



TOOTH DEVELOPMENT IN THE EARLY DEVONIAN SARCOPTERYGIAN *POWICHTHYS* AND THE EVOLUTION OF THE CROWN OSTEICHTHYAN DENTITION

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Abstract: In osteichthyans (bony fishes) the dentition is characterized by marginal tooth rows replaced by basal resorption. Basal resorption was present in the stem osteichthyan *Andreolepis*, which also possessed overgrowing tooth-shaped odontodes, a possible intermediate state between external odontodes and teeth. *Andreolepis*, however, lacked the enlarged marginal tooth rows found in more advanced osteichthyans, and how these evolved from the stem osteichthyan condition is unknown. Here we present computed tomography and synchrotron-based x-ray phase-contrast imaging of the jaws and teeth of the Early Devonian sarcopterygian *Powichthys*. We reveal the presence of fields of overgrowing tooth-like odontodes, resembling the dentitions of stem-group osteichthyans, alongside the marginal tooth row. In the

inner dental arcade, we show a continuous variation between regions of tooth-like and external odontode-like replacement, apparently driven by variations in the relative rates of bone growth, odontode addition and odontode size. These results suggest that there is a degree of plasticity in oral odontode development. We propose that the tooth rows of crown osteichthyans develop in an essentially similar manner to the teeth of stem osteichthyans, with differences explained by increased resorption activity linked to the larger size of the teeth. Therefore, the external odontodes and teeth of both stem and crown osteichthyan lie on the same developmental continuum.

Key words: osteichthyan, Devonian, x-ray tomography, tooth replacement, resorption, evolution.

THE teeth of living osteichthyans are highly disparate in terms of their functional morphology and replacement mechanisms. The origins of this important functional system can be traced to the relatively simple tooth rows of early osteichthyans. The earliest members of the osteichthyan crown group have dentitions characterized by a single row of large conical teeth on the margins of the dermal jaw bones (Jarvik 1972; Gardiner 1984; Andrews *et al.* 2006). Similar tooth rows are also found in the ‘psarolepid’ osteichthyans (Yu 1998; Zhu & Yu 2004; Zhu *et al.* 2009), which may be sarcopterygians but more likely to be stem osteichthyans (Qu *et al.* 2015; King 2019). On the other hand, the marginal jawbones of the Silurian stem osteichthyans *Andreolepis hedei* and *Lophosteus superbus* lack these tooth rows (Botella *et al.* 2007). Instead, their marginal teeth are only slightly larger than the external dermal odontodes and lack organization into longitudinal rows. The enlarged tooth rows of osteichthyans are therefore inferred to have evolved on the osteichthyan stem after the divergence of *Andreolepis* and *Lophosteus*.

The dentitions of the stem osteichthyans *Andreolepis* and *Lophosteus* have been studied using three-dimensional reconstructions of phase-contrast synchrotron microtomography (PC-SμCT) scans, revealing valuable insights into the origins of tooth replacement (Chen *et al.* 2016, 2017, 2020). *Andreolepis* marginal jaw bones show tooth-shedding by basal resorption, as well as overgrown, partially resorbed tooth-shaped odontodes on the labial side of the jaw (Chen *et al.* 2016). It has been suggested that the latter represent a transitional zone between external odontodes and teeth (Johanson 2017). *Lophosteus* tooth cushions (small tooth bearing plates probably forming the inner dental arcade) and marginal jaw bones show the presence of semi-basal resorption, in which the bases of previous teeth were retained (Chen *et al.* 2017, 2020). Semi-basal resorption, which occurred alongside complete basal resorption in *Lophosteus*, is hypothesized to be a precursor condition to basal resorption (Chen *et al.* 2017).

Despite these advances, without similarly detailed analyses of more crownward osteichthyans, the evolutionary

steps from a dentition such as that in *Andreolepis* to one with the distinct enlarged tooth rows of more crownward osteichthyans remains unclear. Here we explore tooth development in the Early Devonian crown osteichthyan *Powichthys* using three-dimensional analysis of PC-S μ CT scans. *Powichthys* is generally recovered as a stem lungfish (Ahlberg 1991; Friedman 2007; Zhu *et al.* 2009), most frequently as the sister group to Porolepiformes (Clément & Ahlberg 2010; Lu *et al.* 2012; Clement *et al.* 2018) (Fig. 1).

MATERIAL AND METHOD

Material

The specimens of *Powichthys* investigated here are GZG.V.29285 (previously 100-285; Fig. 2A) and GZG.V.29186 (previously 100-186; Figs 3D, 4A). GZG.V.29285 is an almost complete left lower jaw, described by Jessen (1980). GZG.V.29186 consists of several bone fragments (including parts of two jaws designated GZG.V.29186a and b) left over from acid preparation. All specimens come from the same locality as the holotype of *Powichthys thorsteinssoni*, on the west coast of Prince of Wales Island, Arctic Canada, Early Devonian (Langenstrassen & Schultze 1996). The tooth histology (open pulp cavity, simple plicidentine folding and no bone of attachment between folds)

supports assignment of these specimens to *P. thorsteinssoni*, following previous studies in which isolated material was assigned to the taxon (Chang & Smith 1992).

Institutional abbreviation. GZG, Georg-August-Universität Göttingen Geowissenschaftliches Zentrum, Germany.

CT scanning

All *Powichthys* specimens were scanned on a Zeiss Xradia 510 Versa 3D micro-CT system housed at Naturalis Biodiversity Center, Leiden, The Netherlands (see Table S1). All scans were at 50 kV and taken over 180°. The jaw specimen GZG.V.29285 was scanned for 1401 projections with an exposure time of 18s, with a resulting voxel size of 28.14 μ m. The prearticular fragment from GZG.V.29285 was scanned for 1601 projections with an exposure time of 11s, resulting in a voxel size of 7.09 μ m. GZG.V.29186a was scanned for 1401 projections with an exposure time of 16s, resulting in a voxel size of 3.95 μ m. GZG.V.29186b was scanned for 801 projections with an exposure time of 8s, resulting in a voxel size of 7.91 μ m.

Regions of interest in two jaw fragments from GZG.V.29186 and a detached part of the prearticular (Fig. 2A) from GZG.V.29285 were scanned at higher resolution at the TOMCAT (X02DA) beamline of the Swiss

