Electronic Supplementary Materials for:

First tooth-set outside the jaws in a vertebrate

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The Holocephali (ratfish, rabbit fish and chimaeras) is the sister clade to the Elasmobranchii (sharks skates and rays), which, together, comprise the crown radiation of the Chondrichthyes (Fig. S1) [1-5]. Here, we provide a completely revised description of the dentition of one of the earliest known holocephalans from the Lower Carboniferous (Viséan), Chondrenchelys problematica [6]. We provide the first descriptions of a complete arcade of extra-mandibular teeth in a vertebrate, describe the ontogeny of holocephalan toothplates, and demonstrate the conjunction of characteristic holocephalan toothplates with individual, petalodont-like teeth in a single species.

Materials and Methods

Institutional abbreviations


Systematic Palaeontology

Class: Chondrichthyes [7]

Subclass: Holocephali [8]
Plesion: Chondrenchelyiformes [9]

Family: Chondrenchelyidae [9]

Genus: Chondrenchelys [6]

Species: Chondrenchelys problematica [6]

Geological context and age of Mumbie Quarry

The two new specimens of *Chondrenchelys problematica*, NMS 1998.35.1 and NMS 2002.68.1, originate from the Mumbie Quarry fossil locality. Detailed geologic information for this locality was previously reported by Coates and Gess [10], and is summarized here. In the early 1990’s, S. P. Wood excavated Mumbie Quarry, recovering an early Carboniferous vertebrate assemblage. The locality is adjacent to exposures of the Glencarholm Volcanic Beds, which include the River Esk fish bed horizon: Glencarholm, Dumfries District, Dumfries and Galloway Region, Scotland, Ordnance Survey grid reference NY 376 795 (Fig. S7). Mumbie Quarry is laterally equivalent to the classic Glencarholm Fish Bed [11] that produced the fossil material originally referred to *Chondrenchelys* [6, 12]. The Mumbie Quarry locality is now mostly back-filled [10].

The Glencarholm Fish Bed forms a thin member within the larger Glencarholm Volcanic Beds, themselves a subunit of the Upper Border Group of the Calciferous Sandstone [13]. The Glencarholm Volcanic Beds span the Holkerian/Asbian Substage boundary of the Viséan (Lower Carboniferous) [14, 15], implying an age 332±5 Ma for the Glencarholm Fish Bed, and therefore for Mumbie Quarry, as well [ICS 2004 Timescale: 16]. Schram’s [17] assessment of the depositional environment for the Glencarholm biota was a near-shore marine environment. Because calcareous shells are
rare in these faunas, it is thought that these units represent quick burial in conditions with low oxygen/low pH. This would result in intact body fossils, but with mineral content removed through the acidic conditions [17]. However, both the classic Glencarholm Fish Bed and Mumbie Quarry do preserve body fossils with mineralized cartilage and dentine, suggesting that calcareous shells and mineralized skeletal material might be restricted to distinct subfacies, indicative of laterally and/or temporally heterogeneous depositional environments within the larger fish bed unit.

**Examined Fossil Material**

**Specimen NMS 1998.35.1:** This specimen consists of a single slab containing an unusually intact individual, approximately 185 mm in length, preserved in three-dimensions and exposed primarily in lateral view. The cranium is slightly rotated and compressed with respect to the body, such that dorsal and lateral surfaces are visible, with the skull inclined slightly to the animal’s right. The cranium is 26 mm in length from the anteriormost preserved toothplates to the posterior extremity of the occipital region. Unlike the body, the cranium region has been crushed primarily in the dorsoventral plane, and preserves the upper and lower toothplate series in occlusion. This specimen has not been described previously.

