Evolutionary origin of teeth
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Abstract
Teeth and jaws have been widely perceived as key innovations underpinning the adaptive radiation and the evolutionary success of jawed vertebrates. However, the origin, evolution, and developmental evolution of teeth are all the subject of controversy. There are three competing hypotheses that are more or less well supported by the available data: (i) the 'outside-in' hypothesis which contends that odontogenic competence spread from the external dermis to the oro-pharynx – the traditional hypothesis based on the observation that teeth and scales exhibit common patterns of development that extend to the molecular genetic level, combined with evidence that scales appear before teeth within phylogeny; (ii) the 'inside-out' hypothesis that teeth and scales evolved independently, based on the observation that some jawless scale-covered vertebrates also possess oro-pharyngeal scales, and (iii) the 'inside-outside' hypothesis which is effectively agnostic on the question. The available evidence supports an origin of teeth through extension of odontogenic competence from the external dermis to the oro-pharynx.

Key words
Teeth, development, evolution, vertebrates, key innovations, whole genome duplication, neural crest, homology, phylogenetic congruence.

Key concepts
'Outside-in' hypothesis argues for an evolution of teeth after the evolution of jaws from ectodermal epithelium, based on the observation that teeth and scales are considerably similar in their development and morphology.

'Inside-out' hypothesis argues for an evolution of teeth before jaws from an endodermal epithelium, based on the assumption that teeth and scales are considerably different and have no common origin.

'Inside and out' hypothesis argues for a deep homology and ancient gene regulatory network for non-mineralized (taste buds) and mineralized appendages (scales and teeth).

Odontodes are a descriptive observation defined as hard tissue structures that develop in a single papilla, consist of dentine or dentinous tissue and frequently a superficial enameloid layer.

Whole genome duplications as drivers of vertebrate evolution enabling mutations ultimately resulting in the evolution of novelties considered as key-innovations, e.g. jaws and teeth.

Phylogenetic congruence is a test of an evolutionary scenario with cladistics and a well-supported phylogeny.

Introduction

The evolutionary transition from jawless to jawed and tooth-bearing vertebrates constitutes one of the most formative events in vertebrate evolution, precipitating ecological change. Jaws and teeth are widely perceived as the key-innovations that underpinned the adaptive radiation and evolutionary success of jawed vertebrates. Surprisingly, the origin and early evolution of teeth remains hotly debated and far from resolved. Thankfully, there is a rich fossil record of teeth and their development because teeth are mineralized and wear-resistant. These fossil remains are readily studied at a cellular level and beyond, using modern X-ray tomographic methods and, because dental tissues are deposited on a daily cycle, the growth lines preserved within the tissues can be analysed to reveal their pattern of development. Thus, fossilized dental tissues can be studied in much the same way as in living species, allowing for an integrative approach to elucidating the developmental evolution of teeth. When this information is organized within a genealogy of early and primitive vertebrates, it becomes possible to test competing scenarios for the evolution of teeth.

Main text

'Outside in' hypothesis

The first comparative anatomists recognized similarities between external dermal scales and teeth (Agassiz 1833-43; Owen 1843). Are these similarities of shape and composition products of homology or analogy? In order to solve this long-standing question a phylogenetic framework is needed (Figure 1). In living animals with a backbone, the vertebrates, the jawless cyclostomes form a clade comprising lampreys and hagfishes. Cyclostomes from Greek "round mouth" lack true teeth and a dermal skeleton (Figure 1). The tooth function is instead fulfilled by keratinous tooth-like structures (Krejsa et al. 1990). These structures are not homologous to teeth which in living jawed vertebrates are composed of dentine, are capped by an enamel or enamel-like tissue, and have a bone of attachment. Living jawed vertebrates include the chondrichthyans (sharks, rays, and chimaeras) and osteichthyans (bony fishes and tetrapods, Figure 1), have both teeth and jaws. Chondrichthyans and especially sharks, have been considered the most primitive living jawed vertebrates when looking for the ancestral condition of characters like teeth. However, this perspective ignores the fact that chondrichthyans are also specialized and the result of hundreds of millions of years of independent evolution, just like osteichthyans. Therefore, the nature of recent sharks might not be informative about ancestral jawed vertebrate characters. Their dermal skeleton is made of tiny tooth-like scales and their endoskeleton is composed of unmineralized cartilage, fulfilling expectations of a simple skeleton from which a more complex osteichthyan condition evolved.