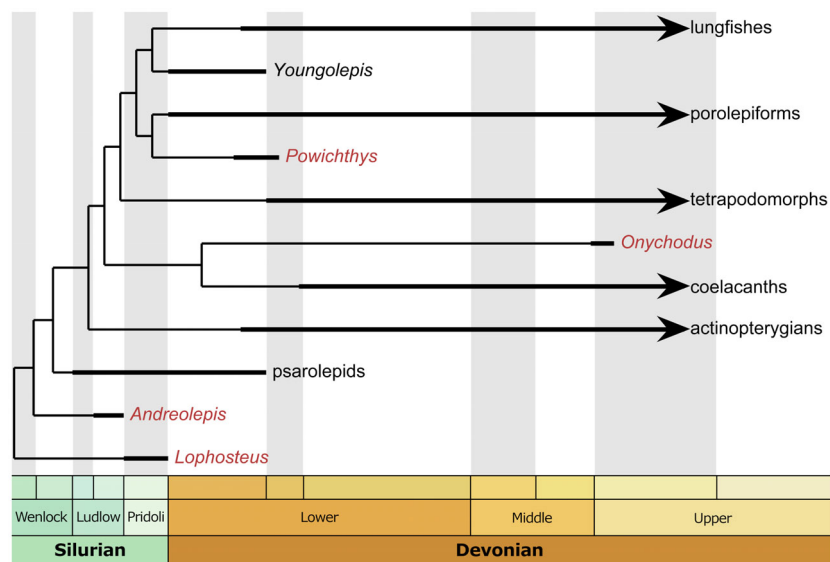
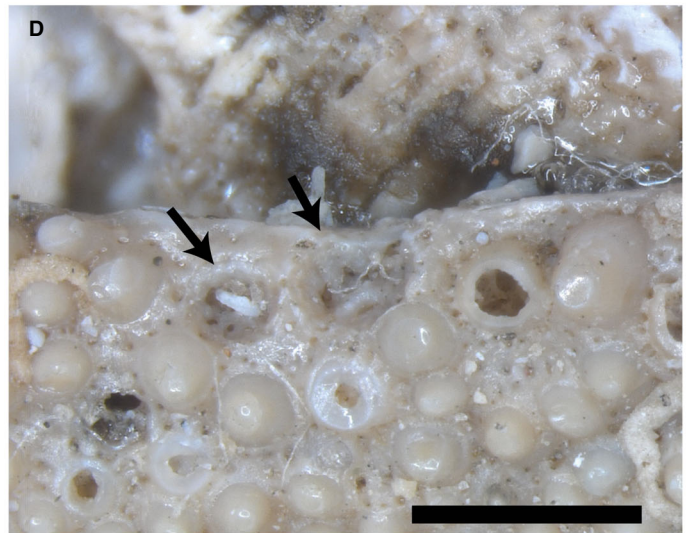
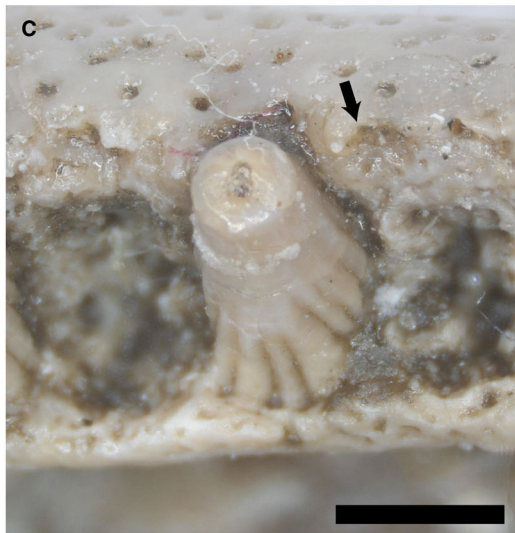
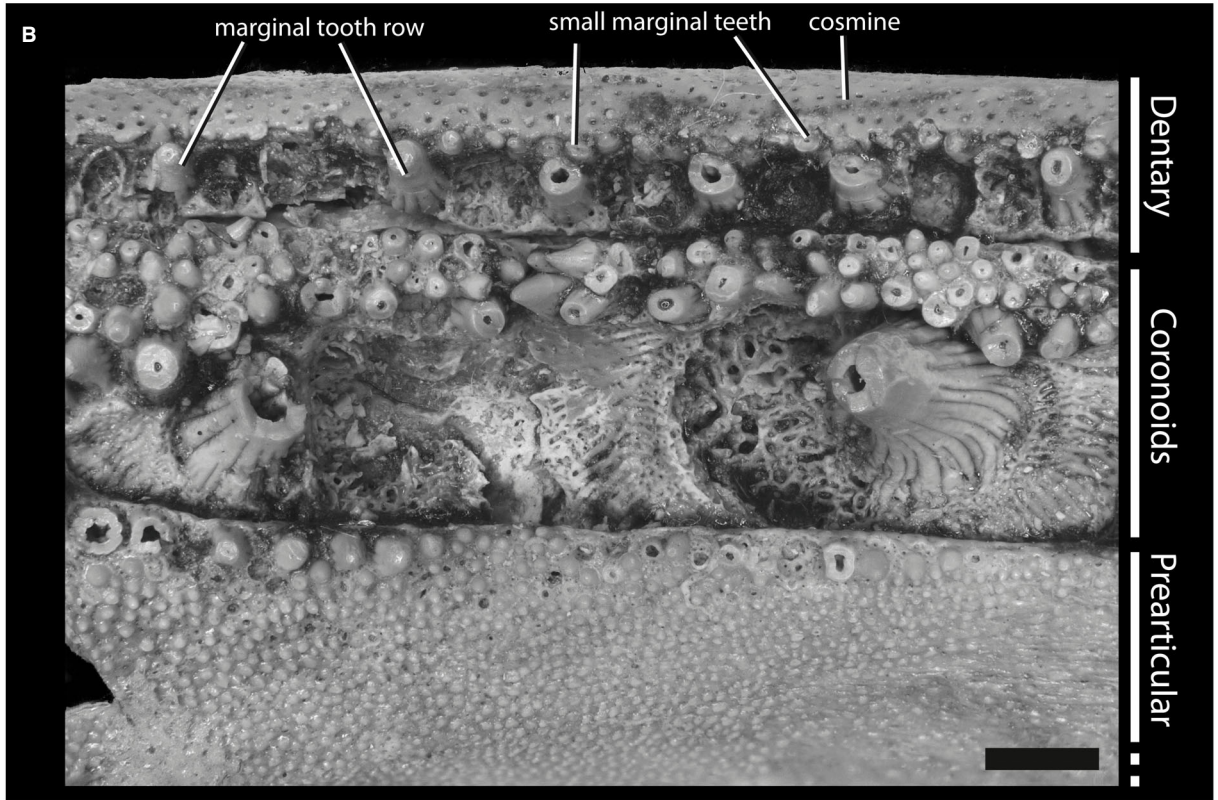
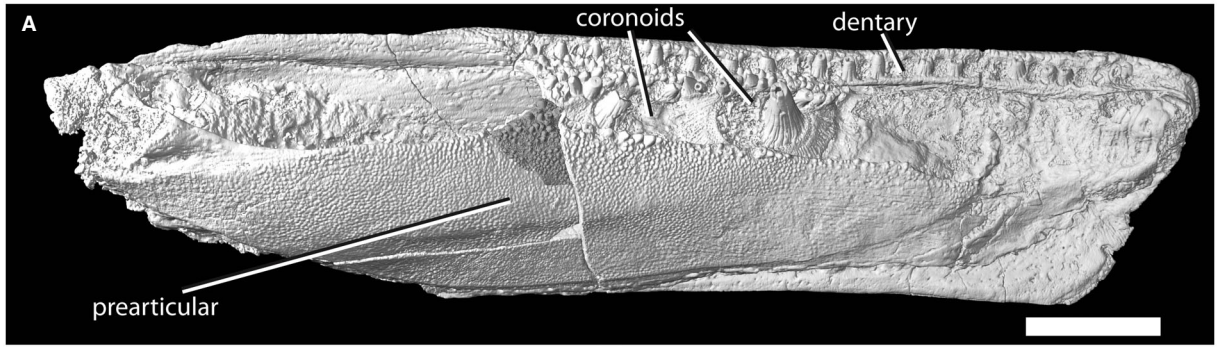


FIG. 1. Phylogeny of osteichthyans, indicating taxa in which labial buried tooth-like odontodes are known to occur in the marginal jaw bones (red). Tree topology based on Clement *et al.* (2018), with position of *Andreolepis* and *Lophosteus* assumed based on (Chen *et al.* 2020).

FIG. 2. The lower jaw of *Powichthys*. A, internal view of the lower jaw, micro-CT data (specimen GZG.V.29285); grey shaded area is a detached fragment, digitally restored to its original position. B, dorsal view of the jaw, photograph. C, dorsal view of *Powichthys* dentary fragment (specimen GZG.V.29186) showing presence of a replacement pit in the narrow field of small lateral teeth (arrow). D, dorsal view of the edge of the prearticular (specimen GZG.V.29285), showing replacement pits (arrows). Scale bars represent: 10 mm (A); 2 mm (B); 1 mm (C, D).



