSSIL INSECT EARS FROM THE EOCENE GREEN RIVER FORMATION OF COLORADO

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ABSTRACT—Tympanal ears in insects are important for both intraspecific communication and for the detection of nocturnal predators. Ears are thought, based on modern forms, to have originated independently multiple times within insects and can be found on multiple regions of the body. Here we describe and document the exceptionally well preserved tympanal ears found in crickets and katydids from the Eocene Green River Formation of Colorado, which are virtually identical to those seen in modern representatives of these groups. These specimens are among the best preserved insect ears in the fossil record and establish the presence of ears in two major clades of Orthoptera 50 million years ago. Also discussed and evaluated are previously described insect ears from the Mesozoic and the implications of the findings of the present study for studying the evolution of ears within insects.

INTRODUCTION

RECENT STUDIES have greatly improved our understanding of the sensory abilities of ancient vertebrates (Schmitz and Motani, 2011; Rowe et al., 2011). In contrast, with the notable exception of the eyes of trilobites and other arthropods (Clarkson et al., 2006; Lee et al., 2011), the sensory organs of fossil invertebrates have been little studied (Plotnick et al., 2010). In this paper we will show that one such organ, the tympanal ears of insects, not only has high preservation potential, but is of major importance in the evolution of insects and of their predators. In particular, we will describe remarkably preserved examples from the Eocene Green River Formation. In addition, we evaluate some of the few examples of fossil insect ears that have been documented in the literature previously and discuss strategies for locating and identifying these important structures on fossil specimens from other fossil deposits.

Tympanal ears are recognized by the presence of the tympanal membrane or eardrum, which consists of a thin layer of cuticle. Its thinness allows it to vibrate in response to sound. The tympanum is usually oval or cylindrical and surrounded by a thickened rim (Yager, 1999; Fig. 1e, 1f). Beneath the eardrum is an air-filled tracheal sac and a chordotonal sensory organ, which detects the vibrations of the membrane. The detailed morphology, biomechanics, and physiology of tympanal ears have been reviewed by Hoy and Robert (1996), Yager (1999), Stumpner and von Helversen (2001), Yack (2004), and Yack and Dawson (2008). With some variation, they all have the same general structure, including at the ultrastructural level.

The consensus is that tympanal ears represent modifications of pre-existing chordotonal mechanoreceptors (Boyan, 1993; Lakes-Harlan et al., 1999; Yager, 1999; Strauss and Lakes-Harlan, 2009), where they were involved in detecting vibrations or in proprioception. As discussed by Yack and Dawson (2009), relatively few changes are needed to modify an existing mechanoreceptor into an organ for detecting sound. These include thinning the nearby cuticle and enlarging adjacent trachea. The seeming ease of converting existing structures into tympanal ears may explain its high frequency of convergent evolution among insects.

Remarkably, despite their morphologic similarity, the tympanal ears of different insect lineages can occur in a number

of places on an insect's body and appendages. Coupled with phylogenetic studies, this indicates that tympanal ears have originated independently at least seventeen times within the insects (Yager, 1999; Yack and Dawson, 2008). For example, tympani have evolved at least twice in the Orthoptera, at least once in the Ensifera (crickets and katydids) and once in the Caelifera (grasshoppers). Grasshopper ears are located on the first abdominal segment. In contrast, the ears of crickets and katydids occur on both of the forelegs, on the anterior and posterior region of the proximal part of the tibia (Fig. 1e, 1f).

There is a great deal of variation in the external and internal morphology of the tympanal region in Ensifera (Bailey, 1990; Mason, 1991; Yager, 1999). In some forms, the two tympani are of near equal size, whereas in others the posterior tympanum, which faces outward, is larger than the anterior. Externally, the tympani may appear as small exposed ovals on the surface of the tibia, can be depressed within the cuticle, or may be partly covered. Depressed and covered tympani are particularly characteristic of the katydids, in which the cuticular coverings can show different degrees of elaboration (Bailey, 1990), including the formation of narrow slits. The functional significance of these cuticular structures has been a source of some controversy, with increasing directionality and/or tuning being commonly suggested (Bailey, 1990; Yager, 1999; Gwynne, 2001). The tibia may also show lateral expansion in the region of the tympanum.