**Specimen NMS 2002.68.1:** This specimen is preserved as a part and counterpart, and contains an individual approximately 140 mm in length. Uniquely, NMS 2002.68.1 was split through the oral cavity, such that NMS 2002.68.1p preserves the mandible in dorsal view, while NMS 2002.68.1cp preserves the upper tooth series and base of the neurocranium in ventral view. As such, both the lower and upper dentitions are preserved
in oral view. Therefore, between the two Mumbie Quarry specimens, we are able to evaluate the complete dentition of *Chondrenchelys* both in occlusal view and in occlusion. Although this specimen has not been described previously, an image of the mandible and several toothplates before preparation does appear in [18, Fig. 8A].

**Identification of specimen HM V.7173:** Precise locality information for HM V.7173 is not available. It is known that the specimen was collected around 1881 by one A. R. Pratt, and that it was donated to the Hunterian Museum, University of Glasgow, Scotland, UK from a private collection in 1964. In 1965, ostracods from the associated matrix were analyzed by J. W. Mackay. He concluded that the ostracods were consistent with those of the Calciferous Sandstone of the Lower Limestone Group, and that HM V.7173 likely originated from the Glencartholm Fish Bed [13] (see above: Geologic Context). Therefore, HM V.7173 is probably contemporaneous with previously-described *Chondrenchelys* specimens and also the new Mumbie Quarry specimens. In 1980, HM V.7173 was misidentified in the collections as *Phanerosteon mirabilie* (an actinopterygian fish); it was subsequently correctly attributed to *Chondrenchelys problematica* in a survey of the Hunterian Museum collections by L. C. Sallan in 2010. This specimen has not been described previously.

**Specimen HM V.7173:** This specimen consists of a single slab, preserving a partial individual. The dentition is visible primarily in dorsal view, with the posterior toothplates preserved in occlusion. The rostrum has been crushed, and the anterior toothplates are damaged, and displaced to the anterior of the individual. In addition, the anterior half of the chondrocranium has been broken away, exposing the aboral surfaces of the upper posterior toothplates, which have been displaced slightly from life position,
exposing portions of the lower toothplate occlusal surfaces.

**Additional specimens of Chondrenchelys:** The quality of preservation of these three specimens permits re-evaluation of several previously described specimens of *Chondrenchelys*, furthering our understanding of its dental morphology. These included the type specimen, NHM P 4085 [6, 12], and RSM 1885.54.5/5A (part/counterpart), part of Moy-Thomas’ [12] description of *Chondrenchelys*. NHM P 4085 preserves a damaged dentition, while RSM 1885.54.5 preserves an individual with a highly crushed cranium, although the toothplates are generally well preserved. RMS 1891.53.33, referred to *Chondrenchelys* and figured by Lund [19], preserves a crushed specimen with several identifiable toothplates, as well as portions of the cranium and axial skeleton. BGS-GSE 13328, also referred to *Chondrenchelys* by Lund (listed as "IGS-GSE 13328" in his referred specimens) [19], was figured by Lund [19] and Ginter and Sun [18]. This specimen preserves an incomplete cranial fragment with associated toothplates.

**Examination of additional fossil chondrichthyans:** To facilitate our redescription of the dentition of *Chondrenchelys problematica*, we studied specimens of other early Carboniferous chondrichthyans from the Serpukhovian Bear Gulch Limestone of Montana, USA, in the collections of the Carnegie Museum of Natural History, Pittsburgh, PA, USA, including its sister taxon in the Chondrenchelyidae, *Harpagofututor volsellorhinus* [19]. Where appropriate, we refer to individual specimens with their CMNH accession numbers in our description below.

**Description of the dentition of Chondrenchelys problematica**

*Toothplate dentition*
The two previous descriptions of the dentition in *Chondrenchelys* differ substantially from one another. Lund [19] reconstructed one pair of large posterior toothplates in both the upper and lower jaws. Anterior to these, he reconstructed two paired, anterior toothplates and a midline symphyseal toothplate in the mandible, and a single pair of upper anterior toothplates in the palatal dentition. In contrast to this, Moy Thomas [12] reconstructed two longitudinally-oriented posterior toothplates (one medial, one lateral) in both the upper and lower dentitions. Moy-Thomas’ reconstruction also reversed the counts of the anterior toothplates, proposing two pairs of upper anterior toothplates and a single pair of lower anterior toothplates, and did not include a symphyseal toothplate in either the palatal or mandibular dentitions [12].

