Diverse stem-chondrichthyan oral structures and evidence for an independently acquired acanthodid dentition

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Abstract

The teeth of sharks famously form a series of parallel, continuously replacing files borne directly on the jaw cartilages, in contrast to the site-specific, dermal plate-borne dentition of bony fishes. A major obstacle in understanding how this system evolved is the poorly understood relationships of the earliest chondrichthyans and the profusion of morphologically and terminologically diverse bones, cartilages, splints and whorls that they possess. Here we use tomographic methods to investigate mandibular structures in several early branching 'acanthodian'-grade stem-chondrichthyans. We show that the dentigerous jaw bones of disparate genera of ischnacanthids are united by a common construction, being growing bones with non-shedding dentition. Mandibular splints, which support the ventro-lateral edge of the Meckel's cartilage in some taxa, are formed from dermal bone and may be an acanthodid synapomorphy. We demonstrate that the teeth of *Acanthodopsis* are borne directly on the mandibular cartilage and that this taxon is deeply nested within an edentulous radiation, representing an unexpected independent origin of teeth. Many or even all of the range of unusual oral structures may be apomorphic, but they should nonetheless be considered when building hypotheses of tooth and jaw evolution, both in chondrichthyans and more broadly.

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

1. Introduction

The structure and position of teeth and jaws are amongst the major anatomical distinctions between crown osteichthyans (bony fishes: ray-finned fishes, lobe-finned fishes, and tetrapods) and crown 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 as part of outer and inner dental arcades. In crownward chondrichthyans, teeth grow, shed, and are replaced in parallel rows of labiolingually-directed series directly on the jaw cartilages. The origins of these dental structures can be traced back to Palaeozoic taxa, 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 [2–7]. However, oral structures in many of these taxa remain poorly characterised, with their relevance to the evolution of teeth poorly understood.

The advent of micro-computed tomography has led to a renewed interest in tooth evolution and development in Palaeozoic gnathostomes. These have mostly focussed on stem-gnathostome ‘placoderms’ [2,5,6,8] and osteichthyans [9–14] and have revealed an unexpected range of morphologies. Stem-group gnathostomes have non-shedding dentitions borne on an underlying dermal bone, which may be arranged radially [5,8] or in parallel rows [6]. The homology of the dermal jaw bones to the inner and outer dental arcades of crown gnathostomes is uncertain [6,15,16]. Meanwhile

many early osteichthyans possessed shedding dentitions comparable to more recent osteichthyans, although early in their history have dental structures that are more broadly comparable in the gnathostome total group such as symphyseal tooth whorls [14] and marginal cusps organised into rows [9,10,11,12,13] Early-branching members of the chondrichthyan total-group (including ‘acanthodians’), have received less attention, with just three taxa described using CT data [7,17-20]. This is despite a remarkable array of dermal oral structures across the assemblage: various early chondrichthyans possess tooth whorls [17,21,22], gracile or molariform teeth not organised into whorls [18,23,24], dermal plates of differing constrictions with and without teeth [22,23,25-28], or may lack dermal mandibular structures entirely [29]. A variety of extramandibular ‘dentitions’ and other oral structures are also known [29,30].

The file-like arrangement of teeth in extant chondrichthyans has a long evolutionary history. In the larger of the two constituent chondrichthyan clades (elasmobranchs: sharks and rays), teeth are continuously replaced [1]. They grow on the inner margin of the jaw, move through a labiolingual file (figure 1a), and are shed at the jaw margin [1]. In holocephalans (chimaeras and relatives), the dentition is modified to two upper pairs and one lower pair of non-shedding hypermineralised toothplates [31]. The elasmobranch condition of file-like teeth is present in stem-group elasmobranchs [32] and stem-group holocephalans [33], which alongside the file-like whorls of stem-chondrichthyans [17], implies that this arrangement is plesiomorphic for chondrichthyans. However, the joined tooth of stem-group chondrichthyans [17], and evidence that at least some stem-group elasmobranchs had non-

shedding dentitions [34], indicating that this mode of tooth replacement was a later acquisition. Tooth whorls are common in animals in the chondrichthyan stem-group, and may form the entire dentition (e.g. *Ptomacanthus* [21]; *Doliodus* [17]) or be present at and/or restricted to the symphysis (e.g. ischnacanthids: [20,22]). It is unclear whether teeth were shed from whorls on mandibular rami [17].

In addition, a ream of stem-group chondrichthyans have unusual dentitions that do not conform to a file-like arrangement, and which are less commonly considered in hypotheses of tooth evolution (figure 1b-f). The most well-characterised of these are dentigerous jaw bones: large, tooth-bearing dermal plates which sit on both the upper and lower jaw cartilages in 'ischnacanthid' stem-group chondrichthyans [22]. Dentigerous jaw bones bear one or more rows of antero-posteriorly aligned teeth, the cusps of which can be quite morphologically and presumably functionally variable [25]. The tooth rows have been shown to grow via anterior addition of new cusps in one taxonomically unidentified specimen, but the bone's wider construction and different morphologies remain poorly characterised [7]. Others stem-group chondrichthyans, such as Gladbachus [24], *Pucapampella* [18] and *Acanthodopsis* [23] have teeth that are not part of dentigerous jaw bones or tooth files, but which are not arranged into files. Diplacanthid stem-group chondrichthyans [26,27] bear smooth, toothless dermal plates on their lower jaws. Numerous stem-group chondrichthyans lack teeth altogether, and the lower jaws of many of these taxa bear poorly-characterised mandibular splints [29,35] which have also been identified in some diplacanthids and ischnacanthids [36,37].

Further confounding this diversity of oral structures are competing and unsettled hypotheses of relationships for early chondrichthyans. While 'acanthodians' are now established as stem-group chondrichthyans [24,32,33, 38-42], there is limited certainty over the monophyly of 'acanthodian' subgroups. There is some evidence that an assemblage of diplacanthiform, ischnacanthiform, and acanthodiform taxa may form a clade or grade subtending the remainder of the chondrichthyan total-group [24]. 'Climatiid' acanthodians, which have overlapping character complements with more shark-like chondrichthyans [18], tend to be recovered in a more crownward position (although see [33]). Beyond this, however, different phylogenetic analyses present very different schemes of relationships, often with low support. These conflicting patterns of relationships present major obstacles to understanding patterns evolution for many of the dental structures seen in early chondrichthyans, although likelihood-based methods provide a possible approach [7].

Here we use computed tomography to image the teeth, jaws and associated oral structures of several early-diverging stem-group chondrichthyans with the aim of more broadly sampling the diversity of their oral structures. We aim to characterise the anatomy of several different ischnacanthid gnathal plates of different constructions, the mandibular splint of acanthodids, and the 'teeth' of *Acanthodopsis*. We contextualise our new data within a wider review of stem-group chondrichthyan oral structures and identify those that represent synapomorphies, while also discussing challenges in reconstructing dental evolutionary histories and homologies.

2. Materials and Methods

2.1 Taxa examined

All specimens studied here are housed at the Natural History Museum, London (NHMUK), and comprise: an isolated jaw of *Taemasacanthus erroli* (NHMUK PV P.33706); an isolated jaw of *Atopacanthus* sp. (NHMUK PV P.10978); an isolated jaw of *Acanthodopsis* sp. (NHMUK PV P.10383); a partial head of *Acanthodes* sp. (NHMUK PV P.8065); and an isolated jaw of *Ischnacanthus* sp. (NHMUK PV P.40124).

Taemasacanthus erroli is known from eight isolated jaws from the Emsian (Lower Devonian) Murrumbidgee Group in New South Wales, Australia [43]. Other species, also based on isolated jaw bones, have been assigned to the genus [44,45], but no articulated animals are known. *Taemasacanthus* is understood to be an ischnacanthid on the basis of its dentigerous jaw bone [43]. NHMUK PV P.33706, described here (figure 2), is a right lower jaw, and comprises two main parts: a dermal dentigerous jaw bone and the articular ossification of Meckel's cartilage. The external morphology of this specimen of *Taemasacanthus* has been fully described [43] but is briefly redescribed here to contextualise our new information. An additional ventral fragment of the articular (previously figured [43]) has become detached from the rest of the ossification and was not included in the CT scan.

Atopacanthus is known throughout the Middle-Upper Devonian [46]. The type species, *Atopacanthus dentatus*, is known from several dentigerous jaw bones from near Hamburg, New York and is presumed to be an ischnacanthid

[23,47]. The sole articulated specimen attributed to *Atopacanthus* sp., from the Upper Devonian of the Rhineland [48,49], has since been referred to *Serradentus* [50] and so the genus is known only from disarticulated remains. The specimen described here, NHMUK PV P.10978 (figure 3), is a dentigerous jaw bone collected from Elgin, Scotland, and is Middle Devonian in age. It was originally labelled as a possible dipnoan toothplate before later being referred to *Atopacanthus*, and its morphology conforms with that of other specimens described as *Atopacanthus*. It is not associated with any endoskeletal material, and it is impossible to tell whether it is from a right lower jaw or upper left jaw. For ease of comparison with other specimens, we describe its morphology as if it were a part of the lower jaw.

Ischnacanthus is the best known ischnacanthid ‘acanthodian’, represented by numerous articulated specimens of Lochkovian (Lower Devonian) age from the Midland Valley in Scotland [22]. The material described here (NHMUK PV P.40124; figure 4) is an isolated left lower jaw from the Lower Devonian (Lochkovian) Midland Valley in Tealing, Forfarshire [51]. It is fairly complete, but parts of the dorsal and anterior margins have been lost to the counterpart (which is preserved, but was not CT scanned), and the whole jaw is laterally flattened. It comprises a dentigerous jaw bone and Meckel’s cartilage.

Acanthodopsis is known from the Carboniferous of the UK and Australia. *Acanthodopsis* has been previously considered an ischnacanthid on the basis of its “dentigerous jaw bones”, but in terms of its skeletal anatomy it is more similar to acanthodids [23,43]. The material described here, NHMUK PV P.10383 from the Northumberland Coal Measures (figure 5), comprises a

laterally flattened lower right jaw, consisting of a Meckel's cartilage with teeth and a mandibular splint.