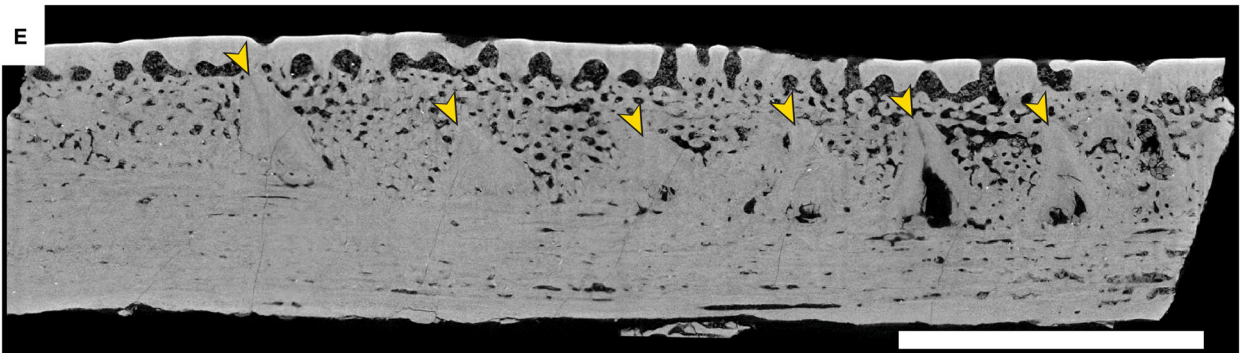
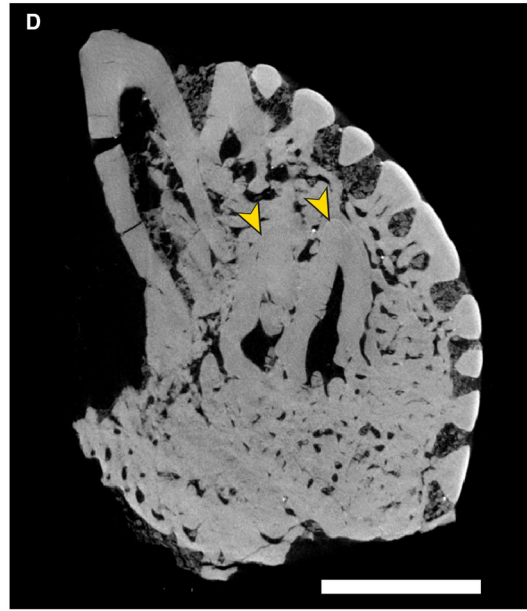
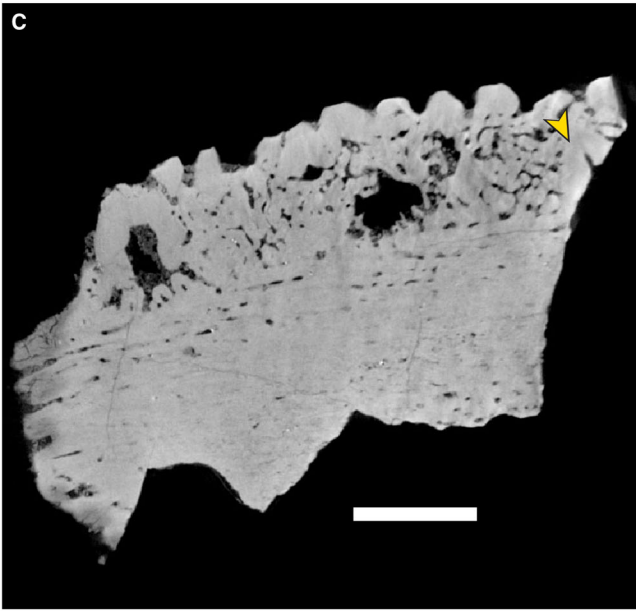
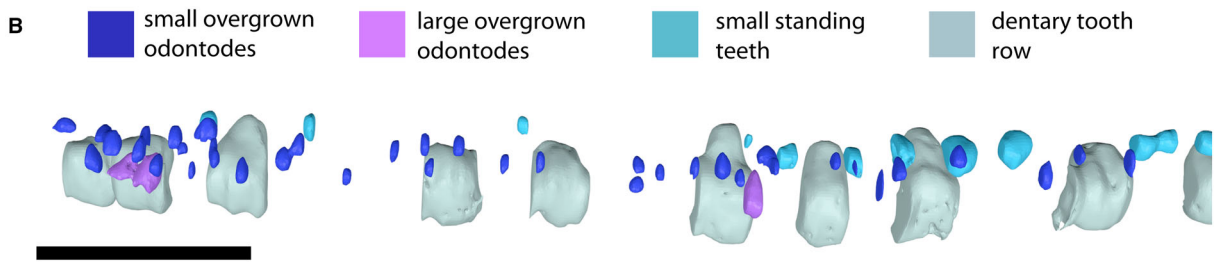
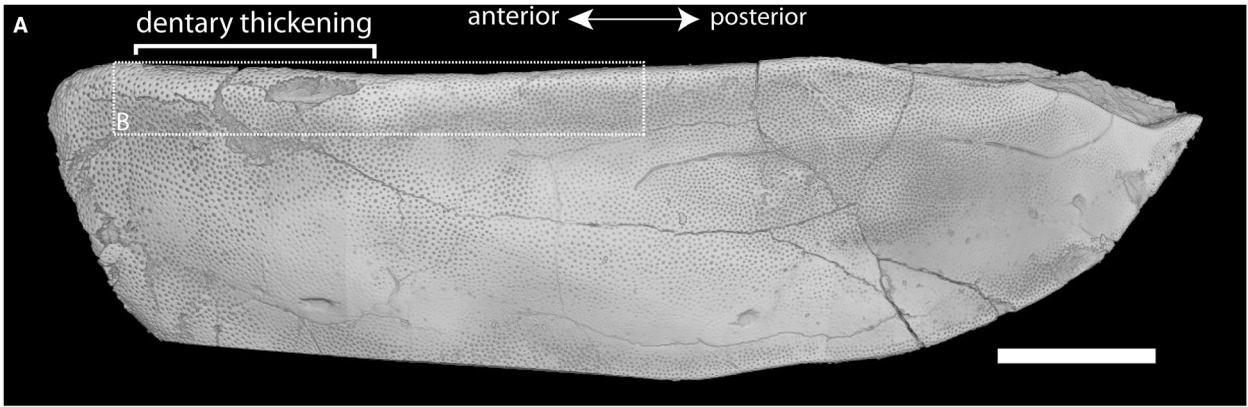


FIG. 3. Buried tooth-like odontodes in *Powichthys*, micro-CT data. A, lateral view of the lower jaw of *Powichthys*. B, segmentation of odontodes in the anterior part of the jaw. C, oblique slice from micro-CT scan of GZG.V.29186b, showing a single buried tooth-like odontode (yellow arrowhead). D–E, micro-CT scan of GZG.V.29186a, showing buried tooth-like odontodes (arrowheads): D, transverse; E, longitudinal slice. Scale bars represent: 10 mm (A); 5 mm (B); 1 mm (C, D); 3 mm (E).

Light Source, Paul Scherrer Institut, Switzerland (Stampanoni *et al.* 2006). Acquisition of all scans was with 1501 projections over 180° using a 10× objective with a resulting voxel size of 0.65 μm. For GZG.V.29186 an energy of 31 keV with an exposure time of 1.8 s (scan 1018_03) and 32 keV with 2 s exposure time (scan 1018_04) were used. The prearticular fragment from GZG.V.29285 was scanned at 35 keV with 2 s exposure time (scans 1018_06 and 1018_07) and 31 keV with 1.4 s exposure time (scan 1118_03). Prior to tomographic reconstruction, the corrected projections were phase retrieved using the Paganin algorithm (Paganin *et al.* 2002). Volume rendering and figures of CT slices were produced in AvizoLite 9.5 and Avizo 9.5.0. Segmentation was performed in Mimics v21.0 and ply files were exported to Blender for visualization.

