LETTERS

Tetrapod-like middle ear architecture in a Devonian fish

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Few fossils show the incipient stages of complex morphological transformations[1]. For example, the earliest stages in the remodelling of the spiracular tract and suspensorium (jaw suspension) of osteolepiform fishes[2–4] into the middle ear of tetrapods have remained elusive[3]. The most primitive known tetrapods show a middle ear architecture that is very different from osteolepiforms such as *Eusthenopteron*[3], with little indication of how this transformation took place. Here we present an analysis of tetrapod middle ear origins that is based on a detailed study of *Panderichthys*, the immediate sister taxon of tetrapods. We show that the spiracular region is radically transformed from osteolepiforms and represents the earliest stages in the origin of the tetrapod middle ear architecture. The posterior palatoquadrate of *Panderichthys* is completely tetrapod-like and defines a similarly tetrapod-like spiracular tract. The hyomandibula has lost its distal portion, representing a previously unrecognized advance towards a stapes-like morphology. This spiracular specialization suggests that the middle ear of early tetrapods evolved initially as part of a spiracular breathing apparatus[5,6].

The spiracular tract of fishes is bounded by the lateral wall of the braincase, the hyomandibula, and the mesial face of the palatoquadrate. The palatoquadrate governs nearly the whole lateral wall of the tract and is therefore crucial in defining the architecture of the spiracle or middle ear. In osteolepiforms (the paraphyletic group