Acanthodes is the latest occurring genus of 'acanthodian' found as articulated body fossils from the Mississippian (Carboniferous) into the Lower Permian [29]. It is the only genus of 'acanthodian'-grade animal known from extensively preserved endoskeleton, seen in specimens of *Acanthodes confusus* from Lebach, Germany [52]. The material described here (NHMUK PV P.8065) comprises part of the ventral half of the head of a specimen from the Knowles Ironstone of Staffordshire (figure 6). As the dorsal margins of the jaw bones are obscured within the rock, it was originally referred to '*Acanthodopsis* or *Acanthodes'*. As CT scanning shows that dentition is absent, we can confirm it to be *Acanthodes* sp. Most of the left jaw is preserved, and of the right jaw only the mandibular splint is preserved, as are some of the lower branchiostegal ray series and isolated dermal gill rakers. Scattered parts of the rest of the head endoskeleton are also present, including parts of ceratobranchial and a hyomandibular.

2.2 CT scanning

Full details of scanning parameters are given in supplementary table 1. The voxel size for each scan are as follows: *Acanthodes*, 44.9 *µ*m; *Acanthodopsis*, 22.6 µm; *Atopacanthus*, 19.508 *µ*m; *Ischnacanthus*, 24.6 *µ*m; *Taemasacanthus erroli*, 17.3 *µ*m.

206 Reconstructed tomographic datasets were segmented in Mimics v.19
207 (biomedical.materialise.com/mimics; Materialise, Leuven, Belgium) and
208 images were generated using Blender (blender.org).

209 **2.3 Phylogenetic analyses**

210 Our dataset is based on Dearden *et al*. [42], the most recently published
211 phylogenetic dataset specifically tackling stem-group chondrichthyan
212 relationships. We have added one taxon and four characters and made minor
213 modifications to some codes (full details given in the supplementary text). We
214 performed a parsimony analysis in TNT [53] with the following settings: a
215 parsimony ratchet with 10,000 iterations, holding 100 trees per iteration, with
216 TBR branch swapping. Galeaspida was set as the outgroup and the following
217 constraint applied: (Galeaspida(Osteostraci(Mandibulate Gnathostomes))).
218 We also performed a Bayesian analysis, with Galeaspida set as the outgroup,
219 mandibulate gnathostomes constrained as monophyletic, and the following
220 settings. We used a uniform prior with the Mkv model and gamma-distributed
221 rates; searched for 10,000,000 generations, sampling every 1,000
222 generations; and calculated the majority rule consensus tree with a relative
223 burn-in of 25%.

224

225 # 3. Results

226 **3.1 *Taemasacanthus***

227 The dentigerous jaw bone of *Taemasacanthus* is approximately half the full
228 depth of the jaw and is sinusoidal in dorsal view (figure 2). A circular ridge,

229 previously suggested to be for a labial cartilage attachment [43] but more
230 likely the attachment site for a ligament, is present on the lateral surface
231 approximately ¼ of the way along its length (figure 2b,c). Posteriorly, the bone
232 curves laterally and broadens to wrap around the articular. The lateral
233 expansion is larger than the medial expansion, and both are rounded
234 posteriorly. Ventrally, a groove formed by the posterior confluence of these
235 two processes runs underneath the entire length of the dentigerous jaw bone,
236 and would have overlain Meckel's cartilage (figure 2c). The dentigerous jaw
237 bone is approximately trapezoid in cross section, and bears three rows of
238 teeth (figure 2a,b,d,f,g). Histologically the underlying dermal plate comprises
239 heavily vascularised dermal bone, similar to that observed in thin sections of
240 other ischnacanthid dentigerous jaw bones [7,22,54], with a relatively thin
241 layer of less vascularised bone around the plate margins (figure 2f; figure
242 S1a-d). The vascularisation comprises an interlinked network of tubules,
243 which are strongly anteroposteriorly polarised in the tooth-bearing section of
244 the bone. Vascular channels occasionally open onto the surface of the bone,
245 particularly the ventral groove. On the lingual surface of the bone, a change in
246 orientation of the vascularisation (from anteroposterior to more random)
247 indicates the presence of a separate plate-like unit of growth (Figure S1d).
248 The more posterior, wrapped part of the bone has a radial arrangement of
249 vasculature suggesting that the bone grew posteriorly and ventrally as well as
250 anteriorly as the underlying endoskeletal jaw grew. The circular ridge is
251 formed of avascular bone, but is otherwise a similar tissue to that forming the
252 outer margin of the dermal plate; it's position at the apparent point of radiation
253 of the vascularisation suggests that it could also be an artifact of growth.

Three rows of teeth are borne on the biting edge of the dermal plate, all starting approximately at the level of the mesial ridge: a lateral, medial, and lingual row (figure 1a,b,d). Teeth of the medial row are far smaller and less distinct than those of the lateral and lingual rows. Teeth within the lateral and lingual rows are fused to the jaw, but the base of the tooth is marked by an increase in the density of random and dorsally-oriented vascular canals (figure 1f; figure S1a-c). The medial row lies on the mesial ridge and comprises a single row of small disorganised cusps that are continuous with the underlying dermal plate and do not appear to overlap with each other. Vasculature in the medial row is only visible in the more posterior cusps and does not seem related to size. The lateral and lingual rows of teeth are much larger and ridged, with a vascular base topped with a mostly avascular crown. The younger, larger, more anterior teeth of both rows have extensively vascularised crown. The smaller, more posterior cusps have less—or even no—vascularisation, indicating that the crown was infilled in older teeth. The basal vasculature has occasional connections with the vasculature of the underlying dermal plate. The teeth seemingly lack a continuous enameloid covering (figure 1f), contra recent reports of enameloid in an ischnacanthid (Rucklin et al 2021 ref), although we caution that this may be due to the resolution of our dataset. Both tooth rows grow by the addition of new teeth onto the anterior end of the row, as evidenced by anterior teeth partially overlying posterior ones, and cusps becoming progressively larger in the direction of growth. The sole exception to this is in the lingual tooth row, where, in what is probably a pathology, the eighth cusp of the lingual row is incomplete and is either damaged or its growth has been aborted (figure 1a).

Both the damaged eighth cusp and the undamaged tenth cusp are overgrown by the youngest cusp in the row. This, the ninth cusp, is oriented noticeably more medially than other cusps and may have disrupted the growth of the smaller tenth cusp, although the underlying bone appears unaffected. The vasculature of the ninth cusp appears to be isolated from the surrounding vasculature, while the vasculature of the underlying eighth cusp's opens into a large, central hollow. The lateral tooth row comprises around twelve cusps, and its teeth are laterally unornamented and continuous with the lateral surface of the dermal bone, connected to one another via antero-posterior lateral ridges (figure 1b). The lingual side of each cusp is rounded, and ornamented with a number of ridges, which become longer and progressively more tuberculated on more anterior cusps. The lingual tooth row comprises ten cusps, which curve away from the occlusal surface anteriorly.

Only the posteriormost portion of the Meckel's cartilage, the articular ossification, is preserved (figure 2). It is formed from a sheath of perichondral bone and would have been filled with cartilage in life. Some spongy texture is apparent on the interior surface of the perichondral bone. A shallow groove on the posterior surface does not appear to continue ventrally, making it unlikely to have accommodated a mandibular splint as previously suggested [43]. Articulation with the palatoquadrate appear to be via an open, oval, fossa [43] (figure 2d). The tissue forming this is notably ill-formed, and appears to lack a solid perichondral covering; as Burrow [22] suggests it seems likely to be a broken articular process like that in ischnacanthids [22,25].

3.2 *Atopacanthus*

303 The dentigerous jaw bone is robust, trapezoid in cross-section, but flatter and
304 taller proportionate to its length than in *Taemasacanthus* (figure 3). It is
305 slightly medially convex. The anterior fifth of the preserved bone (it is broken
306 both anteriorly and posteriorly) is toothless and tapers slightly. A narrow,
307 shallow groove to accommodate the mandibular cartilage runs along its
308 ventral surface (figure 3c). The histology is similar to *Taemasacanthus*, with
309 heavily vascularised dermal bone surrounded by a less vascular layer, but the
310 vascular tubules are even more strongly polarised in an antero-dorsal
311 direction (figure 3e; figure S1e-g). Again, the vasculature principally opens
312 into the ventral groove. Towards the surface, bone vascularisation is less
313 dense, and not polarised. The lingual face of the dentigerous jaw bone
314 supports a distinct thin, lingual, tooth-bearing plate (figure 3a,d,e), which is
315 comparable in position and vascularisation to the plate-like region in
316 *Taemasacanthus* (figure S1d). This plate is still heavily vascularised, but
317 tubes are polarised dorso-lingually. On the outer perimeter of the lateral face
318 of the main bone, the vasculature is oriented obliquely.

319 As in *Taemasacanthus*, lateral, mesial and lingual tooth rows are borne on the
320 dorsal surface of the underlying dermal plate (figure 3a,b,d). The medial ridge
321 bears two disorganised rows of cusps along its anterior half, with the posterior
322 half being smooth. All cusps are vascular, and are histologically continuous
323 with the medial ridge. The lateral tooth row comprises eight cusps, which
324 become progressively larger anteriorly, and their lateral surfaces are
325 continuous with the outside of the dermal plate (figure 3b). Their lingual
326 surfaces are rounded and ornamented with untuberculated ridges. The inner
327 tooth row comprises ten main cusps, which curve medially across the

dentigerous jaw bone. Two additional small cusps are present near the posterior margin of the dermal plate, ventral to but independent from the main lingual tooth row, which are closest in appearance to the teeth of the medial ridge. This tooth row lies on top of a lingual plate, which is apposited onto the lingual surface of the main dermal plate (figure 3a,d,e) . As in the lateral row and in *Taemasacanthus*, cusps become larger anteriorly, and are ornamented with ridges. The histology of the teeth of the lateral and lingual rows comprises a vascular base topped with an avascular cap lacking enameloid, with the vascular canals oriented distinctly from the underlying dermal and lingual plates (figure 3e). As in *Taemasacanthus*, younger teeth are more heavily vascularised with an extensively vascularised crown, and the anteriormost tooth still posseses a clear pulp cavity (figure S1e-g), suggesting that teeth vasculature became infilled with age. Teeth in both the lateral and lingual rows were added anteriorly, with anterior cusps partly overlying their posterior fellows.

