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Jaws for a spiral-tooth whorl: CT images reveal novel adaptation and phylogeny in fossil *Helicoprion*

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New CT scans of the spiral-tooth fossil, *Helicoprion*, resolve a longstanding mystery concerning the form and phylogeny of this ancient cartilaginous fish. We present the first three-dimensional images that show the tooth whorl occupying the entire mandibular arch, and which is supported along the midline of the lower jaw. Several characters of the upper jaw show that it articulated with the neurocranium in two places and that the hyomandibula was not part of the jaw suspension. These features identify *Helicoprion* as a member of the stem holocephalan group Euchondrocephali. Our reconstruction illustrates novel adaptations, such as lateral cartilage to buttress the tooth whorl, which accommodated the unusual trait of continuous addition and retention of teeth in a predatory chondrichthyan. *Helicoprion* exemplifies the climax of stem holocephalan diversification and body size in Late Palaeozoic seas, a role dominated today by sharks and rays.

1. Introduction

The iconic spiral-tooth whorl of *Helicoprion* is one of the most unusual evolutionary novelties among ancient chondrichthians. For more than a century, palaeobiologists have puzzled over its form and function in the absence of fossilized cranial or postcranial elements, leading to numerous creative but largely untested reconstructions ([1–12]; figure 1a–i). Bendix-Almgreen [5] described the only known *Helicoprion* specimen (IMNH 37899) that preserves endoskeletal elements in association with the whorl. The fossil is imbedded in a slab of phosphatic limestone from the Early Permian (270 Ma) Phosphoria Formation of Idaho, USA. With limited exposure, Bendix-Almgreen interpreted calcified layers of cartilage as the jaws and anterior portion of the neurocranium. His reconstruction placed the tooth whorl at the front midline of elongate lower jaws (figure 1j; [5,13]), and his interpretation of a neurocranial capsule and rostrum led to his assessment that *Helicoprion* belonged to the Elasmobranchii, an ill-defined group of sharks and rays. Bendix-Almgreen’s ‘symphyseal’ reconstruction ([6,14]; figure 1j–k) has not been challenged by new physical evidence in the intervening decades. Phylogenetic interpretations of *Helicoprion* and its spiral-tooth relatives have been less stable; however, most recent analyses based on dental characters have placed *Helicoprion* among the Euchondrocephali, which include modern chimaera and ratfish [15,16].

In this study, we re-examine IMNH 37899 using computer tomographic scans to describe the cranial anatomy of *Helicoprion*. Our reassessment of the anatomy partly confirms Bendix-Almgreen’s symphyseal reconstruction, but
2. Material and methods

The rock slab containing IMNH 37899 (figure 2a), also known as ‘Idaho 4’ [5], is 32.9 × 30.2 × 13.1 cm. It was collected in 1950 from the historic Waterloo Mine near Montpelier, Idaho (42.3° N, 111.2° W) and deposited at the Idaho Museum of Natural History. Bendix-Almgreen [5] diagnosed the specimen as mostly as external impressions, so a model of the whorl was generated for figure 2. This computer generated model was produced by scanning fig. 12 of [5], and sculpting a three-dimensional whorl using BLENDER v. 2.64a software. Fig. 2b of [5] was used to accurately model the thickness of teeth and root. The model whorl was then scaled to match a surface scan of IMNH 37899 (figure 2b), made using a KonicaMinolta Vivid911 non-contact laser scanner at the Idaho Virtualization Lab of IMNH.

3. Description

IMNH 37899 has a whorl measuring 23 cm in diameter and bearing 117 serrated tooth crowns (figure 2a), most preserved as impressions. The series of tooth crowns are anchored to a continuous osteodentine root and calcified cartilaginous base that forms a logarithmic spiral of 3.2 revolutions, with tooth size increasing outward from the spiral centre. Prismatic calcified cartilage layers of the mandibular arch have lower density than the rock matrix, and are shown in CT scans to be largely intact throughout the specimen.

CT scans reveal the complete left upper and lower jaws in closed articulated position around the medial tooth whorl (see figure 2c–h and electronic supplementary material, figure S1). A large wedge of cartilage extends from the lower jaw and bracess against the outermost root of the whorl. Inner parts of the whorl are surrounded by coarse prismatic tessellated cartilage. No portion of the neurocranium is preserved.

The upper jaw is composed of a triangular palatoquadrate. Its posterior border flares laterally for its entire length, and medial to this is a vertical basitрабecal fossa and basal process. The quadrato process displays dual jointed articular surfaces that correspond with respective articular surfaces of the lower jaw (Meckelian cartilage), a primitive feature of jawed vertebrates. The elongate palatine ramus tapers anteriorly, with a pronounced medial circular dome-shaped ethmoid process. Quadrate and palatine fossae are located on the lateral surface for quadratomandibular muscle attachment. There is no evidence of a groove on the medial surface of the quadrato to accommodate the hyomandibula, and the CT scans provide no evidence for dentition associated with the palatoquadrate.

The Meckelian cartilage of the lower jaw is incomplete in its anteroventral region. Its anteroventral surface flares laterally to border the quadratomandibular fossa ventrally. On the Meckelian cartilage anterior to the jaw joint, a process projects dorsally and abuts a descending process of the palatoquadrate (figure 2g). These processes may serve to restrict closure of the lower jaw, and consequently prevent the tooth whorl from puncturing the neurocranium.