Our reconstruction differs significantly from both of these descriptions. The occlusal view of upper and lower jaws, afforded by NMS 2002.68.1p/cp, and confirmed in BGS-GSE 13328, clearly demonstrates that the posterior toothplates are single units in both jaws [19]. In NMS 1998.35.1 and HM V.7173 a pronounced descending lamina, a distinctive feature of crown group Holocephali and a subset of stem relatives [20], separates the aboral surface from the symphyseal and labial surfaces of the upper posterior toothplates (UPT). NMS 2002.68.1 clearly shows only a single pair anterior toothplates in the mandible [12]. Additionally, NMS 1998.35.1 demonstrates that there is a single pair upper anterior toothplates (UAT). The anterior toothplate counts are confirmed upon re-examination of RSM 1885.54.5A. We find no evidence of a symphyseal lower toothplate in either of the Mumbie Quarry specimens or HM V.7173, nor is there any midline toothplate preserved in the classic *Chondrenchelys* specimens, contra Lund [19]. In this respect, *Chondrenchelys* differs from *Harpagofututor*, in which
the presence of a symphyseal toothplate in the mandible is unambiguous (CM 27330, CM 35524, CM 37521). Therefore, we reconstruct the dental formula of *Chondrenchelys* as follows: each quadrant of the mandibular dentition consists of a large lower posterior toothplate (LPT) and a single, smaller LAT, and each half of the palatine dentition houses a large UPT and one, smaller UAT.

The LPT occlusal surface is partially exposed on the left side of NMS 1998.35.1, and the occlusal surfaces of the LPTs are completely exposed in NMS 2002.68.1. The general form of the LPTs is an obliquely-oriented spiral whorl, oriented in a postero-lingual/antero-labial direction. Pallial dentine is visible along the occlusal surface of the toothplates; this is especially evident on the relatively unworn BGS-GSE 13328. The morphology of the LPT surface is characterized by two obliquely-oriented ridges: areas of high relief that are separated by a large median trough, giving the tooth a distinct “ridge and valley” appearance. The axis of each raised “ridge” is lined, and presumably reinforced, by vertically-oriented, highly mineralized tritors, which exhibit differential wear relative to the surrounding dentine. A third ridge reinforced by mineralized tritors is also visible at the anteriormost extent of the LPT, and is oriented linguo-labially, with respect to Meckel’s cartilage.

Transversely-oriented bands of dentine connect tritors of different ridges across the valleys, marking apparent generations within the tooth families. The composition of the tritors resembles those observed in the posterior toothplates of extant *Hydrolagus*, although in *Chondrenchelys* tritors appear in each tooth generation as determined by the transverse banding, whereas in *Hydrolagus* tritors are less frequent, with multiple tooth generations between tritors. This composition also differs from *Harpagofutuor*. 
Toothplate surfaces in *Harpagofututor* are covered in a dentine surface with regularly-spaced dimples, which, in cross-section, are shown to be vertically-oriented mineralized tubules (denteons) (CM 35503, CM 35506). Unlike *Chondrenchelys*, no large tritor-like structures are preserved in *Harpagofututor*. The tubules are arranged in regular linear bands, indicative of individual generations.

In *Chondrenchelys*, the orientation of the transverse banding changes during ontogeny. In NMS 2002.68.1, the angle of the anterior-most transverse dentine banding in the LPT indicates a linguo-labial orientation of tooth propagation in the toothplate. The orientation of the transverse ridges changes to one parallel with the coronal plane at the posterior margin of the toothplate, therefore implying a parasagittal propagation at the caudal margin of the toothplate. In all, three linear series of mineralized tritors are visible in the LPTs of NMS 2002.68.1. Each series constitutes a longitudinally fused tooth family, centered on a mineralized tritor. These families are also joined laterally to adjacent tooth families via the transverse dentine bands, to form the complete toothplate.

