Cover illustration

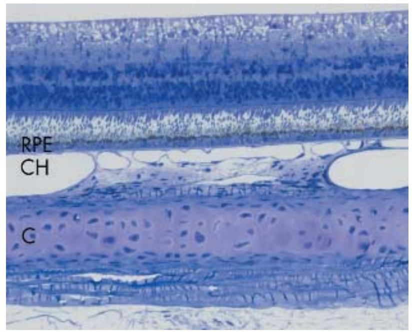
How do I fit in?

A few million years after tetrapods came ashore, approximately 375 million years ago, an odd creature lived among the giant amphibians and represented the next great evolutionary leap. It may not have appeared so at the time. This creature was the initial common amniote that started the clade of tetrapods which includes all reptiles, birds, and mammals. This small protoreptile boasts its evolutionary position because it had an egg that could survive out of water. This required an amnion, and an impermeable shell or, later, internal protection in the form of a uterus. These adaptations constituted major evolutionary advances in the move from an aquatic existence to at least a partial terrestrial existence.

As the tetrapods expanded to fill empty terrestrial niches, they radiated into birds and mammals. Despite the evolution and radiation into other classes, fragments of the reptilian antecedents remain in all descendant groups. Even among mammals, echoes of a reptilian beginning persist in extant creatures.

The echidnas, *Tachyglossus aculcatus* (cover, upper) and *Zaglossus bruijni* (cover, lower) are primitive mammals representing a group that diverged from the other two mammalian groups, the marsupials or Metatherians, and placentals or Eutherians, approximately 125 million years ago. The monotremes, the two echidnas and the platypus, came from a common, but now extinct reptilian ancestor, probably in separate stages. The two extant species of echidna are Prototherian mammals. Although mammalian, they retain many whispers of our reptilian, and for that matter, amniotic beginnings, while displaying features of mammalian specialisations. For example, the Prototherians (echidnas and platypus) are the only mammals that excrete milk (the echidna's milk is pink from the iron content) from pores on the female's belly, have a cloaca (hence the name monotreme or ''one opening''), and still lay eggs.

Amphibian eggs are surrounded by a gelatinous mass and an outer membrane and rely upon diffusion for nutrient and waste exchange very much like the egg of a fish, and must have direct access to water or have a coating of mucus to inhibit evaporation. Between 400 million and 350 million years ago, however, the protoamniote evolved a leathery or cleidoic (essentially meaning to hold water) egg. This first amniotic egg may not have been too different from the egg laid by the present day echidna. Requirements for all amniotes include membranous tissues that remove wastes, exchanges gases, provides nutrients, and an amnion to bathe the fetus in fluid—even amniotes cannot escape our watery beginnings.



Histopathology of echidna globe. Note scleral cartilage, avascular retina. RPE, retinal pigment epithelium, Ch, choroid, C, cartilage.

Before the hegemony of the mammals that began following the Cretaceous extinction, reptiles had evolved an eye with a cartilaginous cup within the sclera, an avascular retina, an annular pad for the crystalline lens, and for some reptiles and birds, a Harderian gland (reviewed in the *BJO*, January 2004). The echidna retains all these features (see fig) and even has a keratinised corneal epithelium, presumably to protect its eyes from the formic acid produced in defence by the ants upon which it preys. A few other ant eating mammals such as the aardvark also have keratinised corneas, but this adaptation is seen much more frequently in reptiles.

The iris musculature of the echidna is restricted to smooth muscle found as a sphincter. This represents the only intraocular muscle as there are no dilator or ciliary body muscles to be found (O'Day KJ, *Trans Ophthalmol Soc Aust* 1952;**12**:96–103). This again bears similarity to the reptilian eye.

The brownish colour of the fundus resembles that of some reptiles, but the choroid lacks a tapetum. The retina is composed of nearly all rods, which suits its crepuscular and nocturnal lifestyle, although some few cones have been found. Oil droplets similar to those found in turtles and birds (discussed in *BJO*, May 2004) have recently been discovered although they are not numerous. The retina has no fovea or area centralis but does have a hint of a horizontal visual streak. The multilayered retinal structure typical for mammals is present; however, it is primitive and undifferentiated. What investigation of the visual capabilities that has been performed suggests that the echidna has visual abilities resembling those of a rat. Because of these poor visual abilities, the echidna relies heavily upon other senses and can detect minute electrical currents with its snout. Recent work evaluating and comparing retinal neurons has shown that the echidna is closer to reptiles or even birds than Metatherian or Eutherian mammals, at least neurologically.

The anatomical similarities to reptiles and birds but dissimilarities to other extant marsupials and mammals suggests that we cannot assume direct lineage from the more primitive monotremes to marsupials and to mammals. Although the Prototheria are surely related to the other mammalian lineages with various mammalian features, these anatomical studies suggest that the monotremes, and perhaps only the echidnas, diverged and radiated from a common lineage, but not necessarily a common ancestor, before radiation of the marsupials and mammals. It is even possible that these three families developed more independently from different but related common ancestors.

Direct lineage may still be possible because we cannot examine the retinas of extinct animals, but the gross and cellular morphology of the eye of the echidna suggests that it is a pivotal species in understanding mammalian evolution. Further studies of ocular morphology may be important to understand just where this eye fits in.

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