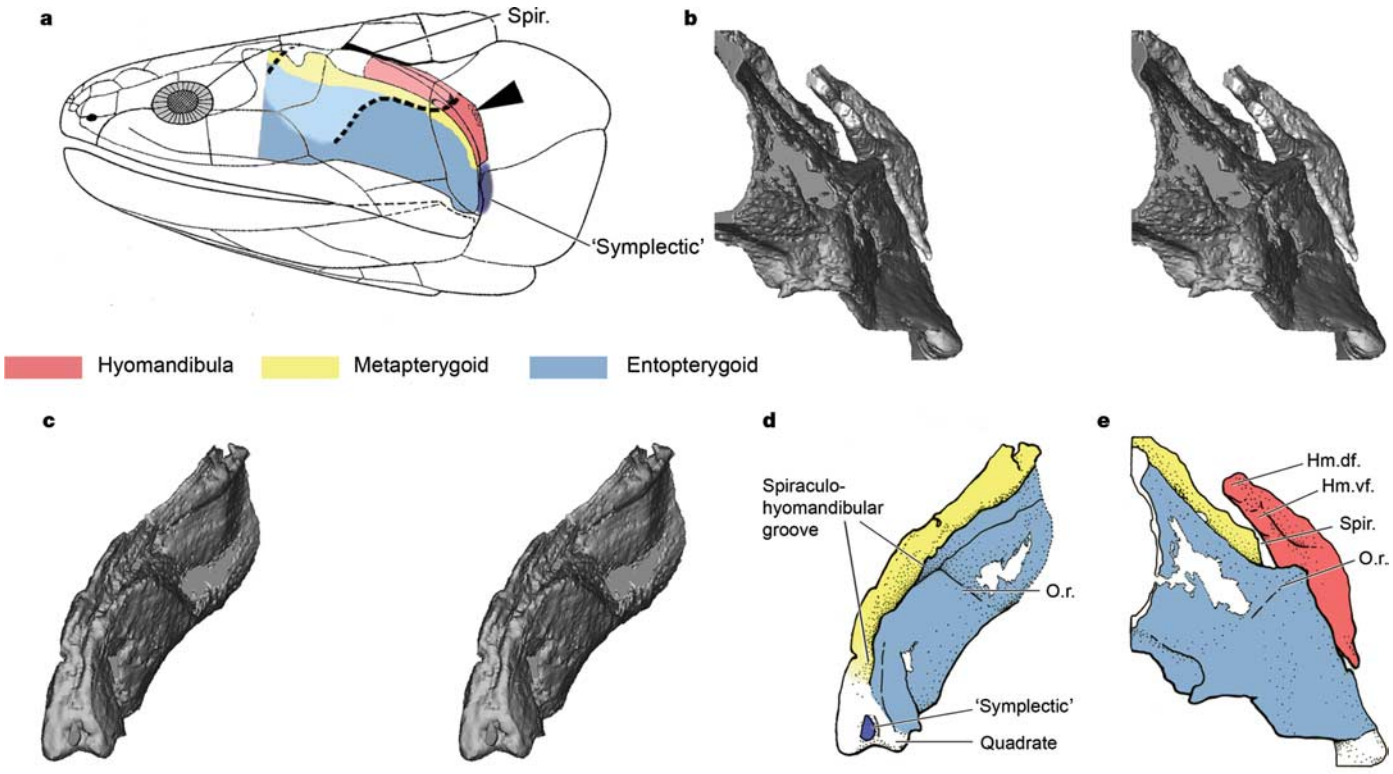

Figure 1 | Hyomandibula and subdivisions of the palatoquadrate of *Eusthenopteron foordi*. Figure is based on computed tomography scans of MHMN 06-538 showing the 'osteolepiform'[7] condition ancestral for tetrapods. **a**, Left lateral view of skull showing, in colour, the region of the palatoquadrate recorded in the scan (modified, with permission, from ref. 26). Lighter coloured area bounded by broken lines shows extent of spiracle. **b**, Stereopair of a three-dimensional computer model of the right palatoquadrate in oblique antero-ventro-mesial view with hyomandibula in place. **c**, Stereopair of a computer model of the left palatoquadrate in oblique postero-dorso-mesial view. **d**, **e**, Interpretive drawings of the computer models in **c** and **b**, respectively. Arrowhead indicates the position of the hyomandibula–opercula linkage. Hm.df, dorsal foot of hyomandibula; Hm.dv, ventral foot of hyomandibula; O.r., oblique ridge; Spir., spiracle.

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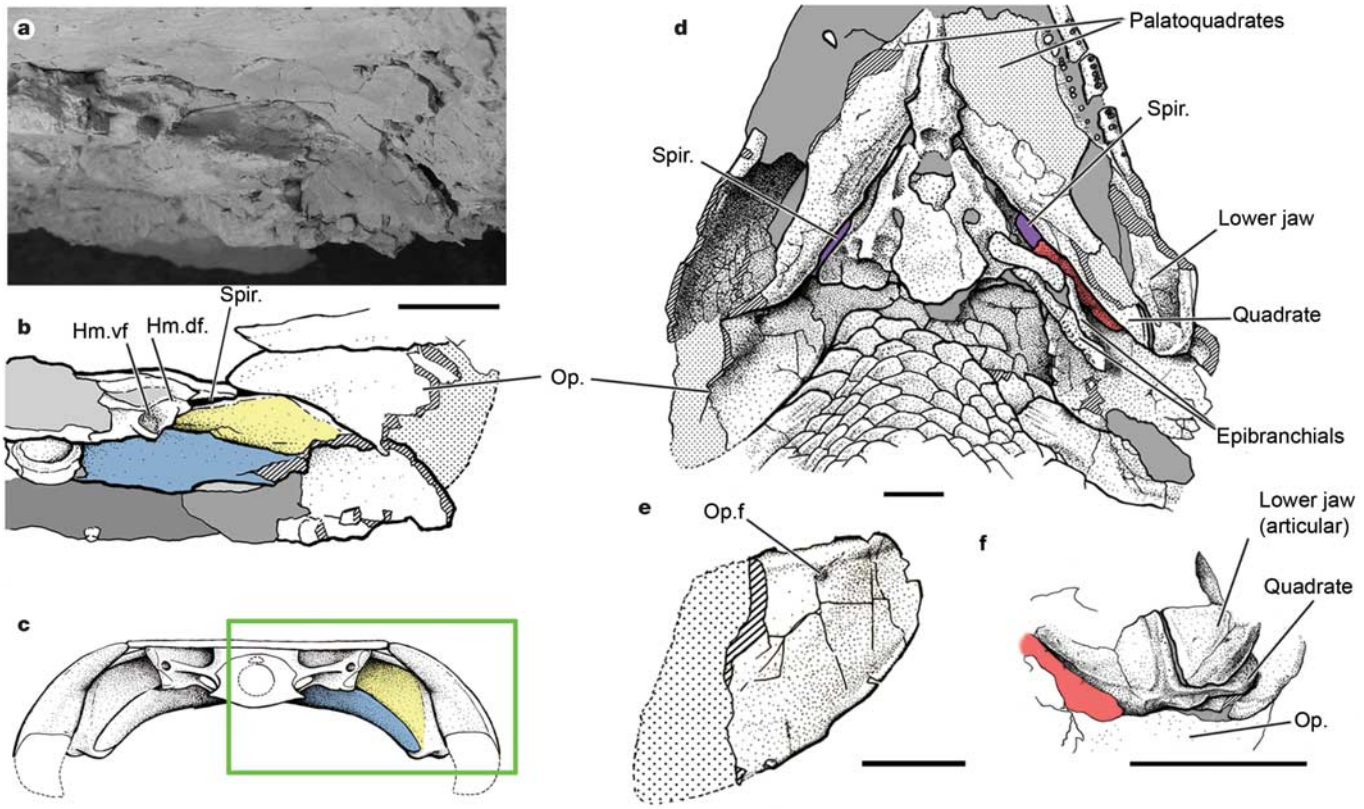