Slight imperfections in the alignment of the transverse ridges in the “valleys” between tritural ridges are evident in the LPT of NMS 2002.68.1 and in the UPT of BGS-GSE 13328 (Figs. 3, S3), further supporting the interpretation that these represent families of individual teeth fused into a composite toothplate. Similar imperfections in the alignment of the mineralized tubules are visible in *Harpagofututor* (e.g., CM 41023), indicating that its toothplates are also composite structures of at least two tooth families.

The axis of anteriormost tooth family in the LPT is oriented approximately orthogonally to those of the more caudal tritual ridges (Figs. 3, S3). This can be understood in terms of ontogeny, in which accretion of the early tooth family proceeded
approximately linguo-labially. By tracing the transverse dentine bands laterally to the adjacent tooth family, it is apparent that tooth generation at the earliest tooth generation sites is either discontinued or substantially slowed, so that tooth generation is displaced caudally and is continued at the other tooth families. Toothplate accretion changes to a postero-lingual/antero-labial orientation in the adult with respect to the jaw cartilage. However, given the angle of Meckel’s cartilage from its articulation with the palatoquadrate to the midline symphysis, the absolute direction of tooth accretion in the adult mouth was approximately parasagittal, as it is in modern chimaeroids. This stands in contrast to Harpagofututor, wherein there does not appear to be any change in the orientation of the arrangement of the mineralized tubules; the direction of tooth generation appears to be caudal-rostral throughout the ontogeny of the toothplate (CM 35503, CM 35524).

The occlusal surface of the UPTs are missing in NMS 2002.68.1 due to post-preservation breakage, with only the general form of the toothplate and the mineralized basal material preserved. The UPT is posteriorly broad, narrowing mesially, and in overall form is similar to extant Callorhinchus [20, see also Main Text Fig. 3]. Each UPT extends anteriorly from a level about halfway along the length of the orbit, to contact its complement from the other quadrant along a broad symphyseal margin. The two UPTs in NMS 2002.68.1 form a diagnostic horseshoe-shaped mesial recess at the caudal toothplate margin, along the midline (Fig. 3). This morphology contrasts with both living holocephalans (e.g., Callorhinchus, Hydrolagus) and Harpagofututor (CM 35524, CM 46108, CM 62831), wherein midline contact is complete to the caudal margin of the UPTs.
Specimen BGS-GSE 13328 (Fig. S4) deserves specific re-description and clarification in light of the context provided by the Mumbie Quarry material. Lund [19, Fig. 5F] figured BGS-GSE 13328, without providing a specific description of the specimen. In assigning two isolated toothplates from China to the genus *Chondrenchelys*, Ginter and Sun [18, Fig. 8B] interpreted BGS-GSE 13328 as consisting of two LPTs, a single UPT, with two damaged anterior toothplates. However, Ginter and Sun [18] confused the upper and lower dentitions. BGS-GSE 13328 actually preserves two UPTs (their LPTs) in oral view and the left LPT (their UPT) rotated in partial oral view. The UPTs are diagnosable based on the presence of the horseshoe-shaped mesial recess, preserved in both upper toothplates. In addition, neither of the features they identified as anterior toothplates are such. One is clearly composed of tesserae of calcified cartilage. The second is not a distinct toothplate, but rather a fragmented block of dentine, which is derived from the anterior end of the right LPT in aboral view. Three partial anterior toothplates are preserved in BGS-GSE 13328, but are highly damaged and not in life position, so no useful information can be gleaned from these.

