First tooth-set outside the jaws in a vertebrate

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Holocephalans (ratfish, rabbitfish and chimaeras) figure with increasing prominence in studies of gnathostome evolutionary biology. Here, we provide the first complete description of the teeth and toothplates of one of the earliest known holocephalans, Chondrenchelys problematica, including the first unambiguous evidence of a gnathostome with an extra-mandibular dentition. We further demonstrate that holocephalan toothplate ontogeny differs fundamentally from all other extant gnathostome examples, and show how the conjunction of these teeth and toothplates challenges the monophyly of an extinct chondrichthyan clade, the Petalodontiformes. Chondrenchelys provides a novel perspective on the evolution of dentitions in shark-like fishes, expands the known repertoire of gnathostome dental morphologies and offers a glimpse of radically new chondrichthyan ecomorphs, now lost from the modern biota, following the end-Devonian extinctions.

Keywords: Chondrichthyes; Holocephali; extra-mandibular teeth; Palaeozoic

1. INTRODUCTION
Living chimaeroids are the remnants of a major Palaeozoic radiation of cartilaginous fishes. As such, they represent a significant component of extant gnathostome diversity and, in terms of their morphological and genomic heritage, provide unique insights into conditions among early vertebrates [1,2]. Genome sequencing of the elephant shark (Callorhinus milii) [3] has raised interest in holocephalans as a model system in comparative evolutionary biology, evolutionary developmental biology and genomics [4–6]. Extant holocephalans are characterized by a distinctive suite of anatomical specializations [7–10]; however, we have little appreciation of the deep evolutionary history of this clade and its diagnostic features.

Most Palaeozoic holocephalans are known only from isolated teeth [9], and the few known body fossils present strikingly different ecomorphs compared with those observed today [7,11,12]. In practice, the parallel, and often independent, treatments of data drawn from the abundant record of isolated teeth, on the one hand [13], and the more rarely preserved articulated skeletal remains, on the other [14,15], present a persistent problem in the study of early vertebrate diversity. Here, we describe the dentition of the Lower Carboniferous (Viséan) holocephalan Chondrenchelys problematica (Traquair [16]; figure 1), using new and previously unrecognized specimens. We provide (i) the first description of a complete arcade of extra-mandibular teeth, (ii) a new description of holocephalan toothplate ontogeny, and (iii) the conjunction, within a single species, of characteristic holocephalan toothplates with individual, petalodont-like teeth. These novel features have important implications for the evolution of disparity in modern gnathostome dentitions, interpretations of the patterns of early fossil vertebrate diversity from records of isolated teeth and the range of ecomorphs among early chondrichynans.


2. MATERIAL AND METHODS
The new Mumbie Quarry specimens, NMS 1998.35.1 and NMS 2002.68.1, are more complete than previously described examples, and benefit from more precise preparation and consolidation. NMS 1998.35.1 is a single slab containing an unusually intact individual with the upper and lower dentitions preserved in occlusion. NMS 2002.68.1 is preserved as a part and counterpart. The specimens are split through the oral cavity, such that both the mandibular and palatal dentitions are preserved in oral view. The previously misidentified specimen, HM V.7173 (see the electronic supplementary material), is a single slab preserving the dentition primarily in a dorsal view, with the posterior toothplates preserved in occlusion and damaged anterior toothplates, displaced rostrally. New data preserved in these specimens motivated a re-evaluation of the dentitions in previously described Chondrenchelys specimens (including NHM P 4085 and RSM 1885.54.5), part of Moy-Thomas’s [11] original description, and referred specimens RMS 1891.53.33 and BGS-GSE 13328 [12]. The wealth of new information from these specimens facilitated the complete redescription of the dentition of Chondrenchelys (see the electronic supplementary material for complete description).
3. RESULTS

The new specimens demonstrate unambiguously the presence of an extra-mandibular dentition, consisting of individual teeth (figures 1b and 2; electronic supplementary material, figures S3–5), with complete mandibular and palatal cartilages preserved, an unusual quality of preservation for Palaeozoic holocephalans. The outer surfaces of these extra-mandibular teeth have a pin-cushion appearance, reflecting vertically oriented, closely spaced tubules emerging onto the outermost dentine surface [9,13,18] (figure 2; electronic supplementary material, figure S4). The crowns are labio-lingually compressed, and the tooth bases are deep and likewise labio-lingually thin (electronic supplementary material, figure S4). This combination of characters closely resembles that of taxa associated with the Petalodontiformes [9,13,18].

Each quadrant of both the mandibular and palatal dentitions consists of a large posterior toothplate and a single, smaller anterior toothplate (figure 3). Upper and lower posterior toothplates (UPT and LPT, respectively; electronic supplementary material) preserve complete developmental sequences and display distinct shifts in the orientation of tooth generation (figure 3). Transverse dentine bands in the anteriormost portion of the LPT and UPT, and the mineralized triturae within the anterior-most ridge, show that the oldest part of each toothplate was generated linguo-labially as in Helodus and chochliodonts [8,9,19] (electronic supplementary material, figure S2). In the posterior (younger) portion of each toothplate (figure 3), the dentine bands are reoriented, such that they pass transversely across the toothplate.
condition of elasmobranchs (figure 1c). Lyodont (‘loose tooth’) dentitions are characterized by individual, unrooted teeth, generated in a dental lamina that is set in a trough along the lingual margin of the jaw cartilage [22]. Later teeth sequentially replace earlier ones at each tooth generation site, or family, with replacement proceeding linguo-labially [19,22], more or less perpendicular to the tangent of the tooth row. This pattern has been proposed for Palaeozoic holocephalans, of which the scrolled toothplates of cochliodonts (electronic supplementary material, figure S2) are the most striking examples [8,19].

