

MORB that have formed in conjunction with continental rifting and where EM-1 component signatures occur. □

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The origin of the internal nostril of tetrapods

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The choana, a unique ‘internal nostril’ opening from the nasal sac into the roof of the mouth, is a key part of the tetrapod (land vertebrate) respiratory system. It was the first component of the tetrapod body plan to evolve, well before the origin of limbs, and is therefore crucial to our understanding of the beginning of the fish–tetrapod transition. However, there is no consensus on the origin of the choana despite decades of heated debate^{1–9}; some have claimed that it represents a palatally displaced external nostril^{4,6}, but others have argued that this is implausible because it implies breaking and rejoining the maxillary–premaxillary dental arcade and the maxillary branch of nerve V^{2,6}. The fossil record has not resolved the dispute, because the choana is fully developed in known tetrapod stem-group members^{8,10,11}. Here we present new material of *Kenichthys*, a 395-million-year-old fossil fish from China^{12–14}, that provides direct evidence for the origin of the choana and establishes its homology: it is indeed a displaced posterior external nostril that, during a brief transitional stage illustrated by *Kenichthys*, separated the maxilla from the premaxilla.

Most jawed fishes have anterior and posterior external nostrils but no connection between the nasal sac and mouth. The only living exception is the lungfishes, in which the posterior nostril is palatal, but this differs structurally from the tetrapod choana and is regarded as convergent^{2,3,6}. Among those sarcopterygian fishes (lobe-fins) with a complete maxillary–premaxillary arcade, the nasal region comes in two patterns. In fishes belonging to the Tetrapodomorpha, the tetrapod total group^{10–12}, there is a single external nostril that lies between lateral rostral and tectal (Fig. 1f, g). On the palate, the anterior end of the maxilla splits into two diverging processes that surround a choana^{3,15}. In non-tetrapodomorphs such as *Youngolepis*^{16,17}, which lack a choana (Fig. 1b, c), the anterior external nostril lies between the lateral rostral and tectal bones and the posterior nostril between the lateral rostral and lacrimal^{3,9}. On the palate, the maxilla and premaxilla meet in a simple butt joint. *Kenichthys campbelli*, from the Emsian Chuan-dong Formation of Yunnan, China, presents the only known intermediate between these two patterns.

Kenichthys is the earliest known and most phylogenetically basal tetrapodomorph^{11–14}, a conclusion that we confirm here on the basis of a new expanded character suite (Supplementary Information). The snout and cheek bones of *Kenichthys*, including 19 ethmosphenoid and 10 maxilla specimens, are not preserved in articulation but are very well preserved and show little individual variation in morphology. This allows their positional relationships to be reconstructed with reasonable certainty, even though it is not possible to reassemble individual skulls (Figs 2 and 3). The anterior nostril occupies its usual position between lateral rostral and tectal (Fig. 1a, d). Unusually, however, the ventral margin of the lateral rostral extends some way beyond the posterior end of the premaxilla (Figs 1a, d, e and 2e). The end of the premaxilla is narrow and capped by cosmine (dentine with a thin enamel covering), without a sutural surface for the maxilla, and the free ventral edge of the lateral rostral is also cosmine-covered rather than sutural (Fig. 2a–h, j). It seems that these margins were free and wrapped in epithelium rather than sutured to the maxilla as in other lobe-fins. The small

space that is bounded anteriorly by the posterior end of the premaxilla, and laterally by the ventral margin of the lateral rostral, lies immediately below the fenestra endochoanalis (Figs 2a, c and 3c, d). The posterior margin of the lateral rostral, which would carry the posterior nostril in non-tetrapodomorph lobe-fins, is entirely sutural and matches perfectly the anterior margin of the lacrimal (Fig. 2i). The final piece of the puzzle is provided by the maxilla (Figs 2k, l and 3f), which lacks the two diverging processes that frame the choana in other tetrapodomorph fishes, ending instead in a simple thin edge (Fig. 1a) and carrying no obvious sutural surface for the premaxilla.

Kenichthys clearly does not display either the primitive sarcopterygian condition with two external nostrils (Fig. 1b) or the tetrapodomorph condition with a single external nostril and a large choana framed by diverging processes of the maxilla (Figs 1g and 3g). We reconstruct the posterior nostril as opening in the upper lip, separating the maxilla from the premaxilla (Fig. 1d, e). No alternative reconstruction makes sense of all the morphological characteristics of the nasal region.

