West Antarctic glacier. However, it is just a small region of a single glacier, and there is an urgent need to obtain a similar level of understanding of other Antarctic glaciers, each of which has its own unique features.

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Palaeontology

Fish fossil unfolds clues to vertebrate brain evolution

Hugo Dutel & Matteo Fabbri

A 319-million-year-old fossil provides the oldest known evidence of preserved vertebrate brain tissue. This specimen offers insights into the brain evolution of ray-finned fishes, the most diverse group of living vertebrates. **See p.486**

The diversity of modern animal forms that we might encounter in our day-to-day lives is only the latest chapter in hundreds of millions of years of evolution. Fossils are therefore pivotal in reconstructing the sequence and timing of the evolution of living animals' defining features. However, although mineralized tissues such as bone commonly fossilize, soft tissues, such as the brain and muscles, usually leave no trace. Therefore, our understanding of how living animals became how they are is incomplete. On page 486, Figueroa *et al.*[1] report the stunning discovery of a fossilized brain in an early ray-finned fish, presenting findings that overturn textbook narratives about the brain evolution of vertebrates.

Ray-finned fishes represent about half of all living vertebrates[2], and encompass most of the animals described as fish that we might encounter in everyday life, such as tuna and monkfish at the fishmongers. Their brain anatomy and the way in which the brain forms are among the most distinctive features of these animals[3]. In vertebrates, including our species, brain regions called the cerebral hemispheres are generally formed by a developmental process called evagination. The tip of a structure in the embryo called the neural tube bulges and folds inwards to form two cerebral hemispheres that enclose a hollow space called a ventricle (Fig. 1a).

However, the cerebral hemispheres of living ray-finned fishes are formed by a different process, known as eversion. In this case, the neural tube folds and extends outwards. Eversion results in solid cerebral hemispheres separated by a narrow ventricle, and this type of brain development was considered to have arisen when ray-finned fishes first appeared[3,4].

This evolutionary scenario was established on the basis of the study of living species only, but Figueroa and colleagues' examination of a small fossil of an extinct species named *Coccocephalus wildi* now turns this view on its head. The fossil, of a skull preserved in 3D, was discovered in rocks of the Carboniferous period (estimated to be 319 million years old) in north-west England, and first described around a century ago[5].

At first glance, *Coccocephalus* looks like a typical early ray-finned fish. It has a bulky skull, a short snout and large eye sockets, and other work[6] provides evidence consistent with the view that it is an early-diverging, distant cousin of all living ray-finned fishes. When studying its internal anatomy with X-ray scanning and 3D reconstruction techniques, Figueroa *et al.* found not only that the main regions of the brain and cranial nerves were fossilized in stunning detail, but also that the forebrain is evaginated – a feature previously unknown in ray-finned fishes (Fig. 1b).

Fossilized soft tissues in such ancient vertebrates are unusual, and this fossil is the oldest known fossilized vertebrate brain. Before this discovery, a slightly younger 3D fossilized brain was described in an extinct relative of ratfishes[7], and other fossilized organs have been described for fossil fishes called placoderms[8].

This discovery and the position of *Coccocephalus* in the vertebrate family tree have crucial implications for our understanding of brain evolution. The fact that *Coccocephalus* is unequivocally a ray-finned fish – but in a branch distinct from that of modern ray-finned fishes – means that an everted

