Dental diversity in early chondrichthyans and the multiple origins of shedding teeth

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Abstract

The teeth of sharks famously form a series of parallel, continuously replacing files borne directly on the mandibular cartilages. In contrast, bony fishes possess site-specific shedding dentition borne on dermal plates. Understanding how these disparate systems evolved is challenging, not least because of poorly understood relationships and the profusion of morphologically and terminologically diverse bones, splints and whorls seen in the earliest chondrichthyans. Here we use tomographic methods to investigate the nature of mandibular structures in several early branching ‘acanthodian’-grade stem-chondrichthyans. We characterise the gnathal plates of ischnacanthids as growing bones, and draw similarities between early chondrichthyan and stem gnathostome teeth and jaws. We further build the case for *Acanthodopsis*, a Carboniferous taxon, as an acanthodid, and show that, unexpectedly, its teeth are borne directly on the mandibular cartilage. Mandibular splints are formed from dermal bone and appear to be an acanthodid synapomorphy. The development of a unidirectionally growing dentition may be a feature of the chondrichthyan total-group. More generally, ischnacanthid and stem gnathostome gnathal plates share a common construction and are likely homologous, and shedding teeth evolved twice in gnathostomes.

Keywords (3-6): dentitions, early vertebrates, acanthodians, chondrichthyans, tooth evolution, Palaeozoic

1. Background

The structure and position of teeth and jaws are one of the major anatomical distinctions between osteichthyans (bony fishes: ray-finned fishes, lobe-finned fishes, and tetrapods) and chondrichthyans (cartilaginous fishes: sharks, rays, and chimaeras) (1). In osteichthyans, teeth are partially resorbed, shed, and replaced in position on dermal bones lateral to and overlying endoskeletal jaw cartilages. These form inner (dermal: coronoids, dermopalatines; endoskeletal: Meckel's cartilage, palatoquadrate) and outer (dermal: dentary, maxilla, premaxilla) dental arcades. In chondrichthyans, teeth grow, shed, and are replaced in parallel rows of labially-directed series directly on the jaw cartilages (endoskeletal: Meckel's cartilage, palatoquadrate). These two conditions are difficult to reconcile. Their origins can be observed in the morphologies of Palaeozoic gnathostome fossils, which suggest that the last common ancestor of jawed fishes (gnathostomes), as well as crownward stem gnathostomes (a paraphyletic assemblage referred to as 'placoderms'), possessed non-shedding teeth fused to the underlying dermal jaw bone (2–4).

The advent of micro-computed tomography has led to a renewed interest in tooth evolution and development in 'placoderms' (3–5) and osteichthyans (6–10). However, 'acanthodians', the earliest-branching members of the chondrichthyan total-group, have received comparatively little study (but see: (11–13)), despite a bewildering array of dermal oral structures (e.g. (11,14–18)).

Here we provide new tomographic data on teeth and jaws in several early-diverging stem chondrichthyans. We place this in the context of what we know about early chondrichthyan relationships, and discuss its implications for the early evolution of gnathostome dentitions.

2. Materials and Methods

All specimens studied here are housed at the Natural History Museum, London (NHM), and comprise: an isolated *Taemasacanthus erroli* jaw (NHMUK PV P33706); an isolated *Atopacanthus* sp. jaw (NHMUK PV P.10978); an isolated *Acanthodopsis* sp. jaw (NHMUK PV P.10383); and a partial head of *Acanthodes* sp. (NHMUK PV P.8065). Full descriptions, as well as details of an additional isolated *Ischnacanthus* sp. jaw (NHMUK PV P.40124) are given in the supplement.

CT scanning of two specimens took place at the Imaging and Analysis Centre, NHMUK, using a Metris X-Tek HMX ST 225 with the following settings: *Taemasacanthus erroli*: 3142 projections, 130 kV, 131 *μ*A, 0.1 mm copper filter, voxel size 17.3 *μ*m; *Atopacanthus*: 3142 projections, 130 kV, 154 *μ*A, 0.1 mm copper filter, voxel size 19.508/07/2020 18:05:00 *μ*m.