The origins and evolution of tympanal ears in insects have been attributed to two main causes (Hoy and Robert, 1996; Stumpner and Helversen, 2001; Senter, 2008). The first of these is intraspecific communication, such as within cicadas (Hemiptera: Auchenorrhyncha) and crickets (Orthoptera: Ensifera). As discussed by Stumpner and von Helversen (2001), these ears should be adapted for song recognition and sound localization. The second is the detection of predators, in particular microchiropterid bats. These ears should be adapted for maximum sensitivity to ultrasound. In some cases, such as within the crickets and katydids, they can perform both functions.

The use of sound for intraspecific communication has been extensively examined within the Orthoptera (see papers in Drosopoulos and Claridge, 2006). Among ensiferans, the sounds are generated by tegminal stridulation, the rubbing between specialized front wing veins (Jost and Shaw, 2006).

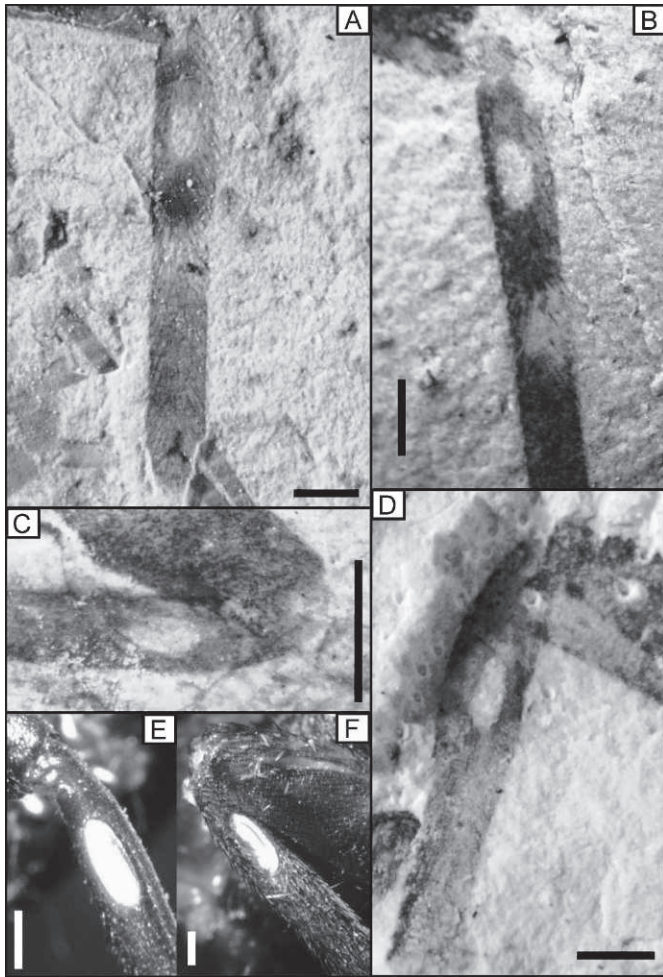


FIGURE 1—Examples of tympana preserved on fossil Gryllidae from the middle Eocene Green River Formation of Colorado: *a*, USNM 138819; *b*, UCM 45502; *c*, UCM 45236; *d*, USNM 30868; *e, f*, modern Gryllidae from UCM-Entomology. All scale bars=0.5 mm.

The presence of these specialized wing areas are taken as direct evidence for sound production and detection in both recent and fossil forms (Grimaldi and Engel, 2005; see below). There have been numerous studies of “singing” in katydids, crickets, and grasshoppers (Alexander, 1962; Otte, 1992; Gwynne, 2001). Probably the most familiar use of sound and hearing is by crickets to attract mates (Hoy and Robert, 1996).

Bats, in particular the Microchiroptera, are major predators of nocturnal flying insects, which they find using echolocation (Gunnell and Simmons, 2005). A number of insect groups are thought to have concomitantly evolved the ability to detect the ultrasonic sounds emitted by bats and to modify their flight behavior accordingly (Spangler, 1988; Hoy, 1990; Miller and Surlykke, 2001; Ratcliffe, 2009). Ears that are sensitive to bat ultrasound have been found in moths (Lepidoptera), green lacewings (Neuroptera), tiger beetles (Coleoptera), mantises (Mantodea), crickets, locusts, and katydids. In addition, it has been strongly suggested that bats have correspondingly modified their hunting strategies in response to being detected by their insect prey (Miller and Surlykke, 2001), however the evidence for this is still not clear (Ratcliffe, 2009).

