REVIEW

Voices of the past: a review of Paleozoic and Mesozoic animal sounds

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Here, I present a review and synthesis of fossil and neontological evidence to find major trends in the pre-Cenozoic evolution of animal acoustic behaviour. Anatomical, ecological and phylogenetic data support the following scenario. Stridulating insects, including crickets, performed the first terrestrial twilight choruses during the Triassic. The twilight chorus was joined by water boatmen in the Lower Jurassic, anurans in the Upper Jurassic, geckoes and birds in the Lower Cretaceous, and cicadas and crocodilians in the Upper Cretaceous. Parallel evolution of defensive stridulation took place multiple times within Malacostraca, Arachnida and Coleoptera. Parallel evolution of defensive and courtship-related sound production took place in Actinopterygii, possibly as early as the Devonian. Defensive vocalisations by tetrapods probably did not appear until their predators acquired tympanic ears in the Permian. Tympanic ears appeared independently in Diadectomorpha, Seymouriamorpha, Parareptilia, Diapsida and derived Synapsida. Crocodilians and birds acquired vocal organs independently, and there is no anatomical evidence for vocal ability in bird-line archosaurs basal to the avian clade Ornithothoraces. Acoustic displays by non-avian dinosaurs were therefore probably non-vocal. Other aspects of the evolution of acoustic behaviour in these and other lineages are also discussed.

Keywords: acoustic behaviour; vocalisation; hearing; Crustacea; Insecta; Orthoptera; Coleoptera; Hemiptera; Crocodylia; Aves; Mammalia

Introduction

The fossil record does not include audio recordings. As a result, few researchers lose sleep over such questions as whether Triceratops heard crickets chirping in the evening, whether Mesozoic treetops resounded with birdsong or frogsong, or whether the immense corpses of sauropods were surrounded by the buzzing of bottle flies. Questions such as these seem silly at first but are nevertheless worthwhile to ask for three reasons: (1) inferable acoustic details must be included if the paleontologist is to accomplish one of paleontology’s main goals: the reconstruction of the ancient world in as much detail as possible, (2) acoustic signals are of great importance to many animals, so the reconstruction of the lifestyles of ancient organisms must take acoustic signals into consideration, and (3) many studies have addressed whether or not extinct animals could hear (e.g. Reisz 1981; Allin 1986; Wu 1994; Clack and Allin 2004) and the evolution of sound production in the insect orders Orthoptera and Hemiptera (e.g. Sweet 1996; Rust et al. 1999; Béthoux and Nel 2002; Gorochov and Rasnitsyn 2002). However, many other paleobioacoustical issues can be addressed with available data from fossil and neontological evidence. For example, the first appearances of fossils of sound-producing taxa can be used to constrain the times of origin of their characteristic sounds. Also, knowledge of directional selection on extant animal sounds can be used to infer characteristics of the sounds produced by their ancestors. In addition, because the functions of animal sounds depend on their reception by the intended recipients, information on the evolution of hearing can be used to constrain the times of origin of certain animal sounds. For example, one can reasonably infer that certain courtship sounds, territorial sounds and other sounds directed at conspecifics were absent in taxa that lacked appropriate sensory structures. Similarly, one can also reasonably infer that certain anti-predator sounds were absent before the appearance of predators with appropriate sensory structures. Much information pertinent to the
reconstruction of ancient acoustic behaviour has been published, but before now no attempt has been made to pool available information to illuminate broad trends in such behaviour across large geologic time spans. Here, I present a review of the available literature so as to perform such a synthesis for the Paleozoic and Mesozoic Eras.

Major themes in the evolution of aerial sound production and reception

Sound reception

Most invertebrates are aquatic, and several lineages have independently evolved sense organs that perceive water displacement (Budelmann 1992a,b; Coffin et al. 2004). However, it is difficult to say whether most possess a true sense of hearing, both because the definition of ‘hearing’ varies among researchers and because in aquatic environments the distinctions between sound, vibration and water flow are blurred (Budelmann 1992b). In any case, among extant invertebrates acoustic communication is unknown outside Arthropoda, and there is no reason to believe that the case was different among extinct invertebrates.

Airborne sound reception is typically accomplished with tympanic ears. In such ears airborne sounds cause vibrations in a thin membrane, the tympanum (Figure 1), internal to which is an air-filled chamber; mechanoreceptors that are linked to the tympanum detect its movement in response to sounds (Wever 1978; Yager 1999; Kardong 2006). Among insects, tympanic ears have appeared independently in Cicadidae (cicadas), Corixidae (water boatmen), Tachinidae (tachinid flies), Sarcophagidae (flesh flies), Neuroptera (lacewings), Mantodea (mantises), Cicindelidae (tiger beetles), Scarabaeidae (scarab beetles), and several times within Orthoptera (crickets and grasshoppers) and Lepidoptera (moths and butterflies) (Yager 1999; Flok et al. 2000; Robert and Hoy 2000; Čokl et al. 2006) (Figure 2). Tympanic ears in cicadas, water boatmen and crickets are associated with intraspecific acoustic communication (Bailey 1991; Gerhardt and Huber 2002; Čokl et al. 2006). Those of tachinid and flesh flies are used to find their cricket hosts when the latter stridulate (Yager 1999; Robert and Hoy 2000). The tympanic ears of lepidopterans, lacewings, mantises, beetles and grasshoppers are tuned to frequencies produced by echolocating bats (Mammalia: Chiroptera), the sounds of which stimulate evasive behaviours in these insects (Bailey 1991; Yager 1999; Flok et al. 2000). Such ears are an evolutionary response to predation by bats (Bailey 1991; Flok et al. 2000) and, like bats, were therefore absent before the Cenozoic. Courtship sounds of grasshoppers and lepidopterans are secondary and appeared after the advent of tympanic hearing in those taxa (Yager 1999), and were therefore absent before the Cenozoic. In addition to receptors attuned to frequencies used in intraspecific communication, some cricket ears also have a

![Figure 1](https://example.com/figure1.png)

Figure 1. Sound production (A–D) and reception (E–H) devices of extant animals. (A) Left cheliped of male ghost crab (*Ocypode quadrata*), ventral view, showing sound-producing stridulatory structures. (B) Male cicada (*Pomponia intermedia*) with wings and operculum (exoskeletal covering of tymbal) removed to show sound-producing tymbal. (C) Sagittally sectioned larynx of late-term fetal pig (*Sus scrofa*) in medial view, showing sound-producing laryngeal vocal cord and laryngeal cartilages mentioned in text, with edges of airway outlined with broken line. (D) Female katydid (*Siliquofera grandis*), showing tibial tympanum for reception of airborne sound. (E) Head of toad (*Bufo americanus*), left dorsolateral view, showing tympanum for reception of airborne sound. (F) Skull of turtle (*Trachemys scripta*), showing posterior skull

small number of acoustic receptors for much higher frequencies produced by echolocating bats (Imaizumi and Pollack 1999) (Figure 3), a secondary innovation that presumably appeared after the Cenozoic appearance of bats.

In tetrapod vertebrates with tympanic ears, a bony connection transmits vibrations from the tympanum to the inner ear, where resulting fluid vibrations stimulate mechanoreceptors (Wever 1978; Kardong 2006). This mechanism appeared independently in Anura (frogs and toads), Diapsida (lizards, crocodilians, birds and kin) and Synapsida (mammals and kin) (Clack and Allin 2004), and apparently also in the extinct tetrapod groups Seymouriamorpha (Ivakhnenko 1987), Diadectomorpha (Berman et al. 1992) and Parareptilia (Laurin and Reisz 1995) (Figure 4). Whether the tympanic ears of turtles (Testudines) appeared independently depends on whether or not turtles arose from within Diapsida or Parareptilia, an issue that is disputed (e.g. Rieppel and deBraga 1996; Lee 1997a,b). Osteological evidence, reviewed later in this
Methods of animal sound production fall into five main categories: stridulation, vocalisation, percussion, forced airflow and the tympanic mechanism. Stridulation, the rubbing together of body parts, is the most common means of sound production in arthropods. Usually one of the stridulatory parts (the file) is ridged, while the other (the scraper or plectrum) is not (Figure 1). Stridulation has evolved convergently in several arthropod groups (Figure 2) and is especially prevalent among groups with highly sclerotised (hardened) exoskeletons such as Malacostraca (shrimps, crabs and kin), Arachnida (spiders, scorpions and kin), Orthoptera (crickets and grasshoppers), Hemiptera (true bugs) and Coleoptera (beetles) (e.g. Dumortier 1963b).

Unfortunately for paleontology, arthropod fossils are rarely preserved in enough detail to determine whether or not stridulatory structures are present. An exception is the taxon Orthoptera, in which the stridulatory structures are modified wing veins and can easily be discerned on fossil wings (e.g. Béthoux and Nel 2002). Stridulation can be effective even if the intended recipient lacks an auditory apparatus. Arthropods often detect the stridulation of conspecifics via substrate-borne vibrations (Crowson 1981; Gogala 1985, 2006; Barth 2002). Stridulation by prey upon seizure by a vertebrate or arthropod predator stimulates the predator's tactile receptors – and auditory receptors, if present – and often stimulates the predator to release the prey (Masters 1979; Crowson 1981). In many cases the predator's release of the stridulating prey may be a hardwired response to an honest warning, for stridulating prey items often follow stridulation with painful stimuli (e.g. stinging) or emission of noxious chemicals, or are externally tough and therefore difficult to eat (Masters 1979).

Many tetrapod vertebrates (Tetrapoda) produce sounds by vocalisation, the vibration of mucosal folds called vocal cords that extend into the lumen of the respiratory tract (Figure 1). Vocal cords occur in Anura (frogs and toads), Ambystoma + Dicamptodon (mole salamanders), Mammalia (mammals), Gekkonidae + Eublepharidae (geckos), Pituophis melanoleucus (the bull snake), Crocodylia (crocodilians), and Aves (birds) (Reese 1914; Maslin 1950; Kelemen 1963; Gans and Maderson 1973; King 1989; Young et al. 1995). Morphology, topology and phylogenetic distribution indicate that vocal cords arose independently in each of these groups (Figure 5). In all but Aves the vocal cords are in the larynx (Reese 1914; Maslin 1950; Kelemen 1963; Gans and Maderson 1973; King 1989; Young et al. 1995); in birds they are in a unique organ called the syrinx (King 1989).

Percussion is the hitting of a body part against a substrate. Examples include nuptial abdomen tapping by stoneflies (Plecoptera) and booklice (Psocoptera) and the aquatic head-slap displays of crocodilians (Pearman 1928; Garrick et al. 1978; Thorbjarnarson 1989; Stewart and Sandberg 2006). These are discussed in more detail below.

Some insects produce defensive sounds by forcing air through spiracles (Roth and Hartman 1967; Aiken 1985). However, sound production by forceful airflow is more characteristic of the vertebrate taxon Amniota, many members of which hiss by forced ventilation. Hissing as a threat device, often directed at potential predators, is widespread among extant amniotes, including lizards, snakes, turtles, crocodilians, basal birds and basal mammals (Greene 1988; Davies 2002; Kear 2005; Nowak 2005). It may therefore be a behavioural symplesiomorphy for Amniota. If that is correct, then the
hiss was present by the Pennsylvanian Period (Ruta et al. 2003), at which time no vertebrate predator had yet acquired tympanic ears (Clack and Allin 2004). A Pennsylvanian hiss therefore had no value as an acoustic display unless it exhibited the extraordinary intensity necessary to be heard with atympanic ears. If hissing is a behavioural symplesiomorphy of Amniota, its sound may therefore have originally been the passive result of a visual, inflationary display, as is the case with some extant reptiles (Kinney et al. 1998). A hiss can be produced during inspiration (Kinney et al. 1998; Young 1998) or expiration (Gans and Maderson 1973; Young 1998). Either way, forced inspiration occurs, and this increases apparent body size in an amniote with movable ribs (e.g. Kinney et al. 1998). In turtles and birds, hissing is not accompanied by bodily expansion because their ribcages do not allow it. However, hissing in the earliest turtles and birds already had value as an acoustic display because tympanic ears were present in a variety of tetrapod predators by the time turtles and birds appeared (reviewed below).

Tymbals, which are unique to Hemiptera (true bugs), are series of external folds on the first abdominal segment. Tymbals are buckled by internal muscles to produce substrate-borne vibrations (Leston and Pringle 1963; Gogala 1984; Claridge 1985). In cicadas (Cicadidae), discussed more fully below, tymbals are coupled with air bladders to produce airborne sounds.
Temporal patterns

Across taxa, certain temporal patterns in sound production are nearly universal. Animals tend to be noisiest at dawn, dusk and night, with very little sound production during the day (Schneider 1967; Marcellini 1977; Garrick et al. 1978; Welty and Baptista 1988; Thorbjarnarson and Hernández 1993; Zelick et al. 1999; McCauley and Cato 2000; Gerhardt and Huber 2002). A circannual pattern is also present across taxa, with more sound production during summers than during winters (Garrick et al. 1978; Aiken 1985; Thorbjarnarson and Hernández 1993; Morton 1996; McCauley and Cato 2000; Gerhardt and Huber 2002). There is no reason to believe that such temporal patterns were absent before the Cenozoic.

Parallel evolution

Certain body plans are more conducive than others to the evolution of certain sound-producing or -receiving organs, and parallel evolution of such structures is common in taxa with appropriate body plans. For example, posterior and internal to the tetrapod cheek is a bone called the stapes (Figure 1) that primitively served as a brace between cheek and braincase (Clack 1992). Due to its opportune location the stapes has been coupled with an external tympanum for transmission of airborne sound to the inner ear in several tetrapod lineages independently (Clack and Allin 2004) (Figure 4). Another example of acoustic parallelism in tetrapods is the parallel evolution of sound-producing vocal cords within the larynx (Maslin 1950; Kelemen 1963; Gans and Maderson 1973) (Figure 5).

Caveats

Sound-producing structures often fossilise poorly or not at all. Because of this the inference that a given animal sound was present during a given geological period is rarely certain. If a sound producing structure is present in all extant members of a given crown clade, then it is most parsimonious to infer that the structure was present in the common ancestor of the clade. However, confidence in such inferences cannot always be absolute, because in some cases the prevalence of acoustic parallelism renders hypotheses of homology of acoustic structures and behaviour uncertain even among closely related species. Even when such an inference is correct, it places only a tentative bound on the time of origin of the structure, because the crown clade may have appeared earlier than its earliest known fossils and also because it may be impossible to determine whether the structure was present in fossil members of the lineage that are basal to the crown clade. Another compounding factor is the fact that some taxa with extant members are not defined as crown clades. The earliest members of such taxa therefore do not necessarily possess the features characteristic of the crown clade. For these reasons the paleobiacoustical inferences presented here must be treated as hypotheses to test, rather than firm conclusions. Nevertheless, available evidence...
allows enough inferences to be made to make paleobioacoustical studies worthwhile.