3.3 *Ischnacanthus*

Only the anterior part of the dentigerous jaw bone is preserved in the part (figure 4), although the mould of the posterior region is visible in outline. The underlying dermal plate is much shallower than in *Taemasacanthus* and *Atopacanthus*. A lateral tooth row and a medial ridge are present. The lateral tooth row preserves four cusps, the third of which is exposed on the surface and therefore incomplete dorsally. The cusps are linked by a cuspidate ridge along their lateral faces. Relative size and age are difficult to determine due to the mode of preservation, but the anteriormost cusp is the largest, and cusp

overlap indicates that teeth were added anteriorly. Although the ventralmost parts of the dermal plate are missing, the ventral margin of the teeth is marked by a noticeable shift in density and orientation of the vascular canals (figure 4d). The tissue forming the teeth is similar to *Taemasacanthus* and *Atopacanthus*, with a vascularised base and an avascular crown apparently lacking enameloid [22]. The internal vasculature of the bone in *Ischnacanthus* is also longitudinally polarised and connected, although less well-visualised in our scan data (figure S1h,i).

The large Meckel's cartilage is near-complete and preserved as a single ossification (figure 4). It is curved posteriorly and tapers anteriorly. The dentigerous jaw bone is borne on its dorso-lingual surface. A laterally-directed articular condyle is present at the posterior extent, and a shallow groove extends ventral to the condyle. The majority of the Meckel's cartilage is formed of globular calcified cartilage. Parts of its lateral surface, as well as its ventral, anterior, and posterior extents, are covered by a thin, densely mineralised tissue that appears to be perichondral bone [22]. This tissue thickens ventrally and posteriorly and is fractured. The perichondral sheath is avascular, but has fractured in such a way that cracks and voids artificially resemble the vasculature of the dentigerous jaw bone. A thickened ridge along the posteroventral and posterior margin is continuous with the perichondral rind that extends onto the lateral surface, but externally gives the appearance of a separate ossification (figure 4bc,). In section this is closely comparable to the so called "mandibular bone" that Ørvig [37] described in *Xylacanthus and* is probably responsible for accounts of mandibular splints in ischnacanthids.

3.4 *Acanthodopsis*

The lower jaw in *Acanthodopsis* comprises a tooth-bearing Meckel's cartilage and a mandibular splint (figure 5). The Meckel's cartilage is long and thin and similar in form to that of *Acanthodes* (figure 5; 23,50], with an identical articular cotylus and marked preglenoid process. It tapers anteriorly, terminating in a small, cup-shaped anterior symphyseal fossa (figure 5c,e). The Meckel's cartilage is formed from a shell of what we infer to be perichondral bone [23], which has collapsed and cracked under compression and appears to beunmineralized internally (figure 5g,h), although some mineralisation appears to be present in the jaw articulation. Unlike *Acanthodes confusus*, it is perichondrally mineralised along its entire length (figure 5), rather than in separate articular and mentomandibular sections.

Ten monocuspid, triangular teeth form a row along the dorsal surface of the Meckel's cartilage (figure 5). 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, each with a smooth (but possibly weathered) lateral face and a longitudinally striated lingual face. Previous descriptions of the teeth [23] were undecided as to their tissue makeup. The tissue comprising them comprises distinct inner and outer layers. The outer layer is thick and covers the outside surface of each tooth but does not close ventrally: unlike the perichondral surface of the cartilage it is not crushed and the surface appears intact. The inner layer has a a spongy texture, which may reflect internal vasculature: no obvious pulp canals are present. Although the contrast between teeth and jaw bone is poorly defined, a difference can be seen in slices between the spongy texture of a tooth's internal tissues and the

solid perichondral bone. Based on our data, we infer these to be dermal due to this histological distinction from the Meckel's cartilage as well as their separated gross structure and ornamentation. We consider it likely that these tissues are dentinous but more detailed study is needed to establish these tissues' identity. The direction of growth is difficult to infer. In successive tomograms viewed in sequence, the largest tooth appears to be overlapped by the anterior and posterior teeth, possibly making it the oldest. This contrasts to the order of growth in *Taemasacanthus*, *Atopacanthus* and *Ischnacanthus*, where teeth are added anteriorly. However, as with the identity of the tissue, we express caution at this interpretation.

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 (figure 5a,b). This groove was likely originally much shallower, and its depth has been exaggerated by lateral flattening of the specimen. The tissue forming the splint is solid, and is organised into multiple concentric lamellae likely representing lines of arrested growth. It is pierced by a series of thin, longitudinally oriented canals (figure 5g,h). This tissue is distinct from that forming Meckel's cartilage, in particular being denser and better organised, and can be interpreted as dermal bone, especially given the ornamentation of the mandibular splints of some acanthodids [55]. Burrow [23] reported that the mandibular splint in *Acanthodopsis* was formed from cartilage and bone based on thin sections, but the cartilage identified in these reports may have been the Meckel's cartilage above the bone instead (CJB pers. comm. July 2020).

428 **3.2 *Acanthodes***

429 The left lower jaw comprises ossified articular and mentomandibular parts of
430 Meckel's cartilage, as well as a mandibular splint (figure 6). Mineralised parts
431 of the Meckel's cartilage are formed from thick perichondral bone, and are
432 slightly laterally crushed (figure. 6a-d). The articular is as previously described
433 [52]. The mentomandibular has a distinct cup-like symphyseal fossa at its
434 anterior tip, forming part of the mandibular symphysis (figure 6c). The
435 mandibular splint is unornamented, slightly sinusoidal in shape, and ellipsoid
436 in cross-section. It sits in a groove in the lateral faces of the mentomandibular
437 and articular. Internally it is solid and vascularised by sparse long, thin canals
438 running its length (figure 6e,f), as in *Acanthodopsis*. A single tooth-like cusp
439 sitting in (although separate from) a cushion-shaped base is probably a
440 branchial or hyoid raker (figure 6b,e).

441

442 **3.6 *Phylogenetic results***

443 Our parsimony analysis recovered 26101 most parsimonious trees with a
444 length of 704 steps. The strict consensus of these results (figures 7a, S2) is
445 consistent with other recent analyses in finding all 'acanthodians' to be stem-
446 group chondrichthyans. We recover "Acanthodii" *sensu* Coates *et al.* [24] as a
447 clade subtending the remainder of the chondrichthyan total group, with
448 *Euthacanthus* as the sister group to the "Acanthodii". However,
449 acanthodiforms (i.e. cheiracanthids, mesacanthids, and acanthodids) are
450 paraphyletic. Ischnacanthids plus diplacanthids form a clade, but
451 ischnacanthids themselves are paraphyletic, and diplacanthids are a clade to

the exclusion of *Tetanopsyrus*. Remaining stem chondrichthyan taxa, including climatiids, *Gladbachus* and Doliodus, are recovered in a polytomy along with a monophyletic chondrichthyan crown group. Support values aside from the chondrichthyan total group and crown group nodes are typically low. The Bayesian majority rule consensus tree (figure 7b, S3) is broadly consistent with the parsimony strict consensus tree, although “Acanthodii” decay into a polytomy subtending all more crownwards chondrichthyans. *Acanthodopsis* is recovered as the sister-taxon to *Acanthodes* in both analyses.

4. Discussion

4.1 Stem-chondrichthyan oral structures

Our new data show that the dentigerous jaw bones of all ischnacanthids, including articulated taxa such as *Ischnacanthus* and those only known from isolated jaws (e.g. atopacanthids and taemasacanthids), were united by a common construction. These follow the model of tooth growth supposed by Ørvig [56] and demonstrated by Rucklin *et al.* [7] on the basis of directional wear and overlapping cusps. These teeth were fused to, but distinct from, the underlying bone, which grew with the endoskeletal component of the jaw, based on the vasculature of *Taemasacanthus* outwards from a point posterior to the tooth row. This condition and the positions of tooth rows relative to the underlying dermal plate is common to the three different morphologies of dentigerous jaw bone that we describe and we infer it to have been a common

476 feature of ischnacanthid dentigerous jaw bones The presence of an out of
477 sequence tooth in *Taemasacanthus*, where the youngest tooth has partially
478 overgrown a cusp anteriorly (figure 2), suggests that non-sequential growth
479 was possible in the otherwise ordered tooth rows, likely in response to a
480 pathology. Dentigerous jaw bones are broadly comparable with the condition
481 in stem-gnathostomes in the sense that non-shedding teeth are ankylosed to
482 and growing on a basal bone. However, phylogenetic topologies supporting
483 homology between these conditions are in limited supply (figure. 7,8), and is
484 not supported by our topology or by more detailed analysis [7].

485 Although dentigerous jaw bones are typically contrasted with tooth whorls [7],
486 we suggest that dentigerous jaw bones can be usefully interpreted by
487 comparison to antero-posteriorly “stretched out” tooth whorls. Teeth and
488 tooth-like structures are added directionally across the gnathostome total-
489 group and this may be a plesiomorphic feature of gnathostome dentitions [6].
490 However, tooth rows on dentigerous jaw bones are more comparable to
491 whorls than to these other structures in that they comprise site-specific tooth
492 files, growing in a single direction in a specific position on an underlying
493 dermal plate. This stands in contrast to single-directional, but haphazardly
494 arranged, tooth files reported in stem-gnathostomes and early osteichthyans
495 [6,9]. Notably, symphyseal tooth whorls and whorl-like cheek scales in some
496 ischnacanthids could suggest common patterning mechanisms affecting
497 dermal structures in and around the mouth of early chondrichthyans [57]. This
498 site-specific placement of tooth files could be apomorphic for
499 chondrichthyans if osteichthyan tooth whorls are optimised as homoplasious

[7], and could potentially be a character uniting chondrichthyan dentitions more inclusively than the presence of tooth whorls.