Secondary loss of hearing is also common among some ensiferans, but apparently only among species that have also lost the ability to fly (Otte, 1992). This is not always coupled with the loss of sound production (muteness). For example,

among Australian species all deaf species do not fly and all flying species can hear, even if they apparently do not stridulate. This suggested to Otte (1992) that these tympana are kept in order to detect bats.

The apparent co-evolutionary relationship between echolocating microchiropterid bats and their insect prey has suggested to entomologists (e.g., Yack and Dawson, 2008) that the origin of hearing in many insect groups should have followed the origin of these nocturnal predators. The oldest documented echolocating bat fossils are from the Eocene (Habersetzer et al., 1994; Gunnell and Simmons, 2005; Simmons et al., 2008), in particular from the Green River Formation of Utah and Colorado, U.S.A., which dates from approximately 48–51 Ma (Smith et al., 2008) and the slightly younger (47.8 Ma) Grube Messel of Germany (Franzen, 2005).

Three approaches have been used to reconstruct the evolutionary history of hearing and development of the tympanum in various insect lineages. The first of these is to use a phylogenetic approach and infer the first appearance of ears based on which groups are known to possess ears today (Yager, 1999). Unfortunately, the phylogenetic relationships within most insect clades are still poorly understood. For example, there is not much agreement on the evolutionary relationships of members of the Ensifera, including questions as to whether the group is actually monophyletic or not (Legendre et al., 2010). Morphological and molecular evidence have been used to both argue for a single origin of ears early in the evolutionary history of the group (Otte, 1992; Jost and Shaw, 2006), as well as for multiple originations occurring later (Gwynne, 1995; Desutter-Grandcolas, 2003; Strauss and Lakes-Harlan, 2009).

A second approach has been to look to the fossil record for evidence of organs that are used for sound production. The assumption is that sound producing organs and ears would be characters that evolved together, so if one finds sound producing organs, ears would have been there as well. A detailed synopsis of the fossil record of these structures was published by Senter (2008), who also summarized other aspects of the history of animal sound production. Sound producing organs are found on Triassic orthopterans, but not on any Paleozoic forms (Gorochov and Rasnitsyn, 2002). A very large stridulatory structure on a wing of a Triassic representative of the extinct orthopterid group, Titanoptera, was discussed by Grimaldi and Engel (2005), who also illustrated a well-preserved cricket stridulatory mirror from the Cretaceous of Brazil. Rust et al. (1999) illustrated a stridulatory structure in an Eocene bushcricket (katydid), as well as a well preserved foreleg tibial tympanum from the same specimen. This was described as an open (uncovered) tympanum, similar to that in the modern subfamily Phaneropterinae.

The final approach, of course, is to identify tympanal ears in the fossil record. In addition to the Eocene example of Rust et al. (1999), their occurrence has occasionally been documented for individual fossils. All of these specimens are members of the Orthoptera, in particular the Ensifera (Table 1). No tympani have been identified in Paleozoic orthopterans (Gorochov and Rasnitsyn, 2002) or from any other insect group.

The oldest possible orthopteran tympanum is from the Rhaetian (Late Triassic) Cotham Marble at Aust Cliff, Avon, U.K. The specimen is an isolated leg, comprising only the femur and tibia (Fig. 2). The tibia is quite slender, being 17.2 mm long and 0.5 mm wide (Zeuner, 1939). The specimen was originally

TABLE 1—Previously described fossil orthopteran (Ensifera) ears. Family assignments are from the Orthoptera Species File (<http://orthoptera.speciesfile.org/>) or Carpenter (1992).

Family	Species	Locality	Age	References
Prophalangopsidae?	<i>Liadolocusta auscultans</i>	Aust Cliff, Forthampton, Gloucestershire	Triassic (Rhaetian)	Brodie, 1845; Handlirsch, 1906; Zeuner, 1939
Haglidae	<i>Hagla gracilis</i>	Binton, Warwickshire	Jurassic (lower Lias)	Zeuner, 1939
Prophalangopsidae	<i>Pycnophlebia speciosa</i>	Solnhofen	Jurassic	Deichmüller, 1886
Prophalangopsidae		Karatau, Kazakhstan	Jurassic	Sharov, 1968
Tettigoniidae	<i>Pseudotettigonia amoena</i>	Jylland, Denmark	lower Eocene	Rust et al., 1999
Tettigoniidae	<i>Rammea laticeps</i>	Böttingen, Germany	upper Miocene (Sarmatian)	Zeuner, 1939
Gryllidae	<i>Trichogryllus macrocercus</i>	Baltic ('East Prussia') (amber)	lower Oligocene	Chopard, 1936
Gryllidae	<i>Amusurgus africanus</i>	East Africa, copal	Quaternary	Chopard, 1936; Zeuner, 1939