The labial cartilage is a distinct element that forms a synchondrosis with the dorsal surface of the Meckelian cartilage—a unique articulation found only in Helicoprion. Widened portions of the blade-shaped labial cartilage match the dorsal position of successive roots in the whorl, suggesting a gliding articulation with the base of the root (figure 2d,g). The posterior region of the labial cartilages forms a cup-shaped structure that surrounds the developing root of the last whorl. This is the only structure that was reoriented in producing the CT model, shifting three collapsed fragments of the posterior margin approximately 1 cm in a medial-anterior direction.

Part of the tessellated cartilages that surround the inner parts of the whorl are visible in scans and do not appear to articulate directly with either the lower jaw or the labial cartilages (figure 2f). From the surface view of the imbedded fossil,
these thin cartilage layers are restricted to the ventral and central parts of the whorl. Only the outermost eight tooth crowns and a short arc of root appear in the scan (figure 2f).

4. Comparison

Bendix-Almgreen’s [5] contention that the fossil was severely crushed and disarticulated from burial largely explains why our interpretations of the fossil differ. Our most substantial anatomical revision concerns the upper jaw. The anterior part, which we interpret as the palatine region, was interpreted by Bendix-Almgreen as the neurocranial cavity and rostrum, but CT evidence demonstrates continuity of the calcified cartilage through the palatine and quadrate regions of the upper jaw. Scans also show that the anterior part of the lower jaw does not include a projection beyond the whorl, as suggested by Bendix-Almgreen, nor do we find CT evidence for a tooth pavement associated with the upper jaw. Finally, identification of labial cartilages concealed by the rock matrix is a new observation afforded by CT imaging. Although, its articulation with the Meckelian cartilage is unique to *Helicoprion*, designating them as labial cartilage is conservative because these elements are common to chondrichthyans.

**Figure 2.** *Helicoprion* specimen IMNH 37899, preserving cartilages of the mandibular arch and tooth whorl. (a) Photograph and (b) surface scan of fossil, positioned anterior to the right, imbedded in limestone slab. (c) CT model of specimen in lateral, (d) medial, (e) posterior, (f) oblique lateral, (g) oblique medial and (h) ventral views. Modelled tooth whorl (grey, black outline) surrounded by palatoquadrate (green), Meckelian (blue) and labial (red) cartilages. (d) Asterisks mark widened part of labial cartilage corresponding to successive root volutions. (f) Palatoquadrate removed to show scanned portion of root (dark yellow), tooth crowns (pale yellow) and tessellated cartilages of the inner whorl (purple). Arrow indicates direction of root growth and advancement to form spiral. (h) Right side of image mirrored to show paired jaw elements surrounding the whorl. bf, basitrabecular fossa; bp, basal process; c, cup-shaped portion of labial cartilage; ep, ethmoid process; lj, labial joint with base of root; pf, lateral palatine fossa; pp, process limiting jaw closure; qf, lateral quadrate fossa; qmf, quadratomandibular fossa; qp, quadrate process. Scale bar applies to all but oblique views (f–g).
5. Discussion

Our reconstruction posits that the tooth whorl is a singular, symphysial structure of the lower jaw that occupied the full length of the mandibular arch. This contrasts with previous symphysial reconstructions (figure 1j,k; [5,6]) which place the whorl at the anterior end of an elongate jaw, creating a space between the whorl and the jaw joint. In our model, the posterior region of the lower jaw is the site where larger tooth crowns are produced atop a continuous root that is buttressed laterally by the labial cartilage. The gliding articulation between the root and labial cartilage serves as the linkage between the left and right lower jaws (figure 2h). Continual growth of the whorl pushes the tooth—root complex in a curved direction towards the front of the jaw, where it eventually spirals to form the base of the newest root material, and this process continues to form successive revolutions (figure 2f). At some time, prior to a complete 360° rotation of spiral growth, tooth crowns are concealed within tessellated cartilage.

Retention of teeth in a continuously growing whorl necessitates specialized morphologies, including the buttressing of soft and rigid elements, maintaining rigidity and alignment of the whorl, as it occludes between the upper jaws. With the jaw articulation next to the whorl, closure of the lower jaw rotates the teeth dorso-posteriorly, providing an effective slicing mechanism for the blade-like serrated teeth and forcing food to the back of the oral cavity.

Accommodating the continuous growth of the logarithmic whorl required commensurate anterior and dorsal expansion of the mandibular arch to house the symphysial structure. Based on the largest diameter whorls in the IMNH collections, Helicoprion jaw length and height could exceed 50 cm, nearly double the size of IMNH 37899. Pre-mortem tooth wear or breakage is rare in Helicoprion [5,6]. This may be a result of rapid tooth production—some whorls exceed 150—along with prey selection of soft-bodied animals, such as cephalopods [6] or poorly armoured fish.

CT scans demonstrate that Helicoprion possessed an autodiastic jaw suspension [17] characterized by a two-point articulation of the upper jaw to the neurocranium via ethmoid and basal processes, and the absence of a dorsal extension (otic process) and hyomandibular articulation site on the upper jaw [18]. An autodiastic jaw suspension is diagnostic of euchondrocephalans [19], which confirms previous dentition-based phylogenies placing Helicoprion among the Euchondrocephali. This result provides new insight into the evolutionary history of early holocephalans, including their high degree of specialization and large body size during the Late Palaeozoic, which may correspond to the increased diversity and abundance of cephalopod prey at this time.

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