**Pre-Cenozoic paleobioacoustics of non-insect invertebrates**

**Incidental sounds**

Extant squid make a popping sound that appears to be due to fluttering of mantle lips during expulsion of water from the siphon (Iversen et al. 1963). Although cephalopods are the only invertebrates outside Arthropoda that possess organs for unambiguous underwater sound reception (modified statocysts) (Coffin et al. 2004), there is no evidence that their locomotor sounds are involved in communication. Cephalopods appeared during the Upper Cambrian and stem-group squid (Teuthidea) during the Upper Triassic (Doyle 1993; King 1993). Squid popping sounds may therefore have existed as early as the Upper Triassic, and such sounds may have been present as early as the Cambrian if other cephalopods made them. However, no extant teuthid family has a known pre-Cenozoic fossil record (Doyle 1993), so if popping sounds are restricted to crown-group squid such sounds may have been absent from the Mesozoic.

Saltwater mussels (Mollusca: Bivalvia: Mytilidae) attach themselves to the substrate with protein secretions from the foot called byssal threads. When a mussel uses its foot for locomotion, the stretching and breaking of the byssal threads make loud snapping sounds (Fish and Mowbray 1970). Summation of the snaps produced by the various colony members produces a continuous crackling sound (Fish and Mowbray 1970). The family Mytilidae is known from as early as the Lower Triassic (Skelton and Benton 1993). Members of several other bivalve families use byssal threads as anchors, but only in Mytilidae are the threads used in locomotion (Ruppert and Barnes 1994), so we should not expect that the snapping sounds were present before the appearance of mytilids.

Colonies of sea urchins (Echinodermata: Echinoidea) make sustained crackling sounds that have been likened to the sound of something frying (Fish and Mowbray 1970). Individuals contribute to the sound by movement of spines and possibly by action of the calcareous feeding apparatus called Aristotle’s lantern (Fish and Mowbray 1970). Sea urchins are known from as early as the Upper Ordovician; their diversity exploded during the Jurassic Period (Kier 1987), at which time their frying sounds presumably became more prevalent.

Extant barnacles (Arthropoda: Cirripedia) make crackling sounds during feeding as their appendages scrape against their calcareous shells (Budelmann 1992a,b). These sounds are often continuous due to high population density (Dumortier 1963b). Convergent acquisition of calcareous shells, and presumably crackling sounds, by various lineages of barnacles occurred in the Triassic Period and continued through the Mesozoic (Foster and Buckeridge 1987). Paleozoic barnacles lacked calcareous shells (Wills 1963; Schram 1975; Collins and Rudkin 1981) and therefore probably did not produce the crackling sounds.

The appendages of non-sessile arthropods sometimes produce low-amplitude clicking or ticking sounds during locomotion when the appendages contact the substrate or other body parts. Arthropods are known from early in the Cambrian Period (Briggs et al. 1993), so their incidental locomotor sounds may have been present that early.

**Crustaceans (Arthropoda: Crustacea)**

Many members of the crustacean taxon Malacostraca (shrimp, lobsters and crabs) stridulate when seized (Budelmann 1992a). The taxonomically erratic distribution of malacostracan stridulatory structures, along with their great variety and lack of transitional forms, suggests multiple parallel origins of stridulation within the group (Dumortier 1963b) (Table 1). While most malacostracans stridulate with hard exoskeletal parts, spiny lobsters (Palinuridae) stridulate by rubbing a soft plectrum at the base of the antenna over a file beneath the eye; the mechanism of the resulting rasping sound resembles that of the bow and string of a stringed instrument (Patek 2001). The oldest known malacostracans are from the Upper Devonian (Briggs et al. 1993). The bauplan that allowed repeated evolution of stridulation was therefore present that early, and it is possible that anti-predator

<table>
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<th>Location of scraper</th>
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<td>Cephalothorax</td>
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<td>Right cheliped</td>
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<td>Lower Triassic</td>
<td>First abdominal segment</td>
<td>Posterior Cephalothorax</td>
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<tr>
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<td>Uropods</td>
<td>Lower surface of telson</td>
</tr>
<tr>
<td>Xanthididae (mud crabs)</td>
<td>Lower Cretaceous</td>
<td>Cheliped</td>
<td>Walking legs</td>
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Arachnids (Arthropoda: Arachnida)

Stridulation in response to disturbance is present in a wide variety of arachnids, including spiders (Araneae), scorpions (Scorpionida), windscorpions (Solifugae) and harvestmen (Opiliones) (Dumortier 1963a,b; Uetz and Stratton 1981; Cloudsley-Thompson and Constantinou 1984). While the sounds produced by arachnid stridulation are often of low intensity and cannot be heard further away than a few centimetres, in some cases spider and scorpion stridulation produces a loud buzz or hiss (Uetz and Stratton 1981; McCormick and Polis 1990). Only six of the many extant arachnid families with known stridulating members (Dumortier 1963b; Uetz and Stratton 1981) have known pre-Cenozoic fossil records, and all six are spider families (Selden 1993; Penney et al. 2003) (Table 2). However, the known pre-Cenozoic fossil record of Arachnida is so spotty that many extinct lineages probably existed long before their known fossil records reveal (Penney et al. 2003). Also, the wide variety of arachnid stridulatory structures (Dumortier 1963b; Uetz and Stratton 1981; Hjelle 1990) indicates that parallel evolution of stridulation is rampant in Arachnida, which in turn suggests high likelihood that many extinct arachnids also stridulated in response to disturbance. A patch of spines found on a limb fragment of a Middle Devonian arachnid of unknown affinity from New York may be a stridulatory structure (Shear et al. 1987).

The earliest known arachnids are from the Silurian (Jerm et al. 1990). The earliest known harvestman is from the Devonian (Dunlop et al. 2003), and the earliest known solifuge and amblypygid are from the Pennsylvanian (Selden 1993; Dunlop 1994). The earliest terrestrial scorpions are from the Devonian (Selden and Dunlop 1998). Basal spiders are known from as early as the Lower Devonian, with representatives of extant clades present by the Pennsylvanian (Mesothelae), Middle Triassic (Mygalomorphae) and Middle Jurassic (Araneomorphae) (Penney et al. 2003). Stridulation by or directed toward those taxa may have been present by those times.

In addition to defensive stridulation, members of several extant spider families stridulate during courtship or interspecific aggression (Uetz and Stratton 1981), and the same is conceivably true of members of extinct spider families. Some spiders make courtship sounds by means other than stridulation. Giant crab spiders (Sparassidae) vibrate their appendages like tuning forks, and crab spiders (Thomisidae) drum body parts against the substrate (Uetz and Stratton 1981). Both families were present by the Cretaceous Period (Grimaldi et al. 2002a,b).

Trichobothria, sensory hairs sensitive to the air movements, have evolved convergently in several extant arachnid taxa (Sissom 1990; Barth 2002). The trichobothria of spiders can detect low-frequency sounds of 10–950 Hz, with peak sensitivity from 50 to 120 Hz, and spiders use this ability to locate flying flies and other prey (Barth 2002). Extant scorpions use trichobothria to detect air currents caused by prey movements (McCormick and Polis 1990), but it is uncertain whether their trichobothria are used for sound reception. Either way, Paleozoic scorpions lacked trichobothria (Sissom 1990) and therefore did not locate prey by means of airborne sound.

Millipedes and centipedes (Arthropoda: Myriapoda)

Some myriapods stridulate in response to disturbance, and in some cases detached appendages make creaking sounds by an unknown mechanism, apparently to distract a predator while the myriapod escapes (Dumortier 1963a,b). Centipedes (Chilopoda) are known from as early as the Upper Silurian (Jeram et al. 1990) and millipedes (Diplopoda) from as early as the Lower Devonian (Shear 1997). Defensive stridulation by myriapods, directed at arachnid or centipede predators, may therefore

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<td>Uloboridae (hackled orb weavers)</td>
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<td>Pedipalp</td>
<td>Chelicera</td>
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References: Uetz and Stratton 1981; Grimaldi et al. 2002a,b; Penney et al. 2003.
have existed this early. However, airborne predator-distracting sounds, such as the creaking of detached appendages, would have been ineffective against deaf predators and so were probably absent before terrestrial tetrapods acquired the ability to hear airborne sounds in the Permian Period (see below).

The earliest terrestrial animal communities, from the Silurian Period, included centipedes and arachnids (Jeram et al. 1990), both of which are predatory. The earliest known millipedes and basal insects (Insecta) appeared shortly thereafter, in the Lower Devonian (Jeram et al. 1990; Shear 1997). Anti-predator stridulation is known in extant members of all four taxa (Dumortier 1963a, b; Uetz and Stratton 1981) and may therefore have existed in these early communities. Anti-predator stridulation is most likely to have evolved first in taxa with especially tough exoskeletons or in taxa capable of producing unpleasant stimuli such as stings, bites, or noxious emissions, so that it functioned as an honest warning to predators, as in extant arthropods (Masters 1979).

Directions for further research
To my knowledge, stridulatory structures have not been described in fossil arthropods outside Insecta with the exception of the Devonian arachnid and the Cretaceous lobster mentioned above. A search for stridulatory structures among fossil malacostracans, trilobites, eurypterids and perhaps other pre-Cenozoic arthropods would be worthwhile. It would also be informative to compare sound-producing structures across Malacostraca and Arachnida to determine whether any such structures are homologous between families or genera.

Pre-Cenozoic insect paleobioacoustics

Stoneflies (Plecoptera)
Intraspecific acoustic communication is characteristic of the extant stonefly clade Arctoperlaria (Stewart and Sandberg 2006). After emergence, arctoperlarian stoneflies perform male-female vibratory duets at aggregation sites while the males search for the females (Stewart and Sandberg 2006). The duets consist of vibrations with species-specific rhythms, produced by audible tapping of the abdomen on the substrate (Stewart and Sandberg 2006). Tapping duets are known in all extant arctoperlarian families and appear to be a behavioural synapomorphy of the clade (Stewart and Sandberg 2006). If this is correct then the resulting sounds were present at the time of origin of the arctoperlarian crown clade, the earliest known fossils of which are from the Middle Triassic (Grimaldi and Engel 2005).

Members of some extant stonefly families augment the courtship tapping with scratching of the abdomen on the substrate (producing a raspy sound), or rubbing of specialised abdominal parts on the substrate (producing a squeak) (Stewart and Sandberg 2006). However, none of these families has a pre-Cenozoic fossil record (Smitschenkova 2002).

Crickets and kin (Orthoptera)
Males of several extant orthopteran taxa stridulate during courtship by rubbing together specialised parts of the wings, producing sounds with species-specific rhythms. Such stridulation often stimulates chorusing and aggression from nearby males, and the approach of one male too close to another may elicit a different temporal pattern of stridulation called a disturbance song (Dumortier 1963a). Stridulatory wing venation patterns are absent in Paleozoic orthopterans, the earliest known of which are from the Pennsylvanian (Béthoux and Nel 2002; Gorochov and Rasnitsyn 2002). Stridulatory mechanisms on the wings were present in the extinct, Upper Triassic orthopteran family Mesoedisciidae and in members of Ensifera (crickets) from the Upper Triassic and later (Béthoux and Nel 2002; Gorochov and Rasnitsyn 2002). The earliest known members of the extant stridulating ensiferan taxa Gryllidae (true crickets) and Gryllotalpidae (mole crickets) are from the Lower Cretaceous (Ross and Jarzemkowski 1993). Stridulation is also characteristic of ‘Prophalangopsidae’ (hump-winged and sagebrush crickets), a taxon that is probably paraphyletic with respect to Tettigoniidae (katydids) (Desutter-Grandcolas 2003). ‘Prophalangopsids’ are known from as early as the Lower Jurassic, while katydids, grasshoppers (Acridoidea), and other extant orthopteran families with stridulating members have no known pre-Cenozoic fossil record (Ross and Jarzembowski 1993; Rust et al. 1999; Gorochov and Rasnitsyn 2002).

Extant stridulating crickets simultaneously perceive both the substrate-borne vibrations (via mechanoreceptors in the legs) and the airborne sounds (via tibial tympana; Figure 1) generated by the singing of conspecifics (Kühne et al. 1985). Morphological phylogenetic analyses of extant ensiferans suggest that stridulatory structures and tibial tympana were absent in the common ancestor of extant orthopterans and have evolved in parallel a number of times within the ensiferan crown group (Gwynne 1995; Desutter-Grandcolas 2003). However, stridulatory wing venation is present in all members of a long phylogenetic series of Upper Triassic crickets that are basal to crown Orthoptera (Béthoux and Nel 2002), which indicates that stridulatory behaviour is plesiomorphic for Upper Triassic and later crickets. This suggests that either stridulation was lost once in the crown clade’s ancestor and then regained multiple times by its descendents, or that it was present in the crown clade’s ancestor and was lost multiple times within the crown clade. The latter interpretation is supported by a recent molecular phylogenetic analysis,
the results of which differ greatly from those of morphological phylogenetic analyses (Jost and Shaw 2006). Most of the non-stridulatory extant families are fossorial (Gwynne 1995), and there may be a connection between the acquisition of such a lifestyle and the loss of stridulatory behaviour in crickets.

Gryllacrididae (locust crickets and leaf-rolling crickets) are non-stridulating crickets without tympana, some of which are fossorial. Males and females duet by drumming the tarsus or abdomen on the substrate (Hale and Rentz 2001). This family is known from as early as the Upper Cretaceous (Ross and Jarzembowski 1993).

Among extant orthopterans of various lineages, females generally prefer male calls that are longer and occur at higher rates (Gerhardt and Huber 2002). If selective pressure for these traits has existed long enough, then within each orthopteran lineage male calls were originally of shorter duration and occurred at lower rates than those of their extant descendants.

Rust et al. (1999) used comparison with extant orthopterans to calculate the dominant frequency of the stridulatory sounds produced by the wings of a Cenozoic fossil katydid. The same may be possible with Mesozoic orthopterans but has not yet been attempted.

Stridulatory wing structures are also present in members of the extinct, Middle and Upper Triassic taxon Titanoptera (=Mesotitanida). This taxon is closely related to Orthoptera and consists of large (wingspans up to 40 cm) insects from Eurasia and Australia (Gorochov and Rasnitsyn 2002; Grimaldi and Engel 2005).