RESULTS

Jaw morphology

The dentary of *Powichthys* bears a single row of large teeth, and a narrow field of much smaller teeth on the labial side (Fig. 2A, B). Replacement pits are present infrequently amongst these smaller teeth (Fig. 2C), whereas approximately half of the main tooth row consists of empty replacement pits. On the lingual face of the jaw, the prearticular is covered with small odontodes (Fig. 2A, B). Odontode size increases towards the occlusal (dorsal) margin of the bone, where resorption pits are visible (Fig. 2D). A series of coronoids sits on the dorsal side of the jaw between the dentary and prearticular (Fig. 2A, B), which bear large teeth (coronoid fangs) and many smaller teeth. This pattern of jaw bones and teeth is similar to that in many early osteichthyans (Jarvik 1972; Gardiner 1984; Zhu & Yu 2004; Andrews *et al.* 2006), as well as the extant coelacanth (Meunier *et al.* 2015).

Dentary

Overgrown pointed odontodes are present in the dentary of *Powichthys* (Fig. 3). Segmentations of tomograms reveal that they occur along the length of the dentary, but are particularly common at the anterior end (Fig. 3B) where the dentary shows a slight lateral thickening

(Fig. 3A). Overgrown odontodes lack organization into defined rows or tooth families (Fig. 3B).

Scans of two *Powichthys* jaw fragments offered higher resolution than was available from scans of the complete jaw. GZG.V.29186b, is probably from a posterior position and contains only a single small overgrown odontode (Fig. 3C), while GZG.V.29186a, probably from an anterior position, had many (Fig. 3D, E). In the latter, buried tooth-like odontodes occur in two size classes, with smaller odontodes present in a more superficial position (Fig. 4B, C). We interpret these smaller buried odontodes as earlier generations of the small labial teeth, while the larger buried odontodes probably represent the first generations of the tooth row. All odontodes sit above a basal plate with longitudinal vasculature (Fig. 4B). Bone covers the top of the buried odontodes and is further covered by a sheet of cosmine (Fig. 5A).

PC-SμCT scans of the *Powichthys* dentary fragments reveal partial resorption of the overgrown tooth-like odontodes (Figs 5, 6). The larger odontodes closest to the main row of dentary teeth show resorption bays at their base on the lingual side (Figs 5A, 6A), which cut through

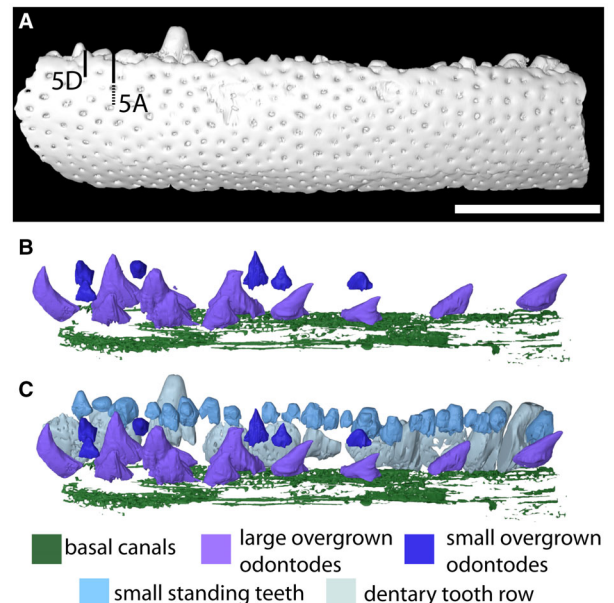


FIG. 4. Three-dimensional reconstruction of *Powichthys* dentary fragment from micro-CT data of GZG.V.29186a. A, specimen in lateral view (sections illustrated in Fig. 5 indicated). B, overgrown odontodes. C, all odontodes including marginal teeth. Scale bar represents 3 mm.

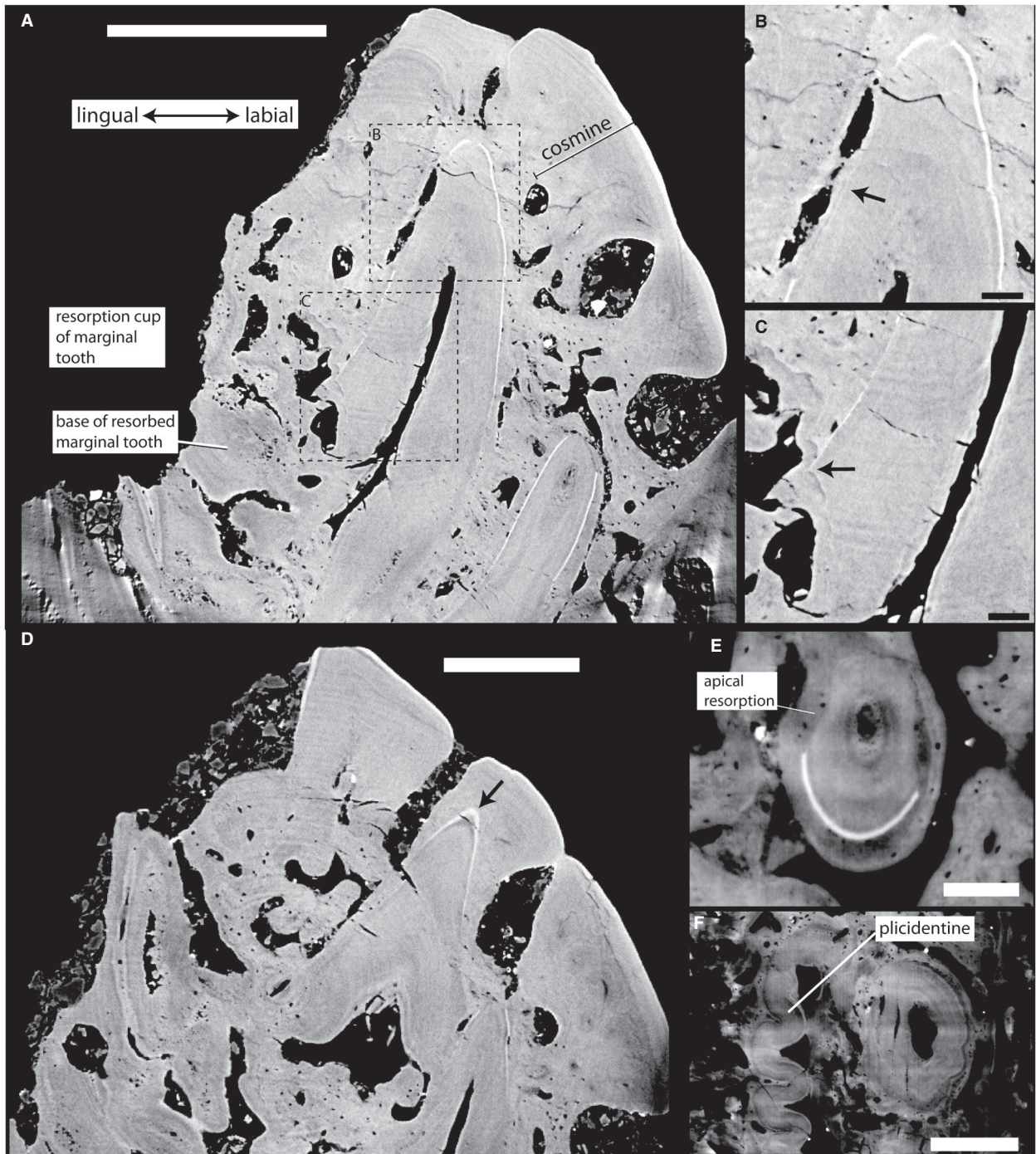


FIG. 5. Synchrotron microtomography scans of *Powichthys* dentary fragment. Specimen GZG.V.29186a. A, cross section of overgrown odontode (positions of enlargements B and C indicated). B, apical region of overgrown odontode. C, basal region of overgrown odontode; arrows indicate resorption lines. D, overgrown odontode with tip inside the cosmine layer. E, apical resorption of overgrown odontode. F, plicidentine at the base of an overgrown odontode. Scale bars represent: 500 μm (A); 50 μm (B, C, E); 300 μm (D); 200 μm (F).

the odontode and surrounding bone. There are small areas of local resorption elsewhere including apically, associated with bone remodelling around vascular canals (Figs 5B–C, 6B–C). Some of the buried odontodes are surrounded by the cosmine layer (Fig. 5D).