In modern chimaeroids, tooth replacement is described as proceeding in a caudal-to-rostral direction [26]. Individual tooth units are thought to traverse the jaw cartilage margins, with earlier generations abraded and replaced anteriorly [19,26]. Consequently, it appears that tooth replacement has been reoriented in holocephalans, from a primitively radial to a modern caudal–rostral direction [9,19] (compare figure 1a,c). The Carboniferous holocephalan Helodus simplex possesses distinct families of mostly separate teeth, successively replacing one another linguo-labially, as in extant sharks. But it also possesses tooth families that are fused into incipient toothplates (compare electronic supplementary material, figure S2a with figure 1c). As such, Helodus has been presented as a transitional form between the presumed ancestral and derived conditions [8,18].

The new data on Chondrenchelys toothplate ontogeny call this long-accepted scenario into question. The orientations of the transverse dentine bands and mineralized tritors in the posterior toothplates show that the direction of toothplate growth was reoriented during life. In Chondrenchelys, the older (anterior) portion of the posterior toothplates is generated radially with transverse bands oriented similarly to modern elasmobranch teeth, whereas the younger (caudal) portion matches modern chimaeroids, with transverse bands oriented in coronal section, thus perpendicular to an antero-posterior direction of tooth generation (figure 3a,c). As such, Helodus has been presented as a transitional form between the presumed ancestral and derived conditions [8,18].

Gross toothplate morphology in Mesozoic and Cenozoic holocephalans is essentially identical to Chondrenchelys (compare figure 1a, with electronic supplementary material, figure S2c). Within the LPT of Chondrichthyes, three reinforced tritral ridges are arranged in what appear to be tooth family whorls (figure 3a,c, electronic supplementary material, figure S3). The anteriormost ridge is oriented labio-lingually, and obliquely to the more posterior ridges, which fan out in an increasingly parasagittal array. This is similar to more recent holocephalans, such as the Mesozoic Myriacanthidae and the extant families Callorhinchidae and Rhinocnemidae [8,9]. However, these ridge patterns are unlike those observed in the classic Palaeozoic holocephalan groups, such as Chochliodontidae, Psammodontidae or Helodontidae [8,9], in which whorl orientations are strictly radial (compare electronic supplementary material, figure S2a,b with electronic supplementary material, figure S2c and figure 3a).
If elasmobranchs exemplify the primitive condition, then the lyodont model would imply net movement of individual teeth relative to the jaw cartilage [19,26]. In *Chondrenchelys*, the anteriormost portions of the posterior toothplates remain in position throughout life (figure 3). We interpret this as coordinated, episodic growth between the mandible and LPT. Intriguingly, toothplate growth via accretion resembles patterns observed in several evolutionarily remote clades (e.g. dipnoan sarcopterygians [27,28] and arthrodire placoderms [29]). Caudal accretion further emphasizes the fundamental dissimilarity between the dentitions of *Chondrenchelys* and conventional sharks [22,29].

The extra-mandibular dentition displays characters that resemble teeth normally ascribed to the Petalodontiformes [9,13,18]. Petalodonts are an enigmatic group of Palaeozoic chondrichthyans of uncertain phylogenetic affinity [13,15,18,30] (electronic supplementary material, figure S1). In particular, we note that the extra-mandibular teeth are strikingly similar to the teeth of *Debeerius* (electronic supplementary material, figure S6), both of which have been allied with or included within the Petalodontiformes [9,13,18]. The extra-mandibular dentition displays characters that resemble teeth normally ascribed to the Petalodontiformes [9,13,18]. Petalodonts are an enigmatic group of Palaeozoic chondrichthyans of uncertain phylogenetic affinity [13,15,18,30] (electronic supplementary material, figure S1). In particular, we note that the extra-mandibular teeth are strikingly similar to the teeth of *Debeerius* (electronic supplementary material, figure S6), both of which have been allied with or included within the Petalodontiformes [9,13,18]. The extra-mandibular teeth are strikingly similar to the teeth of *Debeerius* (electronic supplementary material, figure S6), both of which have been allied with or included within the Petalodontiformes [9,13,18]. The extra-mandibular teeth are strikingly similar to the teeth of *Debeerius* (electronic supplementary material, figure S6), both of which have been allied with or included within the Petalodontiformes [9,13,18]. Therefore, it is possible that the Petalodontiformes is not monophyletic, and we predict that an increasing number of species will be removed from it as additional body fossils with more or less ‘petalodont’ dentitions emerge in the Palaeozoic chondrichthyan record.

The *Chondrenchelys* raises new questions about the evolution of jawed vertebrate dentitions in the wake of the end-Devonian extinction [35]. Furthermore, it reveals experimentation with ecomorphologies that are never again observed in the Holocelphal. Dental and histological character data are important, but early vertebrate phylogeny cannot be successfully resolved using these materials alone. The importance of tooth, scale and histological data can only be fully appreciated when understood in context with more inclusive sets of character data, hence the importance of fossils such as *Chondrenchelys*.

For access to specimens we thank: the British Geological Survey of Edinburgh, J. Liston, N. Clark, C. Beard, A. Henrici, R. Paton and S. Walsh. We acknowledge S. P. Wood for discovery and primary preparation of the Mumbie Quarry specimens and academic collaboration. We thank L. C. Sallan for identification of the Hunterian Museum specimen and B. Masek for painstaking preparation of the new specimens. This project was supported by National Science Foundation grant DEB-0917922.

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