Roaches (Blattaria)
Roachlike insects from as early as the Carboniferous Period are often placed in Blattaria, but as a group Paleozoic ‘roachoids’ are paraphyletic with respect to Isoptera (termites), Mantodea (mantises), and Blattaria (true roaches) (Grimaldi and Engel 2005). The earliest known members of Blattaria sensu stricto are from the Lower Cretaceous (Grimaldi and Engel 2005). Many extant roaches make courtship or disturbance sounds by a variety of means, but most such noisy roaches are members of Blaberidae (Roth and Hartman 1967), which is unknown before the Cenozoic (Grimaldi and Engel 2005). Members of other roach families are generally silent, although one member of Blattellidae, a family known from the Lower Cretaceous (Grimaldi and Engel 2005), makes a clicking sound before taking flight, and another blattellid is known to squeak when caught (Roth and Hartman 1967).

Termites (Isoptera)
Termite soldiers tap their heads on the substrate with a rhythm that is recognised by conspecifics, in response to disturbance, most likely as an alarm signal (Kirchner et al. 1994). This behaviour is taxonomically widespread within Isoptera and may therefore be a behavioural symplesiomorphy for the group (Virant-Doberlet and Čokl 2004). Early termites are known from most continents in the Lower Cretaceous, including Laurasian members of the extant head-tapping family Termopsidae (Grimaldi and Engel 2005).

Booklice (Psocoptera)
A widespread behaviour among booklice is the tapping of the abdomen on the substrate by females to call males; it makes a ticking or creaking sound (Pearman 1928). The earliest known booklice are from the Upper Jurassic; fossils from as early as the Lower Permian have been attributed to Psocoptera but more likely belong to some related taxon (Grimaldi and Engel 2005). Extant psocopteran families with tapping species and known pre-Cenozoic fossil records include Psociidae (Upper Jurassic) and Trogiidae (Upper Cretaceous) (Rasnitsyn 2002).

True bugs (Hemiptera)
Extant hemipterans comprise five major clades: Sternorrhyncha (aphids, scale insects and kin), Fulguromorpha (planthoppers), Coleorrhyncha (peloridiid bugs), Prosorrhyncha (water bugs, assassin bugs, stink bugs and kin), and Clypeomorpha (cicadas, leafhoppers, froghoppers and kin). Members of the latter four clades possess tymbals, which are buckled by internal muscles in species-specific rhythms to produce vibrations called ‘songs’ during courtship and, in some cases, during copulation (Leston and Pringle 1963; Gogala 1984; Claridge 1985; Sweet 1996). Tymbals are absent in Sternorrhyncha, and their presence in the other four clades suggests that the presence of tymbals is a synapomorphy that unites the other four clades into a taxon (hereafter called the ‘tymbaled superclade’ below) that excludes Sternorrhyncha (Sweet 1996). That interpretation of hemipteran phylogeny is supported by molecular systematics (Campbell et al. 1995; von Dohlen and Moran 1995).

In most members of the tymbaled superclade the tymbals are simple and do not produce airborne sound but instead cause vibrations in the substrate, usually a plant stem (Leston and Pringle 1963; Claridge 1985; Gogala 1984, 1985, 2006; Sweet 1996). Both sexes sing, lack tympana and perceive the songs of conspecifics via mechanoreceptors in the legs (Leston and Pringle 1963; Claridge 1985; Gogala 1985, 2006; Sweet 1996). This appears to be the plesiomorphic condition for the tymbaled superclade (Sweet 1996). The earliest known members of the tymbaled superclade, which is a crown clade, are from the Lower Permian (Shcherbakov and Popov 2002), and...
the use of tymbals for substrate-borne courtship songs presumably originated then.

Within the tymbaled superclade are several taxa in which courtship is modified such that it produces airborne sounds. The most familiar example is probably the treetop singing of members of Cicadidae (cicadas), the earliest known fossils of which are from the Upper Cretaceous (Turonian) of New Jersey (Grimaldi et al. 2002b). In cicadas the females have lost the tymbals, so singing is done only by the males, in which the tymbals are elaborate in comparison with those of other hemipterans (Leston and Pringle 1963; Claridge 1985). Air sacs internal to the tymbals amplify the songs so that they are audible from several meters away and attract members of both sexes to a congregational area for reproduction (Dumortier 1963a; Claridge 1985). Cicadas hear each other’s songs with tympanic ears that are ventral to the tymbals on the abdomen (Leston and Pringle 1963; Claridge 1985). After attracting a female, a male cicada changes the rhythm of his song; in some species he also adds audible wing-flicking, and in some species the female responds with wing-flicking of her own (Boulard 2006). Some cicada species also have stridulatory structures, the behavioural significance of which is unknown (Boulard 2006). Another enigmatic acoustic behaviour by cicadas is the drumming of the wings on the substrate in some species, especially in those that have lost tymbals altogether (Boulard 2006).

In many members of Prosorrhyncha, the earliest known members of which are from the Upper Triassic (Shcherbakov and Popov 2002), tymbal songs are augmented by simultaneous, audible stridulation, which adds higher frequencies to the songs (Gogala 1984, 1985, 2006; Sweet 1996). Often, after the female has been attracted by the male’s calling song, he switches to a courtship song (Dumortier 1963a). The variety of stridulatory structures in Prosorrhyncha (Table 3) indicates that augmentation of tymbal songs with stridulation arose multiple times in parallel within Prosorrhyncha (Leston and Pringle 1963). Trichothorbia are present in many prosorrhynchans, fulgurormorphs, and coleorrhynchans, but not in clypeomorphs (Sweet 1996). They appear to be used as acoustic receptors for low-frequency, low-amplitude, audible song and differences between the trichothorbia of various taxa suggest that they appeared in parallel multiple times in the tymbaled superclade (Sweet 1996).

In the prosorrhynchan taxon Nepomorpha a switch has occurred from the ancestral hemipteran plant-dwelling habitat to an aquatic one (Shcherbakov and Popov 2002). The new habitat required that plant stems be traded for the watery environment as a medium to carry vibrational signals to conspecifics. Accordingly, many nepomorphs stridulate underwater. Among nepomorph families with known pre-Cenozoic fossil records, stridulation is known in Corixidae (water boatmen), Naeororidae (creeping water bugs), Nepidae (waterscorpions), and Notonectidae (backswimmers) (Dumortier 1963b). In Corixidae and Notonectidae stridulation by males is known to attract females (Dumortier 1963a; Čokl et al. 2006). The variety of nepomorph stridulatory structures (Table 3) suggests that stridulation arose multiple times independently in Nepomorpha. Because evolution of stridulation is rampant in Nepomorpha, it may have been present in extinct nepomorphs as early as the Upper Triassic, from which time period the earliest nepomorphs are known (Shcherbakov and Popov 2002). Non-stridulatory courtship sounds (buzzing or chirping) are made by members of Belostomatidae (giant water bugs) by expulsion of air

Table 3. Prosorrhynchan families that are known from before the Cenozoic with members that are known to stridulate, and their stridulatory organs.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Earliest record</th>
<th>Location of scraper</th>
<th>Location of file</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alydidae (broad-headed bugs)</td>
<td>Upper Jurassic</td>
<td>Femur</td>
<td>Hemelytra</td>
</tr>
<tr>
<td>Aradidae (flat bugs)</td>
<td>Lower Cretaceous</td>
<td>Hind femur</td>
<td>Abdomen</td>
</tr>
<tr>
<td>Coreidae (leaf-footed bugs)</td>
<td>Upper Jurassic</td>
<td>Hind tibia</td>
<td>Abdomen</td>
</tr>
<tr>
<td>Corixidae (water boatmen)</td>
<td>Lower Jurassic</td>
<td>Pronotum</td>
<td>Fore wing</td>
</tr>
<tr>
<td>Cydnidae (burrowing bugs)</td>
<td>Lower Jurassic</td>
<td>Fore tarsus</td>
<td>Opposite fore femur</td>
</tr>
<tr>
<td>Lygaeidae (seed bugs)</td>
<td>Lower Cretaceous</td>
<td>Fore femur</td>
<td>Head</td>
</tr>
<tr>
<td>Miridae (plant bugs)</td>
<td>Upper Jurassic</td>
<td>Abdomen</td>
<td>Wing</td>
</tr>
<tr>
<td>Nabidae (damsel bugs)</td>
<td>Upper Jurassic</td>
<td>Hind femur</td>
<td>Abdomen</td>
</tr>
<tr>
<td>Nepidae (waterscorpions)</td>
<td>Upper Triassic</td>
<td>Foreleg</td>
<td>Prosternum</td>
</tr>
<tr>
<td>Notonectidae (backswimmers)</td>
<td>Upper Triassic</td>
<td>Coxa</td>
<td>Embolium</td>
</tr>
<tr>
<td>Reduviidae (assassin bugs)</td>
<td>Lower Cretaceous</td>
<td>Fore femur</td>
<td>Head or fore coxa</td>
</tr>
<tr>
<td>Thaumastellidae (no common name)</td>
<td>Lower Cretaceous</td>
<td>Tibia</td>
<td>Rostrum</td>
</tr>
</tbody>
</table>

through spiracles (Aiken 1985); belostomatids are known from as early as the Upper Triassic (Ross and Jarzembowski 1993).

In one nepomorph family, Corixidae (water boatmen) – known from as early as the Lower Jurassic (Ross and Jarzembowski 1993) – perception of conspecific stridulation is truly auditory. Water boatmen receive such vibrations with tympana that are surrounded by air bubbles, whereas other nepomorphs use atympanic mechanoreceptors for reception of water-borne vibrations (Cokl et al. 2006). Unlike the low-amplitude calls of most nepomorphs, which are audible to humans only if the bug is close to the listener’s ear, the underwater songs of corixids are quite loud; resonance by the same air bubbles that enable tympanic hearing in corixids amplifies the songs so that they are audible from beyond the shoreline (Aiken 1985).

Courtship sounds are not the only sounds made by hemipterans. Many clypeomorphs cryaudibly when caught and during rough treatment (Dumortier 1963a; Leston and Pringle 1963; Claridge 1985). Many prosorrhynchs stridulate audibly when caught, including members of Cydnidae (burrowing bugs), Lygaeidae (seed bugs) and Reduviidae (assassin bugs) (Dumortier 1963a; Leston and Pringle 1963; Gogala 2006). In some reduvid species the female stridulates upon being mounted, deterring the male, if she is unwilling to mate (Lazzari et al. 2006). Members of the prosorrhynch family Coreidae (leaf-footed bugs), the earliest known members of which are from the Upper Jurassic (Ross and Jarzembowski 1993), make sounds by unknown means (Dumortier 1963b); the biological significance of these sounds is unclear, and they are probably by-products of locomotion (Gogala 1985). Among members of Sternorrhyncha, some colonies of aphids (Aphididae) make scraping sounds when disturbed (Leston and Pringle 1963). These stridulatory sounds are made by rubbing the hind tibiae on rough spots on the abdomen (Dumortier 1963a). The earliest known aphids are from the Lower Cretaceous (Ross and Jarzembowski 1993).

Stridulatory structures are known in some fossil hemipterans. Members of the stem-hemipteran family Dysmorphoptilidae possessed a stridulatory apparatus with a scraper on the hind knee and the file on the underside of the fore wing; the family is known from the Upper Permian to the Upper Jurassic (Shcherbakov and Popov 2002). A similar stridulatory apparatus is present in Triassic members of the extinct prosorrhynch family Ipsviciidae (Shcherbakov and Popov 2002).

**Beetles (Coleoptera)**

Beetles of many extant families produce sounds, often by stridulation (Alexander and Moore 1963; Dumortier 1963b). Adult and larval beetles often stridulate in response to disturbance, although some adult males stridulate to attract females or repel rival males (Dumortier 1963a; Rudinsky and Ryker 1976; Aiken 1985). The broad taxonomic span of families with stridulating members and the wide variety of stridulatory structures shows that repeated parallel evolution of stridulation is rampant in Coleoptera (Table 4). Beetle stridulation may therefore have been present as early as the Lower Permian, from which the earliest beetle fossils are known (Ponomarenko 2002).

Various beetles are also known to make non-stridulatory sounds. Female members of Anobiidae (death-watch beetles), a family known from as early as the Lower Cretaceous (Ross and Jarzembowski 1993), attract males by drumming the head on the substrate (Dumortier 1963a). In some members of Buprestidae (metallic wood-boring beetles), a family known from as early as the Middle Jurassic (Ross and Jarzembowski 1993), members of both sexes drum their abdomens on the substrate and answer each other’s drumming in like manner (Crowson 1981). Drumming of body parts against the substrate is also known in Cerambycidae (long-horned beetles) (Crowson 1981), the earliest known members of which are from the Lower Cretaceous (Ross and Jarzembowski 1993). Some cerambycids also make purring sounds by vibrating the body within a crevice in bark (Dumortier 1963b). Larvae of some members of Dytiscidae (predaceous diving beetles), a family known from as early as the Upper Jurassic (Ponomarenko 2002), squeak by expelling air through spiracles when disturbed (Aiken 1985). Larvae of some members of Hydrophilidae (water scavenger beetles), a taxon known from as early as the Upper Triassic (Ponomarenko 2002), hiss by an unknown mechanism upon disturbance (Aiken 1985). Members of Elateridae (click beetles), produce a loud click by snapping a spine on the prosternum into a notch on the mesosternum, which suddenly flexes and bounces the beetle and is used to right the beetle when upside-down or to make it difficult for predators to hold (Grimaldi and Engel 2005); the earliest known elaterids are from the Upper Triassic (Ponomarenko 2002). The wings of members of Scarabaeidae (scarab beetles), a family known from as early as the Lower Jurassic (Ponomarenko 2002), often buzz loudly during flight. The exoskeletons of these beetles are particularly tough, so it is possible that the loud scarabaeid flight buzz is an honest warning of culinary difficulty to potential predators.

**Lacewings and kin (Neuroptera)**

The supraordinal insect taxon Neuroptera includes the order Raphidioptera (snakeflies) and the sister orders Megaloptera (dobsonflies and alderflies) and Neuroptera (lacewings). Courtship in all extant families of Raphidioptera and Megaloptera involves abdominal tremulation, sensed via substrate- (stem- or leaf-) borne vibrations with species-specific rhythms; in Corydalidae (dobsonflies)
only the males tremulate, but in Sialidae (alderflies) and Raphidioptera the sexes perform tremulatory duets (Henry 2006). While tremulation does not produce airborne sounds, it is often accompanied by audible wing fluttering in Raphidioptera or by audible drumming of the abdomen on the substrate in Sialidae, and is replaced by audible wing fluttering in some species of Corydalidae (Henry 2006).

Among lacewings, wing fluttering during courtship is known in Coniopterygidae (dustywings) and Berothidae (beaded lacewings) (Henry 2006), known from as early as the Upper Jurassic and the Lower Cretaceous respectively (Grimaldi and Engel 2005). Tremulation, wing fluttering and abdominal drumming during courtship are all known in Chrysopidae (green lacewings) (Henry 2006), a family known from as early as the Lower Cretaceous (Grimaldi and Engel 2005).