It is evident that there was no posterior external nostril on the suture between the lacrimal and lateral rostral, and no notch for a choana in the anterior end of the maxilla. If the maxilla is pushed forwards to contact the premaxilla and lateral rostral, we are left with no space for a posterior nostril or choana at all, except conceivably in a very mesial position internal to the maxillary-premaxillary arcade, which seems implausible. Such a reconstruction also fails to account for the clearly non-sutural character of the posterior end of the premaxilla and the free ventral margin of the lateral rostral.

The morphology of the maxilla itself also conflicts with this reconstruction. In ventral view (Fig. 2a, c), the free ventral margin of the lateral rostral runs at about 45° to the long axis of the head; the maxilla, in contrast, must have had an alignment closer to 30° to the long axis (because any other alignment results in an implausible head shape), so to suture with the ventral margin of the lateral rostral as in other tetrapodomorphs, the anterior end of the maxilla would have needed a distinct mesial deflection. In fact there is no

such deflection (Figs 1e and 2k, l). Furthermore, the dorsal margin of the maxilla shows a single continuous contact area anteriorly (Figs 2k, l and 3f), suggesting that this margin sutured with only one bone. Where a single long bone sutures with two shorter elements, such as the anterior part of the lacrimal suturing with the tectal and prefrontal, the boundary between the two sutures is usually marked by a slight step (Fig. 2i, red arrow). The overlapped area in the anterior part of the maxilla also excludes the possibility that the maxilla formed the ventral margin of the posterior nostril as in non-tetrapodomorph fishes.

We conclude that the anterior part of the maxilla sutured only

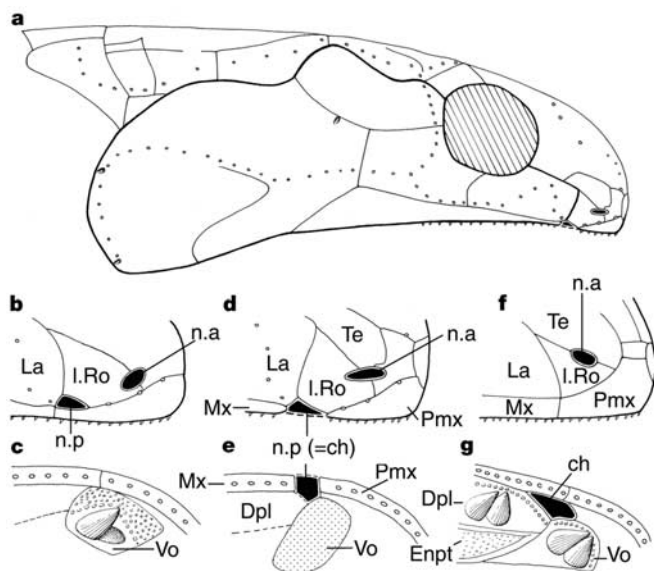


Figure 1 Nostril positions on the heads of sarcopterygian fishes. **a**, reconstruction of *Kenichthys campbelli* head and cheek in lateral view. **b, c**, *Youngolepis*. **d, e**, *Kenichthys*. **f, g**, *Eusthenopteron*. **b, d, f** are lateral views; **c, e, g** are ventral views. In **e**, the (unknown) vomer is represented by its attachment area on the ethmoid. Not to scale. ch, choana; Dpl, dermopalatine; Enpt, entopterygoid; La, lacrimal; I.Ro, lateral rostral; Mx, maxilla; n.a, anterior nostril; n.p, posterior nostril; Pmx, premaxilla; Te, tectal; Vo, vomer.