Figure 2 | Suspensorium of *Panderichthys* LDM 60/123 (Middle to Late Devonian). **a**, **b**, Photograph and interpretive drawing of the right palatoquadrate in posterior view. **c**, Reconstruction of skull in posterior view (with location of **a** and **b** outlined in green). **d**, Skull in palatal view showing large, straight spiracular canals. The hyomandibula (red) terminates at the level of the opercular facet. **e**, The right opercular showing opercular facet (Op.f.). **f**, Left quadrate in postero-mesial view. The hyomandibula can be seen in close association with the opercular. Diagonal lines indicate broken bone surface; mechanical stippling indicates natural mould; grey indicates matrix (the three shades represent depth in the viewing plane, where light grey is the closest). Abbreviations and colours are the same as in Fig. 1; purple indicates spiracular opening in dermal skull roof. Scale bar, 2 cm.

ancestral to tetrapods[7]) and porolepiforms (stem-group lungfishes[8]), the palatoquadrate morphology is well known[9–12], giving us a clear understanding of the spiracular condition that was ancestral to the tetrapod middle ear. This condition proves to be very different to that in *Panderichthys*.

As in most basal osteichthyans[13], the osteolepiform palatoquadrate is deep and laterally flattened posteriorly, with an entopterygoid bone forming an expansive denticle field over its mesial (buccal) surface (Fig. 1). The dorsal part of the posterior palatoquadrate, the metapterygoid region (or 'epipterygoid' in early tetrapod terminology[14]; Fig. 1) defines the anatomically lateral wall of the spiracular tract. In cross-section, it is narrow, dorsally concave and laterally deflected relative to the entopterygoid. An oblique ridge running across the buccal face of the entopterygoid demarcates two distinct zones: anterior to this ridge, the hyomandibula is separated from the palatoquadrate by a slot that transmitted the spiracle in life; posterior to it, the entopterygoid forms a long, intimate contact with the hyomandibula (Fig. 1). The oblique ridge evidently marks the posterior wall of the 'Eustachian tube' connecting the spiracular tract to the buccal cavity. The spiracular tract, extending between the buccal cavity and the small spiracular opening on the skull roof, could not have been more than a narrow, slot-like, dog-leg passage between the palatoquadrate, braincase and hyomandibula[9–11]. Past analyses have emphasized similarities between the osteolepiform and tetrapod palatoquadrate, giving rise to the impression that it has not changed greatly during the emergence of tetrapods[15,16].

The palatoquadrate of *Panderichthys*, from the Givetian (Upper Devonian) of Latvia, was only briefly described[17] without detailed comparisons to osteolepiforms or early tetrapods. Apart from its elongate external spiracular opening[17,18], *Panderichthys* has generally

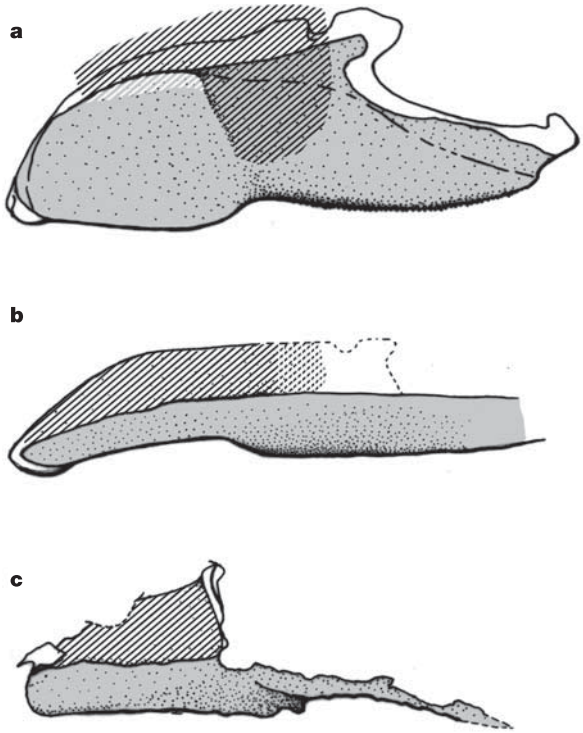

Figure 3 | Palatoquadrates. Shown are the left palatoquadrates of *Eusthenopteron* (**a**; after ref. 9), *Panderichthys* (**b**) and *Acanthostega* (**c**) in mesial view. Grey shows extent of entopterygoid; hatches show extent of the spiracular space over the palatoquadrate.