The similarities of dermal scales and teeth in sharks are obvious, extending from commonality of composition (dentine pulp, enameloid cap and bone of attachment) down to the manner in which they develop (Debiais-Thibaud et al. 2011). Hertwig (1874) hypothesized early in the history of comparative anatomy that both systems share a common ancestry and teeth represent a co-option of scales to an oral position. The same observation of similarity led to the lepidomorial theory of Stensiö and the odontode theory of Ørvig which contends that both teeth and scales develop from a common developmental module which has been termed an odontode (Ørvig 1977; Reif 1982; Donoghue 2002). This long tradition of recognizing a common development and evolution of scales and teeth has more recently been coined the "outside-in" hypothesis based on their idea that internal teeth evolved from external scales (Figure 2A). The fossil record seems to support this view with the discovery of jawless and toothless vertebrates shielded with hundreds of external dermal scales or even encased into an extensive dermal armor resembling the plating of a medieval knight. This fossil record of jawed and tooth-bearing vertebrates evolving long after their armored jawless and toothless "ostracoderm" antecedents, has long been interpreted to support the outside-in hypothesis.

'Inside out' hypothesis

One major problem with the 'outside-in' hypothesis is that up to now no animal, fossil or living, has shown evidence for the extension of external dermal scales into the mouth. The so-called 'spiny shark' acanthodians have been proposed to evidence this evolutionary transition, with tooth-like scales surrounding the mouth (Blais et al. 2011). However, these fossil jawed fish (Figure 1) already have an impressively developed dentition of replacement teeth.

The competing 'inside-out' hypothesis draws a fundamental distinction between internal teeth and external scales on the basis that they develop from different tissues: teeth from oral endoderm and scales from the external dermis (Figure 2B). Furthermore, a range of fossil groups have been interpreted to evidence an origin of oral teeth evolving before dermal scales and before the origin of jaws – evidence that would appear to contradict the traditional outside-in hypothesis.

Conodonts

Conodonts are an extinct group of jawless vertebrates that strongly resemble the living cyclostomes, but possessed mineralized tooth-like elements. Conodont elements are composed of a cap of hypermineralized material that is similar to enamel and a basal tissue that is similar to dentine, and the two tissues appear to have grown in a manner that is directly comparable to teeth and scales (Donoghue 1998). As such, conodonts have been interpreted to be more closely related to living jawed vertebrates, but more primitive than the fossil armored ostracoderms (Figure 1). Thus conodont elements have been interpreted as evidence of tooth-like structures occurring deep inside of the mouth of vertebrates, evolving long before the first vertebrates with external dermal skeleton (Smith and Coates 1998; Smith 2003; Fraser et al. 2010).

However, researchers have argued that conodonts are not vertebrates (Turner et al. 2010) and others have demonstrated that the tooth-like condition of conodont elements has evolved convergently. Specifically, it has been shown that the structure of conodonts evolved piecemeal, with early ‘paraconodonts’ possessing only the dentine-like basal tissue, and later ‘euconodonts’ evolving the hypermineralized enamel-like cap. Given their independent evolution within the conodont lineage, these tissues and structures cannot be homologous to the teeth or scales of other vertebrates (Figure 1; Murdock et al. 2013). As such, evidence from conodonts is not informative on the question of how teeth evolved.

Thelodonts

Proponents of the inside-out hypothesis have also marshalled evidence for teeth evolving before jaws in a group of extinct jawless ostracoderms called the thelodonts. Thelodonts like *Loganellia scotica* possess an external dermal skeleton comprised of tiny shark-like scales, but some also possess an internal skeleton of even smaller scales lining the mouth and pharynx (Figure 1; Van der Brugghen and Janvier 1993). These scales possess a pulp cavity with dentine and an enameloid cap, and base formed from acellular bone (Donoghue and Sansom 2002, Rücklin et al. 2012).

Internal scales come in three different styles, as minute individual scales at the front of the mouth, combined scales growing together deeper in the mouth, and in the gill area scales are found arranged together as though on a string of pearls, that apparently grew successionally, aligned in one direction (Smith and Coates 2000).