The majority of the occlusal surfaces of the UPTs are preserved in BGS-GSE 13328, and the LPT is in partial occlusion with the corresponding left UPT, but has been rotated such that its occlusal surface is visible. The occlusal surfaces of the UPTs, as with the LPTs, are characterized by transverse bands of dentine, which mark tooth generations within the tooth whorl. The overall form of the UPT surface is a set of “ridge and valley” forms similar to those observed in the LPTs. There is evidence for mineralized tritors in positions of high relief. BGS-GSE 13328 also demonstrates that, as with the LPTs, the direction of UPT tooth accretion changes during ontogeny, with an early radial accretion
shifting to antero-posterior accretion later in life. As with the lower dentition, our observations in *Chondrenchelys* contrast sharply with the upper posterior toothplates in *Harpagofututor*, which do not show a change in the orientation of tooth generation (CM 35506, CM 41023).

The lower anterior toothplates are roughly triangular in cross-section at the base, tapering crownward to a more oval cross-section, giving the anterior toothplates a sectorial appearance. The posterior margin of the LAT has a prominent basal heel, which interlocks with mesial margin of the LPT such that the LAT has a distinct hook-like appearance when observed in isolation (e.g., NMS 19998.35.1). The isolated anterior toothplates figured by Ginter and Sun [18, Fig. 8E] provides a good model for the three-dimensional shape of the UATs in *Chondrenchelys*. The general form of the UATs is approximately tetrahedral in three-dimensions, imparting the distinctive triangular shapes observed in the flattened specimens described earlier [12, 19]. The grinding surfaces of both lower and upper anterior toothplates are marked by a ridge of circular bumps [12], which are mineralized tritors, as seen in the posterior toothplates. LATs preserve a single ridge of tritors, which in lateral view is reminiscent of the parasymphyseal tooth whorls known in a variety of early gnathostome taxa [21, 22]. The UAT display two tritural ridges.

**Reconstruction of the occlusion between the mandibular and palatine dentitions**

Because of the extraordinary completeness of the preservation of the toothplate dentition in the examined specimens, we are able to reconstruct the manner of occlusion between the posterior toothplates of the palatine and mandibular dentitions (Fig. 3C). We
used digital representations of the occlusal surfaces of the LPTs (taken from NMS 2002.68.1) and UPTs (taken from BGS-GSE 13328), scaling these dentitions to a common size using comparisons with the preserved crania in NMS 1998.35.1 and NMS 2002.68.1.

The LPTs and UPTs are comprised of topographically complex sets of high “ridges” and low “valleys.” However, there is not a correspondence between the topographies of the palatal and mandibular toothplates during occlusion. Both of the more longitudinally-oriented tritoral ridges of the LPT are positioned laterally to the main tritual ridge of the UPT when the toothplates are brought into occlusion. Interestingly, the large area of low relief to along the midline of the UPT does not come into contact with the LPT when the bite is closed, and therefore does not appear to function with respect to food processing.

Both the LATs and UATs meet their compliments at an oblique angle to the midline. The occlusal surface preserves two raised tritural ridges flanking and interior flat shelf. The tritors face anteriorly in the LATs, and posteriorly in the UATs. This orientation for the UATs differs substantially from the reconstruction offered for the isolated anterior toothplate identified by Ginter and Sun as an upper anterior toothplate [18, Fig. 8C]. Occlusion occurs between the forward facing LATs and rear-facing UATs, and the neither set of anterior toothplates contacts the posterior toothplates during biting.

