changes in the emissions of carbon dioxide. Such actions need to be supported by a good understanding and prediction of the climate role of black carbon. Writing in the *Journal of Climate*, Sand *et al.*[3] report climate simulations that provide insights into these issues. The results highlight challenges for upcoming international initiatives aimed at better understanding how the climate responds to changes in the composition of the atmosphere.

Sand and colleagues used a numerical simulator of Earth's atmosphere and ocean to compare the effects on climate of artificially large increases in the emission of carbon dioxide and black carbon. They find that, although the increases were designed to exert similar perturbations in Earth's energy budget (the net flow of incoming and outgoing energy), changes in the planet's surface temperature and rainfall are considerably weaker in the simulation with elevated concentrations of black carbon.

This result confirms the importance of rapid responses in the atmosphere to changes in black carbon. These responses manifest themselves as warming at height and changes in cloud properties that lead to a net decrease in mid- and high-level cloud (Fig. 1). Moreover, they act to offset the initial artificially large perturbation, mainly because the warming and cloud loss at altitude effectively radiate energy to space, before the surface climate is able to respond. However, the magnitude of the rapid responses reported by Sand *et al.* — roughly seven times stronger than those to carbon dioxide — will come as a surprise to many climate scientists.

The researchers also highlight another result, which has implications for numerical simulations of climate change. By using a pair of experiments, both of which explore the climate impacts of black carbon and differ only in whether black-carbon changes can also adjust to atmospheric-circulation responses, Sand *et al.* demonstrate the role of the two-way black carbon–atmosphere interactions in driving the full climate response. Their findings are unexpected because these interactions seem to be the dominant cause of the climate response to changes in black carbon. The change in global surface temperature varies by a factor of two between the two experiments, with considerably larger differences at altitude. Indeed, many rainfall responses appear only when feedbacks of black carbon-to-atmosphere-to-black carbon are included.

The authors point out that the feedback loop of black carbon to itself through changes in climate may be particularly strong in their simulations because their model contains an unusually active atmospheric convection. Moreover, this strength may be exacerbated further by the artificially large perturbation imposed. Experiments with other numerical models may find weaker responses. Nevertheless, the large differences in the climate impacts of black carbon, when its two-way interaction with meteorology is also included, may make it harder to determine black carbon's full climate impact.

The various groups of climate scientists each focus on specific aspects of the climate system to better understand the effects of atmospheric changes. For those who work on atmospheric particulates, such as black carbon, an important aim is to quantify the particulates' impact on Earth's energy budget. A largely separate community studies atmospheric feedbacks, such as convection and clouds. Plans are already under way to design climate-model experiments under the Coupled Model Intercomparison Project, Phase 6 (ref. 4), which will provide improved knowledge of future climate responses and feed results to the next assessment report of the Intergovernmental Panel on Climate Change. Contributions to several of these experiments will either prescribe a fixed meteorology to explore the impacts on Earth's energy balance, or use fixed concentrations of atmospheric particulates to explore atmospheric feedbacks.

Such a pragmatic approach enables groups to concentrate resources on particular aspects of the climate-change problem and gain better insight into the processes involved. However, Sand and co-workers' findings suggest that when it comes to understanding the full climate impact of black carbon, it will be crucial to account for both how black carbon influences atmospheric circulation and also how these changes feed back on the atmospheric distribution of black carbon. This highlights the risk of simplified or idealized approaches, which may produce misleading conclusions about the total climate impact of changes in black-carbon concentrations. ■

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EVOLUTIONARY BIOLOGY

The origin of terrestrial hearing

A study of the African lungfish reveals that it has a rudimentary ability to detect pressure waves caused by sound. The finding expands our knowledge of how hearing evolved in early tetrapods, the first vertebrates to have limbs and digits.

