

# Wandering nostrils

Philippe Janvier

A small matter of head anatomy has long been a cause of controversy among those interested in vertebrate evolution. An answer that may prove generally palatable now emerges from an ancient fossil fish.

The structures known as choanae may seem obscure. But we've all got them; they are the 'internal nostrils' that form the passage between our nasal cavity and throat that we use for breathing when our mouth is closed. They have also been the subject of much argument among those studying comparative vertebrate anatomy — in particular, the question of how choanae originated in the tetrapods, or land vertebrates, a group that consists of amphibians, reptiles, birds and mammals.

This unique feature of the tetrapod palate was first regarded as an adaptation to breathing air. Now, however, we know

that choanae occurred first in extinct fish relatives of the tetrapods at least 380 million years ago — that is, 30 million years before tetrapods developed limbs and took to the land. So choanae may not have been initially involved in breathing. But did they arise as a novelty within the ancient fish relatives of tetrapods, or were they derived from a pre-existing structure in other fishes? This is a debate that has lasted for about a century, but it is practically settled by new data presented on page 94 of this issue by Zhu and Ahlberg<sup>1</sup>. The subject of their studies is *Kenichthys*, a 395-million-year-old fossil fish from China. The background to the story,

described below, is also outlined in Figure 1.

Most living jawed fishes have two external nostrils on each side of the snout: an anterior one allowing entry of water into the nasal cavity, and a posterior one for its exit. In contrast, tetrapods have only one pair of external nostrils, but their nasal cavity communicates with the mouth cavity by means of the choanae. A single group of living fish, lungfishes, seemed to bridge this gap between fish and tetrapods, as they have 'internal nostrils' in their palate that superficially resemble the choanae. Early evolutionary anatomists thus considered that lungfishes constituted ideal intermediate forms, and were evidence for the piscine origin of tetrapods. Embryological studies then showed that these 'internal nostrils' in fact corresponded to the posterior nostrils of other fishes, but they were also taken to be homologous with — that is, the same as — the tetrapod choanae. The choanae were thus regarded as posterior nostrils that had migrated into the palate in the common ancestor of lungfishes and tetrapods.

Early in the twentieth century, however, that view was shaken by work on certain lobe-finned fishes from the Palaeozoic era (385–280 million years ago). These fishes, later referred to as 'osteolepiforms' and including such examples as *Osteolepis* and *Eusthenopteron*<sup>2</sup>, proved to have a single external nostril on either side of the snout, and choana-like openings in the palate. They became preferred as 'ancestors' to tetrapods because of their close overall resemblance to them and their antiquity, and it soon became received wisdom that the tetrapods had originated from osteolepiforms. The lungfish 'internal nostrils' became increasingly regarded as having merely paralleled the tetrapod choanae in evolution, because of major differences in their relationships to the surrounding nerves, bones and sensory-line canals<sup>3</sup>. This was later confirmed by the discovery of *Diabolepis*, a primitive, 400-million-year-old lungfish, which retains two pairs of external nostrils (and thus lacks 'internal nostrils')<sup>4</sup>.

Several theories have been proposed for the origin of the choanae of tetrapods and of their fossil osteolepiform relatives. The two main possibilities are that choanae are derived from the posterior external nostrils, but independently of development of the 'internal nostrils' of lungfishes, or that they are a novelty, and the posterior external