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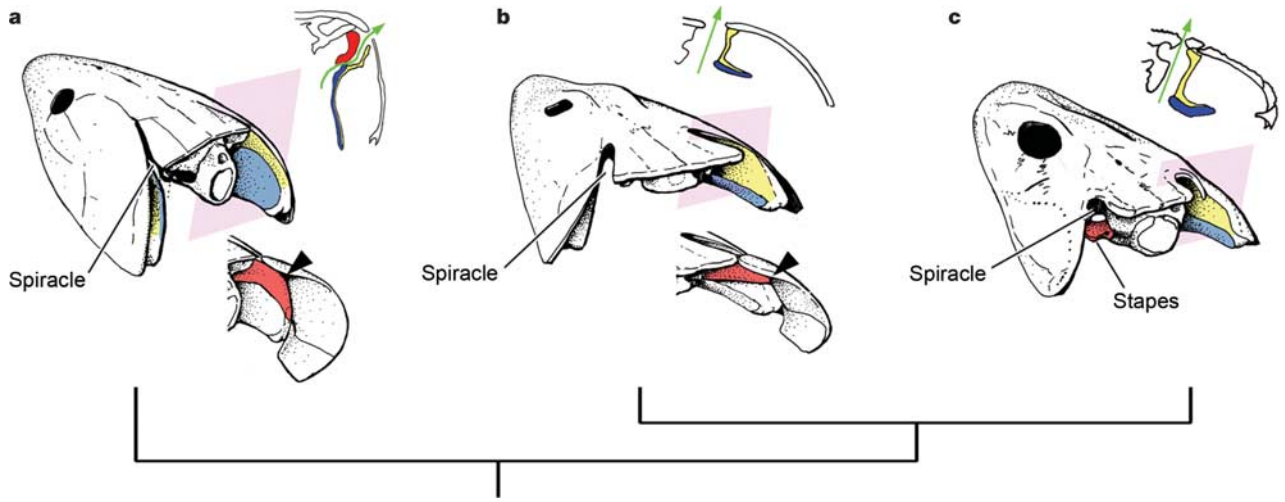

Figure 4 | Early evolution of the tetrapod middle ear space. Shown are the middle ear space of *Eusthenopteron* (**a**), *Panderichthys* (**b**) and *Acanthostega* (**c**) in oblique dorso-lateral view. Top images show cross-section through the spiracle at the approximate level of the pink box. Green arrow indicates the course of the spiracle. Bottom images in **a** and **b** show suspensorium with hyomandibula and opercular series in place. Colours are the same as in Fig. 1. Not to scale.

been excluded from studies of middle ear origins because the braincase, palate and hyomandibula have been thought to be 'fish-like'[17,18]. We examined one *Panderichthys* specimen from the Latvian Natural History Museum, Riga (LDM 60/123; Fig. 2; see Supplementary Information for additional descriptions), that is exceptional in showing these structures in ventral and posterior views[18] and found that its palatoquadrate and hyomandibula in fact differ greatly from the osteolepiform condition.

In *Panderichthys* the palatoquadrate is overall much shallower, shifting the quadrate towards the level of the buccal cavity roof as in Devonian tetrapods. The posterior entopterygoid region is narrowed to a ramus that is about one-third to one-fifth of the depth of the corresponding structure in osteolepiforms (Figs 2a–c and 3). The oblique ridge and dorsal ridge of the osteolepiform entopterygoid are absent, indicating that there was no extensive zone of contact between the hyomandibula and palatoquadrate complex posterior to the spiracular tract. Coupled with the length of the external spiracular opening, this suggests that the spiracle formed an open shaft extending posteriorly almost to the hyomandibular facet on the opercular. In osteolepiforms, by contrast, the ventral and (especially) dorsal openings are smaller and more anteriorly located[9]. *Panderichthys* has a broad, flattened, nearly vertical metapterygoid region, which is much taller than the near-horizontal shelf-and-trough metapterygoid region of osteolepiforms. This creates a wider, straighter and less obstructed spiracle than in osteolepiforms. *Acanthostega*[14,19] and *Ventastega*[20] (personal observation) show a palatoquadrate morphology nearly identical to that of *Panderichthys* in these respects (Figs 3 and 4).