The row of monocuspid ‘teeth’ borne directly on the Meckelian element of *Acanthodopsis* is unlike that of any other known chondrichthyan or gnathostome. Furthermore, the presence of teeth in a Carboniferous taxon deeply nested within an edentulous radiation (figure 7), the oldest of which are Early Devonian in age, strongly suggests that this represents an independent acquisition of dentition. Previous studies of the jaw of *Acanthodopsis* have interpreted it either as a dentigerous jaw bone [56] or as a perichondrally ossified Meckelian bone with ‘teeth’ [23]. Our data confirm the latter view and show that the teeth in *Acanthodopsis* are histologically distinct from the underlying perichondral bone and so are presumably dermal ossifications attached to its surface. Our phylogenetic analysis supports the view of Long [43] and Burrow [23] that *Acanthodopsis* is closely related to *Acanthodes*, with the presence of teeth representing the only difference between the genera. A possible morphological comparison to these teeth lies in the branchial and hyoid rakers found in acanthodiform fishes like *Acanthodes*, *Cheiracanthus*, and *Homalacanthus* [29,58]. As with the teeth of *Acanthodopsis*, these rakers are triangular in shape, sometimes striated ([59] fig. 3), and decrease in size from the centre outwards (Dearden *pers obvs*). An alternative to a cryptic homology between teeth in *Acanthodopsis* and other gnathostomes may be the co-option of hyoid and branchial rakers to form a novel “dentition” on the mandibular arch.

4.2 Distribution of oral structures in the chondrichthyan stem-group

Teeth and other oral structures in stem-chondrichthyans take on a broad variety of forms, raising questions about their homology and the primitive or derived condition for different features. Here we briefly review this diversity and map key characters onto our phylogeny.

A diverse array of **teeth** (light blue icons, figures 7 and 8) are present in the majority of Palaeozoic chondrichthyans, including as tooth whorls, but are also remarkable for the breadth of taxa in which they are absent. Acanthodids (e.g. *Acanthodes*: figure 5, ref. 50) are completely toothless (except for *Acanthodopsis*), as are the likely related mesacanthids (e.g. *Promesacanthus* [35]) and cheiracanthids (e.g. *Cheiracanthus* [58]). In this latter group, tooth-like hyoid rakers have sometimes been mistaken for teeth [60]. Teeth are also absent in diplacanthids [26], with the possible exception of *Tetanopsyrus* (see "Occlusal plates" section below) [27]. A number of toothless taxa with otherwise diverse anatomies, including *Obtusacanthus*, *Lupopsyrus*, *Euthacanthus*, *Brachyacanthus*, and *Kathemacanthus* [61-64], are often resolved as more closely related to the crown-group (figures 7,8). Given the small size and two-dimensional preservation of some of these taxa, it is possible that teeth are present but reduced and so far undetected, as in *Gladbachus adentatus* [24]. Teeth are inferred to be homologous across gnathostomes [7], demanding numerous independent losses of teeth in stem chondrichthyans (figures 7 and 8).

Tooth whorls (dark green icons, figures 7 and 8) are tooth files with a fused bony base, which grow by the lingual addition of new cusps along a single axis [20]. Tooth whorls are understood to be the evolutionary precursor to modern chondrichthyan tooth families, which have a similar morphology but

549 lack a common bony base [65]. Tooth whorls are present in a range of stem-
550 group chondrichthyans with otherwise dissimilar anatomies, including those
551 with dentigerous jaw bones (e.g. *Ischnacanthus* [22]), densely tesserate head
552 skeletons (e.g. *Climatius* [66]), and more shark-like taxa (e.g. *Doliodus* [17]).
553 They have also been described in the acanthodiform-like *Latviacanthus* [67],
554 although as this is based on x-ray plates these may be mischaracterised
555 hyoid rakers as in *Homalacanthus* [58]. Tooth whorls are also present in some
556 stem-group holocephalans such as iniopterygians [68], although these are
557 likely to be secondarily derived given their phylogenetic remoteness from the
558 chondrichthyan stem-group. Some osteichthyan taxa also possess tooth
559 whorls, but here the tooth crowns are shed via resorption of the tooth base, a
560 mechanism not present in statodont chondrichthyan tooth whorls [14].There is
561 variation in their distribution on the jaw: in ischnacanthids and osteichthyans,
562 tooth whorls are few in number and limited to the symphysis [22], whereas in
563 more crownward chondrichthyans they are arrayed along the length of the jaw
564 and comprise the entire dentition (gold and yellow-green icons, figures 7 and
565 8). The distribution of tooth whorls across osteichthyans and within
566 chondrichthyans is complex, with whorl-bearing taxa often nested within
567 whorl-less radiations. Probabilistic ancestral state reconstruction indicates that
568 tooth whorls evolved independently multiple times both within
569 chondrichthyans and across gnathostomes [7]. Within chondrichthyans,
570 different phylogenetic topologies have quite different implications for the gain
571 and loss of tooth whorls and their distribution across the group (figure 8).

572 Some chondrichthyans have **teeth that are not organised into files** but
573 which lie directly on the jaw cartilage (coral icons [in part; this icon also

captures teeth arranged in files that are borne on the jaw cartilages], figures 7 and 8). This condition is present in *Acanthodopsis* (figure 5), *Pucapampella*, and *Gladbachus* [18,24], although presents in different ways. In *Acanthodopsis*, teeth are triangular and diminish in size anteriorly and posteriorly (figure 5). In *Pucapampella*, teeth form a single row along the jaw but show a variety of sizes, shapes, and spacings [18]. In *Gladbachus*, teeth are much reduced and individually separate, although possibly aligned linguo-labially [24]. However, these taxa are scattered across the tree, and their tooth morphologies can be radically different, suggesting that teeth that that lie directly on the jaw cartilage and are not organised into files evolved multiple times independently. Although *Gladbachus* and *Pucapampella* are recovered as a clade in our analyses, this is contrary to most other recent findings (figure 8c,d) and we view this result with extreme caution.

Dentition cones — tooth-like cones with smaller denticles attached — are present in the mouths of some stem-group chondrichthyans. They are only known in partially-articulated ischnacanthids with dentigerous jaw bones: *Zemylacanthus* (*Poracanthodes*), *Acritolepis*, and *Serradentus* [50,69,70]. However, they are absent in the better characterised *Ischnacanthus* and relatives [22,57]. The lack of fully articulated fossils bearing dentition cones leaves open the possibility that they represent a displaced part of the branchial apparatus rather than oral structures [48], and are perhaps comparable to gill and hyoid rakers in cheiracanthids and acanthodids [29,58]. Whether oral or branchial in origin, their presence may unite the subset of ischnacanthids that possess them, although this has not been tested in a phylogenetic context.

Tooth-like scales are present along the oral margin of some stem-group chondrichthyans, and include part of the cheek squamation, the 'lip' and the ventral rostral area. They are best characterised in *Ischnacanthus*-like 'acanthodians' [30] in which they show a variety of morphologies, and in life may have helped with grasping prey. Some of these scales are strikingly similar in organisation to tooth whorls (which are also present within the gape of the same animals), comprising a file of denticles oriented towards the mouth [22,30]. Specialised tooth-like scales have also been identified along the margin of the mouth in *Obtusacanthus* [62]. More generally, tooth-like denticles are common along the oral margin of the tooth row in early osteichthyans [14,71]. Although potentially interesting from a developmental perspective, they seem unlikely to carry any phylogenetic signal.

Dentigerous jaw bones are tooth-bearing dermal jaw bones present in the upper and lower jaws of a number of stem-chondrichthyan taxa [23]. Although isolated dentigerous jaw bones are comparatively common in the rock record, articulated fossils are relatively few and far between: they include *Zemlyacanthus, Nerepisacanthus*, and *Serradentus* [44,50,72]. By far the best anatomically characterised taxa with dentigerous jaw bones are *Ischnacanthus* and similar taxa [22,25]. There are few anatomical characters to group taxa possessing dentigerous jaw bones, but all have a complement of oral structures including some combination of symphyseal tooth whorls, dentition cones, and tooth-like cheek scales. Dentigerous jaw bones themselves display anatomical diversity, for example relating to the structure of the bone, the number and morphology of tooth rows [23], and variance in dentition shapes likely linked to diet [25]. In our phylogeny, taxa with

624 dentigerous jaw bones (i.e. ischnacanthids) are recovered in a polytomy, in a
625 broader grouping of 'acanthodians' with dermal mouth plates (dark purple
626 icons, figures 7 and 8). Dermal jaw bones, both edentulous and tooth-bearing,
627 are also present in 'placoderms' and osteichthyans, but few phylogenetic
628 results support their homology with those of ischnacanthids (Fig. 7,8).

629 **Occlusal plates** are a pair of smooth dermal plates in the gapes of some
630 stem-chondrichthyans (light purple icons, figures 7 and 8). Their detailed
631 anatomy is poorly characterised and in the past they have become
632 terminologically and anatomically confused with the mandibular splint [28].
633 Occlusal plates are present in *Diplacanthus*, *Rhadinacanthus*, *Milesacanthus*,
634 *Uraniacanthus*, *Culmacanthus*, and *Tetanopsyrus* [26-28,73–75]. At least
635 some of these animals have other common morphologies (i.e. similar body
636 shapes, scapular processes with posterior lamina, large postorbital scales,
637 deep, striated dorsal fin spine insertions), and on this basis they are grouped
638 into the diplacanthids [26]. There is some variation in the morphology of
639 occlusal plates. In all taxa but *Tetanopsyrus* [27,76], they are only present in
640 the lower jaws; *Tetanopsyrus* may also have tooth-like denticles along the
641 inner surface of the plates, although this is only known from an isolated
642 Meckel's cartilage associated with a complete *Tetanopsyrus* specimen [27]. In
643 *Uraniacanthus* and *Culmacanthus*, a dorsal process is present [73,77]. We
644 recover diplacanthids as monophyletic in our Bayesian analysis (figure 7, S3),
645 but paraphyletic with respect to *Tetanopsyrus* in our parsimony analysis, and
646 occlusal plates appear to be a character uniting diplacanthids (figures 7, 8).
647 *Tetanopsyrus*, with its upper and lower plates, may represent a link between
648 the occlusal plates of diplacanthids and dermal jaw bones of ischnacanthids.