We also note that the degree of wear on the upper and lower posterior toothplates in *Chondrenchelys* (Fig. 1B) is decidedly unlike what we observe in extant *Hydrolagus* (Fig. 1C). On the occlusal surfaces of the LPTs of both Mumbie Quarry specimens and HM V.7173 the mineralized tritors and transverse dentine bands remain clearly visible
across the entire toothplate surface, including the anteriormost (hence oldest) portion of
the LPTs. In addition, the entire occlusal surface is visible for both the upper and lower
posterior toothplates in BGS-GSE 13328 (Fig. S5), and little wear is evident with pallial
dentine still covering the surfaces between transverse bands. In contrast, the posterior
toothplates in an adult *Hydrolagus* are worn such that no dentine remains covering the
mineralized basal material (Fig. 1C) [23]. While the presence of toothplates in
*Chondrenchelys* could be employed as an ecomorphological indicator of a durophagous
diet, the degree of durophagy in *Chondrenchelys*’ diet cannot be comparable to that
observed in extant chimaeroids. From this, we propose that the large mesial region of the
UPTs that does not contact the LPTs during biting and the long midline contact of the
UPTs are indicative of a structural function for the medial portion of the UPTs, and it is
likely that they buttress the floor of the chondrocranium against bite forces, similar to the
upper toothplates of lungfish [24].

The extra-mandibular dentition

*Chondrenchelys* provides remarkable evidence of an additional series of teeth
positioned anteriorly (i.e., externally) to the mandibular arch. This is the first evidence of
a dentition consisting of individual teeth occurring in conjunction with a conventionally
holocephalan dentition comprised of toothplate. NMS 1998.35.1 preserves 11 such teeth
in two sets: one in aboral (upper dentition) and oral (lower dentition) views. These are
arranged somewhat irregularly to form an extra-mandibular arcade outside the apparent
labial margin of the mandibular arch (Figs. 2, S3, S5, S8).

In NMS 2002.68.1p, a set of at least seven teeth are preserved anterior to the
paired LATs. Notably, these teeth are aligned transversely, and are symmetrically relative to the main anterior-posterior body axis (Fig. S3). Each tooth is small (<0.5 mm in length), labio-lingually narrow, and roughly rectangular in cross-section. It is not certain if the teeth are paired across the body midline or if there is a midline tooth in the extra-mandibular arcade, as a large tooth visible at the center of the extra-mandibular arcade is not part of this series, but is actually a broken piece of dentine from a UAT that has fallen forward and is currently adhered by matrix to the extra-mandibular arcade. The ordered, slightly overlapping arrangement of the teeth in the extra-mandibular arcade suggests that they have been preserved in situ, and form part of the lower dentition. Additionally, an extra-mandibular series is observed, although highly damaged, in HM V.7173 (Fig. S8).

Re-examination of NHM P 4085 revealed a previously unidentified extra-mandibular tooth, with the characteristic bolster-shape observed in several examples in NMS 1998.35.1 (Figs. 2C & D, S4).

The surface morphology of the extra-mandibular teeth is markedly different from that observed in the toothplates, with many small dentine tubules visible on the worn surfaces (NMS 1998.35.1) giving the surface of the extra-mandibular teeth a distinct pock-marked, or “orange-peel,” appearance. The lingual surfaces of several of teeth preserve a distinctive keyhole-shaped recess in the dentine of the tooth crown (Fig. 2C and D). The extra-mandibular teeth possess deep and labio-lingually thin roots (Fig. S4).

It is possible that these teeth are the preserved remnants of a developmentally earlier set of toothplates, which differ in morphology from the full adult dentition. Fossil and recent lungfish have been shown to grow an early set of transient toothplates that are resorbed early in ontogeny [25-27]. However, we argue that these teeth are fundamentally
different and distinguishable from the toothplates found in the mandibular arch. First,

Meckel’s cartilage is complete in both Mumbie Quarry specimens and this dentition is
positioned outside the mandibular arch, therefore the two sets of teeth are positionally
distinct. In addition, the tooth counts of the extra-mandibular teeth are out of register
with, and are more numerous than, the toothplate positions in the mandibular arch. This
would require a re-organization, and a reduction in the number, of the tooth generation
sites within the dental lamina, which would be incompatible with a clonal model of tooth
development [e.g., 21, 28, 29]. Furthermore, the extra-mandibular teeth are also
morphologically distinct from the toothplates in the jaw. There is a distinct surface
morphology to the dentine that is not observed in the toothplates, and the extra-
mandibular teeth possess distinct crowns and roots (Fig S4): NMS 2002.68.1, HM
V.7173, and RMS 1891.53.33 clearly show that toothplates in Chondrenchelys are
unrooted (see above). Taken together, this argues strongly against their identification as
an ontogenetically early toothplate set.

