Ischnacanthiform dentitions and the origin and evolution of vertebrate teeth

by

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ABSTRACT

Living jawed vertebrates can be readily assigned to two major well-supported clades: the cartilaginous Chondrichthyes (sharks and their kin) and the ‘bony fishes’, the Osteichthyes (which include tetrapods, and to which humans belong). Together, these make up the crown group Gnathostomata. Chondrichthyes and Osteichthyes shared a most recent common ancestor no less than 423 million years ago, allowing ample time for the living members of these groups to diverge and acquire new characters and character states, and resulting in a lack of clarity regarding the ancestral conditions of Gnathostomata as a whole. The assignment of fossil taxa to the osteichthyan, chondrichthyan, and gnathostome stem groups is necessary to understand the ancestral conditions and evolutionary origins of these vertebrates, but determining the phylogenetic relationships of Paleozoic gnathostomes presents a challenge, exacerbated by a relative dearth of well-preserved fossil material from the Silurian and Early Devonian.

The Man On The Hill (MOTH) locality in the Northwest Territories of Canada has yielded beautifully preserved fossils of Early Devonian gnathostomes, providing a unique opportunity to investigate their diversity and adding new data to formulate and test hypotheses of evolutionary relationships. In particular, MOTH is one of the only fossil sites in the world to preserve articulated skeletons of an enigmatic group of fishes known as acanthodians. Recently, acanthodians have received increased attention, as they represent a likely sister group to the Chondrichthyes. In this phylogenetic context, acanthodian features may provide insight into the primitive characters of Chondrichthyes, and possibly the primitive conditions for Gnathostomata.

This thesis provides a comprehensive study of acanthodian fossils, particularly those belonging to the order of acanthodians called Ischnacanthiformes. This group is particularly poorly known, being represented primarily by isolated jaw bones. As a part of this study, four new genera comprising six new species of ischnacanthiform acanthodians are described, greatly increasing our comprehension of the diversity of the group. The presence of several closely related species coexisting in a relatively restricted geographic area has been hypothesized to indicate trophic niche partitioning; this hypothesis is indirectly tested here through the use of three-dimensional reconstructions of articulated pairs of jaws, revealing different styles of occlusion and feeding mechanics in different species of ischnacanthiforms from MOTH. The differences in jaw occlusion as well as in patterns of tooth wear support the hypothesized trophic niche differentiation among ischnacanthiform species from MOTH, and suggests that rather than being indiscriminate generalist predators, at least some of these early jawed vertebrates may have specialized in capture and processing of preferred prey items. Previously unidentified morphological and histological structures are also described from MOTH acanthodians, with comments on the potential phylogenetic implications of these discoveries. A new hypothesis is proposed for the mechanism of jaw bone growth and tooth attachment in ischnacanthiform acanthodians.

In providing some insight into the diversity, ecology, and evolutionary history of the Ischnacanthiformes, I hope to have provided a better picture not only of their phylogenetic affinities, but also of the ancient world in which these animals lived, and how they may have interacted with their environment and with each other.

PREFACE

Chapter 2 and Chapter 5 of this thesis have been published in the Journal of Vertebrate Paleontology as collaborative works. Chapter 2 of this thesis was published as Blais, S. A., C. R. Hermus, and M. V. H. Wilson. 2015. Four new Early Devonian ischnacanthid acanthodians from the Mackenzie Mountains, Northwest Territories, Canada: an early experiment in dental diversity. Journal of Vertebrate Paleontology 35: e948546 (13 pages). This study built upon the M.Sc. project of CRH, in which she identified four new species of *Ischnacanthus* from MOTH. I re-evaluated her descriptions and retained three of her specific epithets, but synonymized two of her species and erected three new genera, with new diagnoses, descriptions, and remarks. I was responsible for the examination of the material included in this manuscript, as well as for the composition of the manuscript itself and creation of all figures. MVHW contributed supervisory and funding support, as well as editing of the manuscript.

Chapter 5 of this thesis was published as Blais, S. A., L. A. MacKenzie, and M. V. H. Wilson. 2011. Tooth-like scales in Early Devonian eugnathostomes and the 'outside-in' hypothesis for the origins of teeth in vertebrates. Journal of Vertebrate Paleontology 31:1189-1199. I was responsible for the examination of the material included in this manuscript, as well as for the composition of the manuscript itself and creation of all figures. This chapter builds on part of the M. Sc. project of LAM, in which she described lip scales in *Obtusacanthus* and UALVP 32520 and suggested their connection to the origins of teeth. LAM also contributed the SEM images used in Figure 5.6. MVHW contributed supervisory and funding support, as well as editing of the manuscript.