Prearticular

Sarcopterygian dermal bones and scales contain three layers, which can be distinguished in the *Powichthys* prearticular (Fig. 7). A compact basal layer of bone

FIG. 6. Three-dimensional model of a buried tooth-like odontode (Fig. 5A–C), synchrotron data. A, lingual view. B, lateral view. C, lingual view with vascular system of overgrowing bone, and pore canal system (including both mesh canals and pore canals). Scale bar represents 200 μm .

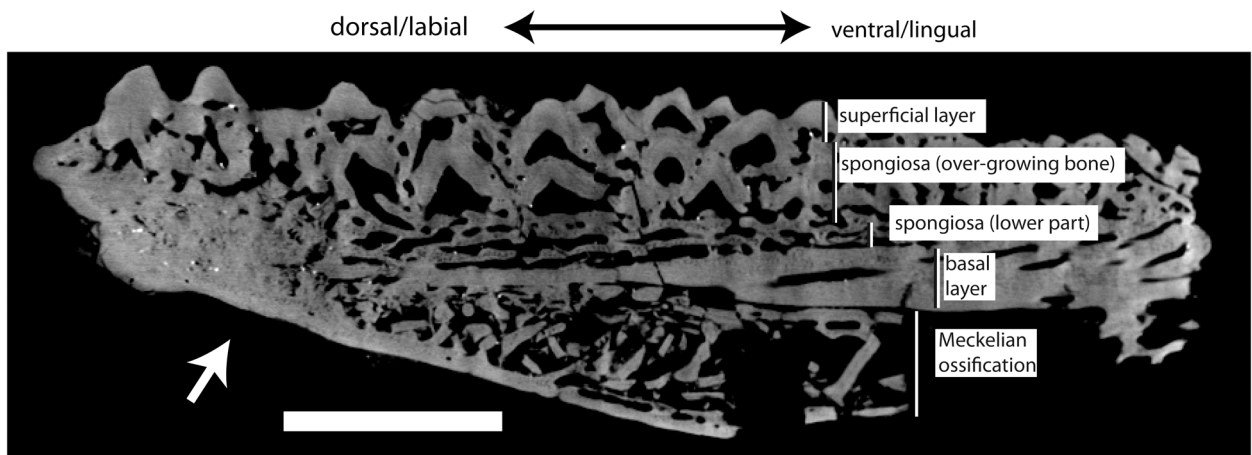
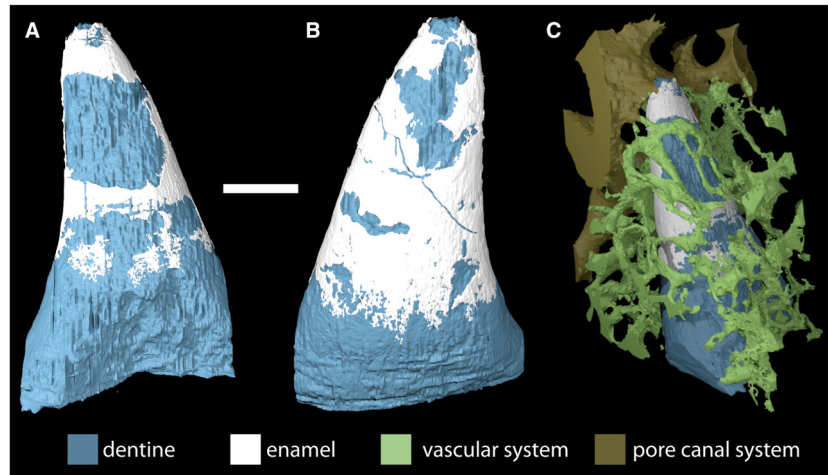


FIG. 7. Overgrown odontodes in the prearticular of *Powichthys*, micro-CT data. Transverse slice through a prearticular fragment from specimen GZG.V.29285. Many overgrown odontodes/denticles are visible. The arrow indicates the region at the margin of the bone where the boundary between the dermal and Meckelian bone breaks down. Scale bar represents 1 mm.

contacts the trabecular bone of the Meckelian ossification, and contains canals forming a pattern radiating from the growth centre. Above this is a layer of vascular bone, comprising most of the bone thickness. Two sub-layers can be distinguished within the vascular bone layer: at the base is a sub-layer in which the vascular canals form a horizontal mesh, above which is a thick zone with disorganized vasculature and overgrown odontodes. Finally, the exposed odontodes correspond to the superficial layer, although there is no distinct boundary between the superficial and middle layers. The basal layer of the prearticular does not reach the dorsal/labial margin of the bone. Here, the boundary between the different dermal bone layers and the underlying Meckelian ossification is obscured, and the bone is particularly dense in this region (Fig. 7, arrow). Overgrown odontodes are

absent from the dorsal/labial margin of the bone, and the most dorsal/labial of the buried odontodes are partially resorbed (confirmed by synchrotron scans, see below).

The growth of the prearticular mirrors that of the dentary (Fig. 8). Evidently the prearticular grew by addition of bone and odontodes to the dorsal/labial margin. Odontodes increase in size towards the labial (occlusal) margin. There is also an increase in odontode size through development, as the largest exposed odontodes are larger than the largest buried odontodes. However, since the margin of the bone shifts during development, overgrowing odontodes are the same size or smaller than the buried odontodes that they directly overgrow, and the largest odontodes are added at the margin and do not overgrow previous odontode generations.

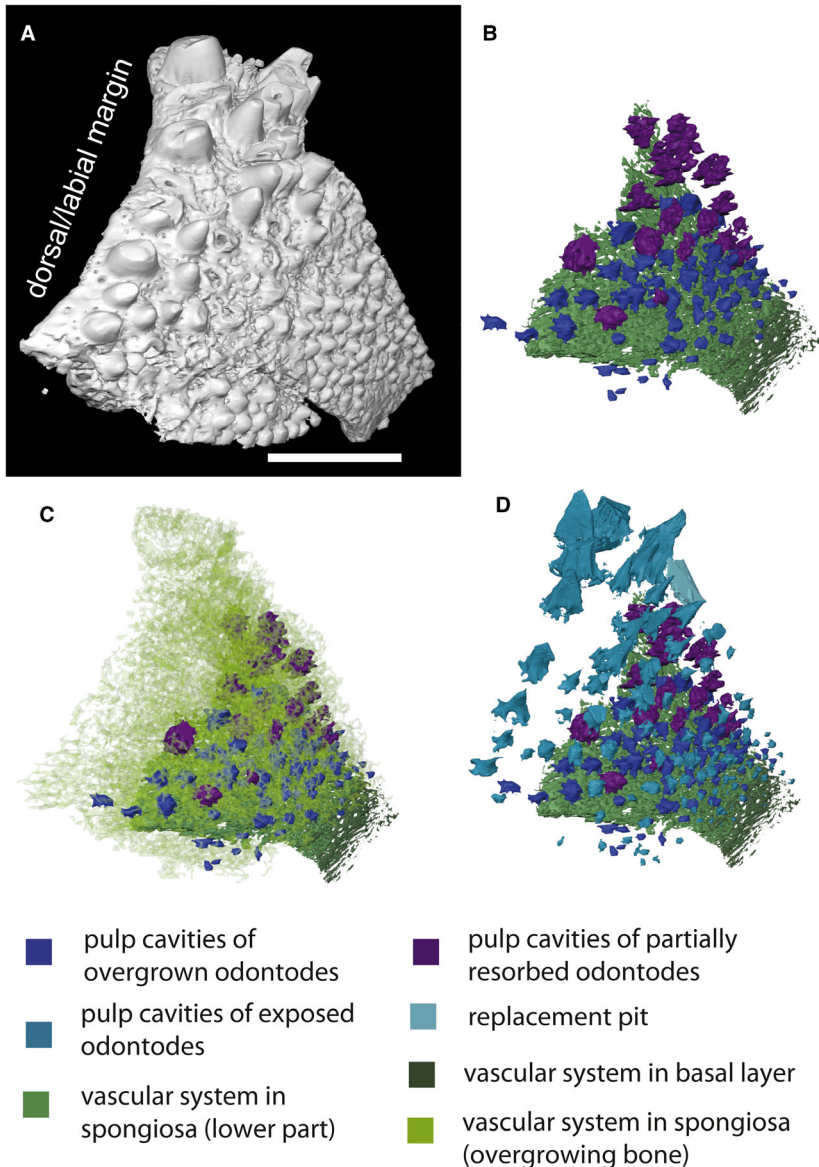


FIG. 8. Three-dimensional reconstruction from micro-CT data of the prearticular of *Powichthys*.