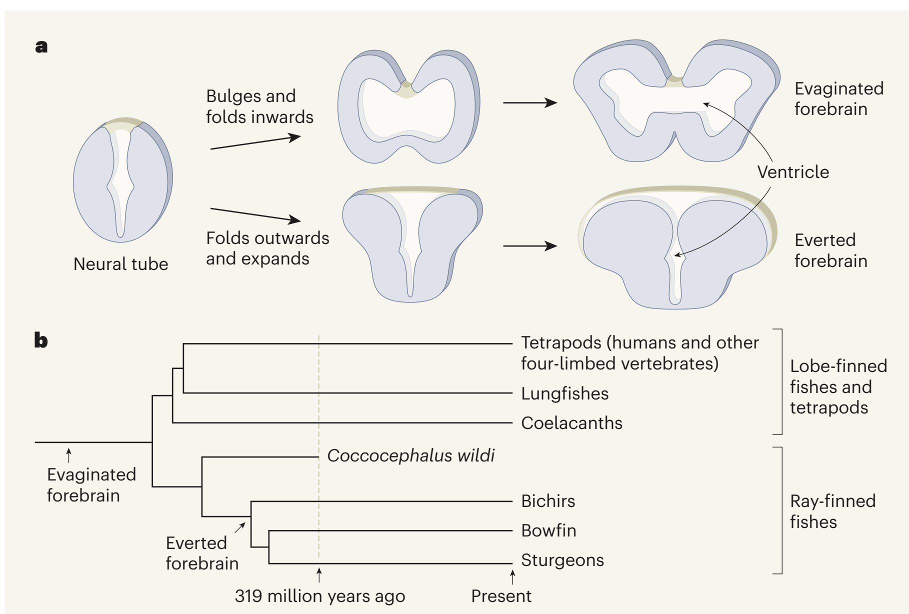

Figure 1 | Brain evolution. a, The vertebrate forebrain forms from the neural tube in the embryo. An evaginated forebrain, such as that of humans, consists of two cerebral hemispheres that enclose a hollow space called a ventricle. An everted forebrain consists of solid cerebral hemispheres that are separated by a narrow ventricle. **b**, Figueroa *et al.*[1] discovered brain tissue in a 319-million-year-old fossil specimen of the extinct ray-finned fish *Coccocephalus wildi*. The specimen has an evaginated forebrain. This is the oldest known vertebrate brain, and its forebrain anatomy contrasts with that of living ray-finned fishes, which have an everted forebrain. The finding offers a revised view of brain evolution for bony fishes (lobe-finned and ray-finned fishes).

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forebrain is not a specialization of ray-finned fishes, but instead evolved later than was previously thought. Moreover, although a small forebrain had been seen as an innovation in modern ray-finned fishes, it now seems that they inherited this ancestral condition of bony fishes — which consist of all ray-finned fishes and their sister group, lobe-finned fishes. Furthermore, insights from the analysis of *Coccocephalus* also now cast uncertainty on the evolution of other neural features that are used to classify ray-finned fishes. This study therefore shows distinctly how fossils can change our understanding of evolution by revealing combinations of anatomical features that are not observed in living animals.

The brain is a delicate organ that generally decays quickly after death. Therefore, palaeontologists usually rely only on imprints of brain cavities, termed endocasts, to infer the fossil neuroanatomy[9]. In many cases, however, we cannot be sure of the extent to which endocasts accurately reflect brain anatomy.

Indeed, *Coccocephalus* indicates that the endocast of other early ray-finned fishes might not closely match brain anatomy, as was previously thought. A discrepancy between the brain and its cavity is also found in coelacanths[10] and in cartilaginous[7] fishes, so it is possible that early ray-finned fishes with their evaginated forebrains have retained what might be a general characteristic of jawed vertebrates. However, it is unclear how much fossilization might have caused distortion and shrinkage in the *Coccocephalus* brain.

Indeed, we still have a poor understanding of how soft tissues can retain such remarkable details when fossilized, and experimental studies of the process of fossilization (taphonomy) will help to decipher the parameters that underpin this process[11]. Despite these limitations, *Coccocephalus* reveals key clues about what can be learnt about neuroanatomy from the endocasts of early ray-finned fishes.

How and why ray-finned fishes acquired an everted forebrain remains an open question. The evolution of small body size in ray-finned fishes during the Devonian period (around 419 million to 360 million years ago) was thought to have constrained the space in which the brain develops[4]. This would have had the potential to hinder forebrain evagination — a scenario that the *Coccocephalus* findings now call into question.

Yet our current knowledge about the developmental mechanisms at work in the forebrain in ray-finned fishes is scarce, and mostly limited to experimental work on zebrafish. These are the most commonly used model fish, but they are so evolutionarily distant from early ray-finned fishes that generalization from the observations made using zebrafish should be done with caution. Comparative and experimental data on the development of other ray-finned fishes, such as gars and bichirs, will be crucial for answering this curious brain teaser.

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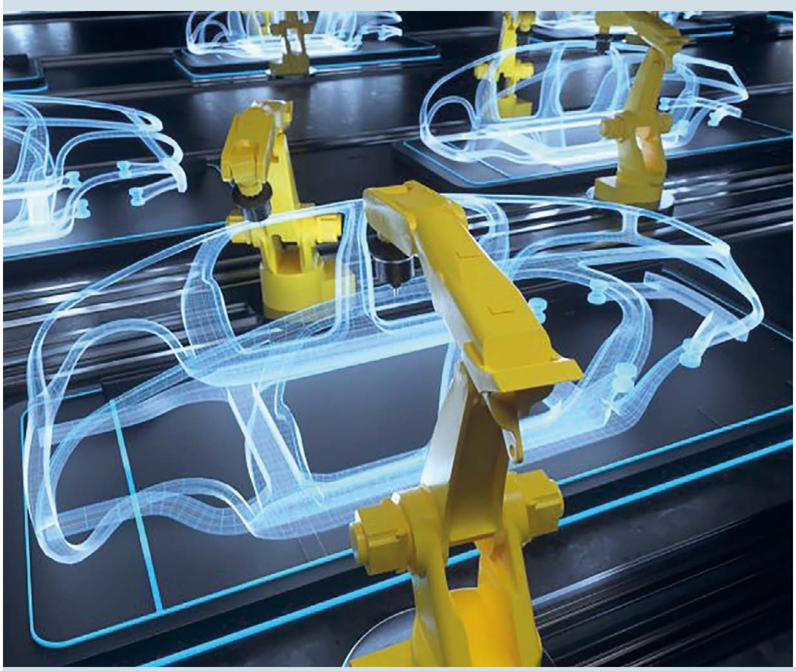

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