A **mandibular splint** (variously termed dentohyoid, extramandibular spine, splenial, or mandibular bone) is a slightly sinusoidal dermal bone that underlies the Meckel's cartilage ventrolaterally (grey icons, figures 7 and 8). Unlike the other structures discussed here, it did not lie within the gape, and likely reinforced the lower jaw. Mandibular splints are present in *Acanthodes*, *Acanthodopsis*, *Halimacanthodes*, *Howittacanthus*, and *Protogonacanthus* [52,55,78,79]. They have also been incorrectly identified in a variety of other taxa. Mandibular splints in mesacanthids [35,61] are more similar in size to gular plates, and may represent displaced elements of this series. Reports in diplacanthids [73,75] are better interpreted as occlusal plates [28]. Although a mandibular splint has been identified in the putative cheiracanthid *Protogonacanthus* [55], the taxon in question is likely not a cheiracanthid but an acanthodid [58]. Finally, as we show, descriptions of mandibular splints in ischnacanthids [37,48] instead represent a reinforced ventral margin of the endoskeletal mandible. Mandibular splints in acanthodids are very conservative in form, although may be ornamented as in *Acanthodes sulcatus* [55]. Its similarity to the ventral branchiostegal rays in *Acanthodes* (figure 6a,b), which are also dermal, tubular, and slighty sinusoidal, suggests that it may be part of this series that has been co-opted to support the jaw. Our phylogeny suggests that a mandibular splint unites *Acanthodes* and *Acanthodopsis* but either evolved convergently in *Halimacanthodes* (figure. 7) or was lost in *Homalacanthus*; we consider it most likely that it unites acanthodids to the exclusion of other stem-chondrichthyans, and that this distribution is a result of undersampling acanthodids and their characters in our phylogeny.

674 **4.3 The evolution of chondrichthyan teeth**

675 Although phylogenetic topologies for early chondrichthyans are poorly
676 resolved and often suggest conflicting hypotheses, there are some signals
677 that may provide insight into the evolution of a modern shark-like dentition.
678 The placement of 'climatiid' acanthodians in a relatively crownwards position
679 on the chondrichthyan stem-group [24,40-42] (Fig. 7,8a-c) suggests that taxa
680 with a dentition entirely formed from tooth whorls share a last common
681 ancestor to the exclusion of other taxa. Not all topologies support this
682 hypothesis, however: Frey *et al.* [33] recover climatiids as remote from the
683 chondrichthyan crown node, with an extensively whorl-based dentition borne
684 on the jaw cartilages either developing independently in the crownward
685 lineage or being lost in "Acanthodii". Either scenario still invokes multiple
686 episodes of secondary tooth loss (e.g. *Lupoposyrus*) and divergences from a
687 whorl-like tooth anatomy (*Gladbachus*, *Pucapampella*). In our phylogeny,
688 tooth-shedding is restricted to the crown node, although if the condition
689 described in cladodonts [34] is more widespread then shedding may be
690 limited to a subset of elasmobranchs. This suggests a 'two-step' development
691 of the stereotypical chondrichthyan dentition, with an initiall shift towards tooth
692 whorls borne exclusively on the jaw cartilages, followed by the eventual loss
693 of fused bases and concomitant development of tooth shedding in crown-
694 group chondrichhtyans. However, significant phylogenetic uncertainty
695 persists, and this scenario warrants further testing as hypotheses of
696 relationship stabilise. Despite this, the interposition of multiple lineages of
697 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 [6,7,11,14].

In stark contrast to the clade comprising chondrichthyans with tooth whorls, the clade or grade including diplacanthids, acanthodids, and ischnacanthiforms exhibits a diverse array of oral structures, none of which seem to persist beyond the end of the Palaeozoic [24]. In phylogenetic analyses, this grade is consistently recovered at the base of the chondrichthyan total-group, with the exception of Frey *et al.* [33], who recover it in a more crownward position. A number of likely apomorphic oral morphologies are present within this clade, including diplacanthid occlusal plates, ischnacanthid dentigerous jaw bones and toothless acanthodids with mandibular splints. Many of these morphologies are known from the Late Silurian and Devonian, approximately contemporaneously to 'acanthodians' with tooth whorls and the unusual dentitions in more shark-like taxa (e.g. *Pucapampella*, *Gladbachus*. Novel oral morphologies have been linked to a period of rapid gnathostome evolution [7,41]. Furthermore in the Devonian small-bodied chondrichthyans were significant in of freshwater nektonic faunas [24]: diverse oral structures seem likely to have accompanied their radiation into these niches. While the latest surviving lineage of the 'acanthodian' grade was the remarkably morphologically conservative acanthodids [78], *Acanthodopsis* shows that experimentation with novel oral apparatus continued well into the Late Carboniferous.

4. Conclusion

721 ‘Acanthodian’ stem-group chondrichthyans display a diverse array of oral and
722 dental morphologies, including an apparently independent origin of teeth deep
723 within an edentulous clade. However, interpreting patterns of tooth evolution
724 is complicated by conflicting and unresolved phylogenetic hypotheses, both
725 for the chondrichthyan (figure 7; figures S1,2) and gnathostome stem
726 [6,58,82–84]. CT- and synchrotron-based investigations seem likely to provide
727 the anatomical information necessary to resolve these instabilities, and
728 likelihood-based methods provide another potential way of overcoming
729 uncertainties [7]. However the proliferation of different tree shapes in
730 conjunction with generally low support values means that morphologies
731 should be considered across multiple potential topologies. This illustrates the
732 challenges of drawing broad scale conclusions for gnathostome tooth
733 evolution on the basis of unstable relationships or tentatively-placed taxa.

734

735 **Acknowledgements**

736 We thank E. Bernard and Z. Johanson (NHMUK) for assistance with
737 specimen access, V. Fernandez and B. Clark (both NHMUK) and T. Davies
738 (University of Bristol) for assistance with CT scanning. M. Brazeau (Imperial
739 College London), B. Davidson, and C. Burrow (Queensland Museum) and P.
740 Ahlberg (Uppsala University) contributed to helpful discussion. M. Colfer
741 (University of Oxford) carried out preliminary segmentation and interpretation
742 of the Mimics files. Four anonymous reviewers provided helpful comments,
743 and we also thank two anonymous reviewers for their comments on an earlier
744 version of this manuscript.

Funding

This work was supported by a Junior Research Fellowship, Christ Church, Oxford, and a Royal Society Dorothy Hodgkin Research Fellowship, both to S.G.. R.P.D. was supported by a Paris Île-de-France Région – DIM "Matériaux anciens et patrimoniaux" grant (PHARE project).

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 for the purposes of review((Acanthodes_NHMUK_PV_P.8065 PLY files: https://www.dropbox.com/sh/7mmrrdo0shhhkc3/AABG5jhLrbghHeMghpYgizJAa?dl=0; Acanthodes_NHMUK_PV_P.8065 TIFF stack: https://www.dropbox.com/sh/ao3hua7467kat40/AADUb_etPMoD_CK-c7m-E5kba?dl=0; Acanthodes_NHMUK_PV_P.8065 Mimics file: https://www.dropbox.com/s/x8hfru687hs8lqj/Acanthodes_NHMUK_PV_P.8065_mimics.mcs?dl=0; Acanthodopsis_NHMUK_PV_P.10328 PLY files: https://www.dropbox.com/sh/2ip4lzsd56yjpyz/AAAqqq2BU6EbJ8x8Xm0TJWuTa?dl=0; Acanthodopsis_NHMUK_PV_P.10328 TIFF stack https://www.dropbox.com/sh/n24djy5n4de82bd/AABDEmru9PVyOqSHg-f_GCqNa?dl=0; Acanthodopsis_NHMUK_PV_P.10328 Mimics file: https://www.dropbox.com/s/9y9r7yac7p4gc0n/Acanthodopsis_NHMUK_PV_P.10328_mimics.mcs?dl=0 Atopacanthus_NHMUK_PV_P.10978 PLY files: https://www.dropbox.com/sh/0kgc31bw6b1sb78/AAB0kvTiCeA__Nw4JTrKd5f

3a?dl=0; Atopacanthus_NHMUK_PV_P.10978 TIFF stack: https://www.dropbox.com/sh/6ceer4qkelkv8be/AABZGZqJ-tneqFvX8Ff_K7UZa?dl=0 Atopacanthus_NHMUK_PV_P.10978 Mimics file: https://www.dropbox.com/s/gxiyur8qo54mcxw/Atopacanthus_NHMUK_PV_P.10978_mimics.mcs?dl=0; Ischnacanthus_NHMUK_PV_P.40124 PLY files: https://www.dropbox.com/sh/mrskv03iztott7s/AAChCylP9LMOYOXbYDymN_pCa?dl=0; Ischnacanthus_NHMUK_PV_P.40124 TIFF stack: https://www.dropbox.com/sh/x82rgb6dx5zjv1g/AAB8f6psZiuwY-m-R-_SiK76a?dl=0; Ischnacanthus_NHMUK_PV_P.40124 Mimics file: https://www.dropbox.com/s/4d2bboluoes51l4/Ischnacanthus_NHMUK_PV_P.40124_mimics.mcs?dl=0; Taemasacanthus_erroli_NHMUK_PV_P33706 PLY files: https://www.dropbox.com/sh/521y1zjasuff2c7/AABeQ16MiFbNKbSyMuvCG4Rva?dl=0; Taemasacanthus_erroli_NHMUK_PV_P33706 VOL file: https://www.dropbox.com/sh/tm798rx0ilmutqo/AADob3ja5rCoZV5Hd_D5qlt_a?dl=0; Taemasacanthus_erolli_NHMUK_PV_P33706 Mimics file: https://www.dropbox.com/s/qm90cxvlivd4zf8/Taemasacanthus_erolli_NHMUK_PV_P33706_mimics.mcs?dl=0.) 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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Figure captions