This pattern of aligned growth was interpreted to resemble tooth replacement in the tooth whorls of living sharks and the extinct acanthodians (Van der Brugghen and Janvier 1993). As with conodonts, this was regarded as evidence that teeth evolved before jaws inside of the mouth probably from an internal, endodermal tissue, and that shark-like tooth replacement had evolved in association with the gills. The ensuing evolutionary scenario that tooth replacement had evolved in the pharynx, later to be reused (co-opted) in the mouth, is even in agreement with the idea that jaws and branchial arches share a common developmental origin.

However, the mode of development and replacement of tooth-like scales in the mouth and pharynx of the thelodont *Loganellia*, was largely guesswork that had to be tested. High resolution X-ray tomography was used to characterize the three dimensional structure of specimens extracted from a key specimen. This work confirmed the initial inference of the scales growing successionally and directionally in some specimens (Rücklin et al. 2011), but there is a great diversity and some scale aggregates from the mouth and pharynx of the thelodont *Loganellia* show no coherent pattern, with scales are added in both a polarized and unpolarized way (Donoghue and Rücklin 2016).

Mapped onto an evolutionary tree, the thelodont *Loganellia* is resolved as extremely derived, nested deep inside the clade thelodonts, the majority of which appear to lack oral or pharyngeal scales (Rücklin et al. 2011). As such, the evidence indicates that the tooth-like oral or pharyngeal scales of *Loganellia* evolved independently of the teeth of jawed vertebrates and, like conodonts, they cannot be used in evidence to support the inside-out hypothesis.

Placoderm teeth

The extinct placoderms are the first jawed vertebrates and they have traditionally been interpreted to constitute a natural group, sister to the chondrichthyans and bony fishes (Goujet & Young 2004). This critical position in the tree of life, combined with the interpretation that the boney jaws of placoderms were toothless, leant support to the hypothesis that teeth evolved after jaws. Discoveries of teeth or tooth-like structures in derived placoderms (arthrodires), composed of the same tissues seen in the teeth of living jawed vertebrates, challenged this view (Smith and Johanson 2003). Early representatives of each of the main clades of jawed vertebrates, that is, the placoderms, acanthodians, chondrichthyans, and bony fishes, were all interpreted to have lacked teeth, supporting a thesis that teeth had evolved convergently in each derived members of each of these four lineages. All groups, including the jawless thelodonts, were interpreted to share the same developmental process and replacement pattern found in living jawed vertebrates (Johanson and Smith 2003), supporting evidence of a deep homology.

In the intervening years, the phylogenetic framework for interpreting this evidence has undergone its own revolution. In particular, placoderms have been reinterpreted to constitute an evolutionary grade and not a natural group (Brazeau 2009 – though this is still uncertain – see King et al. 2016), with some placoderms resolved as more closely related to living jawed vertebrates than others (Figure 1). As such, the evolution of characteristics such as teeth, have been recast. Thus, evidence of successional teeth in derived placoderms like the arthrodire *Compagopiscis croucheri* (Smith and Johanson 2003, Rücklin et al. 2012, Donoghue and Rücklin 2016) and the more basal buchanosteids, suggests that teeth evolved in closer association with jaws than has been perceived hitherto (Rücklin et al. 2012). Acanthothoracids are among the earliest of placoderm grades, and their jaw plates also display concentric rows of tooth-like denticles (Goujet and Young 2004; Smith and Johanson 2003). Nevertheless, the jaws of the early-branching antiarchs, as exemplified by the ubiquitous *Bothriolepis* (Young 1984), shows no evidence of teeth associated with their lower jaw (Rücklin et al. 2012). This might reflect evolutionary loss, mirrored by absence of dentine-bearing scales from their dermal skeleton (Downs and Donoghue 2009, Giles et al. 2013) or a primary absence deep in the evolutionary grade of placoderms. More placoderms from Silurian strata are needed to inform about the basal conditions.

Odontode regulation hypothesis

For a long time the similarities of teeth and dermal scales in their development have been recognized. These similar developmental modules have been described in the odontode regulation theory as reflecting a common evolutionary origin (Ørvig 1977; Reif 1982; Donoghue and Sansom 2002). This view is not shared by the inside-out hypothesis which instead posits that internal and external odontodes have evolved independently from a common but unmineralised ancestral organ, such as a taste bud. This "deep homology" (Johanson and Smith 2005) is reflect in the shared aspects of development that extends all of the way down to the gene regulatory network that controls the development of teeth, scales and taste buds (Fraser et al. 2010). As such, this hypothesis of homology must extend deep into evolutionary history, before teeth and scales first evolved, into the early stages of vertebrate evolution associated with revolutionary genomic events that distinguish vertebrates from their invertebrate relatives.