A, prearticular fragment from specimen GZG.V.29285 (see Fig. 2A), in posteromesial view. B, buried odontodes (visualized by segmentation of pulp cavities) and basal vasculature in the prearticular fragment.

C, buried odontodes surrounded by vasculature of spongy overgrowing bone. D, buried and surface odontodes, visualized by segmentation of pulp cavities. Scale bar represents 2 mm.

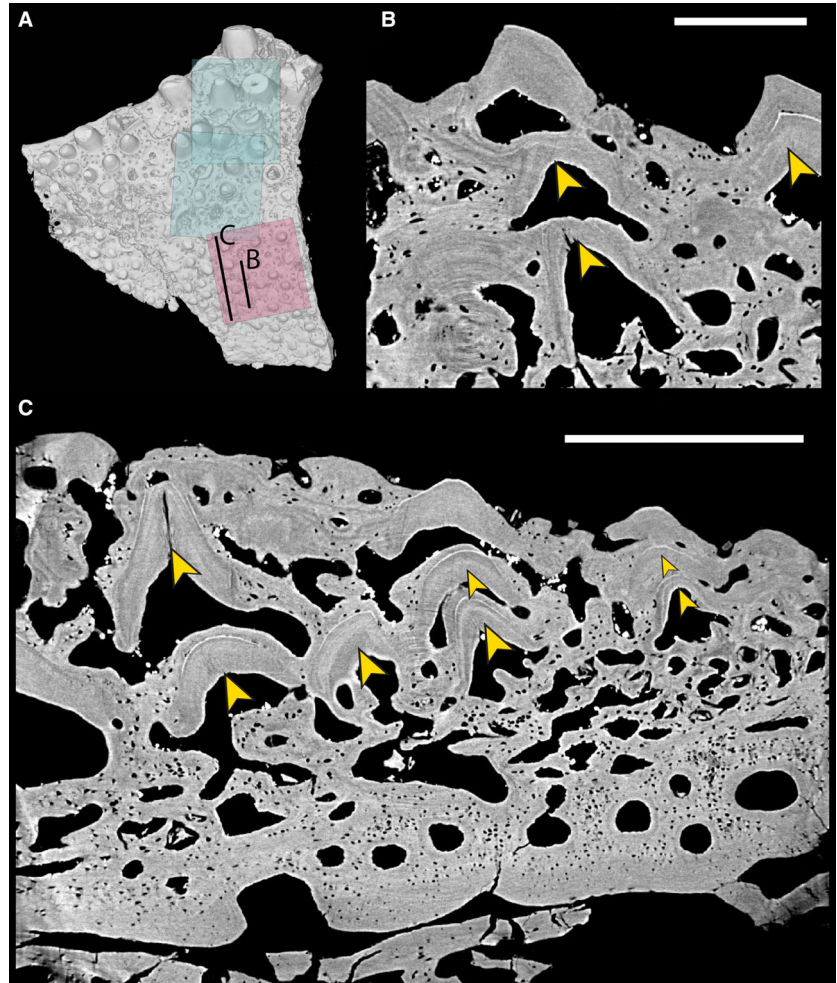
Odontodes in the prearticular show a continuum in the degree of resorption along the lingual-labial axis. Within the ventral-most (lingual) part of the prearticular fragment they are complete or show partial apical resorption (Fig. 9). In the mid-region of the fragment, odontodes show extensive apical resorption and resorption from the pulp cavity (Fig. 10). The most dorsal of the overgrown odontodes show near-complete resorption (Fig. 10E). Semi-basal resorption, in which the base previous generations of odontodes are left as dentine rings, is also evident (Fig. 10C, D). At the dorsal part of the fragment (Fig. 11), the surface odontodes are set within deep sockets, resorption pits are present and there is almost no trace of buried odontodes (possible remnant dentine is labelled in Fig. 11).

DISCUSSION

Teeth versus external odontodes

A continuum in tooth replacement modes is apparent in the *Powichthys* prearticular (Fig. 12A), which has basally resorbed ‘teeth’ at the margin, grading into odontodes with semi-basal resorption, apical resorption and finally little or no resorption away from the margin. Such a continuum is also evident in the marginal jawbones of *Lophosteus* and *Andreolepis* (Chen *et al.* 2016, 2020). To a lesser extent, a resorption continuum is also present in the *Powichthys* dentary in which overgrown, partially resorbed odontodes occur labial to the tooth row. The tooth-like morphology of these odontodes indicates a

FIG. 9. Overgrown odontodes furthest away from the occlusal margin are complete or slightly resorbed. Prearticular fragment from specimen GZG.V.29285 A, position of the three scans of this fragment, with the scan used in this figure highlighted in red. B, buried odontodes with apical resorption. C, transverse slice showing complete buried odontodes. Scale bars represent: 300 μm (B); 700 μm (C).



tooth function prior to bone overgrowth, but the overgrowth and partial resorption is reminiscent of external dermal odontodes. In osteichthyans dermal odontodes can be superimposed directly on one another (Zhu *et al.* 2006) or incorporated into the spongy bone layer and partially resorbed (Gross 1935; Bystrow 1939; Ørvig 1978*a,b*; Meinke 1984; Chang & Smith 1992). The labial buried odontodes of *Powichthys* show the latter condition.

Conserved jaw and tooth development

The growth mode of the jaw bones is conserved between stem and crown osteichthyans. As in the *Andreolepis* dentary, in both the dentary and prearticular of *Powichthys* bone growth extends the dorsal margin and overgrows odontodes. New odontodes are added to the bone margin. This type of growth may be common to dermal bones in general; in *Porolepis uralensis* scales, pointed denticles on the leading edge become buried and overgrown by bone and cosmine (Bystrow 1959). Jaw bones

differ from these scales only by the presence of resorption and shedding of the marginal odontodes/teeth. Lingual tooth addition is a general condition of gnathostomes, found also in acanthothoracid placoderms (Vaškaninová *et al.* 2020).

The labial buried odontodes in the dentary of *Powichthys* resemble the first generation non-shedding odontodes of *Andreolepis* (Chen *et al.* 2016) (Fig. 12B). The similarity even extends to the recurved morphology of the large buried tooth-like odontodes of *Powichthys* and the first generation odontodes of *Andreolepis*. However, in *Powichthys*, there is an abrupt change between these buried odontodes and the dentary tooth row, both in terms of size and morphology (from recurved to conical). The most likely explanation for this is that several intervening generations of teeth are not preserved in the *Powichthys* dentary, having been completely obliterated by resorption associated with replacement teeth. In *Lophosteus*, as many as twenty cycles of shedding and replacement teeth are preserved in stacks at a single position (Chen *et al.* 2020).