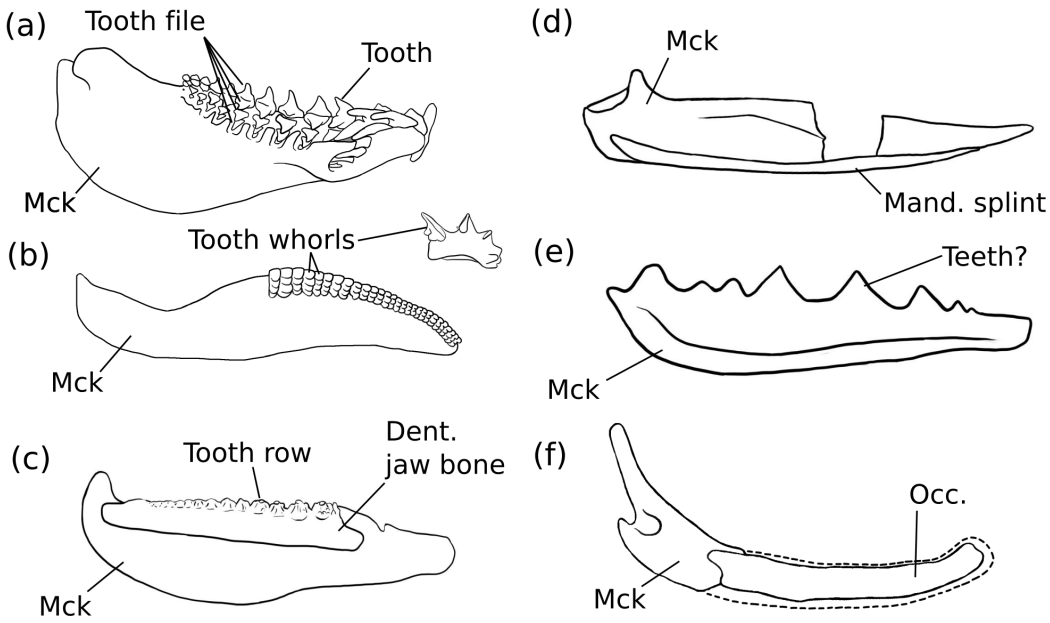
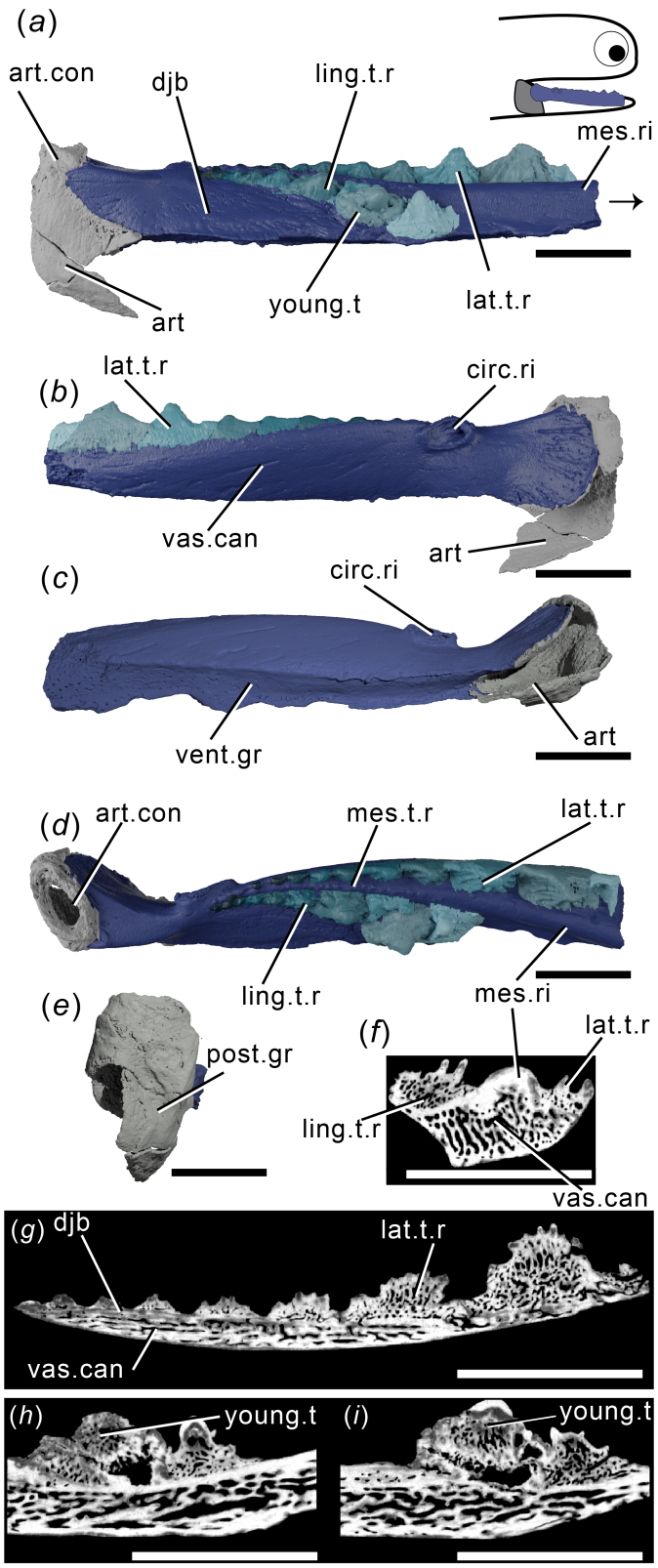


Figure 1. Summary figure showing lower jaws of six chondrichthyans, and major structures discussed in the text. (a) the extant elasmobranch *Isurus* in medial view, drawn from 3D data [80]; (b) the stem-chondrichthyan *Ptomacanthus* in medial view reconstructed from [44] (c) the ischnacanthid stem-chondrichthyan *Erymnacanthus* in medial view redrawn from [25] (d) the acanthodid stem-chondrichthyan *Acanthodes* in lateral view redrawn from [52] (e) the ?acanthodid stem-chondrichthyan *Acanthodopsis* in lateral view redrawn from Burrow [23]; (f) the diplacanthid stem-chondrichthyan *Diplacanthus* in medial view reconstructed from Watson *et al.*[61] and Burrow *et al.* [26] Not to scale.



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1073 **Figure 2**. Tomographic model of the left lower jaw of *Taemasacanthus erroli*

1074 NHMUK PV P.33706 in (*a*) medial view, (*b*) lateral view, (*c*) ventral view, (*d*)

1075 dorsal view, (*e*) posterior view, and reconstructed tomograms showing (*f*) a

transverse section through the lower jaw, (*g*) a sagittal section through the lingual tooth row and (*h*)-(*i)* progressively medial sagittal sections through the aberrant youngest cusp and neighbouring cusps. Teeth in panels (*a*), (*b*) and (*d*) are coloured separately from the dentigerous jaw bone. Arrow indicates direction of anterior, and top right inset shows location of rendered jaw components. Abbreviations: art, articular (Meckel's cartilage); art.con, articular 'condyle'; circ.ri, circular ridge; djb, dentigerous jaw bone; lat.t.r., lateral tooth row; ling.t.r, lingual tooth row; mes.ri, mesial ridge; mes.t.r, mesial tooth row; post.gr, posterior groove; young.t, out-of-order youngest tooth; vent.gr, ventral groove; vas.can, vascular canals. Scale bar = 5 mm.

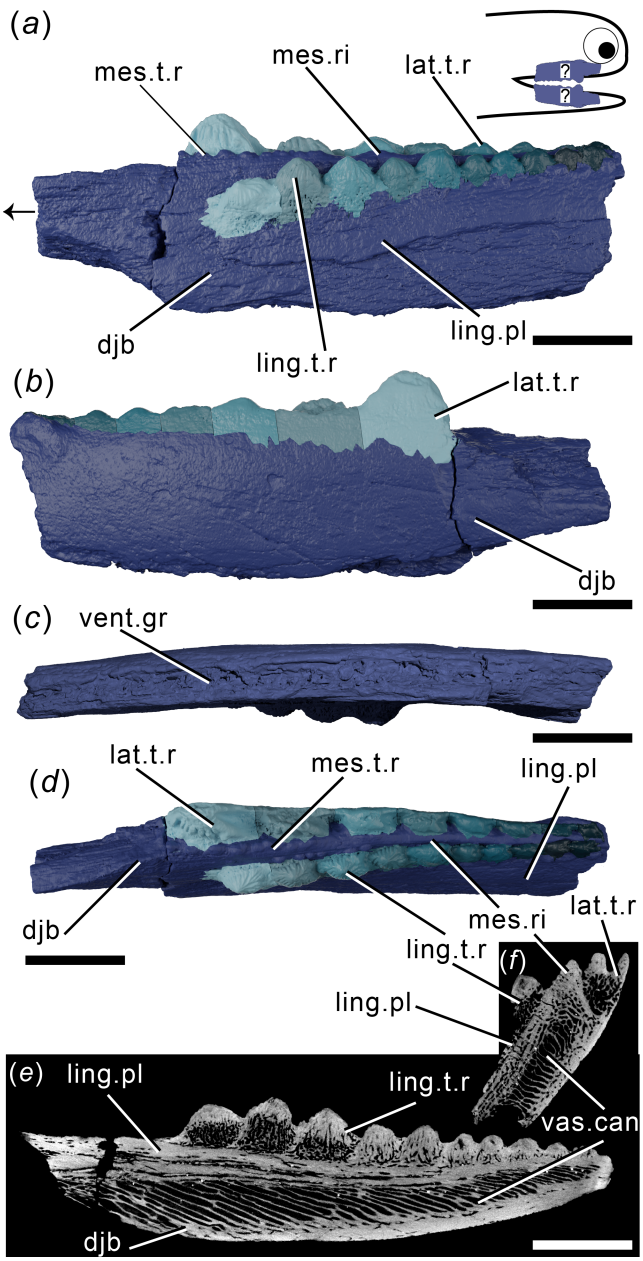

Figure 3. Tomographic model of a dentigerous jaw bone of *Atopacanthus* sp. NHMUK PV P.10978 in (*a*) medial view, (*b*) lateral view, (*c*) ventral view, (*d*) dorsal view and (*e*) a reconstructed tomogram showing a sagittal section through the lingual tooth row. Arrow indicates direction of anterior, and top right inset shows possible locations of rendered jaw components. Teeth in panels (*a*), (*b*) and (*d*) are coloured separately from the dentigerous jaw bone. Abbreviations: djb, dentigerous jaw bone; lat.t.r., lateral tooth row; ling.pl,

lingual plate; ling.t.r, lingual tooth row; mes.ri, mesial ridge; mes.t.r, mesial tooth row; vent.gr, ventral groove; vas.can, vascular canals. Scale bar = 5 mm.