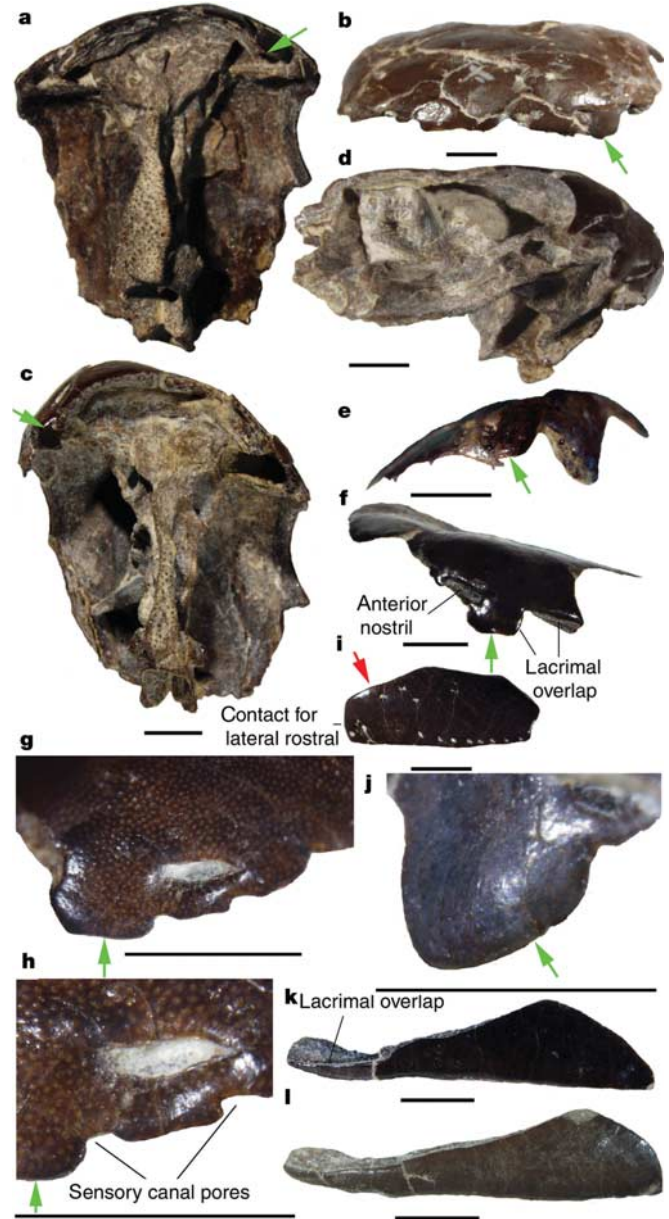


Figure 2 Photographs of *Kenichthys campbelli* specimens. **a, b**, V10493.61, ethmosphenoid in ventral (**a**) and anterior (**b**) views. **c, d**, V10493.60, ethmosphenoid in ventral (**c**) and lateral (**d**) views. **e, f**, V10493.58, ethmosphenoid in antero-lateral view. **f, V10493.1**, holotype, ethmosphenoid in antero-lateral view. **g-h**, V10493.101, ethmosphenoid in anterior view. **i, V10493.81**, lacrimal in external view. **j, V10493.102**, ethmosphenoid in anterior view. **k, V10493.77**, maxilla in external view. **l, V10493.76**, maxilla in external view. The green arrow indicates the free ventral margin of the lateral rostral; the red arrow in **i** indicates the slight 'step' marking the boundary of the tectal and prefrontal sutures. Scale bar, 2 mm.

with the lacrimal, and that the two bones ended anteriorly at the same level (Fig. 1a, d). The maxilla was separated from the premaxilla by a gap of about 1 mm, which communicated directly with the nasal capsule dorsally and was closed dorsolaterally by the free ventral edge of the lacrimal. This gap housed the posterior nostril of *Kenichthys* (Fig. 1a, d). The mesial extent of the nostril onto the palate is uncertain, because the vomer is unknown (apart from its attachment area) and the only known dermopalatine is incomplete and displaced (Fig. 3e), but it seems likely that it was relatively small and that the overall size of the two nostrils was similar.

The nostril morphology of *Kenichthys* forms a perfect intermediate between the non-choanate and choanate conditions. Given the phylogenetic position of *Kenichthys* as the most basal tetrapodomorph (which it maintains even without use of nostril characters¹¹), we infer that the posterior nostril was displaced ventrally at the internode below *Kenichthys*, causing the maxilla and premaxilla to become separated. At the internode between *Kenichthys* and rhizodonts (which have a single external nostril¹⁸, contrary to previous claims for two¹⁹), the maxilla and premaxilla re-established contact lateral to the posterior nostril, which by definition became a choana. *Kenichthys* thus demonstrates beyond reasonable doubt that the tetrapod choana is homologous with the posterior external nostril of fishes. This is further supported by recent work²⁰ disproving the supposed co-occurrence of a posterior external nostril and choana in porolepiforms³, previously one of the main stumbling blocks for that hypothesis^{1,3,4,6}. Furthermore, although *Kenichthys* shows only a single intermediate step, it strongly indicates that the transformation from external nostril to choana was essentially gradualistic in nature; there is nothing to suggest the need for a saltational leap

either before or after the *Kenichthys* node. This contrasts with the apparently abrupt changes in skull and limb structure at the *Panderichthys*–*Acanthostega* internode²¹, but cautions that the discovery of intermediates could similarly overturn our perception of those transformations.