JENNIFER A. CLACK

A long-standing problem in the evolution of land vertebrates has been how they evolved to detect sound. Lungfishes are the closest living relatives of tetrapods (vertebrates that have limbs and digits), and so may help to provide an answer. Until recently, however, there have been few investigations into lungfish hearing. Writing in the *Journal of Experimental Biology*, Christensen *et al.*[1] report their findings about whether the African lungfish *Protopterus annectens* can detect sound, casting fresh light on our understanding of the hearing capabilities of the earliest tetrapods.

The earliest tetrapods seem not to have had a specialized apparatus that would enable terrestrial hearing[2], so to what extent could they pick up air-borne sound as they came onto land? Although there have been many studies of the hearing capacities of ray-finned fishes (actinopterygians), how relevant these findings are to early tetrapods has remained unclear, because ray-finned fishes are a separate branch of bony fishes (osteichthyans) from the lobe-finned fishes (sarcopterygians), the group to which tetrapods and lungfishes belong.

Lungfishes have no obvious adaptations for hearing — that is, they have no middle-ear cavity or a bone equivalent to the stapes bone in tetrapods, through which sound could be conveyed to the inner ear. However, they do have paired lungs, and Christensen and co-workers find that these are key to enabling the lungfish to detect sound.

Overcoming the obstacles to investigating sound detection by fishes is not simple. Ideally, the experiments should be done in open water to avoid the influence of the experimental set-up on the characteristics of the sound field. However, a sound field that can reasonably be used to examine the different aspects of fish hearing[3,4] can be established by creating a standing wave in a metal tube.

By placing lungfish at different locations within the tube, Christensen and colleagues

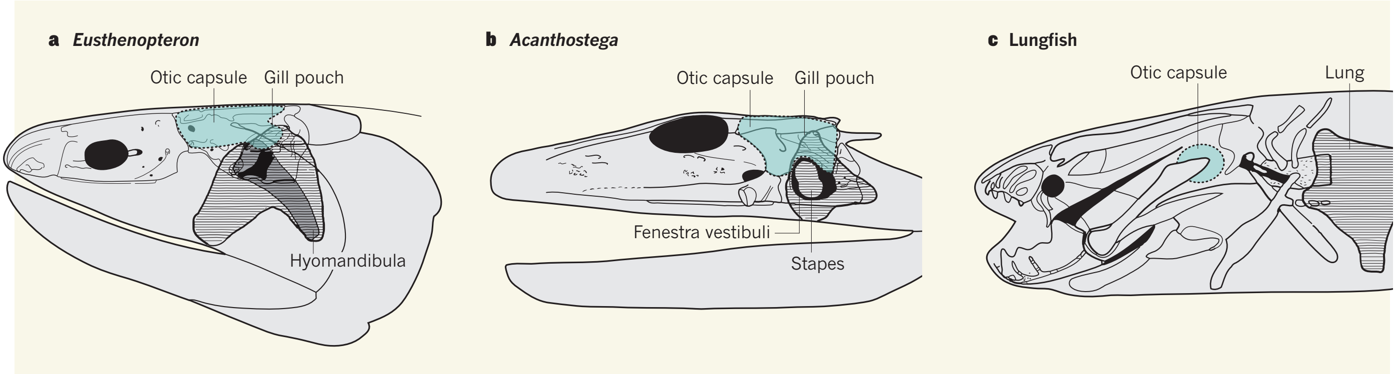

Figure 1 | Evolution of the hearing apparatus in tetrapods. **a**, In the extinct lobe-finned fish *Eusthenopteron*, a bone called the hyomandibula is associated with an air-filled gill pouch and articulates with the otic capsule (the ear region) to control movements of the lower jaw and other parts of the head and throat. **b**, *Acanthostega* is intermediate between lobe-finned fishes and the first tetrapods that were fully capable of coming onto land. A bone called the stapes (formed in part from a reduced-size hyomandibula) penetrates the otic capsule through an opening called the fenestra vestibuli. The stapes could transmit vibrations emanating from sound-induced pressure changes in the air-filled gill pouch to the otic capsule. **c**, Christensen *et al.*[1] report that the modern African lungfish, *Protopterus annectens*, uses its lung to transmit sound vibrations to the otic capsule, and provides a model for hearing in early tetrapods. (**a**, **b** adapted from ref. 10; **c** adapted from ref. 11.)

calibrated both pressure and particle motion in the set-up, to establish which of these components of the sound wave the fish were responding to. They show that the lungfish responds more strongly to the pressure generated by the sound than to particle motion. More specifically, it uses its air-filled lungs to convert pressure to particle motion in its lung that is then perceived by the inner ear. This is similar to the way in which ray-finned fishes use their swim bladder[5] (an internal gas-filled organ that allows a fish to control its buoyancy) for sound detection.