Whole genome duplications
Many of the genes that comprise the gene regulatory networks that underpin tooth and scale development have an evolutionary origin that is associated with whole genome duplication events. In vertebrates, three duplications of the whole gene set are postulated (i) in the ancestral vertebrate lineage, (ii) in the gnathostome stem-lineage, and (iii) in ray finned fishes in the teleost stem lineage. From the perspective of living vertebrate diversity, three events seem to correlate with bursts of character evolution and increasing complexity. However, integrating fossil evidence into this perspective provides a more complete picture in which there is no evidence for a series of evolutionary leaps. For instance, the extinct ostracoderms show that gnathostome anatomical characteristics were assembled piecemeal over a protracted episode of evolutionary history, including a dermal skeleton, a differentiated gut, paired fins, slit-shaped gills, and even jaws and teeth. This episode extends from the first stem-gnathostomes in the Cambrian, to the first definitive crown-gnathostomes in the Silurian (Donoghue & Purnell 2005, Brazeau & Friedman 2015). Therefore, there is no evidence for a direct link between whole genome duplications and evolution of complexity.

Molecular evolution and gene regulation: inside and out
Structures like scales, teeth, hair and feathers all exhibit similar patterns of development and, as such, some developmental biologists have grouped them as a family of like structures known as epithelial appendages. Some researchers have argued that all manifestations of epithelial appendages share a common evolutionary origin (Krejsa 1979) even though there is no phylogenetic evidence to support their homology. Hence, the hypothesis of that scales and teeth may share an evolutionary origin in an unmineralized sensory organ like a taste bud since they certainly share a common suite of genes directing their development (Fraser et al. 2010). Experiments based in the axolotl have shown that teeth can develop from ectoderm, entoderm, and even mixed epithelia (Soukoup et al. 2008) demonstrating that apparently fundamental developmental distinctions between teeth and scales are surmountable. As such, the 'inside and out' hypothesis contends that the question of the topological origin of odontodes is fundamentally irrelevant (Fraser et al. 2010).

Support for the inside and outside hypothesis has found in a comparative analysis of tooth and scale development in the cat shark (Debiais-Thibaud et al. 2011, 2015). These authors found that shark teeth lack the signaling centres associated with cusp development in mammalian teeth, though shark scales exhibit patterns of nested gene expression that is reminiscent of these signaling centres. In this sense, shark scale and mammalian tooth development are more similar than either is to shark tooth development. Comparative analyses including taste buds have further shown similarities in the regenerative capacity of shark teeth and taste buds, not seen in shark dermal scales (Martin et al. 2016).

Testing phylogenetic congruence of hypotheses on the evolution of teeth
Evidently, the competing hypotheses for evolutionary origin of teeth are many and varied, and none have evaded criticism. The ultimate test we can apply is their congruence with phylogenetic hypotheses (Patterson, 1982); as we have seen, however,

phylogenetic hypotheses change over time and so this is not a perfect test, but it remains the key test of any evolutionary scenario. Traditional views mainly based on recent taxa result in the view that chondrichthyans represent the most basal jawed vertebrates and therefore their apparently simple tooth replacement is informative about the basal stage of vertebrate tooth development. However, this perspective ignores evolutionary changes along the stem lineage of chondrichthyans. Recent phylogenetic analyses of fossil data has provided greater support for the view that placoderms constitute an evolutionary grade of stem to crown gnathostomes (Brazeau 2009, Davis et al. 2012; Zhu et al. 2013). This implies that an extensive dermal skeleton is primitive and that the condition both living chondrichthyans and living osteichthyans, is secondarily simplified (Zhu et al. 2013). Extraordinary newly discovered placoderms from China, including *Entelognathus* and *Qilinyu*, possess jaws resembling those of bony fishes (Zhu et al. 2013, 2016), changing our view on the evolution of jawed vertebrates completely. Within this context, it seems clear that teeth evolved long after scales. Commonality of development, extending from the tissue and cell level, down to molecular genetics, must belie any idea that teeth and scales independently evolved their dentine, enamel and bone tissue and cells, even if they inherited a largely preformed gene regulatory network. As such, it seems clear that the inside-out hypothesis must be rejected and with it we can dismiss the inside and outside hypothesis, which is essentially non-evolutionary. This leaves us with the traditional outside-in hypothesis which is compatible with the available evidence, especially the origin of teeth long after the dermal scales. The absence of evidence for a gradual evolution of teeth from marginal scales may be unsettling, but fossils likes *Entelognathus* and *Qilinyu* reveal known-unknowns: that the earliest jawed vertebrates possessed marginal dermal bones that would have borne dermal scales. After all these years of debate focused in the laboratory, it is time to go back out to the rocks in the field and find these critical fossils.