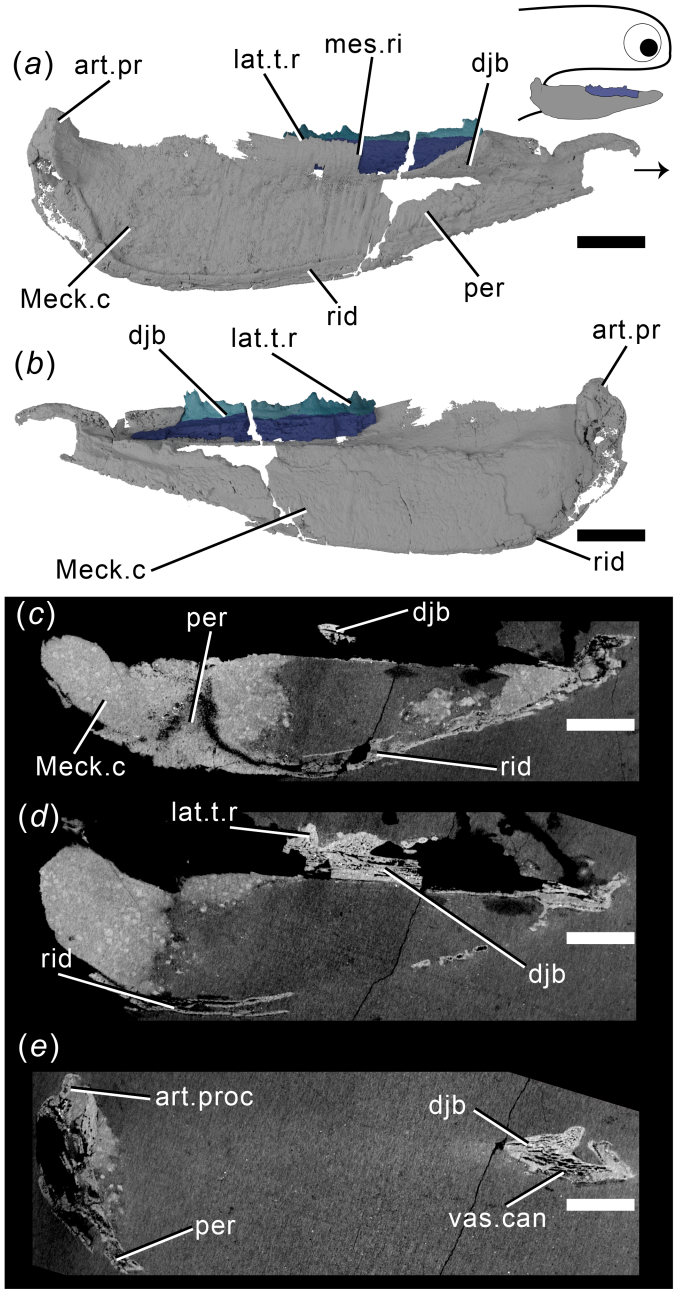

Figure 4. Tomographic model of the left lower jaw of *Ischnacanthus* sp. NHMUK PV P.40124 in (*a*) lateral view, (*b*) medial view, and (*c*), (*d*), (*e*) reconstructed tomograms showing successively deeper sagittal sections. Arrow indicates direction of anterior, and top right inset shows location of rendered jaw components. Abbreviations: art.proc, articular process; djb dentigerous jaw bone; lat.t.r., lateral tooth row; Meck.c, Meckel's cartilage;

mes.ri, mesial ridge; per, perichondral bone; rid, ridge; vas.can, vascular canal. Scale bar = 5 mm.

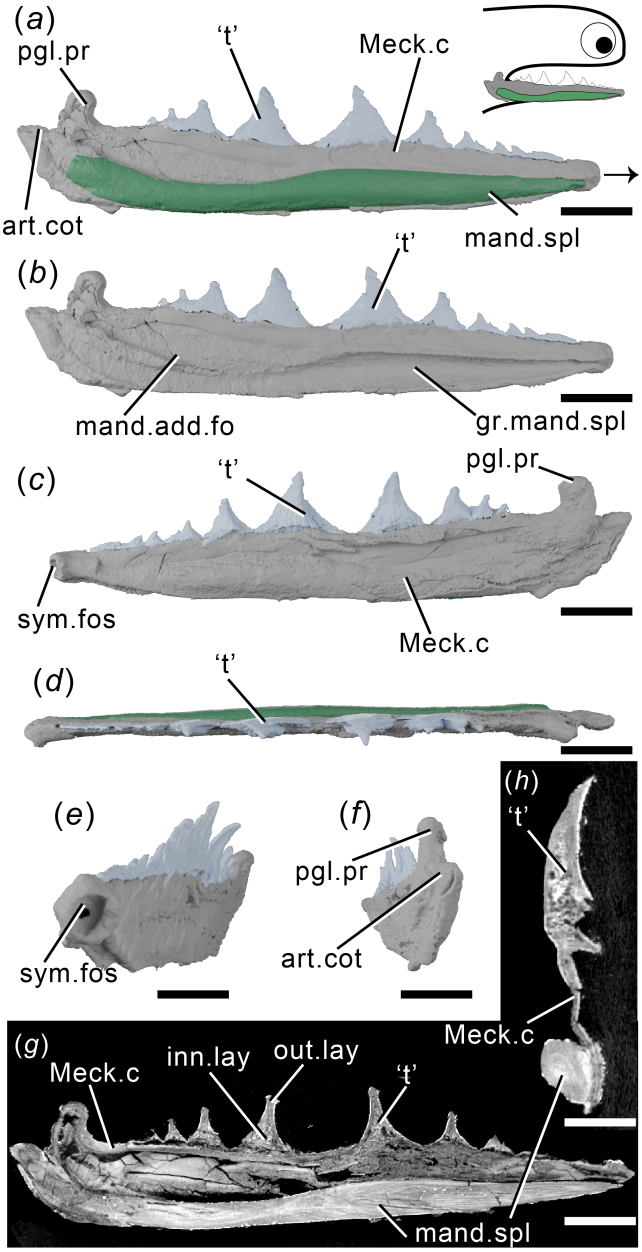

Figure 5. Tomographic model of the right lower jaw of *Acanthodopsis* sp. NHMUK PV P.10383 in lateral view with (*a*) and without (*b*) mandibular splint, (*c*) medial view, (*d*) dorsal view, (*e*) anteromedial view, (*f*) posterior view, and reconstructed tomograms showing (*g*) a sagittal section through the entire jaw and (*h*) a transverse section through the jaw. Arrow indicates direction of anterior, and top right inset shows location of rendered jaw components. Abbreviations: art.cot, articular cotylus; gr.mand.spl, groove for mandibular

splint; inn.lay, inner layer; mand.add.fo, mandibular adductor fossa; mand.spl, mandibular splint; Meck.c, Meckel's cartilage; out.lay, outer layer; pgl.pr, preglenoid process; sym.fos, symphyseal fossa; 't', 'teeth'. Scale bar = 5 mm in (*a*)-(*g*), 2 mm in (*h*).

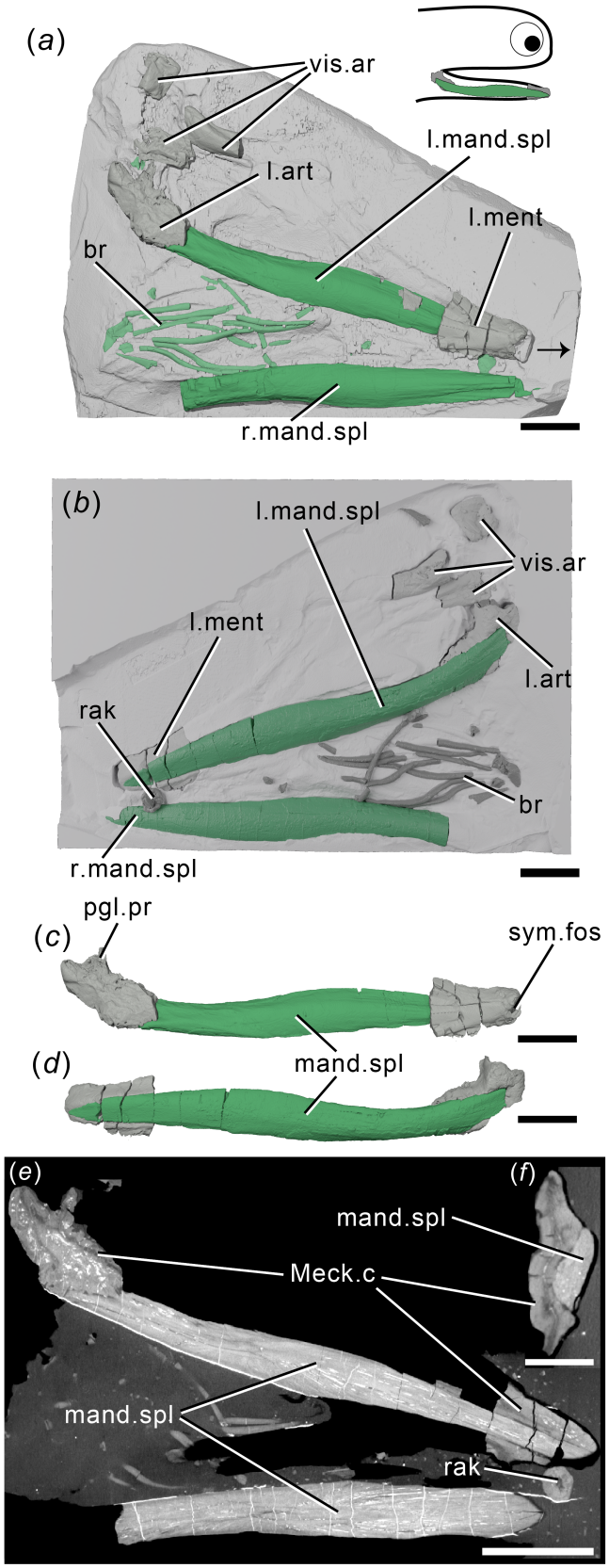

Figure 6. The lower jaws of *Acanthodes* sp. NHMUK PV P.8065 in (*a*) dorsal view against the matrix, (*b*) in ventral view superimposed on a digital mould of

the matrix's surface, the left lower jaw isolated in (*c*) medial and (*d*) lateral view, and reconstructed tomograms showing (*e*) a coronal section through the specimen, and (*f*) a transverse section through a lower jaw. Arrow indicates direction of anterior, and top right inset shows location of rendered jaw components. Abbreviations: art, articular (Meckel's cartilage); br, branchiostegal rays; mand.spl, mandibular splint; Meck.c, Meckel's cartilage; ment, mentomandibular (Meckel's cartilage); pgl.pr, preglenoid process; rak, gill raker; sym.fos, symphyseal fossa; vis.ar, visceral arch fragments. Scale bar = 5 mm in (*a*)-(*e*), 2mm in (*f*).