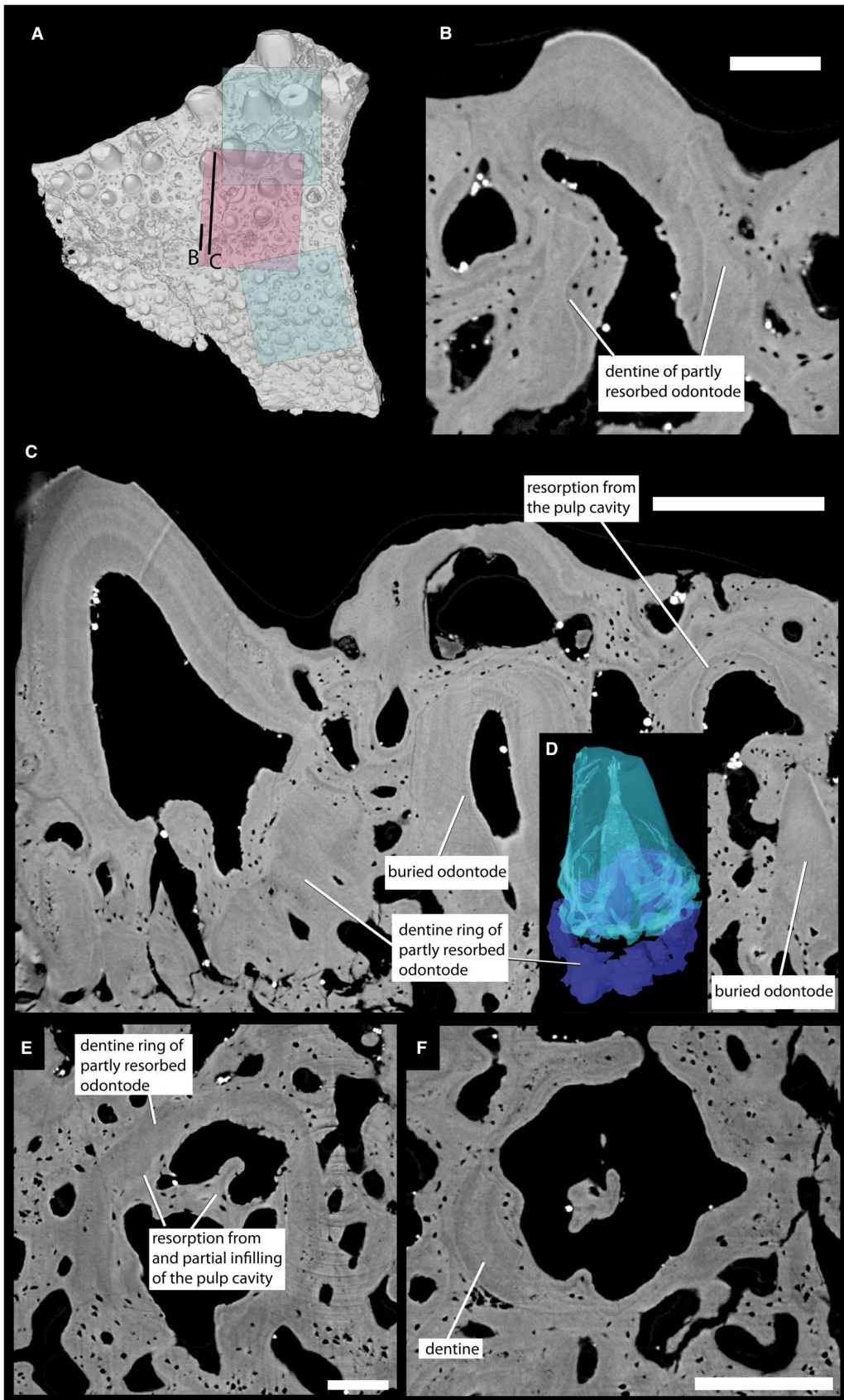


FIG. 10. Overgrown odontodes in the prearticular of *Powichthys* show various degrees of partial resorption. Prearticular fragment from specimen GZG.V.29285 A, position of the three scans of this fragment, with the scan used in this figure highlighted in red. B, buried odontode showing extensive apical resorption, as well as resorption from the pulp cavity. C, transverse section from scan, showing semibasilar resorption (left) and three other partially resorbed odontodes; the partially resorbed odontode in the top right is the same as in B. D, three-dimensional model of remnant dentine ring (semi-basal resorption) and replacement odontode. E, partial infilling of pulp cavity of overgrown odontode. F, dentine remnant of a nearly completely resorbed overgrown odontode. Scale bars represent: 100 μm (B); 300 μm (C); 200 μm (E, F).

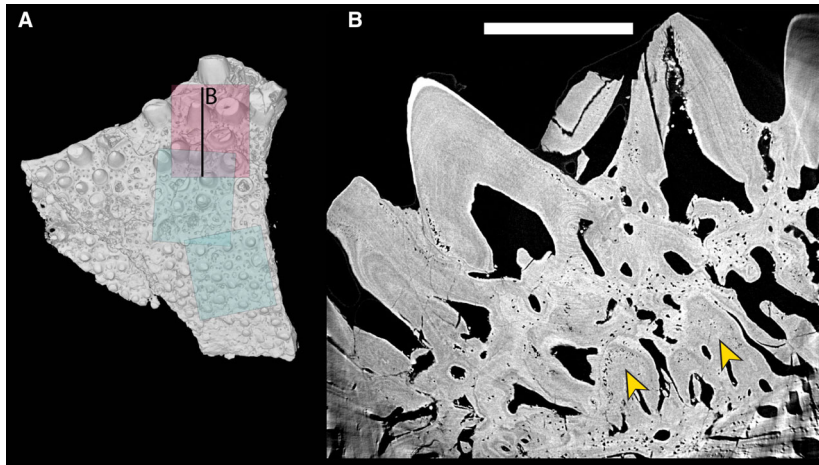


FIG. 11. Odontodes near the bone margin are deeply embedded and there is little evidence for buried odontodes in this region. A, positions of the three synchrotron scans of the prearticular fragment, with the scan used in this figure highlighted in red. B, transverse slice from synchrotron scan, with possible remnant dentine from resorbed buried odontodes indicated with arrowheads. Scale bar represents 500 μm .

Overgrown pointed odontodes, distinct from the dermal ornament, have also been described in the dentary and maxilla of *Onychodus* (Doeland *et al.* 2019), but were not compared to *Andreolepis*. The high-resolution synchrotron scans of the *Powichthys* material reveal the presence of partial resorption in the overgrown tooth-like odontodes, further highlighting similarities with *Andreolepis*. In *Powichthys* there exist two size classes of labial buried tooth-like odontodes, the larger of which we interpret as the earliest generations of the marginal tooth row. In *Onychodus* only the smaller size class is present (Doeland *et al.* 2019). The small labial overgrown odontodes and small labial teeth in *Powichthys* resemble the buried tooth-like odontodes and shedding teeth of *Andreolepis* in their lack of organization into tooth rows, presence of occasional resorption cups, and small size. *Powichthys* therefore possesses the full range of tooth-like odontode morphologies present in *Andreolepis*, but additionally has an enlarged marginal tooth row (Fig. 12B).

The inner dental arcade of early osteichthyans shows the presence of partially resorbed overgrowing odontodes where it has been studied (Bystrow 1939, 1942), and these are retained even in early tetrapods (Bystrow 1938; Hardy *et al.* 2019). Our synchrotron microtomographic data

reveals new details of the development of these overgrowing odontodes, showing a spatial variation in the degree of resorption from lingual to labial, correlated with the size of the odontodes.

Evolutionary development of tooth resorption

Despite the similarities between *Powichthys* and *Andreolepis* there is variability in odontode development between early osteichthyans. Many early osteichthyans also retain a field of small teeth labial to the main tooth row (Gardiner 1984; Zhu & Yu 2004; Zhu *et al.* 2010), but these may not always include shedding teeth (Qu *et al.* 2015; Chen *et al.* 2016). *Powichthys* has occasional large buried odontodes, interpreted here as early generations of the tooth row, which are absent in *Onychodus*. There is also variability in the frequency of overgrown odontodes along the jaw length in *Powichthys*. *Andreolepis* may also have shown variability along the jaw, as the two described fragments have different numbers of shedding teeth and buried odontodes (Cunningham *et al.* 2012; Chen *et al.* 2016).