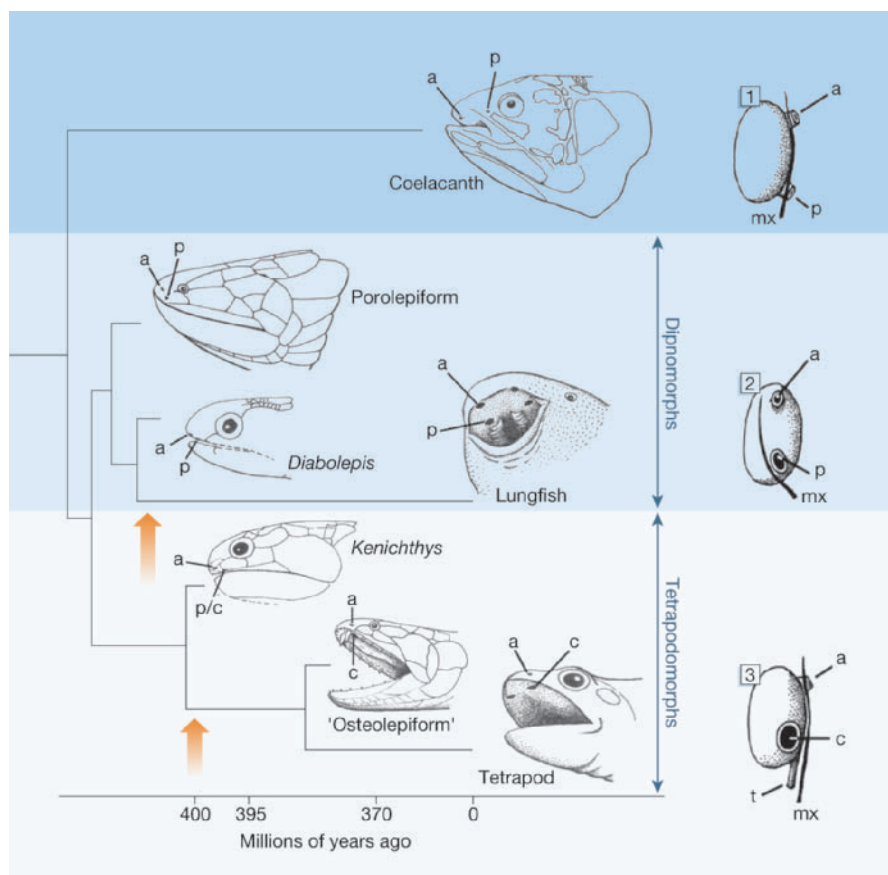


Figure 1 The hole picture. These depictions of the head and palate in some living and fossil lobe-finned fishes and tetrapods show the apertures of the nasal capsule — the anterior (a) and posterior (p) nostrils and the choanae (c). The tree indicates the relationships of the groups, and the orange arrows indicate the two occurrences of the migration of the posterior nostril into the palate. In *Kenichthys*, the fossil studied by Zhu and Ahlberg<sup>1</sup>, the posterior nostril forms a notch in the outer dental arcade, and is intermediate in position between that of an external nostril and that of choanae (p/c). The diagrams (1–3) on the right are of the left nasal cavity, in ventral view, in the three living forms. In lungfishes, the path of the maxillary nerve (mx) is medial to the posterior nostril; in tetrapods it is lateral to the choana. t, tear duct.

nostrils have either disappeared or became the tear ducts. Debate on the matter rumbled on for decades. Rosen *et al.*<sup>5</sup> even revived the theory that lungfishes have true choanae, and claimed that osteolepiforms provide no evidence for choanae, thereby creating a controversy<sup>6</sup> that has had far-reaching consequences for the use of fossil data in reconstructions of evolutionary history<sup>7</sup>.

The current, morphology-based scheme of lobe-finned-fish and tetrapod evolution, first proposed by Ahlberg<sup>8</sup> and shown in Figure 1, displays two major sister groups. These are the dipnomorphs (lungfishes, and the extinct *Diabolepis* and porolepiforms) and the tetrapodomorphs (tetrapods and their closest fossil fish relatives, including the osteolepiforms). If it is now clear, thanks to *Diabolepis*, that the migration of the posterior nostrils into the mouth occurred in the dipnomorphs within the lungfish lineage, there was no comparable fossil evidence for any precursor of the tetrapodomorph choanae.

That changes with Zhu and Ahlberg's report<sup>1</sup> on *Kenichthys*. *Kenichthys* is clearly a tetrapodomorph, and it displays exactly the intermediate condition that would be predicted when assuming that the tetrapod choanae were posterior nostrils displaced into the palate, in the same way as in lungfishes. The posterior nostrils (or already choanae?) of *Kenichthys* are actually right at the margin of the upper jaw, interrupting the outer dental 'arcade' formed by the premaxillary and maxillary bones.

This remarkable discovery, however, does not answer a question that was raised long ago<sup>3</sup> and that centres on other anatomical features. If the posterior nostrils passed into

the palate to form the tetrapod choanae, why did they not leave indelible traces by interrupting the outer dental arcade and the sensory-line canal that runs below the eye sockets, and pushing the maxillary nerve inwards, as they did in lungfishes (Fig. 1)? Zhu and Ahlberg's analysis suggests that this canal and nerve, and the outer dental arcade, were restored laterally to the choanae in more advanced tetrapodomorphs. The restoration of the dental arcade may not be a problem, but that of the maxillary nerve and sensory-line canal certainly is. Further study of the nerve canals inside the snout of *Kenichthys*, or of tetrapod snout development, might offer a solution.