Conclusions and future perspectives

New large-scale phylogenies allow the congruence test of traditional evolutionary scenarios on dental evolution. Tomographic techniques developed in the last decades, advanced computing and 3D reconstruction, enable the reconstruction of growth in fossils. Advances in developmental biology and developmental genetics enable tests of traditional hypotheses. All three important lines of evidence: phylogeny, fossil record and developmental genetic evidence facilitate formulation and tests of hypotheses on the evolution of teeth. Phylogenetic analyses integrating evidence from living and fossil species indicate that the outside-in hypothesis represents the most plausible scenario for the evolutionary origin of teeth, a scenario that will surely be further tested by new discoveries in molecular laboratories and new fossils in the field.

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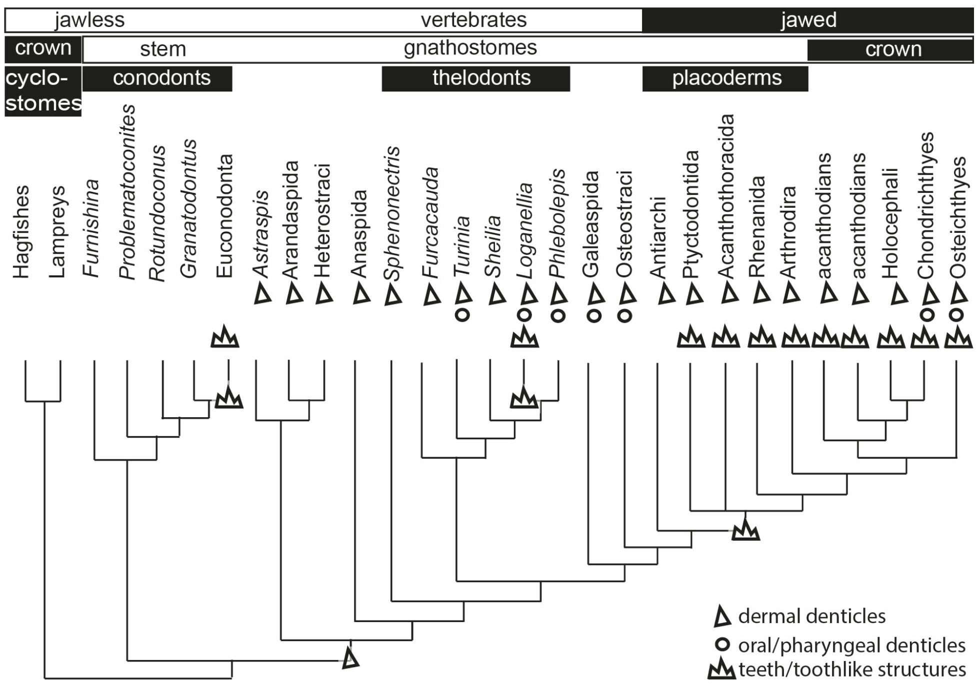
Glossary