In vertebrate paleontology, increasing knowledge leads to triumphant loss of clarity.

Alfred Sherwood Romer

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I've recently been very lucky to get to know the fantastic group of people working in the BioSci Student Services office, and I owe them a debt of thanks as well. Ches, you're a star. I have no idea how you know everything, but you do. Thank you for all the help and advice over the years. Thanks to Heidi, Brenda, Jocelyn, and Heather McDermid, and also to my fellow lab coordinators, Mark, Carla, and Christianne: thanks for the advice, guidance, help, and sometimes commiseration.

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Finally, to Patrick: thank you for being my partner. Thank you for picking up the slack when I couldn't, for shouldering the lion's share of the housework while I sat glued (chained?) to my computer, and for believing in me. Thank you for knowing what an acanthodian is.

And to you, the reader: thank you!

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CHAPTER 1

INTRODUCTION

Gnathostomes, or jawed vertebrates, comprise two major monophyletic taxa with extant members: the cartilaginous Chondrichthyes, and the Osteichthyes, the 'bony fishes', which include tetrapods (and to which clade we belong). These two clades are sister groups, meaning they are each other's closest relatives, and shared a last common ancestor represented on the vertebrate phylogenetic tree by the gnathostome crown node (Fig. 1.1). The divergence between these two groups is the deepest split in the evolutionary history of living gnathostomes: Chondrichthyes and Osteichthyes shared a common ancestor no more recently than 423 million years ago (Zhu et al., 2009). With such a great temporal distance separating the two groups, any extant members of these clades should be considered highly derived fishes with many specialized adaptations. Because of this long divergence time and the probability that living chondrichthyans and osteichthyans have become significantly modified from their ancestral forms, it is necessary to study Paleozoic fossil taxa to understand the origins of the jawed vertebrates and their ancestral features. As well as fossil members of the Chondrichthyes and Osteichthyes, these Paleozoic taxa include members of two extinct assemblages: the heavily armoured placoderms and the generally small, spiny acanthodians.

This thesis is focused on acanthodians in particular. These are represented by the oldest unambiguous fossil remains for any gnathostome, from the Wenlock or Ludlow of the Man On The Hill locality. Acanthodians are mostly small fishes with fusiform bodies, scales composed of concentrically-organized layers of tissue, large eyes, terminal mouths, perichondrally ossified scapulocoracoids, and fin spines on the leading edges of all their fins with the exception of the caudal fin, and including the anal fin (Fig. 1.2). Acanthodians have been traditionally organized into three orders: the Climatiiformes, Ischnacanthiformes, and Acanthodiformes. Of these three, the Climatiiformes are almost certainly paraphyletic (Burrow and Turner, 2010), but the Acanthodiformes and Ischnacanthiformes have been recovered as reciprocal monophyletic sister groups in most recent phylogenetic hypotheses (e.g., Zhu et al., 2013).

Although the acanthodians and placoderms had long been considered to be monophyletic groups (Janvier, 1996), their status as clades has been recently called into question (Brazeau, 2009). Up until the last decade, the Placodermi were widely considered to be the monophyletic sister group to the crown group Gnathostomata, and the Acanthodii were considered to be the monophyletic sister group to the Osteichthyes. Recently, a resurgence in early vertebrate studies, a plethora of new fossil discoveries, and the increased application of phylogenetic analyses has resulted in the rejection of the monophyly of the Placodermi and Acanthodii (although this is not universal; see Young, 2010 and Dupret et al., 2014), and a veritable forest of phylogenetic hypotheses has sprouted regarding their affinities to the crown gnathostome groups (e.g., Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Dupret et al., 2014; Giles et al., 2015; Long et al., 2015).

A consensus regarding the phylogenetic position (and the monophyly versus paraphyly) of placoderms and acanthodians has not been reached at the time of writing of this thesis. Placoderms have been repeatedly recovered in recent analyses as a paraphyletic assemblage of stem-gnathostomes, forming a series of successive sister groups to the crown-group Gnathostomata (Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015; Long et al., 2015). Acanthodians have, in the most recent analyses, been recovered as a paraphyletic assemblage of stem chondrichthyans (Zhu et al., 2013; Giles et al., 2015; Long et al., 2015). However, the discovery of unique claspers in placoderms is a potential synapomorphy of a monophyletic Placodermi (Long et al., 2015) and the position of the acanthodians is poorly resolved in all of these hypotheses.