CT scanning of three specimens took place at the Bristol University Department of Life Sciences using a Nikon XT H 225 ST with the following settings: *Acanthodopsis*: 3142 projections, 180 kV, 92 *μ*A, no filter, voxel size 22.6 μm; *Acanthodes*: 3142 projections, 215 kV, 165 *μ*A, 0.1 mm tin filter, voxel size 44.9 *μ*m; *Ischnacanthus*: 3142 projections, 222 kV, 105 *μ*A, 0.5 mm copper filter, voxel size 24.6 *μ*m.

Reconstructed tomographic datasets were segmented in Mimics v.19 (biomedical.materialise.com/mimics; Materialise, Leuven, Belgium). Images of the resulting models were then generated using Blender (blender.org).

3. Results

The left lower jaw of *Taemasacanthus* (previously described in Long (19): fig. 4A-C) comprises a tooth-bearing dermal gnathal plate (also referred to as a dentigerous jaw bone: Burrow (15)) with a concave ventral surface overlying a partially-ossified Meckel's cartilage (figure 1a,b, figure S1). The *Atopacanthus* specimen examined here belongs to either a right lower or left upper jaw (figure 1d,e, figure S2), and only the gnathal plate is preserved. The jaw bones of both taxa have a broadly similar construction, which also corresponds to that of *Ischnacanthus* (figure S3). The largest component of the dentigerous jaw bone is the gnathal plate. Internally, this plate is highly vascularised with interlinked antero-posteriorly polarised canals (figure 1c,f). Three rows of teeth are borne on the biting edge of the gnathal plate: a lateral, medial, and lingual row. Teeth within the lateral and lingual rows are fused to the jaw but histologically separate from the underlying gnathal plate. The medial row lies on the mesial ridge, formed by the occlusal corner of the gnathal plate, and comprises small disorganised cusps (one row in *Taemasacanthus*, two rows in *Atopacanthus*). All mesial teeth are vascularised in *Atopacanthus*, but only the posteriormost ones are in *Taemasacanthus*. The lateral and lingual rows of teeth in both taxa are much larger, are ridged, and comprise a vascular base topped with an avascular crown (figure 1a,c,f). Both grow by the addition of new teeth anteriorly, as evidenced by anterior teeth partially overlying posterior ones, with cusps becoming progressively larger in the direction of growth. The sole exception to this is the penultimate lingual tooth in *Taemasacanthus* (figure 1a), which partially overlies and is thus younger than the tooth anterior to it. The lateral tooth row in both taxa lies on the dorso-lateral (or ventro-lateral) surface of the gnathal plate. Its teeth are laterally unornamented and continuous with the lateral surface of the dermal bone, connected to one another via antero-posterior lateral ridges. The lingual tooth row grows on the lingual side of the dermal plate, curving away from the occlusal surface anteriorly. These teeth appear to sit on a bony lingual plate, with a distinct histology from the main gnathal plate, something particularly obvious in *Atopacanthus* (figure S2).

The right lower jaw in *Acanthodopsis* comprises a tooth-bearing Meckel's cartilage and a mandibular splint (figure 1g,i,j, figure S4). The Meckel's cartilage is similar in form to that of *Acanthodes* (figure 1k–m, figure S5) (15,20), with an identical articular cotylus and symphyseal fossa, and is mineralised as a thick shell of perichondral bone which would have contained cartilage in life. Unlike in *Acanthodes*, the Meckel's cartilage in *Acanthodopsis* is mineralised along its entire length. A row of ten monocuspid, triangular teeth runs along the dorsal surface of the Meckel's cartilage. The largest tooth is in the middle of the jaw, with teeth becoming smaller and more closely set anteriorly and posteriorly; they are slightly lingually convex, with a smooth (but possibly weathered) lateral face and a longitudinally striated lingual face. Rather than being tooth-shaped extensions of perichondral bone (15) these are histologically distinct from Meckel's cartilage, formed from a thick outer shell and a vascular inner pulp, with no obvious pulp cavity (figure 1i,j). Although indistinct, growth lines suggest that the largest tooth is the oldest, with younger teeth added both anteriorly and posteriorly. The mandibular splint in *Acanthodopsis* is an unornamented, slightly sinusoidal bone that fits into a groove on the ventro-lateral part of Meckel's cartilage, extending almost its entire length. Internally, the element is pierced by a series of thin, longitudinally oriented canals (figure 1i). This, combined with the fact that no other endochondral mineralisation is preserved in either Meckelian element, suggest that it is formed from dermal bone (21), rather than endochondral tissue (15). In all respects the mandibular splint in *Acanthodes* (figure 1l,m, figure S5) is almost identical to that of *Acanthodopsis* (20).