Nevertheless, *Kenichthys* clearly provides the first factual basis for the theory that tetrapod choanae actually are the posterior nostrils, as are the internal nostrils of lungfishes. In a way, the new analysis reconciles Rosen and colleagues' provocative theory<sup>5</sup> and the classical interpretation of the fish members of the tetrapodomorphs — internal nostrils of lungfishes and tetrapod choanae are homologous, but their position in the palate is not. ■

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Materials science

# Lead-free at last

Eric Cross

The most successful piezoelectric ceramics are based on lead zirconate and lead titanate. Environmental concerns over their lead content could disappear with the advent of a new ceramic that is lead-free.

Piezoelectricity is a time-honoured study in crystal physics, initiated by the brothers Jacques and Pierre Curie<sup>1</sup> in 1880. When a piezoelectric crystal is subjected to a suitably oriented elastic stress, the crystal polarizes electrically in proportion to the applied stress; conversely, when a suitably oriented electric field is applied, the crystal changes shape (strains) in proportion to the field level. Such properties lead naturally to possibilities for sensing and actuating elastic changes, but in simple piezoelectrics the effects are too small. Compositions of lead zirconate titanate — the 'PZT' family of ceramics — show much stronger piezoelectric effects, and have come

to dominate the field. Their lead content, however, raises environmental concerns. So the advance reported by Saito *et al.*<sup>2</sup> on page 84 of this issue is welcome indeed: they have created lead-free piezoceramics with properties that closely match those of PZT.

In a normal ceramic, the random orientation of the individual crystallites imparts an infinite degree of rotational symmetry within the ceramic texture; as a result, irrespective of the crystallite symmetry, piezoelectricity is forbidden. What makes piezoelectricity possible in some ceramics, and markedly raises the level of piezoactivity in some single crystals, is the phenomenon of ferroelectricity. In the ferroelectric crystal or crystallite,

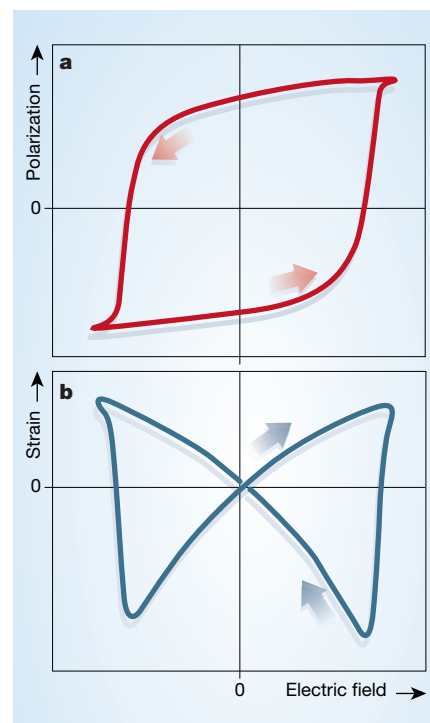


Figure 1 Hysteresis and shape change. a, Hysteresis loop for a ferroelectric composition of lead zirconate and lead titanate. As the electric field is cycled, the polarization of the material changes, but differently depending on whether the field is increasing or decreasing. For zero electric field, there is remanent polarization; to force zero polarization a certain strength of coercive electric field is required. b, For a ferroelectric lead zirconate–titanate ceramic, a cycling electric field changes the elastic strain in the piezoelectric material. The slope of the curve at the origin is indicative of the high 'd<sub>33</sub>' of the ceramic — the induced charge per unit force applied in the same direction — and changes sign with the cycling of the electric field.

there is a substructure of electrically polar domains that can be reoriented by a strong applied electric field. This domain reorientation is demonstrated by the appearance of electric hysteresis and significant shape change (Fig. 1).

In spite of the fact that hysteresis in ceramic ferroelectrics was well known to the physics community, it was an engineer in the United States, R. B. Gray, working at Erie Technological Products in Erie, Pennsylvania, who realized that ferroelectric capacitors under test there were humming at the common 60-Hz power-line frequency. From this he deduced their piezoelectricity, made for himself a piezoceramic phonograph pick-up and pinned down the master piezoceramic patent<sup>3</sup> for Erie. The patent, subsequently licensed to the Clevite Corporation, established an early lead for the United States in the piezoceramic business, and this was strongly reinforced by Clevite's role in the development of the now-dominant PZT family of piezoceramics.