Among lacewings, tremulation is absent in all but three derived families, the relationships between which suggest an independent origin of tremulation in each (Henry 2006). The presence of tremulation in Raphidioptera and Megaloptera but not basal Neuroptera makes it unclear whether tremulation appeared independently in the three neuropterid orders or was present in the common neuropterid ancestor, lost in ancestral lacewings, and then regained in derived lacewings. If tremulation was present in the neuropterid ancestor, then it (and possibly the accompanying sounds of drumming and/or wing fluttering) existed as early as the Permian Period, from which the earliest neuropterid fossils are known (Grimaldi and Engel 2005). If tremulation evolved separately in the three orders, then the times of origin of its separate appearances are less clear. Snakeflies are known from the Lower Jurassic, but the earliest known member of an extant family is from the Tertiary (Grimaldi and Engel 2005). Megalopterans are known from as early as the Upper Triassic, but extant megalopteran families are unknown before the Middle Jurassic (Grimaldi and Engel 2005). Estimated times of origin of tremulation and accompanying sounds in Raphidioptera and Megaloptera therefore depend on whether tremulation was present in each order’s ancestor or only in members of extant tremulating families. It is plausible that the neuropterid bauplan encouraged repeated evolution of tremulation, just as the beetle bauplan encouraged repeated evolution of stridulation. It is therefore possible that these neuropterid

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Table 4. Beetle families that are known from before the Cenozoic in which adults are known to stridulate, and their stridulatory organs, where known.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Earliest record</th>
<th>Location of scraper</th>
<th>Location of file</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anobiidae (death-watch beetles)</td>
<td>Lower Cretaceous</td>
<td>Prosternum</td>
<td>Gula</td>
</tr>
<tr>
<td>Bruchidae (seed beetles)</td>
<td>Upper Jurassic</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Buprestidae (metallic wood-boring beetles)</td>
<td>Upper Jurassic</td>
<td>Elytra</td>
<td>-</td>
</tr>
<tr>
<td>Carabidae (ground beetles)</td>
<td>Lower Jurassic</td>
<td>Femur</td>
<td>Elytra</td>
</tr>
<tr>
<td>Cerambycidae (long-horned beetles)</td>
<td>Lower Cretaceous</td>
<td>Pronotum</td>
<td>Mesonotum</td>
</tr>
<tr>
<td>Chrysomelidae (leaf beetles)</td>
<td>Upper Jurassic</td>
<td>Elytra</td>
<td>Hindfemur</td>
</tr>
<tr>
<td>Curculionidae (weevils)</td>
<td>Lower Cretaceous</td>
<td>Metasternum</td>
<td>Coax</td>
</tr>
<tr>
<td>Dytiscidae (predaceous diving beetles)</td>
<td>Upper Jurassic</td>
<td>Wing</td>
<td>Abdomen</td>
</tr>
<tr>
<td>Endomychidae (handsome fungus beetles)</td>
<td>Upper Cretaceous</td>
<td>Pronotum</td>
<td>Head</td>
</tr>
<tr>
<td>Heteroceridae (variegated mud-loving beetles)</td>
<td>Lower Cretaceous</td>
<td>Femur</td>
<td>Abdomen</td>
</tr>
<tr>
<td>Hydrophilidae (water scavenger beetles)</td>
<td>Upper Triassic</td>
<td>Elytra</td>
<td>Abdomen</td>
</tr>
<tr>
<td>Lucanidae (stag beetles)</td>
<td>Upper Jurassic</td>
<td>Elytra</td>
<td>Hindfemur</td>
</tr>
<tr>
<td>Nemonychidae (no common name)</td>
<td>Upper Jurassic</td>
<td>Pronotum</td>
<td>Head</td>
</tr>
<tr>
<td>Nitidulidae (sap beetles)</td>
<td>Middle Jurassic</td>
<td>Abdomen</td>
<td>Wing</td>
</tr>
<tr>
<td>Passalidae (bessbugs)</td>
<td>Lower Cretaceous</td>
<td>Elytra</td>
<td>Abdomen</td>
</tr>
<tr>
<td>Scarabaeidae (scarab beetles)</td>
<td>Lower Jurassic</td>
<td>Abdomen</td>
<td>Elytra</td>
</tr>
<tr>
<td>Scolytidae (bark beetles and ambrosia beetles)</td>
<td>Lower Cretaceous</td>
<td>Prosternum</td>
<td>Gula</td>
</tr>
<tr>
<td>Silphidae (carion beetles)</td>
<td>Lower Jurassic</td>
<td>Abdomen</td>
<td>Elytra</td>
</tr>
</tbody>
</table>

References: Dumortier 1963b; Ross and Jarzembowski 1993; Ponomarenko 2002; Wessel 2006.
behaviours and their accompanying sounds appeared multiple times before and during the Cenozoic.

**Wasp, bees and ants (Hymenoptera)**
Wasp (Hymenoptera) are known from as early as the Upper Triassic (Grimaldi and Engel 2005). The wasp clade Aculeata, known from as early as the Upper Jurassic, is characterised by modification of the ovipositor into a sting (Grimaldi and Engel 2005). Aculeates tend to buzz audibly in flight, and it is possible that, with the stridulatory sounds of certain other insects, the flight fuzz deters potential predators by warning them of the painful consequences of predatory attempts.

Aculeate flight sounds also serve social functions. Some male braconid wasps (Braconidae) also use their wings to make courtship sounds when near females (Sotavalta 1963); braconids are known from as early as the Lower Cretaceous (Ross and Jarzembowski 1993). Members of Vespidae, which includes hornets and kin, are known to buzz with their wings during flight and during copulation (O’Neill 2001); vespids are known from as early as the Lower Cretaceous (Ross and Jarzembowski 1993). In some members of Sphecidae (mud daubers and kin), a family known from as early as the Lower Cretaceous (Ross and Jarzembowski 1993), males use buzzing as an acoustic threat when defending the nest against marauders or rival males (O’Neill 2001); males of some sphecid species also locate virgin females by the loud buzz made by the females as they dig themselves out of the ground. The buzzing of bees (Apoidea) cannot be heard by fellow bees during flight, but in some bees, once females have alighted, males use the flight buzz to court them (Sotavalta 1963). The earliest known bee is from the Lower Cretaceous (Poinar and Danforth 2006). Reports of pre-Cretaceous bee body and trace fossils exist, but the former have been reidentified as indeterminate insects and the latter are more likely beetle than bee traces (Engel 2001).

A variety of sounds are known in extant bees, particularly those of the closely related tribes Apini (honeybees and kin), Bombini (bumblebees and kin) and Meliponini (stingless bees). Sounds that have been described as tooting, quacking, hissing and piping serve various social functions in Apini and Bombini (Hrncir et al. 2006), but neither taxon is known from before the Cenozoic (Engel 2001). Stingless bees are known from the Upper Cretaceous (Engel 2001). Stingless bees share with Apini and Bombini the tendency for foragers to use thoracic pulsation to make sounds that stimulate nestmates to fly out – sometimes after first buzzing in response – and collect food (Hrncir et al. 2006). If thoracic pulsation is a behavioural symplesiomorphy for stingless bees, honeybees and bumblebees, then it was present at least as early as the Upper Cretaceous. Bees lack tympanic ears and sense the sounds of conspecifics via substrate-borne vibrations and via mechanoreceptors in the antennae that detect air movement caused by the vibrations of the wings of conspecifics engaging in thoracic pulsation (Hrncir et al. 2006).

Ants (Formicidae) are also members of Aculeata. The earliest known ants are from the Cretaceous Period and include members of four extant subfamilies: Ponerinae (trap-jaw ants and kin), Dolichoderinae (cone ants and kin), Formicinae (carpenter ants, wood ants and kin), and Myrmicinae (harvester ants, fire ants and kin) (Moreau et al. 2006). The earliest known fossil records of the former two subfamilies are from the Lower Cretaceous, and those of the latter two are from the Upper Cretaceous (Moreau et al. 2006). Some dolichoderine and formicine ant workers tap their mandibles and abdomens on the substrate to produce alarm sounds in response to nest disturbance (Hölldobler and Wilson 1990). Stridulation is used by ponerine and myrmicine ants – especially in soil-dwelling species – for group cohesion, warning of danger, as a call for help by wounded or imperiled individuals, and as a signal by females to males that copulation is complete (Dumortier 1963a; Hölldobler and Wilson 1990). Stridulation occurs by rubbing the last segment of the petiole against the striated dorsal edge of the first segment of the gaster in Ponerinae and Myrmicinae (Dumortier 1963b); in some myrmicines this is coupled with the rubbing of a second, ventral stridulatory apparatus at the joint between the same two segments (Dumortier 1963b). In small ant species stridulation is inaudible to humans further away than a few centimetres, but in large members of Ponerinae and Myrmicinae it can be audible further away (Dumortier 1963b,c). Ants themselves are deaf to airborne sounds and detect conspecific stridulation via substrate-borne vibrations (Hölldobler and Wilson 1990).

Stridulation between edges of abdominal segments is also known in some members of Mutillidae (velvet-ants) (Dumortier 1963b; O’Neill 2001), an aculeate family known from as early as the Upper Cretaceous (Ross and Jarzembowski 1993). In some species the male makes a honking sound by vibrations of the wings and thorax as he approaches the female, and both members of the pair alternately stridulate during copulation (O’Neill 2001).

**Flies, gnats and mosquitoes (Diptera)**
Dipterans are known from as early as the Middle Triassic (Blagodurov et al. 2002). Audible wing vibration by the male during mounting is widespread in Diptera (Kanmiya 2006). In addition, many dipterans use flight sounds as a means of intraspecific communication. Male mosquitoes (Culicidae) have a hearing apparatus in the antennae, which is used to find the female by her flight hum and to keep together in all-male swarms (Sotavalta 1963); the earliest known mosquitoes are from the Cretaceous (Grimaldi et al. 2002a,b). Male hover flies (Syrphidae)
court females by flying with a high-pitched hum over a female on a flower (Sotavalta 1963); the earliest known hover flies are from the Upper Cretaceous (Blagoderov et al. 2002).

Other dipteran families with audible flight sounds and known pre-Cenozoic fossils include Bombyliidae (bee flies), Tabanidae (horse flies), and bottle flies (Calliphoridae). The oldest known members of Bombyliidae and Tabanidae are from the Lower Cretaceous, and the oldest known member of Calliphoridae is from the Upper Cretaceous (Blagoderov et al. 2002). In some dipteras, morphology and flight sounds mimic those of stinging hymenopterans, apparently to deter predators (Chapman 1975). Such mimicry is unlikely to have arisen before the appearance of stinging hymenopterans, which occurred in the Upper Jurassic (Grimaldi and Engel 2005).

**Directions for further research**

Restudy of fossil insects – especially those that are well preserved in amber – to search for potentially overlooked bioacoustical structures might be worthwhile. A search for stridulatory structures, highly sclerotised ventral surfaces (for percussion), and other sound-producing structures could prove informative. Phylogenetic studies to determine homologies between sound-producing parts could be used to constrain phylogenetic levels at which homologous sound production occurred within given insect taxa, and fossils could then be used to constrain the times of origin of such sounds. For this, a set of reliable phylogenies incorporating these fossil taxa would be necessary to determine historical homology as opposed to convergence. It would also be interesting to examine sound-producing and auditory parts of extant insects for correlations between morphology and dominant frequencies, and to apply the results to fossils to determine more precisely the nature of the sounds produced and heard by fossil insects (e.g. Rust et al. 1999).

**Pre-Cenozoic vertebrate paleobioacoustics**

**Non-bony fishes**

In vertebrates the inner ear exhibits a number of separate neuromast organs, some of which are used for 3D orientation and some of which are used for sound reception (Ladich and Popper 2004). Sound reception has not been demonstrated in the basal taxa Myxini (hagfishes) and Petromyzontida (lampreys) but is present in Gnathostomata (jawed vertebrates) (Ladich and Popper 2004). It may have appeared independently in cartilaginous fishes (Gnathostomata: Chondrichthyens) and bony fishes (Gnathostomata: Osteichthyens) because the former use a neuromast organ called the macula neglecta for hearing, whereas in the latter the macula neglecta is reduced or absent and other parts of the inner ear are used for hearing (Popper et al. 1992; Ladich and Popper 2004).

Cartilaginous fishes are generally silent (Hueter et al. 2004). An exception is the cownose ray (*Rhinoptera bonasus*), which emits clicks in response to a human touch (Fish and Mowbray 1970). The cownose ray is a member of the family Myliobatidae, the earliest known members of which are from the latest Cretaceous (Campanian-Maastrichtian) (Cappetta 1987).

Hearing has been demonstrated in Elasmobranchii (sharks and rays) but has not been studied in Holocephali (ratfishes). Elasmobranchs are known from as early as the Lower Devonian (Cappetta et al. 1993), so it is possible that anti-predator sounds directed at them existed by the late Paleozoic.

**Lobe-finned fishes (Osteichthyes: Sarcopterygii)**

Extant lungfishes (Sarcopterygii: Dipnoi) are generally silent, although the Australian lungfish (*Neoceratodus forsteri*) is known to breathe air noisily and to do it more frequently during the breeding season, sometimes in concert in the evening (Kemp 1986). The sound is more likely incidental than of use in intraspecific communication, because lungfishes lack specialisations for airborne sound reception. Incidental air-breathing sounds that resemble whistling and clucking are also known in extant salamanders (Maslin 1950), so the phenomenon is not limited to sarcopterygians outside Tetrapoda. Sarcopterygians are known from as early as the Upper Silurian (Zhu et al. 2009), so the incidental sounds of air their breathing may have existed that early.

**Ray-finned bony fishes (Osteichthyes: Actinopterygii)**

Many actinopterygian taxa produce grunts, clicks, squeaks, whistles and other sounds for intraspecific communication and when disturbed or apprehended (Fish and Mowbray 1970; Myrberg 1981; Ladich and Bass 2003). Such sounds are typically produced by muscular vibration of the gas bladder, but in some species sound production is accomplished by tendon snapping, pectoral girdle vibration, stridulation of pharyngeal teeth, or other methods (Ladich and Bass 2003). Actinopterygian acoustic behaviour has been studied mainly in teleosts (Teleosteii). Not all teleosts are known to make sounds, and the variety of their sound production mechanisms indicates that acoustic communication evolved independently in several lineages (Schneider 1967; Ladich and Bass 2003). In addition to teleosts, acoustic communication is known in basal ray-finned groups such as sturgeons (Acipenseridae) and bichirs (Polypteridae) (Johnston and Phillips 2003; Ladich and Bass 2003). Although the known fossil records of extant ray-finned fish families that communicate acoustically go back no further than the Upper Jurassic (Table 5), those
Table 5. Families of sound-producing fishes that are known from before the Cenozoic, and details about their sounds.