4. Discussion

Our new data show conclusively that the gnathal plates (also referred to as dentigerous jaw bonens) of ischnacanthids were growing bones with new teeth added in an anterior direction, as supposed by Ørvig (22) based on directional wear. These teeth were fused to, but distinct from, the underlying gnathal plate, which presumably grew with the rest of the jaw. This mode of growth is comparable to that of stem-gnathostome arthrodire gnathal plates in *Compagopiscis* and an unnamed buchanosteid, in which teeth are added in multiple directions onto a growing basal dermal bone (3,5,23). This also appears to be the case in the stem gnathostome acanthothoracid *Romundina*, although its exact mode of growth is disputed (4,24–26). This organisation of dental elements may be a plesiomorphic condition, shared with certain stem-group gnathostomes (figure 2). Unlike these taxa however, the tooth growth in ischnacanthids is unidirectional. This is more comparable to what is seen in ‘acanthodian’ tooth whorls (12,13), where non-shedding cusps are added unidirectionally onto a bony base. This unidirectional mode of tooth growth may be a chondrichthyan synapomorphy (figure 2).

The row of monocuspid dermal teeth borne directly on the Meckelian element of *Acanthodopsis* is unlike any other known chondrichthyan (with the possible exception of *Pucapampella*: (27)), and distinct from that seen in any other known gnathostome. Although in the past *Acanthodopsis* has been considered to have dermal dentigerous jaw bones (15,22), our CT data show conclusively that the main body of the jaw is endoskeletal in origin. A symphyseal fossa and *Acanthodes*-like mandibular splint further support Burrow’s (15) assertion that *Acanthodopsis* is closely related to acanthodiforms, rather than ischnacanthiforms. However, beyond this its dental morphology is difficult to interpret. The teeth are comparable to the tooth whorls of more crownward chondrichthyans in that they are borne directly on the Meckelian element and are apparently oriented perpendicular to the direction of the jaw bone. In this sense they could be interpreted as a non-growing tooth whorl with a single generation. However, this interpretation is confounded by the fact that *Acanthodes* is completely toothless, and phylogenetic analyses recover it as nested within a larger clade of toothless acanthodiforms inferred to be filter-feeders, the earliest members of which existed in the Early Devonian (28). If this phylogeny is correct, and the teeth of *Acanthodopsis* are homologous with tooth whorls, it would demand at least two convergent losses of teeth in this clade (i.e. in deeper-diverging acanthodiforms and *Acanthodes*). Alternatively, teeth may simply be unobserved in some acanthodiform taxa due to their small size: teeth were recently found in the supposedly edentulous filter feeder *Gladbachus adentatus* (28).

Mandibular splints (variously termed dentohyoids, extramandibular spines, splenials, and mandibular bones (29)) have been reported in a range of ‘acanthodian’-grade taxa including acanthodids (29,30), mesacanthids (31,32), cheiracanthids (21), ischnacanthids (33,34), and diplacanthids (35,36). Their small size and unclear association with other bones of the mandibular arch has made them difficult to characterise, of unclear homology, and prone to being mixed up with other mandibular elements; the supposed mandibular splint in diplacanthids has for example been shown to be an “occlusal bone” (18). Our characterisation of the mandibular splint in *Acanthodopsis* and *Acanthodes* as a dermal bone with a distinctive shape allows reassessment of these mandibular bones in other taxa. The morphology in other acanthodids appears likely to match that in the two taxa we describe in that they have a slightly sinusoidal shape, for example in other species of *Acanthodes* (20,29,37), *Halimacanthodes* (30), and *Howittacanthus* (38). In *Ischnacanthus* (figure S3), the ventral margin of Meckel’s cartilage is reinforced and laterally flattened; we suggest this is also likely to be the case in other ischnacanthids with “mandibular splints” (33). This may also be the case in mesacanthids, in which the mandibular splint is not convincingly separate from the Meckel’s cartilage or branchiostegal plates, for example in *Promesacanthus* (31). The condition is uncertain in cheiracanthids: a mandibular splint is absent in *Cheiracanthus* and *Homalacanthus*, and while *Protogonacanthus* is described as having a mandibular splint (21) its morphology looks more similar to the reinforced ventral margin in ischnacanthids. Thus it is possible that a separate "true" mandibular splint, as seen in *Acanthodopsis* and *Acanthodes*, is an acanthodid synapomorphy. Its similarity to the ventral branchiostegal rays in *Acanthodes* suggest that it may simply be part of this series that has been co-opted to support the jaw.