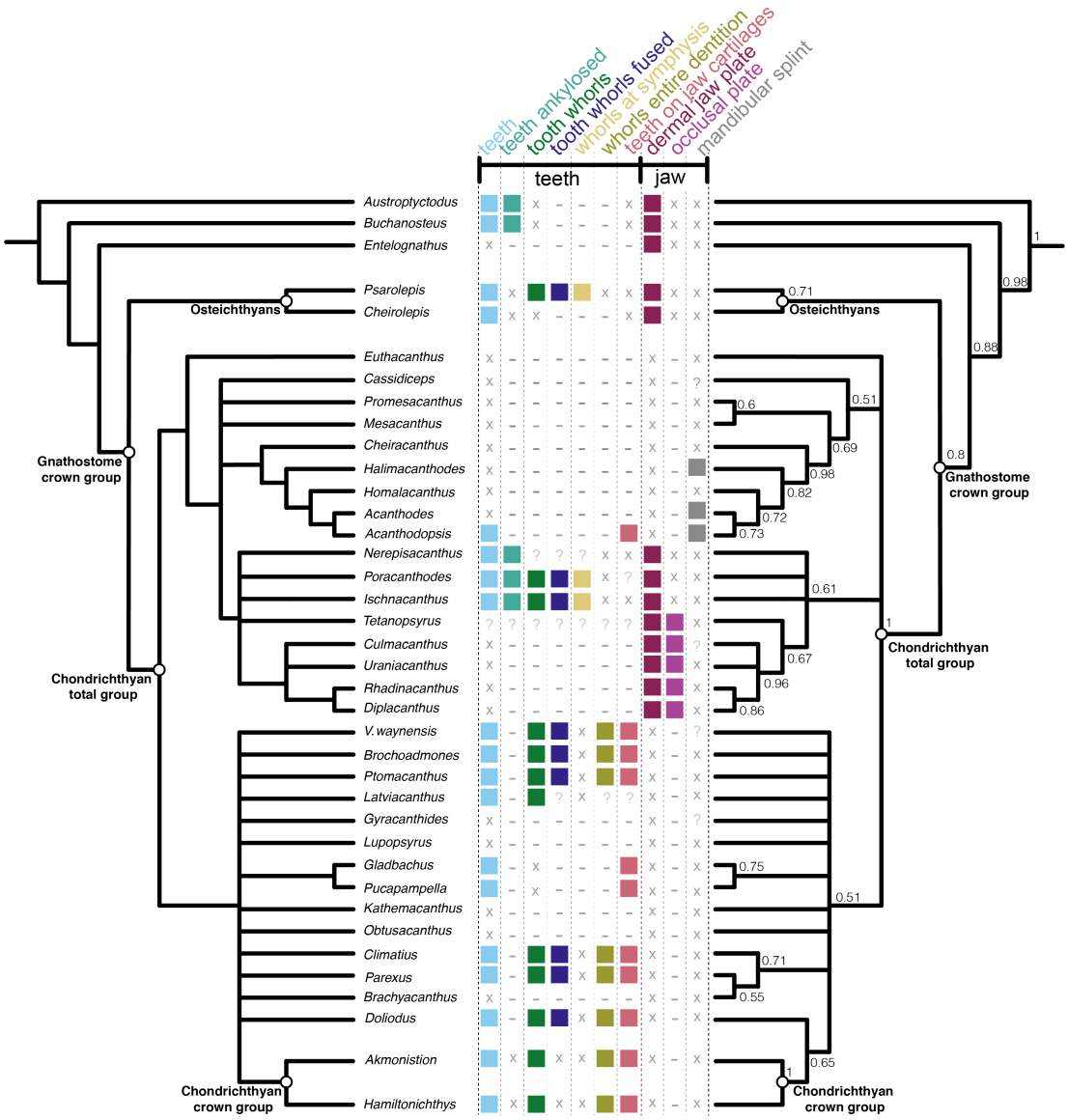

Figure 7. Phylogenetic relationships of early chondrichthyans and distribution of oral structures. Strict consensus of 26101 most parsimonious trees on left and Bayesian analysis on right, with some non-chondrichthyan taxa excluded (full tree with support values in figures S2 and S3). Numbers at nodes on right represent Bayesian posterior probabilities. Character distribtion is based on coding in the data matrix as follows: teeth, character (c.) 82; teeth ankylosed, c.93; tooth whorls fused, c. 85; whorls at symphysis and whorls entire dentition, c.88; teeth on jaw cartilages and dermal jaw plate, c.94 ; occlusal plate, c.269 ; mandibular splint, c.268. Filled boxes indicate presence of

1149 feature; ‘x’ indicates feature absent; ‘?’ indicates uncertainty; ‘-‘indicates

1150 inapplicability.

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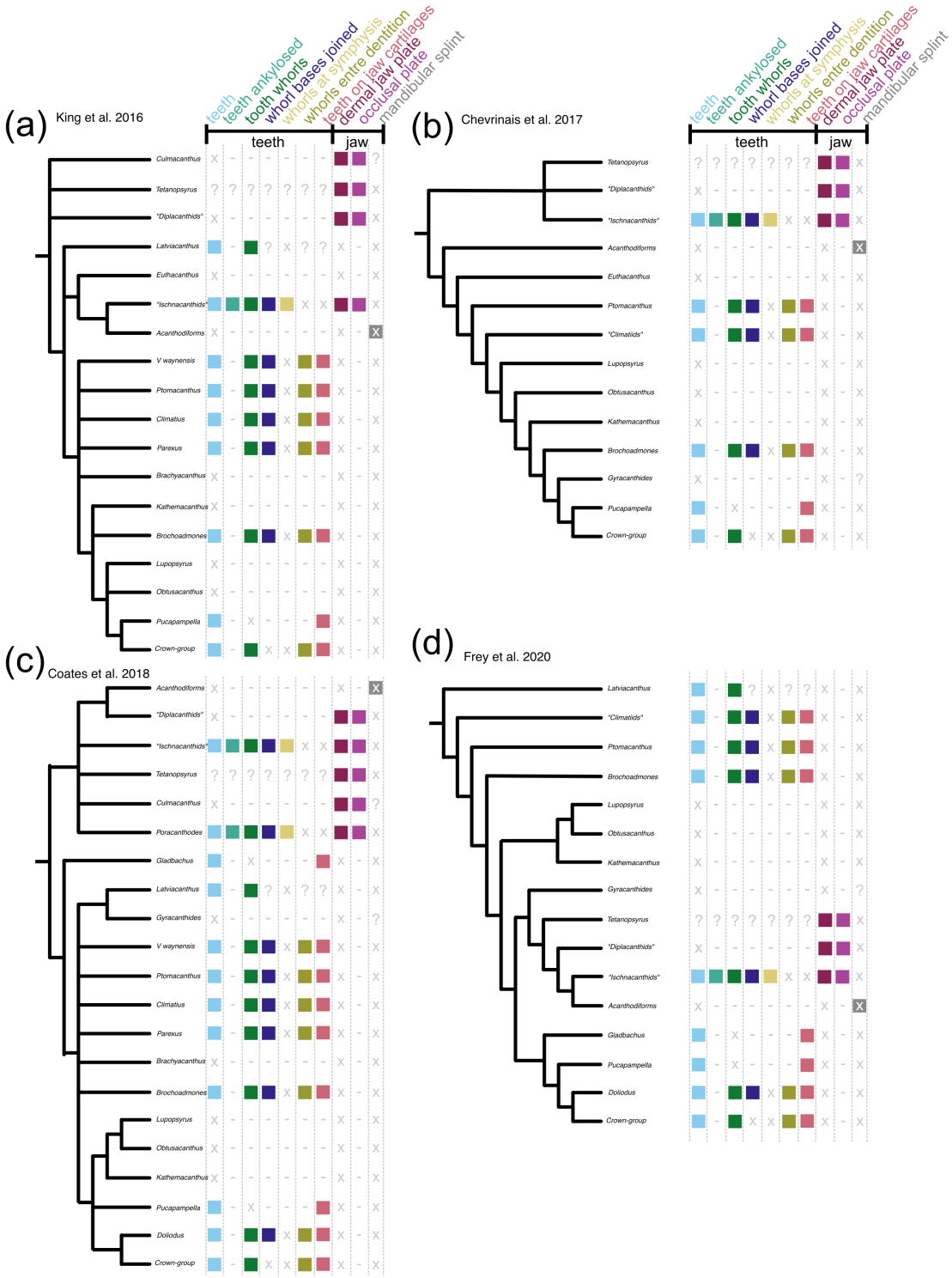

Figure 8. Summaries of four contrasting recent phylogenetic schemes of early chondrichthyans, with distribution of oral characters. (a) King *et al.* 2016 [41], (b) Chevrinais *et al.* 2017 [40], (c) Coates *et al.* 2018 [24], (d) Frey *et al.* 2020

[33]. Icons and character numbers as in Fig. 7 Acanthodiforms includes taxa both with and without mandibular splints.

Supplementary material (separate pdf)

Supplementary information for this manuscript is included as two files. The first includes notes on the phylogenetic analysis (taxon addition, character addition and coding changes) supplementary table 1,and supplementary figures 1-3. The second is a zipped folder containing all files necessary for replicating our Bayesian and parsimony analyses.