illustrated in a line drawing by Brodie (1845, pl. IX, fig. 2), who identified it as the hind leg of a gryllid. Handlirsch (1906) named it *Liadolocusta auscultans*, and mentioned the presence of an ear at the base of the tibia. The naming of a new genus for this specimen was rejected by Zeuner (1939), who considered it as *incertae sedis* within the Ensifera, possibly a member of the Family Prophalangopsidae. The tympanum was described by Zeuner as “comma-shaped.”

A slightly younger example was illustrated by Zeuner (1939, pl. LIII, fig. 1), in a poor quality photograph. It is a specimen of *Hagla gracilis* Giebel from the lower Lias (Early Jurassic) of

Binton, Warwickshire, U.K. The specimen was described in detail by Zeuner (1939) as the femur and tibia of a right foreleg (Fig. 3). The leg again is quite slender, with the tibia being about 15.5 long and 1.0 mm wide. The tympanum was described as being open and oval, although it is difficult to discern in Zeuner’s photograph.

Deichmüller (1886, pl. 2, fig. 2) described the presence of a tympanum on the foreleg of *Pycnophlebia speciosa* Deichmüller from the Upper Jurassic Solnhofen Plattenkalk (Fig. 4). It is illustrated by a line drawing. As pointed out by Zeuner (1939), it is only the presence of the tympanum in this specimen that placed this species within the Ensifera.

The presence of tympanal ears in Jurassic ensiferans of the Family Prophalangopsidae from Karatau, Kazakhstan was mentioned by Sharov (1968), but the specimens were not illustrated. Lin et al. (2008) also described tympani in the prophalangopsid *Ashangopsis daohugouensis* from the Jurassic of Inner Mongolia, China. Their illustrated specimen shows several oval patches of missing cuticle; in their accompanying description they suggest the presence of two tympani, one distal and one proximal. This morphology is unknown in any living ensiferan group and suggests that this interpretation must be viewed with skepticism.

Only a few Cenozoic tympani have been previously cited and none are discussed in detail. Zeuner (1939) described a tympanum in a single specimen of female tettigoniid, *Rammea laticeps*, from the upper Miocene of Germany. He indicated that although tympana are present in the specimen, he could not determine if they were open or covered. A specimen of female cricket (Gryllidae), *Trichogryllus macrocercus* from the