Our new data on 'acanthodian' jaw elements feed into an emerging picture of stem chondrichthyan evolution. A unidirectional mode of tooth growth appears to be a chondrichthyan synapomorphy (with a possible reversal in *Acanthodopsis*; figure 2). While fine-scale relationships remain poorly understood, phylogenetic analyses increasingly recover a stemward grade of ischnacanthiforms, acanthodiforms, and diplacanthiforms (28), with a climatiid-grade more proximate to the chondrichthyan crown. Consequently, a dentition consisting entirely of tooth whorls—which extend along the entire jaw length—as well as absence of dermal gnathal plate, is restricted to climatiids and more crownward taxa (figure 2), although possibly homologous dentitions may be seen in ischnacanthid tooth whorls, *Acanthodopsis*, and *Latviacanthus.* Tooth shedding is restricted to the node proximate to the chondrichthyan crown. Some uncertainty remains, however, largely due to the uncertain position of edentulous taxa such as *Lupopsyrus* and *Kathemacanthus*, and the peculiar site-specific dentition apparently present in *Pucapampella* (27).

Our new data also have a bearing on the broader question of jaw and tooth evolution in gnathostomes. Ischnacanthid gnathal plates (also referred to as dentigerous jaw bones) appear homologous with the gnathal plates of stem-gnathostomes: they are positionally, structurally and histologically similar, being vascularised dermal bones overlying the mandibular cartilage, with non-shedding tooth cusps added onto an underlying dermal plate. These gnathal plates have been homologised with the inner dental arcade of osteichthyans (39–41), and more recently with the outer dental arcade (42,43). In either case, assuming homology between gnathal plates and either the inner or outer dental arcade, this is a rare example of a macromeric skeletal structure preserved on all three branches incident to the gnathostome crown node.

Our reassessment of early chondrichthyan dentitions also presents an opportunity to reconsider the homology of tooth whorls. The rows of denticles on the marginal jaw bones of the stem-osteichthyans *Lophosteus* and *Andreolepis* have been said to recall the tooth “families” of chondrichthyans (6). However, given that multiple rows of tooth whorls are absent in the deepest-diverging chondrichthyans, and that the parasymphyseal tooth whorls that are present grow from the lingual side of the jaw cartilage as in living chondrichthyans (6), we consider any resemblance superficial (9).Similarly, ischnacanthids cheek scales have been argued to be incipient tooth whorls formed from cheek denticles (11,44). However, given the phylogenetic position of ischnacanthids, and the propensity of dermal ornament bordering the mouth to resemble dentition (e.g. *Mimipiscis*, *Ptomacanthus* (45,46)), we consider these structures removed from hypotheses of early tooth evolution. Parasymphyseal tooth whorls in which the teeth replace via resporption and anterior rotation (10) are also known in osteichthyans (e.g. in *Onychodus* (10,47)), but these are phylogenetically and structurally removed from chondrichthyan tooth whorls and unlikely to be homologous. However, it is difficult to assess whether non-shedding parasymphyseal whorls are homologous due to the unclear condition in psarolepids (variably interpreted as stem sarcopterygians or stem osteichthyans (48–52)), in which a whorl is inferred (48,52) but is yet to be described. Finally, the interposition of many non-shedding stem-chondrichthyan taxa between shedding chondrichthyans and shedding osteichthyans confirms that a shedding dentition evolved twice, in two different ways, in crown-gnathostomes (7,10). The teeth of extant chondrichthyans, borne directly on endoskeletal mandibular cartilages, are positionally distinct from both the inner and outer dental arcades of osteichthyans, where teeth are borne on dermal bones.