Given the position of these teeth it is possible that the extra-mandibular dentition
was supported on labial cartilages. Such cartilages are elaborate in modern and fossil
holocephalans [9, 23, 30] and labial cartilage are likely a plesiomorphic feature of
chondrichthyans in general [31, 32]. However, if the extra-mandibular dentition was
supported on labial cartilages, these cartilages were not highly mineralised in
Chondrenchelys, as we found no evidence for such cartilages is preserved in any of the
new specimens, nor in any of the examined classic material.

We find no evidence in any of the examined specimens for a branchial dentition
in Chondrenchelys.
The extra-mandibular dentition of *Chondrenchelys* resembles tooth morphologies described for several taxa either placed within or allied with the extinct chondrichthyan group Petalodontiformes [31, 33-35]. Specifically, *Chondrenchelys* are similar to several chondrichthyans recovered from the Bear Gulch Limestone: *Heteropetalus* [36], *Debeerius* [31], *Gregorius*, and *Srianta* [34]. In the extra-mandibular arcade, more mesially-positioned teeth exhibit a slight cusped shape, whereas more distally-positioned teeth have flatter, bolster-shaped, crowns that are more quadrate in appearance. Furthermore, it is noteworthy that the roots of these teeth are tabular. Unlike the tooth roots of the majority of Paleozoic chondrichthyans, there is no trace of a lingual torus or shelf. In this respect, the extra-mandibular arcade in *Chondrenchelys* resemble the petalodont genus *Petalodus* [33, 35], although there are substantial differences with respect to relative thickness, lack transversely-oriented imbricate basal ridges, and overall size [35]. The extra-mandibular dentition is strikingly similar to that of two taxa that have been allied with the petalodonts, *Heteropetalus* (CM 23664, CM 62837) and most strikingly *Debeerius* (CM 27380, CM 46027) (Fig. S6) [31, 35, 36]. However, despite a high degree of similarity in gross morphology and with the characteristic surface histology between *Chondrenchelys* and these taxa, in no examined specimens of either *Heteropetalus* or *Debeerius* were we able to observe the distinctive keyhole recess.

Grogan and Lund [31] noted similarities between the teeth of *Debeerius* and those of petalodonts. Ginter et al. [35] noted that *Heteropetalus* is similar in appearance to *Debeerius*. Indeed, examination of specimens at the Carnegie Museum reveals that the taxon now identified as *Debeerius* was originally, informally listed as “*Heteropetalus sp.*” *Debeerius* shares characteristic morphologies and histology with petalodonts,
including the morphologies of the cups and tooth roots. Both taxa are known from cranial material and articulated body fossils [36], and toothplates have not been reported for either taxon. Therefore, the extra-mandibular teeth found in conjunction with toothplates in *Chondrenchelys*, resemble those found in isolation in taxa allied with the
Petalodontiformes.