The recent proliferation of early vertebrate phylogenetic analyses is welcome in that these hypotheses provide a starting point and context from which to ask evolutionary questions, but these hypotheses are certainly not universally accepted. Nor should they be treated as definitive, particularly with respect to acanthodian interrelationships and evolutionary affinities. All of the phylogenetic analyses since that of Brazeau (2009) have been performed on incrementally updated iterations of this original data set, meaning none of these analyses represent a completely independent test of a phylogenetic hypothesis. In addition, these analyses resulted in thousands to hundreds of thousands of most parsimonious trees, with low support values for the acanthodian nodes in particular. For example, the most recent analysis (Giles et al., 2015) recovers acanthodians as a series of polytomies on the chondrichthyan stem, with over five hundred thousand most parsimonious trees of over six hundred steps, and Bremer decay indices of 1 or 2 and percentage bootstrap support of 61 or less (not shown) for the acanthodian nodes.

A major contributing factor to the enigma that is acanthodian relationships in particular is the relative dearth of characters that can be used to compare acanthodian groups with other gnathostomes. Many of the characters used in these phylogenetic analyses are found in the braincase, and the braincase is only very well known in *Acanthodes bronni*, one of the youngest and most derived acanthodiform acanthodians (Davis et al., 2012). A partial braincase was recently described for the ‘climatiiform’ acanthodian *Ptomacanthus anglicus* (Brazeau, 2009), but braincases have not been recovered for any other acanthodian taxa. The recent phylogenetic analyses rely heavily on braincase characters that cannot be scored for the vast majority of acanthodian groups, rendering most acanthodian fossils effectively mute and unable to contribute to the discussion of their own affinities. This is a problem, considering that acanthodian taxa most likely represent the sister group (or successive sister groups) to one or both groups of crown gnathostomes, and also represent the oldest unambiguous appearance of these groups in the fossil record. It is becoming increasingly clear that in order to understand the ancestral state of chondrichthyans, and possibly the ancestral state of crown-group gnathostomes, increased understanding of acanthodians is crucial, particularly in those groups not represented by a fossilized braincase.

One such group of acanthodians, the Ischnacanthiformes, is primarily represented by isolated tooth-bearing dermal jaw bones, and only rarely by articulated specimens (Burrow, 2004; Burrow and Rudkin, 2014). It is probably due to this relative lack of data that Ischnacanthiformes are usually represented in phylogenetic analyses by only one or two taxa. Taking this dearth of available information into account and with the understanding that their phylogenetic position is tentative, Ischnacanthiformes are recovered in the most recent phylogenetic hypothesis (Giles et al., 2015) as part of a large polytomy that forms the sister group to the rest of total-group Chondrichthyes. It is due to this position as a potential sister group to the Chondrichthyes, as well as their status as one of the oldest gnathostome groups, that Ischnacanthiformes are the particular focus of this thesis. Ischnacanthiform acanthodians may have retained ancestral features that were lost or obscured by evolutionary innovations in taxa branching from more crownward nodes within total-group Chondrichthyes (or, if they are recovered as sister group to the crown-group Gnathostomata, innovations in crown gnathostomes). An in-depth study of ischnacanthiform material may provide characters that can hopefully be used in future phylogenetic analyses to compare this group with other gnathostome taxa, as well as help to answer unresolved questions about the animals themselves.

Ischnacanthiformes and the MOTH locality

Silurian and Early Devonian fossils of acanthodians are most commonly disarticulated and isolated scales and fin spines. Ischnacanthiform acanthodians are also represented by dermal tooth-bearing jaw bones that rested on the occlusal surfaces of the Palatoquadrate and Meckel's cartilages of the jaw. These dentigerous jaw bones bear one or more rows of teeth, which are fused to the bone of the jaw and are neither replaced nor shed, but retained throughout the life of the animal. These jaw bones have been traditionally considered to be unique structures that are not homologous to the jaw bones in other gnathostome groups, based on two lines of evidence: the interpretation by Ørvig (1973), in the most recent in-depth study of the jaw bones, that their mode of growth was entirely unlike that of any other gnathostome, and the then-resolved phylogenetic position of Ischnacanthiformes, nested within the clade Acanthodii. At the time, 'climatiiforms' were considered to be the sister group to the other acanthodians, meaning it was most parsimonious to interpret the jaw bones in Ischnacanthiformes as having been independently evolved and unrelated to the jaw bones in other gnathostome groups, such as the Osteichthyes (Denison, 1979; Janvier, 1996).