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Ethics. This research is based exclusively on specimens from natural history collections.

Data accessibility. Raw data (.vol or .tiff stacks), Mimics files, and 3D PLY files for each specimen are deposited in Dropbox (see links in supplementary file) and will be permanently deposited in Dryad upon manuscript acceptance.

Authors' contributions. S.G. conceived the project and selected specimens. S.G. and R.P.D. carried out CT scanning. R.P.D. segmented the specimens, made Blender renders and constructed figures with input from S.G. S.G. and R.P.D. drafted the manuscript. Both authors revised and edited the manuscript, approved the final version and agree to be accountable for all aspects of the work.

Competing interests. We have no competing interests.

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Figures

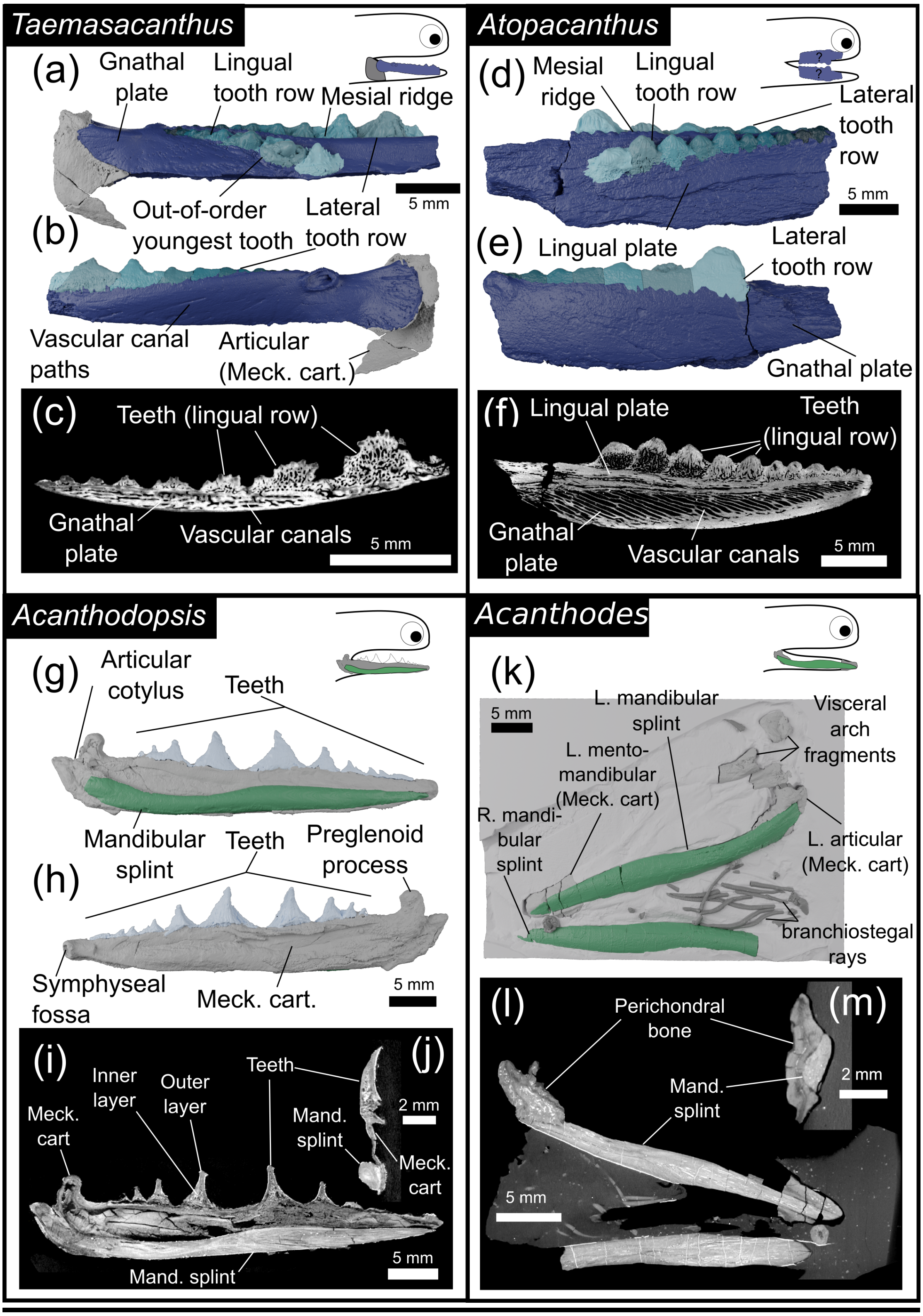
Taemasacanthus
(a)
Gnathal plate
Lingual tooth row
Mesial ridge
5 mm
Out-of-order youngest tooth
Lateral tooth row
(b)
Vascular canal paths
Articular (Meck. cart.)
(c)
Teeth (lingual row)
Gnathal plate
Vascular canals
5 mm
Atopacanthus
(d)
Mesial ridge
Lingual tooth row
?
?
Lateral tooth row
5 mm
(e)
Lingual plate
Lateral tooth row
Gnathal plate
(f)
Lingual plate
Teeth (lingual row)
Gnathal plate
Vascular canals
5 mm
Acanthodopsis
(g)
Articular cotylus
Teeth
Mandibular splint
Teeth
Preglenoid process
(h)
Symphyseal fossa
Meck. cart.
5 mm
(i)
Meck. cart
Inner layer
Outer layer
Teeth
Mand. splint
(j)
2 mm
Mand. splint
Meck. cart
5 mm
Acanthodes
(k)
5 mm
L. mandibular splint
L. mento-mandibular (Meck. cart)
R. mandi-bular splint
Visceral arch fragments
L. articular (Meck. cart)
branchiostegal rays
(l)
Perichondral bone
(m)
Mand. splint
2 mm
5 mm