<table>
<thead>
<tr>
<th>Family</th>
<th>Earliest record</th>
<th>Description of sound</th>
<th>Function of sound</th>
<th>Mechanism, if known</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acipenseridae (sturgeons)</td>
<td>Upper Cretaceous</td>
<td>Squeak, chirp, knock, groan</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Albulidae (bonefishes)</td>
<td>Upper Cretaceous</td>
<td>Click, scratch, knock</td>
<td>R</td>
<td>–</td>
</tr>
<tr>
<td>Ariidae (HS) (marin catfishes)</td>
<td>Upper Cretaceous</td>
<td>Grunt, creak, yelp</td>
<td>R</td>
<td>E</td>
</tr>
<tr>
<td>Elopidae (tarpons)</td>
<td>Upper Jurassic</td>
<td>Thump</td>
<td>R</td>
<td>S</td>
</tr>
<tr>
<td>Gadidae (cods)</td>
<td>Upper Cretaceous</td>
<td>Grunt</td>
<td>A, C, G, R</td>
<td>IN</td>
</tr>
<tr>
<td>Holocentridae (HS) (squirrelfishes)</td>
<td>Upper Cretaceous</td>
<td>Staccato, grunt</td>
<td>A, R, G</td>
<td>E</td>
</tr>
<tr>
<td>Myliobatidae (eagle rays)</td>
<td>Upper Cretaceous</td>
<td>Click</td>
<td>R</td>
<td>I</td>
</tr>
<tr>
<td>Ophidiidae (cusk-eels)</td>
<td>Upper Cretaceous</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Polypteridae (bichirs)</td>
<td>Upper Cretaceous</td>
<td>Thump, moan</td>
<td>A, R</td>
<td>I</td>
</tr>
</tbody>
</table>

A, aggression; C, courtship; E, contraction of extrinsic swim bladder muscles; G, group coordination; HS, hearing specialist; I, sound produced by unknown internal mechanism; IN, contraction of intrinsic swim bladder muscles; R, response to predator, human touch, or startling; S, sound made by swimming. References: Myrberg 1981; Cappetta 1987; Ladich and Tadler 1988; Arratia 1993; Meunier and Gayet 1993; Nolf and Stringer 1993; Patterson 1993; Schwarzhans 1993; Stewart 1993; Johnston and Phillips 2003; Ladich and Bass 2003; Wilson et al. 2003.

families phylogenetically bracket taxa from as early as the Upper Devonian (Carroll 1988; Grande and Bemis 1996). The sounds of actinopterygian communication may therefore have existed through the late Paleozoic and Mesozoic.

Basal ray-finned fishes must have been present by the Upper Silurian, because Sarcopterygii, the sister taxon to Actinopterygii, was present then (Zhu et al. 2009). The lungs of extant basal actinopterygians may be homologous with those of lungfishes (Kardong 2006), in which case the sound of noisy air-breathing by ray-finned fishes may have existed alongside that of their lobe-finned counterparts as early as the Upper Silurian.

Underwater hearing is present in actinopterygians in general. A number of teleost taxa, known as hearing specialists, independently evolved connections between the gas bladder and the inner ear (Ladich and Bass 2003). This increases the upper frequency range through which underwater sounds can be heard (Yan et al. 2000; Ladich and Bass 2003). Accordingly, sounds made by hearing specialist fishes are of higher frequency than those of other fishes (Figure 3) (Ladich and Bass 2003). Hearing specialist taxa include Otophysi (carp, catfishes and kin), Anabantoidea (gouramis and kin), Mormyridae (mormyrids) and Holocentridae (squirrelfishes) (Ladich and Bass 2003). Hearing specialist fishes typically inhabit quiet, shallow water, which enhances high-frequency sound transmission (Ladich and Bass 2003). It stands to reason, then, that high-frequency acoustic behaviour of fossil actinopterygians would have been more prevalent in quiet, shallow water than in noisy or deep water. The earliest known members of extant hearing specialist fish taxa are from the Upper Cretaceous (Table 5).

**Basal tetrapods (Tetrapoda)**

In basal tetrapods a bone called the stapes served as a brace between the palate and braincase (Clack 1992). The stapes of most extant frogs (Anura) and amniotes (Amniota) has been reoriented so that it couples the inner ear to a tympanum, enabling detection of airborne sounds. The sound-sensitive region of the inner ear is homologous in Anura and Amniota (Fritzsch 1992) but its coupling to a tympanum evolved separately in the ancestors of extant frogs, diapsids (Amniota: Diapsida) and mammals (Amniota: Mammalia) (Bol and Lombard 1985; Carroll 1991; Clack and Allin 2004) (Figure 4). The earliest tetrapod skulls exhibit posterior notches that are often called otic (ear) notches because they superficially resemble the posterior skull notches that house tympana in extant frogs and amniotes. However, early tetrapod stapedial and otic morphology are inconsistent with tympanic hearing (Clack et al. 2003). The bony architecture of the notches indicates that they housed spiracles, not tympana (Brazeau and Ahlberg 2006). Even so, early tetrapod inner ears probably detected low-frequency water- and substrate-borne sounds, as do the atympanic ears of extant fishes, salamanders and caecilians (Smotherman and Narins 2004; McCormick 1999; Ladich and Bass 2003).

The early tetrapod *Ichthyostega* exhibits otic modifications analogous to those of hearing-specialist fishes. Uniquely among basal tetrapods, its skull appears to have had an air-filled otic chamber and a mobile stapes with a morphology and position conducive to sound conduction from the air-filled chamber to the inner ear (Clack et al. 2003). The otic chamber apparently functioned as a resonator for high-frequency sounds, as does the gas bladder of hearing specialist fishes, which raises the possibility of high-frequency sonic communication in *Ichthyostega*.

Among members of lissamphibia (the smallest clade including extant amphibians and all taxa phylogenetically bracketed by them), tympanic ears are present in most extant frogs (Anura) but are absent in basal frogs (Ascaphidae and Leiopelmatidae), caecilians (Gymnophiona) and salamanders (Caudata) (Bogert 1958; Smotherman and Narins 2004). This suggests that the lissamphibian ancestor lacked tympanic ears and that within Lissamphibia tympanic ears are a synapomorphy of derived frogs. This interpretation is compatible with all three of the competing hypotheses of lissamphibian origins. According to one hypothesis, Lissamphibia arose from within the otherwise Paleozoic
clade Lepospondyli (Laurin and Reisz 1995, 1997, 1999; Laurin 1998; Vallin and Laurin 2004). According to the second hypothesis, Lissamphibia arose from within the otherwise mostly Paleozoic and Triassic clade Temnospondyli (Milner 1988; Trueb and Cloutier 1991; Ruta et al. 2003). According to the third hypothesis, frogs and salamanders arose from within tymnospondyli but caecilians arose from within Lepospondyli (Carroll 2007; Anderson et al. 2008). Lepospondyls show no osteological evidence of tympanic ears (Clack and Allin 2004). Many temnospondyls exhibit posterior cranial notches that have been interpreted as having housed tympana (Clack and Allin 2004). However, recent studies show that the morphology of the temporal area and the massive size of the stapes in temnospondyls are incompatible with the presence of a tympanum; the notches more likely housed spiracles (Laurin 1998; Laurin and Soler-Gijón 2006). The common ancestor of extant amphibians therefore lacked tympanic ears, regardless of which phylogenetic hypothesis is correct.

Many large temnospondyls had large heads like those of extant crocodilians (Romer 1947), which acoustically advertise presence by slapping their heads on the water (Vliet 1989; Thorbjarnarson 1991; Thorbjarnarson and Hernández 1993). It is therefore tempting to imagine large-headed temnospondyls employing the same communication device. Had they done so, their underwater hearing would have detected the sound and their lateral line systems (Romer 1947) would have detected the location of its source (Coombs and Braun 2003), even without tympana. However, the extreme proximity between shoulder girdle and skull in temnospondyls and other non-amniote tetrapods made the neck extremely short (Romer 1947), so it is unlikely that they could have raised their heads enough to have performed crocodilian-style head-slaps.

This does not necessarily mean that extinct temnospondyls and other basal tetrapods were silent. It is possible that they performed other activities involving audible water displacement. Also, several extant salamander species – which lack tympanic ears – produce airborne anti-predator sounds in response to capture (Maslin 1950). Such defensive sound production may have evolved convergently in extinct basal tetrapods after the appearance of tympanic ears in their predators. Many extant lissamphibians that make such sounds produce noxious chemicals that discourage or even kill predators (Duellman and Trueb 1994). Others, such as amphiumas (Amphiumidae), can deliver a painful bite. Lissamphibian anti-predator sounds may therefore be honest warnings to predators (Duellman and Trueb 1994), as is the case with stridulating insects (Masters 1979). Noxious chemical production in extinct temnospondyls cannot be evaluated, but cranial and dental morphology of many temnospondyls indicates the ability to produce a nasty bite, so they may have made honest warning sounds. While the earliest known predators with tympanic ears are Lower Permian seymouriamorphs (Ivakhnenko 1987) (Figure 6), basal tetrapod anti-predator sounds directed at fishes may have existed before then.

Mechanisms of defensive sound production in extant salamanders are listed in Table 6. Among extant salamander families, Cryptobranchidae (giant salamanders) and Amphiumidae (amphiumas) have a pre-Cenozoic fossil record. The former are known from the Middle Jurassic of China (Gao and Shubin 2003) and the latter from the Upper Cretaceous of North America (Milner 1993). It is therefore possible that their characteristic defensive sounds existed before the Cenozoic.

Arthropod stridulation in response to seizure by tetrapod predators began at the earliest in the Mississippian, at which time the earliest insectivorous tetrapods
appeared (Hotton et al. 1997). Mississippian tetrapods lacked tympanic ears (see below) and therefore would have been deterred by the substrate-transmitted mechanical vibrations produced by stridulation, rather than by the resulting sounds. Predator deterrence by airborne stridulatory sounds would have been effective only after the appearance of tympanic ears in predatory tetrapods in the Permian (see below).

**Frogs (Lissamphibia: Anura)**

In lunged fishes, including lungfishes, the glottis (the opening in the pharynx that leads to the lung) is ringed by a muscular sphincter that closes the glottis (Negus 1949). To this arrangement tetrapods have added the larynx (Figure 1), an organ made of cartilage bodies (arytenoid cartilages cranially and cricoid cartilages caudally) that function as attachment sites for muscles that open the glottis (Negus 1949; Kelemen 1963). In anurans paired vocal cords extend into the lumen from the arytenoid part of the larynx and are vibrated to produce vocalisation during forced expulsion of air from the lungs (Kelemen 1963). In anurans paired vocal cords extend into the lumen from the arytenoid part of the larynx and are vibrated to produce vocalisation during forced expulsion of air from the lungs (Kelemen 1963), or during inspiration in *Bombina* (Duellman and Trueb 1994). Members of Pipidae (clawed frogs) are exceptions; they lack vocal cords but produce a clicking noise by means of the sudden popping movement of a pair of articulating cartilage disks attached to bony rods inside the larynx (Duellman and Trueb 1994). In most frogs, males possess a gular vocal sac that resonates and radiates the sound (Duellman and Trueb 1994).

Members of most families of anurans make anti-predator distress calls when disturbed (Bogert 1958). This is true even of basal taxa such as *Leiopelma* in which tympana, vocal sacs and courtship vocalisations are absent (Bogert 1958). Mesozoic anurans may therefore have made anti-predator sounds before they acquired tympanic ears. Basal crown-group frogs are known from the Upper Jurassic of Argentina (Henrici 1998), so anuran anti-predator sounds may have existed that early.

Tympanic ears and chorusing behaviour are present in the anuran clades Discoglossidae (midwife toads), Mesobatrachia (spadefoot toads, clawed frogs and their relatives) and Neobatrachia (typical frogs, tree frogs, true toads and their relatives), and therefore may be synapomorphies of higher anurans. Discoglossoids and mesobatrachians are known from Laurasia as early as the Upper Jurassic (Henrici 1998) and from Gondwana as early as the Early Cretaceous (Báez et al. 2000). Anuran chorusing therefore likely arose on those landmasses by those times. The only known Mesozoic members of Neobatrachia are South American members of Leptodactylidae from the Upper Cretaceous (Sanchiz 1998). Because no members of arboreal anuran clades are known from the Mesozoic, we can safely infer that Mesozoic anuran choruses took place at ground level.

During choruses, male anurans call to attract mates (advertisement calls) and also emit special aggressive calls in response to the loud vocalisations of nearby male neighbours (Schwartz 2001). Aggressive calls may differ qualitatively or quantitatively from advertisement calls (Schwartz 2001). Females of many anuran species prefer males whose calls are louder, delivered at higher rates, and delivered for longer periods; in fact, male anurans often increase these parameters in their own calls in response to the calls of rivals (Schwartz 2001). If such directional selection by female choice was present through anuran geological history, then Mesozoic anuran calls exhibited lower amplitude, rate and duration than extant anuran calls.

During choruses, male frogs tend to vocalise during the silences between calls of nearby conspecifics – or, for species with multi-note calls, if the songs overlap, notes are sung by one individual between the notes sung by another (Schwartz 2001). Such vocal alternation enables males to detect each other’s calls and enables females to discriminate between individual males’ calls (Schwartz 2001). If vocal alternation during anuran chorusing evolved by means of directional selection, we can safely infer that it was absent or poor in the earliest anuran choruses.