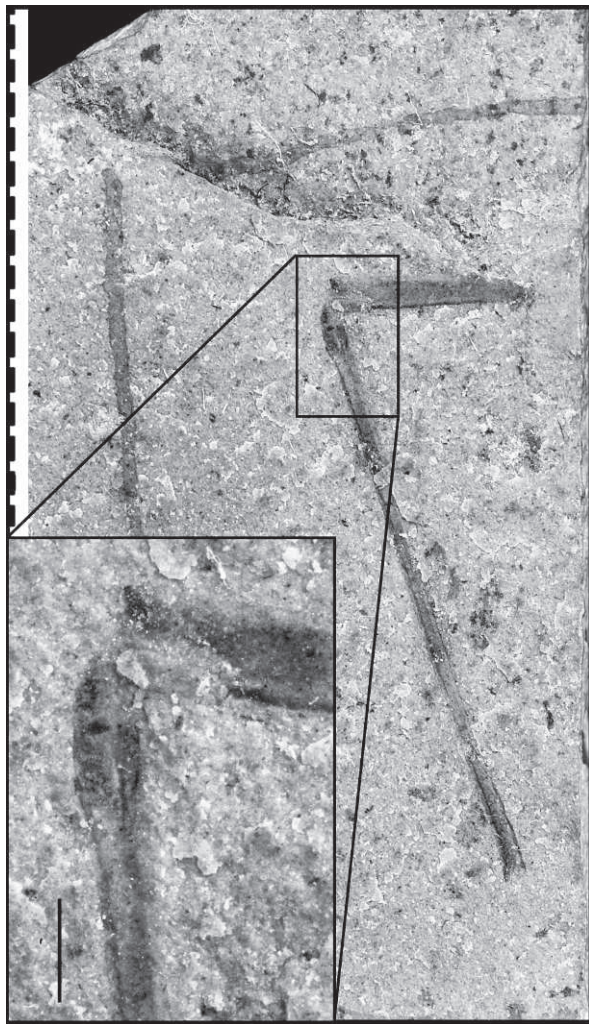


FIGURE 2—Isolated orthopteran leg from Aust Cliff, Forthampton, Gloucestershire, U.K., Triassic (Rhaetian). “*Liadolocusta auscultans*,” BMNH I. 3541. Inset shows area with purported tympanum. Scale bars =1 cm. Photo by Phil Crabb, copyright NHM, London.

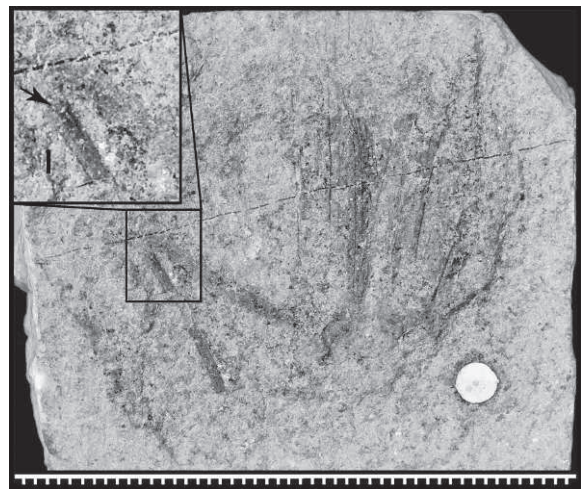


FIGURE 3—Foreleg of *Hagla gracilis* Giebel, BMNH I. 6662, Binton, Warwickshire, U.K., Jurassic (lower Lias). Black arrow indicates region previously described as a tympanum. Scale bars =1 cm. Photo by Phil Hurst, copyright NHM, London.



FIGURE 4—Foreleg of *Pycnophlebia speciosa* Deichmüller from the Upper Jurassic Solnhofen Plattenkalk; BaJ1482-2. The small oval depression (upper arrow) at the proximal end of the foreleg tibia has been described as a tympanum. The lower arrow indicates a similar depression, one of many, on the matrix. Markus Wilmsen at the Dresden Senckenberg Naturhistorische Sammlungen kindly provided the photograph.

lower Oligocene amber of what was East Prussia, possesses a large oval tibial tympanum with a lateral expansion of the tibia (Chopard, 1936; Zeuner, 1939). The cricket *Amusurgus africanus* is preserved in copal from East Africa and is either Pleistocene or Holocene in age (Chopard, 1936; Zeuner, 1939) and is a member of a modern genus. Its fore tibia is expanded at its base and is perforated.

Overall, the empirical fossil record suggests that tibial tympani within the Ensifera may have existed by the beginning of the Jurassic or perhaps the end of the Triassic. The overall poor preservation of these structures, however, indicates that caution must be used in their interpretation. This will be discussed in more detail below.

MATERIAL EXAMINED

Green River Formation insects.—Their association with the oldest documented microchiropteran bats makes the well-preserved insect fauna of the lacustrine deposits of the Green River Formation a logical place to look for evidence of tympanal ears. Over 100 families of insects have been described from the Green River Formation, with many new specimens awaiting examination. All are preserved as compressions and impressions in fine-grained, laminated sediments.

Primary repositories of Green River fossil insect material include the University of Colorado Museum of Natural History (UCM) and the Smithsonian Institution's National Museum of Natural History (NMNH). These two collections combined house approximately 333,333 fossil insect specimens from the Green River Formation. The majority of these materials was collected by Mr. David Kohls (beginning in the mid-1990s) and for the most part represent unbiased collections of material with associated metadata. Orthoptera at UCM are identified to the level of family, whereas those at the NMNH have been further identified by A.V. Gorochov of the Zoological Institute of the Russian Academy of Sciences, who is preparing formal systematic descriptions.