Figure 1. Tomographic models of jaw elements in acanthodian-grade stem-chondrichthyans: (a-c) the left lower jaw of *Taemasacanthus erroli* NHMUK PV P.33706 in (a) medial view, (b) lateral view, and (c) a reconstructed tomogram showing a sagittal section through the lingual tooth row; (d-f) a gnathal plate of *Atopacanthus* sp. NHMUK PV P.10978 in (d) medial view, (e) lateral view, and (f) a reconstructed tomogram showing a sagittal section through the lingual tooth row; (g-j) the right lower jaw of *Acanthodopsis* sp. NHMUK PV P.10383 in (g) lateral view, (h) medial view, (i,j) reconstructed tomograms showing (i) a sagittal section through the entire jaw and (j) a transverse section through the jaw; (k-m) the lower jaws of *Acanthodes* sp. NHMUK PV P.8085 in (k) ventral view against the digital cast of the surface with (l,m) reconstructed tomograms showing (l) a coronal section through the specimen, and (m) a transverse section through a lower jaw. Abbreviations: Mand. splint., Mandibular splint; Meck. cart, Meckel's cartilage; L., Left; R., Right.

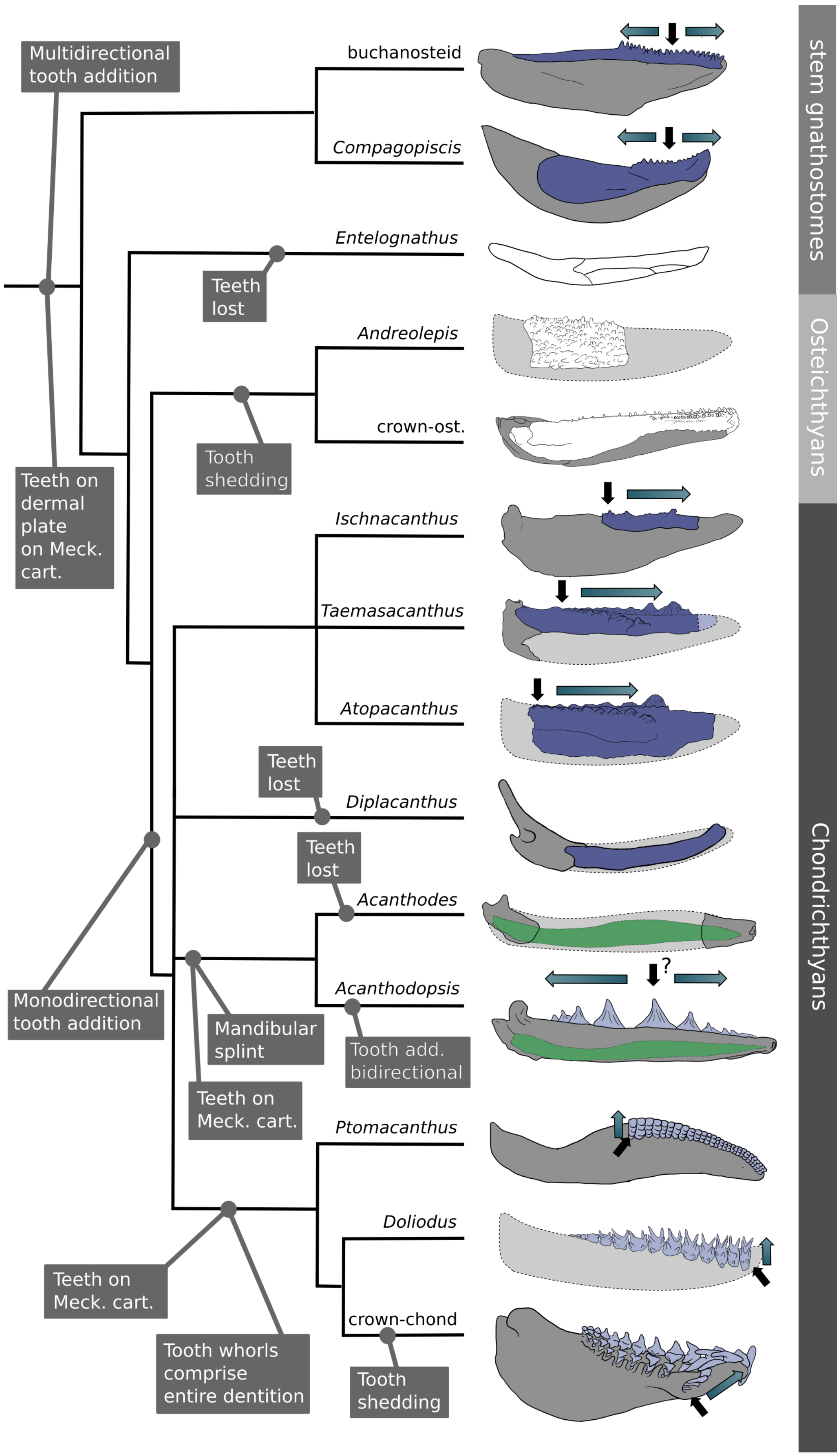
Multidirectional tooth addition
buchanosteid
Compagopiscis
Entelognathus
Teeth lost
Andreolepis
crown-ost.
Tooth shedding
Teeth on dermal plate on Meck. cart.
Ischnacanthus
Taemasacanthus
Atopacanthus
Teeth lost
Diplacanthus
Teeth lost
Acanthodes
Acanthodopsis
?
Monodirectional tooth addition
Mandibular splint