**Previous Reports of Extra-Mandibular Teeth in Gnathostomes**

Extra oral teeth have been reported in at least four extant bony fish taxa [37, 38], however, these are not functional teeth arranged in occluding sets. Rather, these are denticle-like structures covering some portion of the external dermal skeleton, and are thought to be the result of fixed developmental abnormalities [38]. There have been previous reports in the literature of extra-mandibular tooth rows in several fossil taxa. Lund [39] described an extra-oral tooth whorl near the articulation of the mandibular and palatoquadrate cartilages in the Mississippian stethacanthid *Falcatus falcatus*. We examined specimens of *Falcatus* at the Carnegie Museum of Natural History, and in none of the specimens did we find unambiguous evidence for teeth positioned external to the mandibular arch. This includes specimen CM 37532, which was figured by Lund as possessing an extra-oral tooth whorl [39: Fig. 14]. In that specimen, there is a set of teeth at or near the jaw articulation in this specimen, but it is situated entirely on matrix, and it impossible to determine that it is outside the mouth (Fig. S9). Another potential extra-oral dentition was described for the Middle Devonian gnathostome *Ramirosuarezia boliviana* [40]. However, these teeth occlude with those in the mandible, and are therefore neither functionally, nor positionally, distinct from the mandibular arch. As such, they are not
extra-oral, despite not being situated on the palatoquadrate. In this way, the dentition of

*Ramirosuarezia* more closely resembles that placoderms (e.g., *Coccosteus*), wherein the

inferognathal and supragnathal teeth in the palatal dentition occlude with those of the

mandibular dentition [41].
SOM References


the relationships of the Chondrichthyes, and comments on gnathostome evolution. *J Morphol* 243, 219-245.


Figure S1. A simplified cladogram indicting the relationships of crown-clade cartilaginous fishes (Chondrichthyes) [1-3]. The positions of fossil holocephalan *Chondrenchelys problematica* and petalodonts indicated. Note that several potential phylogenetic positions exist for the ambiguously allied petalodonts.
Figure S2. Examples of fossil holocephalan dentitions. A. Palatal dentition of *Helodus simplex*, after [9, 42]. B. Mandible and lower dentition of *Chochliodus contortus* (BMNH P2424). C. Left LPT of *Metopacanthus granulatus* (BMNH P3099) after [23].
Figure S3. NMS 2002.68.1, oral view of the mandibular dentition. Photo A. and interpretive drawing B. **dnt.b.**, transverse dentine bands denoting generations within tooth families. **pr.tr.**, periodic trough morphology, indicating coordinated caudal expansion of the mandible with the growth of the toothplate to the posterior.
Figure S4. Detail of three extra-mandibular teeth in *Chondrenchelys*, showing the characteristic dimpled ("orange-peel") surface and the saddle-shaped morphology. Specimen NMS 1998.35.1: photo A. and interpretive drawing B. cr. crowns of the three extra-mandibular teeth. Roots indicated for two of the three teeth. The third crown is damaged and the identification of its root is speculative.
Figure S5. Photo of BGS-GSE 13328. **UPT**, upper posterior toothplates; **LPT**, lower posterior toothplates; **ATs**, anterior toothplates (highly damaged); **mes. r.**, mesial recess of the upper posterior toothplates.
Figure S6. Close-up of teeth of *Debeerius ellefseni* (specimen CM 27380). Arrow indicates a saddle-shaped tooth in *Debeerius* that bears a striking resemblance to the gross morphology of *Chondrenchelys*’ extra-mandibular teeth (see especially Figs. 4C and D, S4).
Figure S7. Map indicating location of the Mumbie Quarry locality, Glencartholm, Dumfries District, Dumfries and Galloway Region, Scotland, Ordnance Survey grid reference NY 376 795 [10]. The Mumbie Quarry locality is laterally equivalent to the classic Glencarholm fish beds locality that produced the original *Chondrenchelys* material [6, 12]: 
Figure S8. Photo of specimen HM V.7173 with posterior toothplates preserved in occlusion and a damaged set of anterior toothplates and extra-mandibular teeth.
Figure S9. Detail of *Falcatus falcatus* (specimen CM 37532). Arrows point to tooth whorls at the anterior portion of the mandibular cartilage. Oval indicates the position of a tooth whorl at the caudal extent of the mouth, near the articulation of the mandible and palatoquadrate. This whorl was identified by Lund [39] as being extra-oral in position, but there is no unambiguous evidence that this whorl is outside the mouth.