Until the discovery of *Diabolepis*²², a major subject of dispute was the relationship between the tetrapod choana and the palatal posterior nostril of lungfishes^{2,4}. *Diabolepis*, the immediate sister group of the lungfishes within the Dipnomorpha²³, has a posterior nostril that is lateral to the premaxilla and therefore shows that the palatal position of the nostril in lungfishes and tetrapods is not homologous. However, as *Diabolepis* and the less crownward dipnomorph *Youngolepis* both have posterior nostrils that are very close to the lip, it might be that a ventral displacement of the posterior nostril is a shared derived character of Dipnomorpha + Tetrapodomorpha, with a further shift onto the palate accomplished independently through breaching of the maxillary–premaxillary arcade (Tetrapodomorpha) or loss of this arcade and inrolling of the lip (Dipnomorpha)⁶.

It is striking that the development of the nasal region in tetrapods seems in some ways to recapitulate the evolutionary transformation illustrated by *Kenichthys*. In fishes with two external nostrils, such as the paddlefish *Polyodon*²⁴, the premaxilla simply develops on the snout anteriorly to the maxillary prominence of the mandibular arch, without any involvement with the nasal sac. However, in human development, the nasal sac is initially open to the upper jaw margin, and this opening is only closed when the ‘central prominence’ (which will form the premaxilla²⁵) and the maxillary prominence grow together and fuse. Failure of this process results in a cleft lip, mirroring the gap between the premaxilla and maxilla in *Kenichthys*. This joining of the central and maxillary prominences resembles a recapitulation of the re-establishment of maxillary–premaxillary contact at the *Kenichthys*–rhizodont internode. The occurrence of cleft lip and palate are known to be associated with failure of *Bmp* and/or *Shh* + *ptc* expression^{25–27}, regulating the growth of the central and maxillary prominences as well as the epithelial breakdown that allows them to fuse, which indicates that components of this pathway might have been involved in regulating the evolution of the choana. In any event, it seems that a common defect in facial development refers back to an evolutionary event that occurred nearly 400 million years ago. □

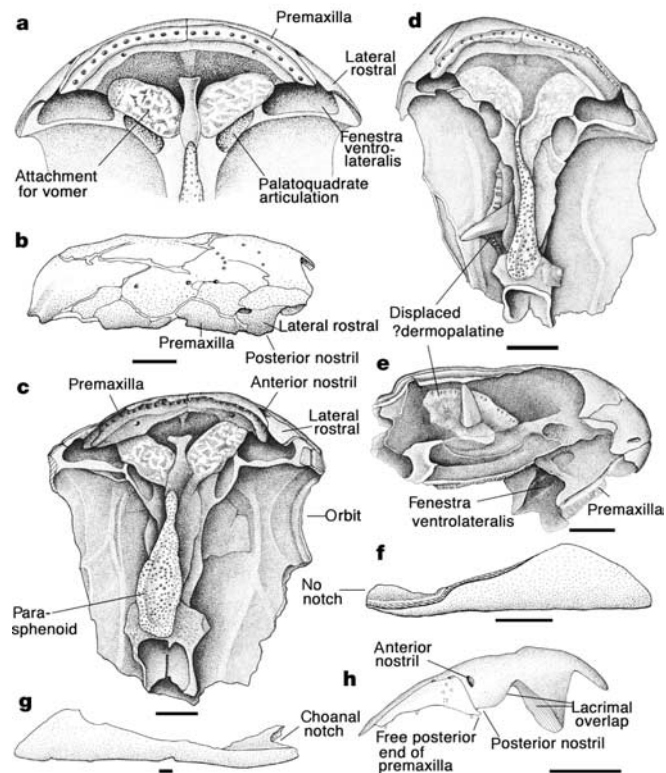


Figure 3 Morphology of *Kenichthys*. **a–f, h**, drawings of *Kenichthys campbelli* specimens. **a**, Restoration of ethmosphenoid in ventral view, based mainly on **c** and **d**. **b, c**, V10493.61, ethmosphenoid in anterior (**b**) and ventral (**c**) views. **d, e**, V10493.60, ethmosphenoid in ventral (**d**) and lateral (**e**) views. **f**, V10493.77, maxilla in external view. **g**, Maxilla of *Medoevia* (ref. 15), showing the diverging processes framing the choana. **h**, V10493.58, ethmosphenoid in antero-lateral view. Scale bar, 2 mm.