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**Table 6. Mechanisms of defensive sound production by extant salamanders (Maslin 1950).**

<table>
<thead>
<tr>
<th>Family</th>
<th>Description of sound</th>
<th>Mechanism (if known)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ambystomatidae (mole salamanders)</td>
<td>Grunt-----------------------------------</td>
<td>Laryngeal vocal cords</td>
</tr>
<tr>
<td></td>
<td>Click, kissing sound---------------------</td>
<td>Forcefully opening mouth (sound produced by breakage of moist seal around mouth)</td>
</tr>
<tr>
<td>Amphiumidae (amphiumas)</td>
<td>Whistle, peep---------------------------</td>
<td>Laryngeal vocal cords</td>
</tr>
<tr>
<td></td>
<td>Cry similar to that of a human infant</td>
<td>Forcing air through gill slits</td>
</tr>
<tr>
<td>Cryptobranchiidae (giant salamanders)</td>
<td>Bark-----------------</td>
<td>Laryngeal vocal cords</td>
</tr>
<tr>
<td>Dicamptodontidae (mole salamanders)</td>
<td>Squeak-----------------</td>
<td>–</td>
</tr>
<tr>
<td>Plethodontidae (lungless salamanders)</td>
<td>Hiss-----------------</td>
<td>–</td>
</tr>
<tr>
<td>Proteidae (mudpuppies)</td>
<td>Peep, squeak, kissing sound</td>
<td>Forcefully opening mouth (sound produced by breakage of moist seal around mouth)</td>
</tr>
<tr>
<td>Salamandridae (newts and kin)</td>
<td>Croak, hiss-----------------------------</td>
<td>–</td>
</tr>
<tr>
<td>Sirenidae (sirens)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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P. Senter
Extinct basal tetrapods with tympanic ears

Skull and the stapes morphology preclude tympana in most basal tetrapods, including basal amniotes (Reisz 1981; Carroll 1991; Laurin 1998; Clack and Allin 2004; Laurin and Soler-Gijón 2006), but there were exceptions. A rodlike stapes oriented toward a strongly embayed posterior skull notch suggests a tympanic ear in the Lower and Upper Permian taxon Seymouriamorpha (Ivakhnenko 1987), which is phylogenetically intermediate between Temnospondyli and Amniota (Laurin 1998; Laurin and Reisz 1999; Ruta et al. 2003) (Figure 4). A posterior skull embayment that suggests a tympanum is also present in the Upper Carboniferous and Lower Permian taxon Diadectomorpha (Berman et al. 1992). Diadectomorpha is phylogenetically positioned immediately outside Amniota (Laurin and Reisz 1995; Ruta et al. 2003) (Figure 4).

A reduced stapes and a posterior skull embayment that suggest a tympanum are present in most members of Parareptilia, a clade of dumpy-looking basal amniotes from the Permian and Triassic (Carroll and Lindsay 1985; Laurin and Reisz 1995; Tsuji 2006; Müller and Tsuji 2007). The embayment is absent in Mesosauridae, the most basal parareptilian group, and its presence is a synapomorphy of higher parareptiles (Laurin and Reisz 1995; Tsuji 2006). Within Parareptilia the otic embayment is particularly well developed in the Upper Permian and Triassic clade Procolophonoidae and a Middle Permian clade informally called ‘nycteroletes’ (Carroll and Lindsay 1985; Müller and Tsuji 2007). The orbits are enlarged in both groups, suggesting crepuscular or nocturnal habits, hence occupation of a visually compromised niche, to which the enhanced auditory apparatus may be functionally related (Müller and Tsuji 2007).

Taxa without tympanic ears fill the phylogenetic gaps between Seymouriamorpha, Diadectomorpha and Parareptilia, and also between these taxa and other amniote taxa with tympanic ears (Figure 4). Such ears therefore appeared independently in each group. The presence of tympanic ears in Seymouriamorpha, Diadectomorpha and Parareptilia made possible the use of airborne sounds in intraspecific communication. However, there is no certainty that it occurred. These groups may have used their tympanic ears for other functions instead of (or in addition to) intraspecific communication. Seymouriamorpha were carnivorous (Hotton et al. 1997) and may therefore have used hearing to locate prey. A prey-locating function is unlikely in the largely herbivorous clades Diadectomorpha and Parareptilia. All three taxa may have used hearing for predator avoidance, as do extant reptiles (Greene 1988).

Lower Permian Seymouriamorpha are the earliest known animals with tympanic ears that preyed on vertebrates. The earliest airborne, anti-predator sounds made by vertebrates may therefore have been directed at Lower Permian seymouriamorphs.

Turtles (Reptilia: Testudines)

Turtles and tortoises are usually silent but do occasionally make sounds by unknown means. During copulation or while chasing the female, males often make sounds that have been described as grunts, groans, moans, bellows and roars (Gans and Maderson 1973; Auffenberg 1977). Such mating sounds are little studied but are known from such a wide taxonomic spectrum of turtle families (Campbell and Evans 1972; Gans and Maderson 1973) that all extant turtles are phylogenetically bracketed by taxa known to produce mating sounds (Shaffer et al. 1997). This suggests that turtle mating sounds were present in the common ancestor of crown group turtles, which appeared in the Lower Jurassic (Rougier et al. 1995). Osteological correlates of hearing in extant turtles are also present in the Upper Triassic and Lower Jurassic family Astrapochelyidae, the sister taxon to the turtle crown clade (Gaffney and Kitching 1990). The situation is ambiguous in the Upper Triassic taxon Proganochelys, the most basal known fossil turtle, because of poor preservation in the relevant region of the skull (Gaffney 1990).

The morphology of the tympanic region of the turtle skull strongly resembles that of some parareptiles, and the same pair of bones (squamosal and quadratejugal) supports the tympanum in both groups (Carroll and Lindsay 1985; Laurin and Reisz 1995; Rougier et al. 1995; Tsuji 2006). If turtles arose from within Parareptilia (Laurin and Reisz 1995; Lee 1997a,b), then the tympanic ears of turtles are probably homologous with those of parareptiles. This introduces the possibility that parareptiles made turtle-like courtship and mating sounds, in which case such sounds may have existed as early as the Permian.

While some phylogenetic analyses of morphological data place turtles within Parareptilia (Laurin and Reisz 1995; Lee 1997a,b), others place them just outside Diapsida (Gauthier et al. 1988) or within crown Diapsida (Rieppel and deBraga 1996; deBraga and Rieppel 1997). Curiously, molecular analyses usually place them within or closely related to the diapsid taxon Archosaurus (Mannen et al. 1997; Platz and Conlon 1997; Hedges and Poling 1999; Zardoya and Meyer 2001), for which there is no documented morphological support, although one recent molecular study places turtles in a phylogenetic position compatible with parareptile status (Frost et al. 2006). If turtles are diapsids then their tympanic ears are homologous with those of other diapsids and not with those of parareptiles.

Lizards and kin (Diapsida: Lepidosauromorpha)

Within the amniote taxon Diapsida are two major clades: Lepidosauromorpha (lizards, tuataras and extinct kin) and Archosauromorpha (crocodilians, birds and extinct kin, including dinosaurs and pterosaurs) (Benton 1985) (Figure 4). Extinct diapsids basal to the clade
Lepidosauromorpha + Archosauromorpha lacked tympanic ears (Reisz 1981; Clack and Allin 2004). Extant lepidosauromorphs and archosauromorphs possess tympanic ears, except for some in which tympanic ears have been lost: snakes (Serpentes), amphisbaenians (Amphisbaenia), California legless lizards (Anniella), chameleons (Chamaeleonidae) and tuatars (Sphenodon) (Wever 1978). Most such groups are subterranean and therefore have no need for airborne hearing (Wever 1978). While most extant snakes are not subterranean, their ancestors probably were subterranean or aquatic (Apesteguía and Zaher 2006; Palci and Caldwell 2007), so their lack of tympanic ears is a vestige of ancestry.

Basal lepidosauromorphs and archosauromorphs exhibit osteological evidence of tympanic ears (posteriorly embayed quadrate, thin stapes) (Gregory 1945; Robinson 1962; Kuhn-Schnyder and Peyer 1973; Carroll 1975; Gow 1975; Evans 1980; Dilkes 1998), which suggests inheritance from a common ancestor. A recently published inference that the two lineages acquired tympanic ears separately is based on the assumption that the basal diapsid Youngina – which lacks evidence for tympanic ears – is a basal lepidosauromorph (Clack and Allin 2004). However, recent phylogenetic analyses place Youngina outside the lepidosauromorph-archosauromorph clade (Laurin 1991; Rieppel and deBraga 1996; Lee 1997a,b; Modesto and Reisz 2002; Senter 2004). Enlarged orbits in basal lepidosauromorphs and archosauromorphs (Robinson 1962; Kuhn-Schnyder and Peyer 1973; Carroll 1975; Gow 1975; Evans 1980, Evans 1991; Modesto and Reisz 2002) suggest crepuscular or nocturnal habits, an interpretation supported by the fact that a reconstructed ancestral archosaur visual pigment seems made for low light levels (Chang et al. 2002). As with parareptiles (Müller and Tsuji 2007), the enhancement of hearing in these animals may be functionally related to ancestral occupation of a visually compromised niche.

The earliest known lepidosauromorphs and archosauromorphs are from the Upper Permian (Carroll 1975; Evans and King 1993). Whether or not the two groups acquired airborne hearing independently, it was present in both by then. Anti-predator sounds directed at diapsids may therefore have appeared in the Upper Permian. The small, peglike teeth of many basal diapsids, including basal lepidosauromorphs and basal archosauromorphs, suggest a diet of invertebrates (Colbert 1970; Carroll 1975; Gow 1975; Evans 1980). Anti-predator sounds directed at Permian diapsids may therefore have included stridulation by arachnids and beetles.

The ability to hear airborne sounds allows acoustic communication, but among extant lizard families with Mesozoic records only geckoes (Gekkonidae and Eublepharidae) vocalise. Using laryngeal vocal cords, geckoes make sounds that are described as squeaks, growls and barks, which carry only for a few meters in some cases and as far as 20 m in others (Gans and Maderson 1973; Marcellini 1977). Single chirps are used for threat calls (when lunging at a predator or conspecific rival) and distress calls (upon being attacked or grasped), both in nocturnal and diurnal geckoes (Marcellini 1977). Temporally patterned multiple chirps are used by nocturnal geckoes, usually males, in intraspecific social situations (Marcellini 1977). Multiple chirps are produced at the beginning of the nocturnal activity period, and may be uttered in response to other individuals’ calls, in response to the sight of rival males, and during courtship (Marcellini 1977). Multiple chirp calls vary between species and appear to be related to spacing and territory (Marcellini 1977). The earliest known geckoes are from the Aptian-Albian (Lower Cretaceous) of Mongolia (Alifanov 1989), and it is possible that gecko calls were present then.

The lepidosauromorph taxon Sphenodontia is today represented by only one genus: Sphenodon (tuataras). Tuataras croak loudly when disturbed (Gans and Wever 1976). Sphenodontians are known from as early as the Upper Triassic (Fraser 1982). Sphenodon lacks tympana and has lost the embayment in the quadrate bone that is associated with the tympanum in lizards. The embayment is present in basal sphenodontians (Evans 1980; Fraser 1982; Wu 1994) but was lost in the lineage leading to Sphenodon by the Lower Jurassic (Reynoso and Clark 1998). The loss of tympanic ears indicates that the use of airborne sounds for intraspecific communication was not important in the lineage.

Without tympanic ears extant tuataras have trouble hearing airborne sounds over 1 kHz but can hear their own croaks, which are of appropriate frequency (Gans and Wever 1976) (Figure 3). Tuataras are not known to vocalise for intraspecific communication, but the fact that they can hear their own voices suggests that they have the equipment with which to do so, even without tympanic ears. This fact might tempt the researcher to conclude that basal, terrestrial tetrapods without tympanic ears may have used low-frequency vocalisations for intraspecific communication. However, such temptation should be resisted. The loss of the tympanum in extant reptiles results not only in a limitation of auditory sensitivity to low-frequency sounds (Figure 3), but also results in an inability to hear such sounds except at very high amplitudes (Wever 1978). Snakes are exceptions to this rule, because they can hear low-frequency sounds at low amplitudes (Wever 1978). However, the example of the snake’s ear is inapplicable to basal tetrapods, for two reasons. First, the quadrate bone of a snake’s skull (Figure 1) is so loose that it vibrates freely and has essentially become a bony tympanum (Wever 1978), whereas no posterior skull bone was loose in basal tetrapods. Second, the staples of a snake is slender and contacts the quadrate as if contacting a tympanum (Wever 1978) (Figure 1), whereas the basal tetrapod staples was a robust, solid brace between the bones of the cheek or palate and the braincase (Carroll 1986; Clack 1992).
Mesozoic marine reptiles

Stapedial and posterior skull morphology indicate retention of tympanic ears in Nothosauria, a marine archosauromorph clade from the Triassic Period (Carroll and Gaskill 1985). This indicates an ability to hear airborne sounds in these animals, despite their aquatic habits. In Plesiosauria, a Mesozoic marine taxon closely related to Nothosauria, a thin stapes suggests evolution from an ancestor with tympanic ears (Hetherington 2008). However, posterior skull morphology indicates that the tympanum was lost in Plesiosauria (Carpenter 1997; Storrs 1997; Hetherington 2008).

A tympanic notch is absent in the Mesozoic marine taxon Ichthyosauria (Maisch 1997), which may or may not be a member of Diapsida (Maisch 1997; Motani et al. 1998). The ichthyosaur stapes is robust and serves as a brace between the cheek and braincase (Hetherington 2008), as in basal amniotes (Clack and Allin 2004). This suggests that ichthyosaur ancestors never passed through a stage with tympanic ears. The lack of tympanic ears in plesiosaurs and ichthyosaurs does not necessarily mean that they were deaf to underwater sounds but does indicate a lack of importance of airborne sounds to them.

Mosasauridae, a marine family of Upper Cretaceous lizards, retained tympanic ears, but they were modified for underwater sound reception. The tympanum was often ossified, increasing resistance to rupture in deep water (Russell 1967). The middle ear cavity was encased in bone and lacked acoustic isolation from the rest of the skull, allowing the skull to conduct sound to the middle ear (Hetherington 2008). Underwater hearing was therefore apparently important to mosasaurs. It is impossible to know, however, whether mosasaur hearing was of importance in prey localisation, avoidance of dangerous animals emitting honest sonic warnings, intraspecific communication, or a combination of factors.

Crocodilians and kin (Archosauromorpha: Archosauria: Crurotarsi)

Basal diapsids appear to have been insectivorous, but the serrated, ziphodont teeth of the archosauromorphp clade Archosauromorphae indicate a switch to a diet of vertebrates (Senter 2003). Archosauromorphs exploded in diversity in the Triassic Period but at least one of its basal members was present in the Upper Permian (Hughes 1963). Antipredator sounds from vertebrates, directed at archosauriforms, may therefore have been present that early.

Members of Archosauromorpha, the archosauriform crown clade, are known from as early as the Middle Triassic (Sereno 1991). Archosauromorpha includes two major lineages, Crurotarsi and Ornithodira (Sereno 1991) (Figure 4). Crurotarsi includes crocodilians (Crocodileia) and several extinct, mostly Triassic taxa (Sereno 1991). Ornithodira includes dinosaurs (Dinosauria) – including birds (Aves) – and pterosaurs (Pterosauria) and a few other extinct forms (Sereno 1991). The vocal organ in extant members of Crurotarsi (crocodilians) is the larynx, whereas in extant members of Ornithodira (birds) it is the syrinx. Because the larynx and syrinx are not homologous, it is most parsimonious to infer that vocalisation arose independently in the two lineages, in which case their common ancestor lacked vocal ability.