The variability in the frequency of buried toothlike odontodes in early osteichthyans, both between taxa and

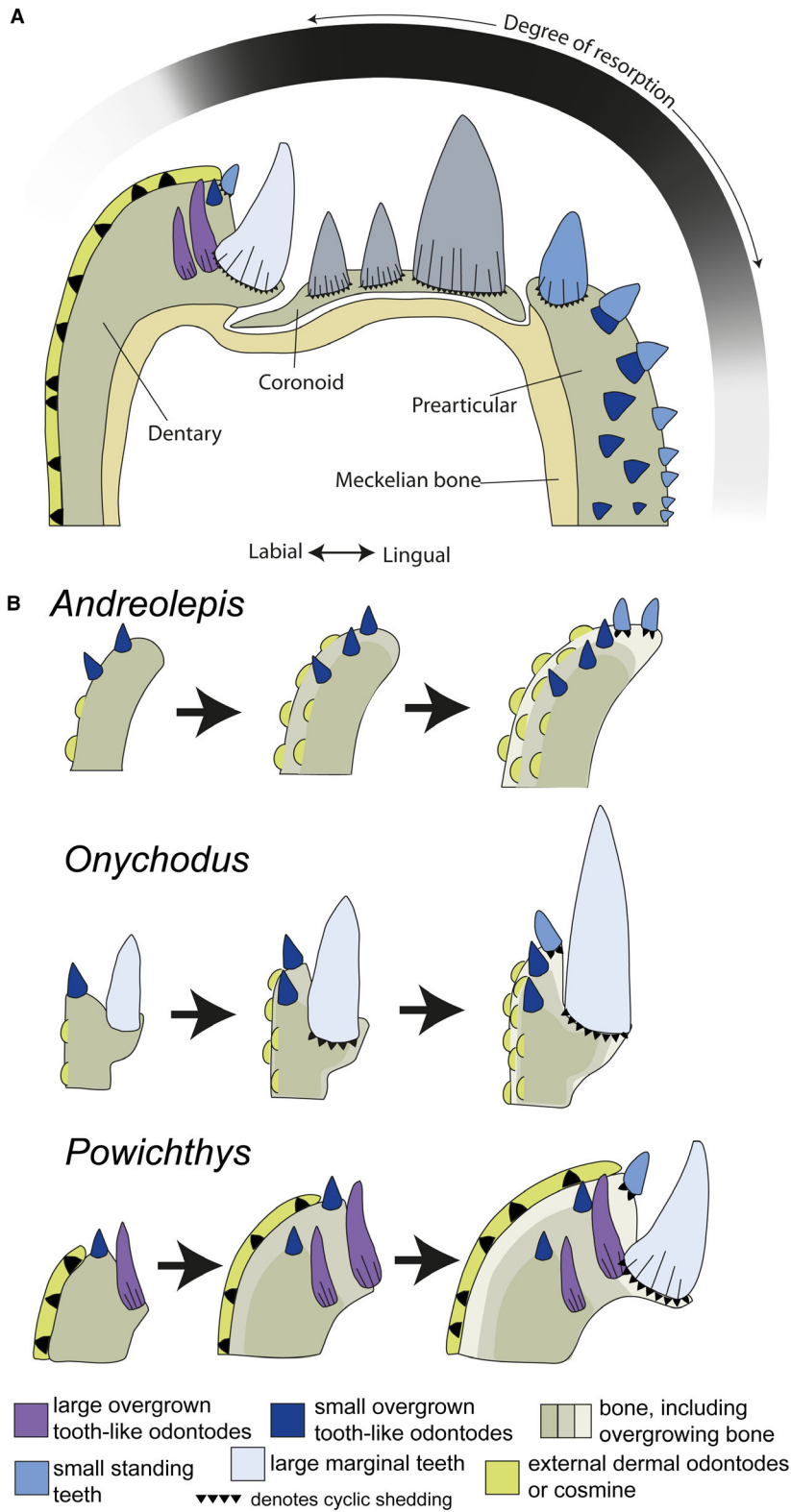


FIG. 12. Summary of oral odontode development in early osteichthyans. **A**, cross-sectional diagram of the dentary, coronoid and prearticular of *Powichthys*; the degree of resorption in both the dentary and the prearticular increases towards the occlusal (dorsal) margin of the bone. **B**, comparison of dentary development in stem and crown osteichthyans: in *Andreolepis*, a stem osteichthyan, early generations of tooth-like odontodes are overgrown, and shedding teeth appear near the bone margin; in *Onychodus* and *Powichthys* a large tooth row (also with on-site replacement) is present; in *Powichthys* only, early generations of the tooth row are buried in the dentary at localized positions. *Andreolepis* and *Onychodus* reconstructions based on Chen *et al.* (2016) and Doeland *et al.* (2019) respectively.

along the jaw within taxa, suggests a degree of plasticity during odontode development. This is consistent with our results showing a continuous variation between teeth

and odontodes, driven by variations in the rate of bone growth, rate of odontode replacement and odontode size. ‘Teeth’ with basal resorption appear where odontodes are

large relative to available space, and replacement outpaces the growth of bone. Conversely, overgrown odontodes (denticles) appear where bone growth outpaces odontode replacement. For example, the large buried odontodes (not described in any early osteichthyan taxon other than *Powichthys*) are mainly present in a localized region at the anterior of the jaw (Fig. 3B, C) where the dentary is thickened laterally (Fig. 3A). Rapid lateral growth of the jaw in this region early in development would explain why odontodes were overgrown rather than resorbed in this region. Plasticity of odontode development related to bone growth is likely to be a widespread phenomenon in gnathostomes; for example, it can explain the varying number of tooth rows among captorhinid reptiles (Leblanc & Reisz 2015).

Our data are consistent with a mode of tooth replacement in which resorption of previous generations of teeth is initiated by the replacement tooth, as occurs in the dentition of the early-diverging actinopterygian *Polypterus* (Vandenplas *et al.* 2014). In *Polypterus*, older teeth are resorbed at the lingual side by odontoclasts associated with the incoming replacement tooth. In actinopterygian tooth replacement, some bone resorption generally occurs following tooth shedding, to prepare a surface for attachment of new teeth (van der Heyden *et al.* 2000; Witten & Huyseune 2009). We propose that the size of the incoming replacement odontode determines the amount of odontoclast/osteoclast activity, and this in turn, together with the amount of bone overgrowth prior to resorption, determines how ‘tooth-like’ or ‘external odontode-like’ the replacement mechanism is.

CONCLUSION

We have shown that the growth and development of the jaw bones in *Powichthys* occurs in a fundamentally similar way to those of the stem osteichthyan *Andreolepis*. *Powichthys* also retains primitive first generation, partially resorbed, overgrown tooth-like odontodes alongside the marginal tooth row. We argue that this demonstrates plasticity in odontode development, and this idea is supported by the observation of a continuum of odontode replacement mechanisms in the prearticular, with progressively more resorption occurring towards the bone margin. The evolution of the osteichthyan dentition can therefore be viewed as a progressive increase in the size of the marginal odontodes (teeth), coupled with progressive increases in resorption activity associated with tooth replacement. This led initially to dentitions such as in *Lophosteus* and *Andreolepis*, with fields of shedding teeth, which were only slightly larger than the external odontodes and stacked generations of resorption surfaces. A continuation of the same trend subsequently led to the

rows of enlarged marginal teeth in ‘psarolepids’ and crown osteichthyans.

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DATA ARCHIVING STATEMENT

CT image data are available in MorphoSource; see Table S1 for a list of DOIs.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. List of micro-CT scanned specimens with DOI links to data files.

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