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Ecosystem remodelling among vertebrates at the Permian–Triassic boundary in Russia

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The mass extinction at the Permian–Triassic boundary, 251 million years (Myr) ago, is accepted as the most profound loss of life on record^{1–3}. Global data compilations indicate a loss of 50% of families or more, both in the sea^{1,2,4} and on land^{2,5}, and these figures scale to a loss of 80–96% of species, based on rarefaction analyses^{6,7}. This level of loss is confirmed by local and regional-scale studies of marine sections^{3,8}, but the terrestrial record has been harder to analyse in such close detail. Here we document the nature of the event in Russia in a comprehensive survey of 675 specimens of amphibians and reptiles from 289 localities spanning 13 successive geological time zones in the South Urals basin. These changes in diversity and turnover cannot be explained simply by sampling effects. There was a profound loss of genera and families, and simplification of ecosystems, with the loss of small fish-eaters and insect-eaters, medium and large herbivores and large carnivores. Faunal dynamics also changed, from high rates of turnover through the Late Permian period to greater stability at low diversity through the Early Triassic period. Even after 15 Myr of ecosystem rebuilding, some guilds were apparently still absent—small fish-eaters, small insect-eaters, large herbivores and top carnivores.

At a time when there is so much focus on global change and threats to biodiversity, it is surprising how little was known about the Permian–Triassic boundary (PTB) event in 1990 (refs 1, 2, 9). Over the past 15 years, our understanding of this mass extinction has become focused in terms of the timescale (perhaps lasting for 500,000 years (refs 3, 10)), the cause (probably associated with massive outpourings of basalt lava, the Siberian Traps, triggering global warming and anoxia, and possibly a runaway greenhouse effect associated with repeated release of gas hydrates^{2,8–12}), and the nature of the event and the immediate recovery phase (mass extinction followed by rapid turnover of weedy species during the phase of maximum anoxia, and then slow rebuilding of ecosystems^{3,8,9}).

The Permian–Triassic succession of the South Urals is about 6 km thick, thinning to 1–2 km in the Moscow basin^{13–15}, and it is subdivided into 13 successive stratigraphic units (Fig. 1). These units are recognized in the field by changes in sedimentary rock type (svitas), and by particular fossil assemblages (gorizonts); they are correlated with each other, and with the global standard, by means of palynomorphs and ostracods^{13–15}. The age range covers the Kazanian and Tatarian stages of the Late Permian and the Induan to Ladinian stages of the Early and Middle Triassic, a total time span of 25–30 Myr.

The Late Permian to Triassic succession in the South Urals starts with a marine episode in the Kazanian, represented by 200 m of limestone, mudstone and halite, followed by about 1 km of river-deposited mudstone and sandstone. The continental succession extends with relatively continuous deposition from the late Kazanian to the Ladinian (Middle Triassic), and consists of repetitions of four main facies types: mudflats, sandy distributary channels, small gravelly channels and large gravelly channel fluvial systems¹³. The basalmost Triassic is marked by thick sandstone units that document a marked, but short-lived, change in sedimentation style to large gravelly channels, with boulders of more ancient rocks, up to 1 m across, swept down from the Ural mountains. These thick conglomerate units were deposited in large-scale alluvial fans that were part of a much larger terminal fan, about 350–400 km in width.

The abrupt change in the size of the basin and the incoming of coarse-grained alluvial fans all along the western margin of the Urals probably resulted from a peak in mountain-building activity in the core of the Urals, and a change at the PTB towards a more arid climate, with higher sediment yield and greater peak discharges in a drainage basin with reduced vegetation cover¹³. These massive changes in style of sedimentation at the PTB have been seen independently in the continental Karoo succession in South Africa¹⁶ and Australia¹⁷. The changes have been linked to the Siberian basalt eruptions and the consequent marked global warming and acid rain. The acid rain may have killed off the vegetation on land, and soils were stripped from the landscape and swept down rivers on to the plains, and eventually into the sea^{2,8,9}. Mountain uplift and soil stripping, rather than increased rainfall, lies behind the switch from low-energy rivers and cyclical deposition in the latest Permian to massive erosion at the base of the Triassic. Environments and sedimentation styles reverted to pre-PTB conditions higher in the Lower Triassic succession.

The range chart of tetrapods in the Late Permian and Triassic of the South Urals (Fig. 1) shows diverse ecosystems in the Late Permian¹⁵. In the rivers and lakes, four to seven genera of small, medium and large aquatic tetrapods (‘amphibians’) fed on the abundant thick-scaled bony fishes and rarer freshwater sharks and lungfishes. On the wooded banks were 5–11 genera of terrestrial tetrapods (‘reptiles’), ranging in size from tiny insect-eaters to rhino-sized plant-eating pareiasaurs and the wolf-sized to bear-sized sabre-toothed gorgonopsians that fed on them. During the 17–18 Myr of the Kazanian and Tatarian, there was considerable turnover of genera and families through the six time zones (Fig. 2).

The percentage extinction of families at the end of the Permian