Despite its tetrapod-like spiracular tract, *Panderichthys* lacks a true stapes[17,18]. Like typical osteolepiforms[21] (Fig. 1a, b, e), *Panderichthys* has a slender, rod-like hyomandibula[17,18]. However, we observe considerable differences in the hyomandibula of *Panderichthys* (Fig. 2d, f) that show the earliest evidence of significant modification in the tetrapod stem lineage. In all other known osteichthyans with a suspensory hyomandibula, this bone[9] (Fig. 1a) connects by means of the opercular process at mid-shaft to a facet on the mesial face of the operculum. It is evident that such a link was retained in *Panderichthys* because an opercular facet is present (Fig. 2e). However, the hyomandibula of LDM 60/123 terminates at the opercular process, rather than having the juncture at mid-shaft (Fig. 2d–f). Instead of having a long contact with the palatoquadrate complex, the hyomandibula bridges only the (posteriorly displaced) lateral commissure[18] to the opercular. These modifications represent an early step towards a free-standing, transversely oriented stapes in early tetrapods[3], and suggest that the tetrapod stapes may correspond to only the proximal half of the primitive osteichthyan hyomandibula. A groove extending ventrally from the hyomandibular facet on the opercular indicates that a cartilaginous element continued the hyoid arch beyond the distal tip of the hyomandibula, perhaps forming a link to the ceratohyal (Fig. 2e).

This analysis enables us to dissect the origin of the primitive tetrapod middle ear into two discrete steps. The first step, below the *Panderichthys* node of the tetrapod stem lineage, involved transformation of the spiracular tract into wider, longer, vertically oriented space, as well as loss of the distal part of the hyomandibula and separation of this bone from the entopterygoid. The second step, between the *Panderichthys* and *Acanthostega* nodes, involved loss of the opercular bone and transformation of the hyomandibula into a transversely oriented stapes with its footplate lodged in the fenestra ovalis, but does not appear to have included any major remodelling of the spiracular tract (Fig. 4). This pattern has clear functional implications.

Because the primitive tetrapod stapedial morphology does not indicate association with a tympanum, it has been repeatedly suggested that the 'otic notch' of the earliest tetrapods in fact housed a persistent spiracle[22]. The data from *Panderichthys* offer strong support for this previously speculative hypothesis. As in osteolepiforms, the hyomandibula of *Panderichthys* formed a brace between the opercular and lateral commissure, and had no direct relationship to the inner ear. There is thus no reason to believe that the remodelling and enlarging of the spiracular tract below the *Panderichthys* node were an auditory adaptation. A more plausible functional model is provided by Recent benthic chondrichthyans such as rays and carpet sharks, which, like *Panderichthys*, have broad, flat skulls and bodies, subterminal mouths, dorsally facing eyes and large spiracular openings[23,24]. These fishes use spiracular inhalation to avoid drawing grit into the gills with the respiratory current when lying on the substrate. Because the spiracular tract of *Panderichthys* seems to have formed a substantially wider and more direct conduit to the pharynx than that of osteolepiforms, and the body form implies a benthic lifestyle, we infer that the remodelling of the spiracle occurred to facilitate spiracular ventilation.

The apparent lack of remodelling between the spiracular spaces of *Panderichthys* and the earliest tetrapods, and the absence of a tympanum, strongly suggest that the ventilatory function of the spiracle was conserved during the origin of tetrapods. The transformation of

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the spiracle into the 'middle ear' of primitive tetrapods such as *Acanthostega* involved the creation of a stapes that contacted the inner ear and may thus have acquired a rudimentary auditory role. Notably, the middle ear of *Ichthyostega*, which does appear to be adapted principally for sound transduction, is markedly divergent from the primitive tetrapod morphology[25]. It does not seem, however, that the earliest stages in the origin of the middle ear were part of a braincase support apparatus[2] or involved in any auditory function. Rather, it seems that they related to the elaboration of the spiracular breathing apparatus and possibly the anchoring of a spiracle valve to the hyomandibula or stapes[6].

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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