Crocodilians vocalise by vibrating three mucosal folds – absent in the avian larynx (McLelland 1989a,b) – that project into the laryngeal lumen under part of the arytenoid cartilage (Reese 1914). Unlike the avian syrinx (see below), the crocodilian vocal organ leaves no trace of its presence on fossil skeletons, so it is impossible to know whether vocalisation was present further down the crurotarsian tree than Crocodylia. We therefore cannot know whether the Triassic and Jurassic Periods were filled with the roaring of basal crurotarsians.

On the other hand, we can infer that the homologous acoustic behaviours of gharials (Gavialidae), crocodiles (Crocodylidae), alligators and caimans (Alligatoridae) were present in their common ancestor (Senter 2008), which appeared in the Upper Cretaceous (Brochu 2003). Juvenile crocodilians of all three groups squeak or grunt when disturbed, sometimes even from within the egg if the nest is disturbed, and the sound attracts adults (Modha 1967; Whitaker and Basu 1982; Cintra 1989; Whitaker and Whitaker 1989). Adult males of all three groups engage in head-slapping, in which the head is raised and then slammed downward onto the water’s surface to create a loud splash that is often followed by a hiss in gharials or a roar in alligators and crocodiles (Garrick et al. 1978; Whitaker and Basu 1982; Thorbjarnarson 1991; Thorbjarnarson and Hernández 1993). The head-slap is used in displays of presence and dominance and in courtship (Garrick et al. 1978; Thorbjarnarson 1989; Whitaker and Whitaker 1989). Courtship in gharials, alligators and crocodiles also involves geysering (shooting jets of water upward from the nostrils, which are held just below the surface) and blowing bubbles in the water with the mouth (Garrick et al. 1978; Whitaker and Basu 1982; Thorbjarnarson 1989; Whitaker and Whitaker 1989; Thorbjarnarson and Hernández 1993). Narial geysering is also used as a territorial display (Modha 1967; Garrick et al. 1978). Territorial fights between crocodilian males often involve loud splashing as bodies are hurled against each other (Modha 1967; Singh and Rao 1990).

The above are all water-based behaviours that would obviously have been absent in the terrestrial precursors of Crocodylia. Aquatic or semi-aquatic habits are characteristic of a large clade, Neosuchia, which includes Crocodylia and several extinct Mesozoic taxa (Clark 1994). If the aquatic acoustic behaviours of crocodilians were present further down neosuchian
phylogeny, they may have been present as early as the Upper Jurassic, from which the earliest non-marine neosuchians are known (Carroll 1988).

Most phylogenetic analyses place the marine taxon Thalattosuchia within Neosuchia (e.g. Clark 1994; Ortega et al. 2000; Sereno et al. 2001; Company et al. 2005). Thalattosuchians, known from as early as the Lower Jurassic (Carroll 1988), had narrow snouts (Clark 1994). Thalattosuchian head-slapping, if it occurred, would therefore have been weak for the sake of protecting the narrow snout, as in the extant gharial (Whitaker and Basu 1982). Snouts were wider in most other extinct neosuchians (Clark 1994), allowing strong head-slaps.

Head-slaps, if present, would have been particularly impressive in the gigantic taxa Sarcosuchus and Deinosuchus, in each of which head length approached 2 m (Sereno et al. 2001; Schwimmer 2002). Sarcosuchus is a neosuchian from the Lower Cretaceous (Aptian-Albian) of western Africa (Sereno et al. 2001), and Deinosuchus is an alligatoroid from the Upper Cretaceous (Campanian) of North America (Schwimmer 2002). Deinosuchus is more certain than Sarcosuchus to have employed head-slapping behaviour because Deinosuchus lies within Crocodylia (Sereno et al. 2001), whereas Sarcosuchus does not (Sereno et al. 2001). Also, Sarcosuchus is phylogenetically bracketed by narrow-snouted forms (Sereno et al. 2001), which increases the likelihood that head-slapping behaviour, if present that far back in neosuchian phylogeny, was lost or weakened in the clade that includes Sarcosuchus.

Members of Alligatoridae (alligators and caimans) employ both head-slapping and a vocal acoustic advertisement display called bellowing (Garrick 1975; Garrick et al. 1978; Gorzula and Seijas 1989). Male and female alligatorids bellow to advertise presence. Bellowing is contagious and its sound is sexually dimorphic (Garrick 1975; Garrick et al. 1978). Alligatoridae is unknown before the Cenozoic (Brochu 2003), but other members of Alligatoroidea, the larger taxon that includes Alligatoridae but excludes Crocodyliidae and Gavialidae, were present in North America as early as the Campanian (Upper Cretaceous) (Brochu 1999). If basal alligatoroids bellowed, then the sound may have been present in the Upper Cretaceous.

**Birds and kin (Archosauromorpha: Ornithodira)**

The syrinx of birds (Ornithodira: Aves) is a series of cartilage rings at the junction of the trachea and primary bronchi, with membranous folds that protrude into the lumen and can be vibrated to produce sound (Brackenbury 1989; King 1989). Vocal production by the syrinx depends on the presence of a clavicular air sac (Brackenbury 1989), a soft structure that invades and pneumatises the bones of the avian pectoral girdle and limb, marking its presence with a characteristic opening on the humerus (McLelland 1989a,b). Such an opening is present in members of the avian clade Ornithothoraces – which includes modern birds and the Lower and Upper Cretaceous taxon Enantiornithes (Chiappe and Walker 2002) – but not in birds basal to Ornithothoraces (Chiappe et al. 1999; Zhou and Zhang 2003).

The clavicular air sac does not develop individually but instead represents a fusion of outgrowths from two pre-existing air sacs and a pair of outgrowths from the lungs. The four outgrowths do not meet in the midline, in the vicinity of the syrinx, until late in embryology (Locy and Larsell 1916). The status of the clavicular air sac as an outgrowth of pre-existing structures, two of which are other air sacs, suggests that it is a later evolutionary acquisition than the original set of ornithodiran air sacs. This is consistent with the interpretation that it arrived relatively late in ornithodiran history. Evidence exists that non-avian ornithodirans, including basal birds, possessed other air sacs homologous with those of birds (Britt et al. 1998; O’Connor 2006; Wedel 2006), but not the clavicular air sac. Outside Ornithothoraces, humeral pneumatisation is present in Pterosauria (O’Connor 2006) but not in the many intervening dinosauromorph taxa (Britt 1997). Humeral pneumatisation in pterosaurs is therefore not homologous with that of birds and so is not evidence for the presence of a clavicular air sac homologous with that of birds. Pneumatisation of the furcula is present in the allosauroid theropod *Aerosteon riocoloradensis*, suggesting the presence of a clavicular air sac (Sereno et al. 2008). However, such a sac is not likely homologous with that of ornithothoracine birds because its osteological indicator (furcular pneumatisation) is absent in phylogenetically intermediate taxa, including other allosauroids (Chure and Madsen 1996), basal birds (Chiappe et al. 1999; Zhou and Zhang 2003; Mayr et al. 2007) and non-avian coelurosaurian theropods (Norell et al. 1997; Makovicky and Currie 1998; Clark et al. 1999; Xu and Norell 2004). Without evidence for a clavicular air sac homologous with that of birds, we should not presume that basal birds and non-avian ornithodirans possessed a functioning syrinx.

The lack of evidence of a syrinx in ornithodirans outside Ornithothoraces will, no doubt, disappoint fans of roaring movie dinosaurs. However, lack of ability to vocalise does not necessarily mean that such animals were silent altogether. Many extant reptiles communicate with each other and with potential predators by non-vocal acoustic means such as hissing, clapping jaws together, grinding mandibles against upper jaws, rubbing scales together, or use of environmental materials (e.g. splashing against water) (Campbell and Evans 1972; Gans and Maderson 1973; Garrick et al. 1978; Thorbjarnarson and Hernández 1993). Birds also use non-vocal acoustic means of communication such as hissing, bill-clapping, stamping and wing beating (Welty and Baptista 1988; Kear 2005; Nelson 2005). Non-avian theropods with feathered wings may have beaten their wings in acoustic displays as extant...
birds often do. Sauropod dinosaurs of the family Diplodocidae, known from the Upper Jurassic of North America and Africa (Upchurch et al. 2004), possessed whiplike tail tips that could have produced loud, whiplike cracking sounds for intraspecific communication or in response to predators (Myhrvold and Currie 1997).

The morphology of the nasal passage in Lambeosaurinae, a Laurasian clade of Upper Cretaceous ornithischians (Horner et al. 2004), suggests a role in sonic resonance (Weishampel 1981). However, resonance need not be for vocal sounds. Some extant snakes lack vocal cords but possess resonating chambers that emphasise the low frequencies of the hiss (Young 1991). The variety of visual display structures in pterosaurs and dinosaurs (Chapman et al. 1997; Molnar 2005; Unwin 2006) shows that visual communication was important to these animals. They may therefore have relied largely on visual means of communication. Extant precedent for such reliance is found among lizards, in which non-chemical communication is primarily visual (Pough et al. 1998), despite their excellent hearing (Wever 1978).

Members of a few extant bird orders are known from before the Cenozoic. Members of Anseriformes (waterfowl) are known from the latest Cretaceous (Campanian-Maastrichtian) of Asia, North America and Antarctica (Hope 2002; Clarke et al. 2005). Several acoustic behaviours are taxonomically widespread within Anseriformes and may be behavioural symplesiomorphies of the group: near-constant contact calls of low amplitude among groups, pairs or parents and offspring; a loud duet called a triumph display by a pair after an agonistic encounter; a special greeting call; a special post-copulatory call; a special alarm call; calling during takeoff and throughout flight; defensive hissing and among juveniles, special distress calls, begging calls and calls expressing sleepiness (Kear 2005). Vocal pitch usually differs between the sexes and is higher in juveniles than adults (Kear 2005).

Members of Galliformes (game birds) are known from the latest Cretaceous (Campanian-Maastrichtian) of North America (Hope 2002). Several acoustic behaviours are taxonomically widespread within Galliformes and may be behavioural symplesiomorphies of the group: frequent utterance of contact calls of low pitch and amplitude among aggregations and pairs; a loud, far-carrying, often multi-syllable advertisement call by the male that is often answered by the female to form a vocally dimorphic duet (You & Currie 1997); and a loud, rapid, multi-syllable call that differs from the usual alarm call, upon takeoff when flushed (Jones et al. 1995; Madge and McGowan 2002). Anseriformes and Galliformes together form the clade Galloanserae, which is the sister clade to all other extant birds except ratites and tinamous (van Tuinen et al. 2000). The frequent occurrence in both Anseriformes and Galliformes of duetting and near-constant, low-amplitude contact calls suggests that they may be behavioural symplesiomorphies for Galloanserae and therefore were present in the Cretaceous.

Members of Gaviiformes (loons) are known from the latest Cretaceous (Maastrichtian) of South America (Hope 2002). Loons emit trains of clucking sounds during flight and a variety of calls in other situations (Oberholser 1974). Far-reaching, drawn-out advertisement calls known as wails or yodels are produced at dawn and dusk during the breeding season (Oberholser 1974). In most loons takeoff involves much noise because a loon has to run along the water’s surface for a long distance to become airborne, and landing may involve a powerful splash (Oberholser 1974).

Members of the extant family Phalacrocoracidae (cormorants, order Pelecaniformes) are known from the latest Cretaceous (Maastrichtian) of Asia and North America (Hope 2002). Several acoustic characteristics and behaviours found in cormorants are widespread in Pelecaniformes and may be behavioural symplesiomorphies for the group. These include general silence away from the nesting colony except for loud communal fishing calls; high-pitched begging calls from chicks; sexual dimorphism in voice; emission of hisses and special disturbance calls during nest-usurpation attempts; copulatory vocalisations and the ability to recognise the voices of offspring and neighbours (Nelson 2005). Other acoustic characteristics that are typical of cormorants but not other pelecaniformes include squeaky complaint calls from chicks when disturbed; loss of the female voice after five to six weeks; growling or loud barks by males in nest defense; and a display by the male when advertising for a female in which he throws his head back and makes neighing or gargling sounds and follows this with ‘Goww, goww, goww,’ if the female approaches (Nelson 2005).

Some fragmentary Upper Cretaceous (Maastrichtian) bird specimens have been referred to Charadriiformes (shorebirds) and Psittaciformes (parrots), but these assignments are doubtful (Hope 2002). We therefore cannot confidently infer that typical shorebird or parrot calls were present before the Cenozoic.

Among extant birds, the vocabularies of basal groups – ratites, tinamous, waterfowl, and galliforms – tend to be differentiated at least into loud advertisement calls, soft contact calls, special alarm calls, and (in Ratitae and Anseriformes) the use of hissing as a threat (Jones et al. 1995; Davies 2002; Madge and McGowan 2002; Kear 2005). Such differentiation also occurs in more derived groups (e.g. Nelson 2005) and therefore may be symplesiomorphic for Neornithes, the clade that includes all birds phylogenetically bracketed by the extant bird orders. The earliest known neornithean birds are from the Upper Cretaceous (Campanian) (Hope 2002), at which time the differentiation was probably present.

Extant bird vocalisations vary in pitch according to body size, with smaller birds emitting vocalisations of higher
frequency (Welty and Baptista 1988). Avian body size is also correlated with the range of frequencies detectable by the inner ear, with smaller birds capable of detecting higher frequencies (Gleich et al. 2004). There is no reason to expect that the same was not true of Mesozoic birds.

Whether or not Mesozoic birds sang is at least partly a semantic issue. According to the technical definition, an avian advertisement call is considered a ‘song’ if it is acoustically complex, multi-syllabic, and exhibits shorter pauses between notes than the pauses between groups of notes (Welty and Baptista 1988). In practice, however, avian advertisement vocalisations are called ‘songs’ if they issue from the mouths of songbirds (Passeriformes), doves (Columbiformes) or tinamous (Tinamiformes), whether or not they are complex or multi-syllabic. This is probably because the advertisement vocalisations of these taxa have a quality that is musical to human ears. The less pleasant (to humans) advertisement vocalisations of other bird taxa are considered ‘calls’ rather than ‘songs,’ despite their similar function and the fact that in some taxa (e.g. galliforms and loons) they fit the technical definition of ‘song.’ In any case, Mesozoic bird sounds probably lacked musical quality because songbirds, doves and tinamous lack Mesozoic records (Unwin 1993; Boles 1995), and musical vocalisations are not the norm in other birds.