Approximately 192 drawers of Green River insect specimens were examined in the UCM invertebrate paleontology collections for any Orthoptera specimens. All Orthoptera were pulled, identified to family and measured using digital

calipers. The quality, completeness and orientation of each specimen were also documented. Specimens that had visible tympani were photographed using a Leica EC3 microscope camera and software.

Approximately 350 drawers of Green River insect specimens at the NMNH were examined. Among these, about 400 specimens had been previously identified as Orthoptera. In addition to Orthoptera, specimens of mantids, cicadas and Lepidoptera were also examined. All specimens were examined for the presence of tympani and specimens with visible ears were photographed.

Mesozoic Orthopteran ears.—The oldest previously described ears are from the Triassic and Jurassic of England and Germany. Published illustrations of these are either line drawings or poor quality photographs (Brodie, 1845; Deichmüller, 1886; Zeuner, 1939). As a result, we arranged with the staff of their current repositories to prepare high quality digital photographs.

The Natural History Museum, London, provided photos of the key specimens of “*Liadolocusta auscultan*” (BMNH I. 6662) and *Hagla gracilis* (BMNH I. 3541). Photos of *Pycnophlebia speciosa* (specimen BaJ1482-2) were provided by the staff of the Dresden Senckenberg Naturhistorische Sammlungen, Dresden, Germany.

RESULTS

Green River Formation insects.—In the CU Museum sample, 50 percent of specimens were complete, with the remainder consisting of fragmented bodies (15 percent) or disarticulated legs and wings (35 percent). Most (77 percent) were exceptionally preserved and 57 percent were oriented in a lateral position. The majority (90 percent) of specimens were missing their fore-tibia. Of the specimens examined at both museums, approximately 545 were Orthoptera and nearly all were in the family Gryllidae, save a few Tettigoniidae. Only seventeen (3 percent) of specimens examined preserved visible tympana (16 Gryllidae and 1 Tettigoniidae). Tympana were not observed in the other taxa (e.g., mantids) examined.

Morphologically, the fossil ears are well-preserved and are essentially identical to those observed in modern Ensifera (for Gryllidae and the single tettigoniid). The fossil gryllid ears are found in the same position on the leg and their overall simple oval shape are the same as found in modern gryllids. Although the thin tympana themselves were not preserved, as might be expected given the fossilization process, there is clear evidence of a raised rim in several specimens, identical to that seen in modern forms (Fig. 1a–1d). The tettigoniid ear (not shown) is less well preserved. It appears to be an open tympanum, with some indication of cuticular thickening at its distal margin, as well as a slight lateral expansion of the tibia.

The mean measured lengths of the twelve gryllid fossil tympana (Table 2) was 0.50 mm (SD=0.31), the mean width was 0.22 mm (SD=0.12), and the mean width/length ratio was 0.45 (SD=0.07). This compares with mean values for the posterior tympana of eight recent gryllid specimens of 0.77 (SD=0.29), 0.24 (SD=0.09), and 0.31 (SD=0.05), respectively. Overall the size range of the fossil and recent ears overlap although the fossil ears have significantly larger width/length ratios (separate variance *t*-test: $P < 0.0001$, 17.8 d.f.). This is likely due to limited sampling and taxonomic coverage of the modern sample.

Mesozoic Orthopteran ears.—The specimen of “*Liadolocusta auscultan*” (BMNH I. 6662) is poorly preserved, with dark and light patches throughout that are not likely to be real anatomical features, but instead represent areas of fading on

TABLE 2—Tympana measurements (in mm) for twelve Eocene and eight modern Gryllidae specimens. UCM=University of Colorado Museum of Natural History, NMNH=National Museum of Natural History.

Category	Specimen number	Tympana length	Tympana width
Fossil	UCM 45502	0.49	0.24
Fossil	UCM 45328	0.26	0.13
Fossil	UCM 45282	0.39	0.17
Fossil	UCM 45236	0.29	0.13
Fossil	UCM 44406	0.43	0.15
Fossil	NMNH 542886	0.32	0.13
Fossil	NMNH 542887	0.44	0.21
Fossil	NMNH 542888	0.85	0.42
Fossil	NMNH 542889	1.37	0.49
Fossil	NMNH 542892	0.30	0.12
Fossil	NMNH 542893	0.50	0.26
Fossil	NMNH 542894	0.38	0.21
Modern	UCM-Gryllidae	1.17	0.32
Modern	UCM-Gryllidae	0.92	0.34
Modern	UCM-Gryllidae	0.81	0.27
Modern	UCM-Gryllidae	0.33	0.12
Modern	UCM-Gryllidae	1.03	0.32
Modern	UCM-Gryllidae	0.72	0.23
Modern	UCM-Gryllidae	0.78	0.19
Modern	UCM-Gryllidae	0.43	0.12

