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Developmental biology

Lungfish dental pattern conserved for 360 Myr

Lungfish, the closest living relatives of four-limbed animals, are unique in that adults lack marginal teeth and have to rely on palatal dental plates for crushing food. We have discovered that an identical pattern of tooth development is used to shape these plates in the hatchlings of fossil and living lungfish species that are separated by 360 million years (Myr) of evolution, even though the adults have very different dental forms; the same pattern is also evident in the transient marginal dentition, despite being functional only until the juvenile stage. This remarkable finding indicates that developmental programming for dentition in lungfish is uniform, unique and conserved for all tooth fields.

Adult lungfish have extensive, continuously growing tooth plates on the palate and the inner side of the lower jaws, which are formed without shedding any teeth. This type of dentition is developed and maintained through continual addition of new teeth labially and dentine from within. In this way individual teeth, arranged in radial rows, are consolidated into dental plates without loss through shedding<sup>1</sup>. This is in contrast to the conventional marginal linear rows of teeth that form the osteichthyan dentition (including tetrapods), in which tooth shedding usually occurs through lingual development of new teeth in each position, with loss of the old tooth. The specialized dentition unique to lungfish is one

example of a strongly conserved structure that is retained through constraints in developmental patterning.

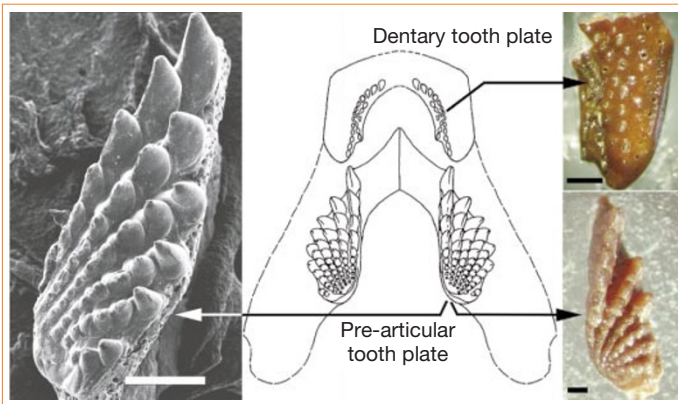
This type of development is shown clearly in the lower jaws of hatchlings of the extant *Neoceratodus* and the Late Devonian *Andrejevichthys*, two lungfish taxa that are separated by 360 Myr. Superbly preserved growth series of *Andrejevichthys* have been uncovered in central Russia<sup>2</sup>. These include not only thousands of specimens, but also the earliest hatchling stages, the only such examples in the current fossil record.

This discovery allowed us to compare the Devonian form with similar developmental stages of *Neoceratodus*. Although the dental plates in adult *Neoceratodus* are non-toothed surfaces for crushing, they develop from toothed rows<sup>3</sup>, with new teeth being added labially to each row of the tooth plate as in adult *Andrejevichthys*<sup>3</sup> (Fig. 1, left arrow).

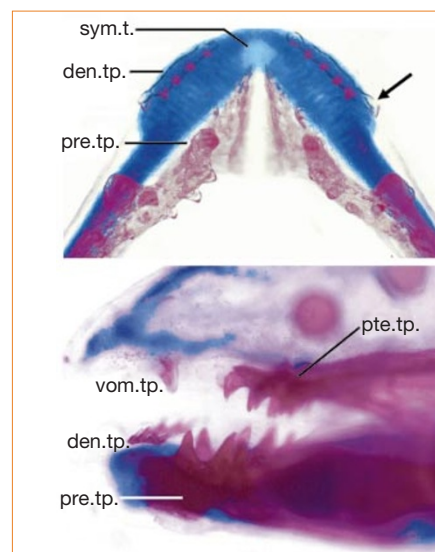
In addition, hatchlings of both taxa develop a marginal dentition, in which the feeding mode is different<sup>4</sup> from that in the adults. This marginal dentition is also organized in both taxa as small tooth plates and is quite unlike that in other osteichthyans. Each marginal set is formed from several rows of joined teeth in the Devonian form (Fig. 1, top right) and from paired single rows in the extant lungfish (Fig. 2). This provides substantial evidence that in lungfish the mode of dentition patterning is consistent in each tooth field, whether marginal or palatal, and that it is unique and specialized. This suggests that it is evolutionarily distinct from that of all other osteichthyans.

We also observed a pattern of selected dental loss through resorption of the marginal dentition from hatchlings to juveniles. In *Neoceratodus* the sequence of loss starts medially, first with the single symphyseal tooth, after which those on the dentary are resorbed, one tooth at a time, until the mar-

**Figure 1** Dorsal views of dentary and pre-articular tooth plates in the Late Devonian *Andrejevichthys epitomus*. The diagram shows a reconstructed outline of the lower jaw in occlusal view and the relative positions of the two types of plate. As in the extant lungfish (Fig. 2), the dentary tooth plate (top right; PIN 1302; arrow originates from and points to the centre of the radiating rows)



is completely resorbed during early ontogeny, and the dentary bone is lost, whereas the pre-articular tooth plate (left and bottom right; PIN 1328, 1548) continues to add new teeth. Both comprise radial rows of teeth. Left, scanning electron micrograph of the pre-articular plate, taken at an angle to show the new teeth at the labial end of each row (arrowhead). Six tooth rows can be seen, all showing a gradation from small, worn medial teeth to larger new teeth; rows 1–4 have 10 teeth, row 5 has 6 teeth and row 6 has 5 teeth. Material courtesy of N. Krupina. Scale bars, 500 μm.



**Figure 2** Tooth plates of the extant *Neoceratodus forsteri*. Images show whole mounts of a hatchling at stage 56, stained red for bone and dentine, and blue for cartilage. Top, occlusal view of lower jaw in which resorption of dentary teeth has begun to occur (one medial tooth from left side). The symphyseal tooth has been completely lost, as shown by the pale blue region. Arrow shows addition of new teeth, which are not yet attached, at the postero-lateral ends of the dentary. Bottom, lateral occlusal view of head, showing the upper and lower tooth plates and the smaller, marginal plates supported by cartilage. In the later stages of ontogeny, the dentary tooth plate is completely resorbed. Material courtesy of J. Joss. Abbreviations: den.tp., dentary tooth plate; pre.tp., pre-articular tooth plate; pte.tp., pterygoid tooth plate; sym.t., symphyseal tooth position; vom.tp., vomerine tooth plate.

ginal tooth plates are lost. Almost the same pattern of loss occurs in *Andrejevichthys* because the marginal tooth plates and the dentary bone of hatchlings subsequently disappear. The hatchling dentition is represented by dozens of dentary tooth plates, but none have been found among the thousands of juvenile and adult specimens.

Our results indicate that a specific developmental mechanism for programmed loss was preserved in these two lungfish throughout 360 Myr of evolutionary history. Early, more basal lungfish<sup>3</sup> have palatal and lingual tooth plates, whereas marginal bones have separate teeth; some later taxa also develop and retain marginal tooth plates as adults<sup>5</sup>, indicating that this programme of development and loss evolved within lungfish, perhaps during the Late Devonian period.

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