Tooth add. bidirectional
Teeth on Meck. cart.
Ptomacanthus
Doliodus
crown-chond
Teeth on Meck. cart.
Tooth whorls comprise entire dentition
Tooth shedding
stem gnathostomes
Osteichthyans
Chondrichthyans

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Figure 2. Hand-drawn cladogram showing relationships of total-group gnathostomes pertinent to tooth evolution and schematics of their lower jaw morphologies. Anterior to right and all specimens in lingual view except for *Compagopiscis*, *Entelognathus*, and *Andreolepis*. Black arrow indicates position of initial tooth growth, blue graded arrow indicates direction of subsequent growth. Colour scheme: grey, Meckel's cartilage; dark blue, gnathal plates and attached teeth; green, mandibular splints; light blue, teeth placed directly on endoskeleton; white, dermal bones of uncertain homology and attached teeth. Abbreviations: Add., addition; Meck. cart, Meckel's cartilage. Images redrawn from (3,5,8,11,16,32,41,45,53,54).

Supplementary material (separate pdf)

Supplementary information for this manuscript is included as a single separate file. It includes supplementary figures 1-5, supplementary text comprising a full description of the elements scanned and a review of acanthodian jaw elements, and supplementary references. It also contains links to 3D models (as plys), mimics files, and tomographic data (as volume files or TIFFs) for all the data used in this study.