**Mammals and kin (Amniota: Synapsida)**

The amniote clade Synapsida includes mammals (Mammalia) and their extinct relatives. Basal synapsids (‘pelycosaurs’) lacked tympanic ears (Carroll 1986). The bones that support the tympanum in mammals and connect it with the stapes are homologous to the posterior bones of the mandible and jaw joint in other synapsids (Allin 1986; Luo and Crompton 1994). In the synapsids most closely related to mammals these bones became smaller and less solidly attached to the anterior mandible (Allin 1986; Crompton and Hylander 1986). In basal mammals – and possibly in *Hadrocodium*, the genus most closely related to mammals (Luo et al. 2001) – these bones detached from the mandible and became incorporated into the middle ear (Wang et al. 2001). This specialisation was present by the Middle Jurassic at the latest (Kielan-Jaworowska et al. 2004), and by the Lower Jurassic if it was present in *Hadrocodium* (Luo et al. 2001). It indicates definitive evidence for tympanic hearing, hence the possibility of acoustic communication, in the earliest mammals. The earliest mammals and their predecessors were probably nocturnal (Crompton et al. 1978), so their evolution of airborne hearing may have been functionally related to their occupation of a visually compromised niche.

The possibility of tympanic hearing in synapsids intermediate between ‘pelycosaurs’ and mammals has received attention. There are strong osteological indicators that these animals lacked a tympanum posterior to the quadratojugal such as diapsids possess (Luo and Crompton 1994). Some researchers have suggested that a mandibular tympanum was present in derived Permian and Triassic synapsids with a posterior mandibular cleft bordered by bones homologous to those that contact the mammalian tympanum (e.g. Allin 1986). However, three lines of evidence support the absence of a tympanum outside a derived synapsid clade that appeared in the Upper Triassic. That clade, hereafter called the DS (derived synapsid) clade for concision, includes mammals and their extinct outgroups Morganucodonta and Tritylodontida (Figure 4). First, the synapsid homologue of the cochlea retained its plesiomorphic, globular shape in other synapsids (Allin 1986) but became elongated, indicating increased auditory acuity, in the DS clade (Vater et al. 2004). Second, osteological evidence suggests that the posterior mandibular bones were muscle attachment sites in other synapsids but not in the DS clade, and the attachment of muscles would have impeded transmission of vibrations from a tympanum (Kemp 2005). Third, the attachment of the posterior mandibular bones was solid, impeding transmission of vibrations from a tympanum, in other synapsids but was loose, facilitating transmission of vibrations, in the DS clade (Crompton and Hylander 1986).

The same three lines of evidence also suggest an increase in auditory acuity at the base of the DS clade. However, they do not demonstrate the presence of tympana. New osteological evidence from a particularly well-preserved skull of *Chiniquodon*, a non-mammalian member of the DS clade, shows that the posterior mandibular bones were acoustically isolated from the anterior mandible and were free to vibrate as a unit about their collective longitudinal axis in response to low-frequency airborne sound (Kemp 2007). However, the arrangement of the rest of the skull bones precludes the presence of an air-filled tympanic cavity, without which a tympanum is pointless (Kemp 2007). Basal members of the DS clade could therefore hear airborne sounds but only at low frequencies (Kemp 2007).

Extant mammals of all three clades – Monotremata (egg-laying mammals: echidna and platypus), Metatheria (marsupials) and Eutheria (placental mammals) – vocalise using vocal cords in the larynx. Their common ancestor, which appeared in the Middle Jurassic (Kielan-Jaworowska et al. 2004), therefore presumably also could vocalise with laryngeal vocal cords. It is uncertain how much, if any, further back in synapsid phylogeny vocal cords were present. Venomous hindlimb spurs are plesiomorphic for the clade that includes Mammalia and its close outgroup Docodonta (Hurum et al. 2006), which phylogenetically bracket Lower Jurassic taxa (Kielan- Jaworowska et al. 2004). If proto-mammals employed acoustic ‘honest warnings’ to predators, as do many insects and amphibians (Masters 1979; Duellman and Trueb 1994), vocal cords may have been present as far
back as the common ancestor of Docodonta and Mammalia in the Lower Jurassic.

In monotremes and the extinct basal mammalian clade Multituberculata, the cochlea is more elongated than in more basal synapsids, indicating that a wider range of frequencies can be heard; even so, monotreme auditory acuity is poor, with a peak at 5 kHz and low ability to hear low-amplitude sounds (Vater et al. 2004). Therefore, in Mesozoic mammals of this grade, any vocalisations used in intraspecific communication likely exhibited low pitch. In contrast, the cochleae of therian (marsupial and placentual) mammals are extremely elongated and coiled, allowing hearing through wide frequency ranges even at low amplitudes (Vater et al. 2004). The frequencies of peak sensitivity for therian ears vary inversely according to body size, with the largest therian ears sensitive to infrasound and the smallest sensitive to ultrasound (Long 1994) (Figure 1). Therefore, in Mesozoic therians, vocalisations used in intraspecific communication likely were of higher pitch in small species and of lower pitch in larger species.

The monotreme and marsupial vocal apparatus is poor, due to fusion of the thyroid cartilage (a mammalian apomorphy) of the larynx with the cricoid cartilage and the possession of primitive laryngeal musculature (Negus 1949; Kelemen 1963). Perhaps because of this, monotreme and marsupial vocal sounds are generally simpler than those of placental mammals, and their vocabularies are smaller. Cooing, purring and snuffing sounds of unclear significance are known in echidnas (Tachyglossidae) (Hutchins 2004). Platypuses (Ornithorhynchus) growl when disturbed, and the female emits pre-copulatory squeaks that are answered by the male; juveniles make squeaking contact calls to each other during play and are also known to hiss (Tembrock 1963; Griffiths 1978). Marsupial vocabularies often include courtship vocalisations, aggressive vocalisations, and hissing as a defensive sound, although in some taxa defensive sounds are vocal (Nowak 2005). More extensive vocalities exist in the marsupial genus Macropus (true kangaroos), but this is probably related to eusociality, a trait characteristic of Macropus and uncharacteristic of marsupials in general (Menkhorst and Knight 2004). It is therefore doubtful that complex vocabularies existed among Mesozoic marsupials.

Stem-group marsupials are known from as early as the Lower Cretaceous (Aptian-Albian) (Kielan-Jaworowska et al. 2004), but no member of the marsupial crown group is known from before the Cenozoic (Rougier et al. 1998). None of the vocalisations characteristic of extant marsupial families can therefore be inferred to have existed before the Cenozoic. However, the fact that vocabularies are differentiated into different vocalisations for different situations in both platypuses and marsupials suggests that such differentiation is an ancient trait. Vocal differentiation may therefore have been present in the common mammalian ancestor in the Middle Jurassic.

Also, the possibility of behavioural homology of defensive hissing in marsupials and reptiles suggests that hissing was a typical defensive behaviour through the synapsid ancestry of mammals.

In placentual mammals the thyroid cartilage has detached from the cricoid cartilage (Figure 1) and the laryngeal musculature is elaborated, so the eutherian larynx facilitates more elaborate vocalisation than is possible in monotremes and marsupials (Kelemen 1963). Perhaps because of this the vocabularies of placentual mammals tend to be larger than those of monotremes and marsupials and can convey information about a wider variety of situations and emotional states (Estes 1991). The earliest known placentual mammals are from the Lower Cretaceous (Barremian) (Ji et al. 2002), and complex vocabularies may have existed among placental mammals that early.

One extant placental order, Soricomorpha (shrews, tenrecs, hedgehogs and kin), is known from the Mesozoic (Kielan-Jaworowska et al. 2004). Echolocation, clicking sounds, defensive hissing and aggressive squeaking are common and taxonomically widespread in extant soricomorphs (Nowak and Paradiso 1983). If these are ancestral acoustic behaviours for Soricomorpha, they were present before the Cenozoic. Soricomorphs are known from as early as the Coniacian (Upper Cretaceous) of Asia and the Campanian (Upper Cretaceous) of North America (Kielan-Jaworowska et al. 2004).

Other extant placental orders are unknown before the Cenozoic, but members of some extant placental supraordinal taxa are present. Basal members of Archonta, which includes the orders Dermoptera (colugos), Chiroptera (bats) and Primates (primates), are known from the latest Cretaceous (Maastrichtian) of India (Kielan-Jaworowska et al. 2004). Basal members of the supraordinal taxon Ungulatomorpha (hoofed mammals) are known from as early as the Upper Cretaceous (Turonian) of Asia and the latest Cretaceous (Campanian-Maastrichtian) of Europe and South America (Kielan-Jaworowska et al. 2004). Sounds made by extant archontans and ungulatomorphs are too varied across taxa (Hill and Smith 1984; Estes 1991) to infer ancestral acoustic behaviour for either group. Basal members of Ferae, which includes the order Carnivora and a few extinct orders, are known from the latest Cretaceous (Campanian-Maastrichtian) of North America (Kielan-Jaworowska et al. 2004). Sounds made by extant carnivorans vary, but three types of sounds are common to so many members of so many carnivoran families that they may be plesiomorphic for Carnivora or perhaps even Ferae: low-pitched growling to communicate threat, high-pitched vocalisations in response to physical pain, and high-pitched distress and contact calls from juveniles (Estes 1991).

Drumming with the hind feet on the substrate is a common method to communicate alarm or the presence of danger among mammals with hindlimbs that are specialised for saltatory locomotion (hopping). This method has
appeared congrengently in Macropodidae (kangaroos and their saltatory relatives), Macroscelididae (elephant shrews), Leporidae (rabbits), Dipodidae (jerboas) and Dipodomys (kangaroo rats) (Nowak and Paradiso 1983; Menkhorst and Knight 2004). It is probably no coincidence that this form of communication is prevalent among mammals of this morphotype and that in all cases it transmits the same type of information. Theoretically, a novel reflexive behavior in response to a given stimulus could most easily evolve by modification of a preexisting reflexive behavior involving the same set of muscles in response to the same stimulus. An oscillatory hindlimb motor reflex (drumming) in response to danger might therefore most easily evolve in mammals that already have a preexisting oscillatory hindlimb motor reflex (hopping) in response to danger. Because of its prevalence among saltatory mammals, it is possible that this method of acoustic communication of alarm/danger was present in Zalambdalestes, a saltatory placental mammal from the Upper Cretaceous (Campanian) of Mongolia (Kielan–Jaworska 1978).

Directions for further research

Rigorous analysis is needed to determine whether the potential acoustic behavioral homologies proposed here within Aves and Mammalia meet tests of homology. It would also be informative to compare aspects of vocalisation across anuran, avian and mammalian phylogeny to determine whether or not it is possible to infer ancestral characteristics of vocal sounds in each group. It would also be informative to study inner ear endocasts of more fossil archosaurian and synapsid taxa to determine hearing ranges, as has been done for a few taxa (Gleich et al. 2004; Vater et al. 2004). In addition, it would be interesting to study sound-producing structures across the phylogeny of ray-finned fishes to determine whether homologies in acoustic anatomy can be assessed.

The big picture

The evidence and inferences presented above suggest that the questions posed in this paper’s opening paragraph can be answered. Triceratops and indeed even the earliest dinosaurs heard crickets chirping in the evening. The Mesozoic treetops did not resound with frogsong, although Upper Jurassic and Cretaceous bodies of water did. Cretaceous treetops were filled with the sounds of honking, cackling and wailing birds in what must have been an awful cacophony that would not become sweet and musical until the advent of songbirds, doves and tinamous in the Cenozoic. The immense corpses of sauropods were surrounded with the buzzing of legions of bottle flies, but not until the Upper Cretaceous.

In addition to such tidbits, a larger paleobioacoustical scenario emerges from the pooled information presented here (Figure 6). Incidental animal sounds were probably present in the oceans by the beginning of the Paleozoic Era, but those sounds were not heard (except perhaps by cephalopods) until much later. The first terrestrial arthropod communities arose in the Silurian Period, and defensive stridulation in terrestrial arthropods may have appeared soon thereafter. In the Silurian Period cartilaginous and bony fishes appeared, and each independently acquired the ability to hear low-frequency water-borne sounds. Parallel evolution of defensive, aggressive and courtship sounds is rampant among ray-finned fishes and may have begun in the Silurian or Devonian. Malacostarcan crustaceans also appeared in the Devonian, and several lineages evolved defensive stridulation in parallel, possibly in response to predation by fishes with underwater hearing. Bony fishes and early tetrapods of the Silurian and Devonian Periods engaged in noisy air-breathing without fear of being overheard by predators, because no vertebrate had yet acquired tympanic ears.

Tetrapods exploded in diversity in the Carboniferous Period. Amniotes appeared in the Pennsylvanian and employed defensive displays that incorporated body inflation as a visual signal. The resulting hissing sound was first heard by seymouriamorph predators in the Lower Permian and by archosauriform predators in the Upper Permian. Arthropod defensive stridulation was heard by diapsid predators for the first time in the Upper Permian, although the mechanical vibrations produced by stridulation may have deterred other tetrapod predators as early as the Mississippian.

An explosion of terrestrial sound appeared in the Triassic Period. Low-frequency twilight choruses may already have existed among ray-finned fishes, but the earliest terrestrial twilight choruses appeared in the Triassic with the advent of crickets and their mesoedicid and titanopteran relatives. The drumming of stoneflies appeared in the Middle Triassic. The hemipteran taxon Prosorrhyncha appeared in the Upper Triassic and radiated into several lineages that evolved defensive and courtship stridulation in parallel. Turtles first appeared in the Upper Triassic; their courtship sounds may have appeared soon thereafter, or those sounds may be evolutionary continuations of courtship sounds that were present in parareptiles from perhaps as early as the Permian.

Water boatmen joined the twilight chorus in the Lower Jurassic, and anurans joined it in the Upper Jurassic. Venomous mammals began making defensive vocalisations in the Lower Jurassic. Tympanic ears appeared in mammals by the Middle Jurassic and may have been used to locate (chorusing?) insect prey. The tapping of booklice, the buzzing of aculeate wasps, and tail-cracking sounds by diplodocid sauropods appeared in the Upper Jurassic.

In the Lower Cretaceous, geckoes and birds joined the twilight chorus. The tapping of death-watch beetles and
termite soldiers, and the buzzing of horseflies, bottle flies and mosquitoes appeared. Mammalian vocalisations increased in pitch as therians gained the ability to hear high-frequency sounds. In the Upper Cretaceous, cicadas and head-slapping crocodilians joined the twilight chorus, along with birds from a few extant orders. The buzzing of bottle flies and the echolocating chirps of soricomorph mammals also appeared, possibly along with the growling of angry basal members of Ferae. High-frequency fish sounds appeared with the advent of hearing-specialist fishes.

This scenario is unlikely to be the last word on Paleozoic and Mesozoic animal sounds. Future discoveries will augment, hone and perhaps even falsify hypotheses put forth here. It is my hope that this synthesis will stimulate more research on the voices of the past.

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