the specimen (Fig. 2). Although there appears to be some widening of the proximal end of the tibia, the putative “comma-shaped” tympanum has an irregular margin and appears to be most similar in shape and color to other pieces of matrix that are flaking off the sample. Although in the right location, it is not the correct shape for a tympanal ear. Rather than a comma, it appears to be a narrow oval, about 1 mm long. It resembles the slits seen in some tettigoniids, but this interpretation is tentative at best.

The specimen of *Hagla gracilis* (BMNH I. 3541) is shown in Figure 3 and the overall preservation quality of the specimen is poor. In this case, there does not seem to be a widening of the proximal portion of the tibia. Again, the exact size and shape of the tympanum is difficult to discern, but there does seem to be an indication of a raised rim surrounding a striated oval area. There does not appear to be any widening of the proximal portion of the tibia and although there is a darkened region, the exact size and shape is difficult to discern. Thus, this example does not have the characteristics necessary to determine it to be an actual tympanal ear.

Pycnophlebia speciosa is shown in Figure 4. Unfortunately, all that is visible is a small oval depression at the proximal end of the foreleg tibia. Although it is in the correct location, there are numerous, identically sized and shaped depressions on the same bedding surface. As opposed to being an actual tympanal ear, it is likely that the indentation is merely a characteristic of the matrix and its location is fortuitous.

DISCUSSION

The presence of stridulatory structures in Triassic orthopteran suggests that tympanal ears should be at least as old. However, a re-examination of available putative Mesozoic examples of tympani shows that the reported structures may be invalid or are so poorly preserved that it is difficult to confirm their presence. Thus, caution must be used in their interpretation.

In contrast, the exceptionally preserved material from the Green River formation contains some of the best documented examples of insect ears from the fossil record. Although most specimens are lacking their forelimbs, the tympani of fossil crickets and katydids, when present, are easy to see and virtually identical, in both position and shape, to the ears of modern crickets and katydids.

The search for cricket ears was aided by their tendency to be laterally preserved and by the occurrence of the tympanum on an appendage, so it was not covered by wings or the body. Among other taxa, where the tympana are hidden by wings or are at the junction of body segments (e.g., most moths), particular attention should be paid to specimens that are partially or fully disarticulated so that these regions can be revealed. Given the large size of many tympana, such as in grasshoppers, they should be readily observable in these cases.

Our data on gryllid and tettigoniid ears, combined with that of the earlier discovery of a tettigoniid ear from Denmark (Rust et al., 1999) shows that these two major clades of ensiferans had modern appearing tympanal ears, and thus by inference social interactions, by the Eocene. Since this occurrence postdates the inferred origin of the clade (Grimaldi and Engle, 2005), earlier examples and a well-supported phylogeny will be needed to determine if these are derived from a common ancestor or represent independent acquisitions.

The obvious preservation of ears among Green River ensiferans suggests that other insect-bearing lagerstätte can be fruitfully explored for the occurrence of tympana. While it is expected that ears will be apparent on specimens preserved in amber, amber does not have the geologic extent of fossiliferous lake deposits (Labandeira, 1999; Smith et al., 2006), and has some taphonomic biases related to insect body size (Henwood, 1993). Having specimens with apparent ears preserved in lacustrine deposits allows for an expansion of fossil deposits that can be examined.

There have been major recent advances in our understanding of the fossil record of insect ecology, especially insect interactions with plants (Lopez-Vaamonde et al., 2006; Labandeira, 2007; Smith, 2008). These workers have extensively documented patterns of insect damage on leaves and developed the ability to identify these patterns and their producers in the geologic past. In addition to feeding damage, a wide variety of insect produced structures are capable of being preserved, such as termite, bee, and ant nests (Hasiotis, 2003), which provide evidence of social behavior in these groups. The study of insect ears will provide another viewpoint of insect ecology, including indirect evidence for predation on insects and for social interactions.

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