The researchers went on to show that lungfish can detect sound pressure waves propagated either through water or through the substrate (the material at the bottom of a lake or stream) and might even have a rudimentary capability to detect such waves in air, despite the absence of a direct anatomical connection between the lung and the inner ear. The groups' earlier work[6] had suggested that lungfish were unlikely to be able to detect pressure waves, but Christensen *et al*. obtained more positive results by using a modified version of the previously reported experimental set-up.

Their findings might have been predicted in the light of what is known about ray-finned fishes. But confirmation was necessary, and has major implications for the evolution of hearing in the earliest tetrapods. It suggests that, if lungfish are capable of sound detection without any obvious connection between an air bladder and the inner ear, then the presence of any such connection — even one not obviously adapted for hearing — would have made sound detection possible.

Both ray-finned and lobe-finned fishes are thought to have possessed air bladders early in their evolution, and may have used them in addition to gills for breathing. The swim bladder of ray-finned fishes is widely considered to have a common evolutionary origin with the lungs in lungfishes and tetrapods. All of the early bony fishes were also equipped with a bone called a hyomandibula that articulated with the ear capsule at a mobile joint and controlled ventilatory movements. It operated the pumping action of the gill chamber, throat and the buccal cavity (the mouth), drawing water or air into these spaces. Air could also pass into the air bladder by this mechanism. Lungfishes, however, lost the hyomandibula during their evolution, although they still breathe air using a similar, but elaborated, buccal-pumping mechanism.

It therefore seems that, even in the earliest osteichthyans, the proximity of the mobile hyomandibula to an air-filled chamber could have allowed pressure-induced vibrations to be transmitted to the inner ear. If air breathing was a primitive osteichthyan characteristic, these animals could, from the time of their origin, have detected sound propagated in water, through the substrate, or possibly even in air, and may have done it rather better than modern lungfishes.

Christensen and colleagues' discovery makes sense of what is known about the earliest tetrapods from the Late Devonian and Early Carboniferous periods (which together spanned from about 387 million to 323 million years ago). Two of the most obvious differences between the ear regions of early bony 'fish' and the descendent early 'tetrapods' are that, in the tetrapods, the hyomandibula had become modified into the stapes, which penetrated the braincase wall at an opening called the fenestra vestibuli (Fig. 1); and that the stapes had developed a structure called a stapedial footplate[7]. These changes must have marked at least some improvement in the transmission of sound waves to the inner ear, even though the stapes was not at that time a slender rod-like bone as it is in most land-dwelling tetrapods today. Rather, it was a bulky bone that was both relatively and absolutely much larger than in modern tetrapods[2] that have an eardrum and a middle-ear cavity, but was nonetheless capable of transmitting vibrations emanating from pressure changes in the air-filled gill pouch with which it was in contact.

The new discovery may also help to resolve an anomaly. One genus of Devonian tetrapod, *Ichthyostega*, had an ear region configured unlike that of any other known tetrapod. It seems to have had an air-filled chamber on each side of its head, roofed by thick walls formed by the skull, braincase and palate, but with a floor occupied in part by a thin, spoon-shaped stapes that articulated with the braincase and fenestra vestibuli[8]. This has been interpreted as an ear adapted for underwater hearing, yet other parts of *Ichthyostega*'s anatomy suggest that the animal had some adaptations for land locomotion[9]. We can now interpret the structure as an ear capable of hearing in both aquatic and terrestrial conditions. ■

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