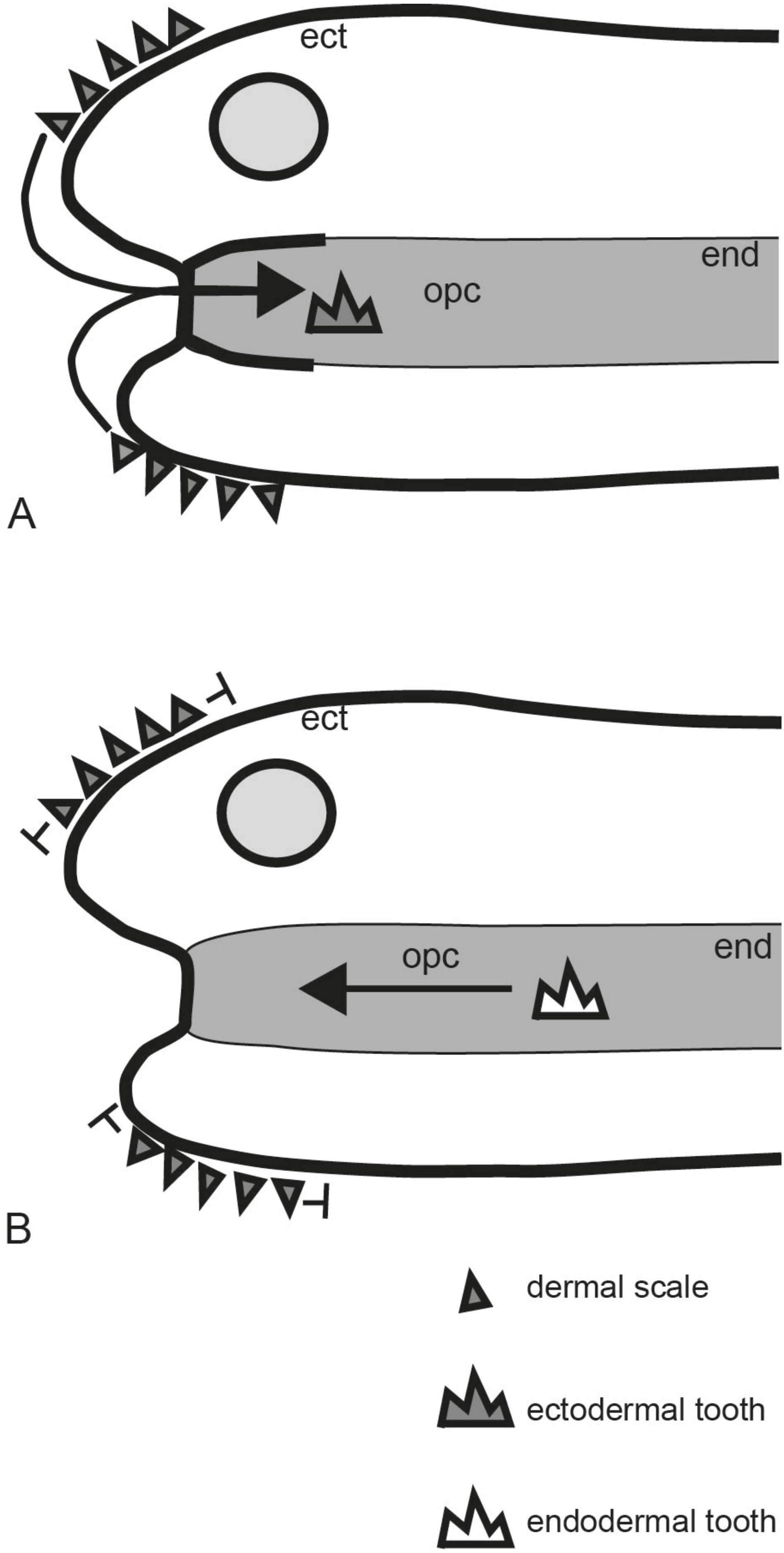
Co-option – is a new use of a trait, comprising the gene regulation and organs.
Odontode – the developmental unit of a tooth or dermal denticle.
Acanthodian – ‘spiny sharks’ are considered as stem chondrichthyans.
Conodont – describes the animal, or oral element of the first mineralizing vertebrates.
Placoderms – are the first jawed vertebrates, probably forming a grade at the stem of living jawed vertebrates.
Thelodonts – are jawless vertebrates with a skeleton of minute scales forming an external dermal, oral and pharyngeal skeleton.

Illustrations
Fig. 1. Phylogeny and distribution of teeth, oral denticles and scales redrawn after Donoghue & Rücklin 2016 changes based on Coates et al. 2018 and Murdock et al. 2013.

Fig. 2. Schematic illustration of hypotheses on dental evolution, redrawn after Fraser et al. 2010. A) Inside out hypothesis and B) outside in hypothesis. ect – Ectoderm; end – Endoderm; opc – oro-pharyngeal cavity

Cross-references to other eLS articles
Placodermi (Armoured Fishes) DOI: 10.1002/9780470015902.a0001533.pub2

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