Articulated specimens of ischnacanthiform acanthodians are extremely rare (Burrow, 2004; Burrow and Rudkin, 2014), and ischnacanthiform species are in many cases distinguished from each other based entirely on the comparative morphology of their jaw bones and teeth (e.g., Long, 1986; Lindley, 2001; Voichyshyn and Szaniawski, 2012). An exceptional fossil locality in the Northwest Territories (Fig. 1.3), known as Man On The Hill after a distinctive rock formation, has provided a unique opportunity to study well-preserved, articulated specimens of acanthodians, including ischnacanthiforms, as well as other early vertebrates. Specimens from this locality were first described by Dineley and Loeffler (1976) and Bernacsek and Dineley (1977), including several acanthodian taxa based primarily on poorly preserved specimens. Since that time, extensive collecting efforts by B. D. E. Chatterton, Mark V. H. Wilson, and their field parties, including G. F. Hanke, L. A. Lindoe, T. Märss, and H.-P. Schultze in 1983, 1990, 1996, 1998, and 2013 (in which the author is extremely grateful to have been included) have yielded many more specimens of exquisite quality.

Currently, more than 75 vertebrate species are known from the MOTH locality (Wilson et al., 2000, 2011), many of which have yet to be formally described. The fossil assemblage includes heterostracans, thelodonts, osteostracans, placoderms, chondrichthyans, and acanthodians, as well as enigmatic taxa that are not readily assignable to a specific group. Interestingly, the only gnathostome taxon not represented by fossils from MOTH is the Osteichthyes. Many of these early vertebrate taxa are represented by articulated specimens, some of which are complete or nearly complete (Wilson et al., 2000, 2011). The number and quality of ischnacanthiform fossils from this locality offer unique insight into a diverse assemblage of these early vertebrates, some of which have features that have been previously undescribed for the group. Many ischnacanthiform acanthodians from MOTH are also represented by articulated upper and lower dentigerous jaw bones and their associated cartilages, allowing the rare opportunity to directly study the occlusion and mechanics of their jaws and revealing a glimpse of the ecology of these enigmatic fishes.

Locality and Age

All of the specimens discussed in this thesis were collected at the Man On The Hill (MOTH) locality, in the Mackenzie Mountains, Northwest Territories, Canada (Fig. 1.3). The MOTH locality is formally designated as the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) locality 129, considered to be equivalent to Geological Society of Canada (GSC) locality 69014, in section 43 of Gabrielse et al. (1973), in the Mackenzie Mountains, Northwest Territories, Canada. The locality is approximately 70 km north-northeast of Tungsten, on the southwest limb of the Grizzly Bear Anticline. There are two main fossiliferous layers from the MOTH locality: the main MOTH fish layer (which is usually what is meant by reference to the MOTH locality), and an older fossiliferous layer that occurs approximately 200 metres below the MOTH fish layer, known as B-MOTH.

The fossils from the MOTH fish layer are preserved in finely interlaminated argillaceous limestone and calcareous shale, within rocks that are considered to be intermediate between basinal Road River Formation rocks and more proximal rocks of the upper part of the Delorme Group and Camsell Formation (Adrain and Wilson, 1994). Adrain and Wilson (1994) used the presence of *Waengsjoeaspis*, a Lochkovian osteostracan, *Canadapteraspis*, a pteraspidid heterostracan, and the placoderm *Romundina* to infer a Lochkovian age for the MOTH fish layer. Hanke (2001) confirmed a middle Lochkovian age based on the presence at MOTH of the putative chondrichthyans *Altholepis composita*, *Polymerolepis whitei*, and *Seretolepis elegans*, taxa that were erected for isolated scales found elsewhere. Zorn et al. (2005) most recently analysed the lithology of the site and interpreted the depositional environment of the MOTH fish layer to be a hypoxic intra-shelf topographic low below storm wave base, on the outer margin of a carbonate platform.

The B-MOTH fish layer is approximately 200 m below the MOTH fish layer, in the same section. The B-MOTH layer is also rich in vertebrate remains, particularly heterostracan scales and shields (Soehn et al., 2000), as well as three acanthodian jaws collected by T. Märss and G. F. Hanke in 1996 and 1998 (Hanke et al., 2001). In 2013, M. V. H. Wilson and T. D. Cook led the most recent field party to the MOTH locality, with A. L. Lindoe, B. R. Scott, L. A. MacKenzie, and myself. Among our findings were two acanthodian jaws from the B-MOTH fish layer described in Chapter 3 of this thesis. The B-MOTH rocks are composed of dark grey limestone with clay inclusions, interpreted by Hanke et al. (2001) as rip-up clasts. Disarticulated fragments of bryozoans, brachiopods, crinoid ossicles, and broken, disarticulated heterostracan shields are commonly recovered from this locality. Similarly to the main MOTH fish layer, the presence of iron minerals, including pyrite, suggests the sediments were hypoxic or anoxic. No articulated vertebrate fossils have been recovered from the B-MOTH layer. Hanke et al. (2001) constrained the age of the B-MOTH fish layer to the late Wenklockian (Homerian) or early Ludlovian (Gorstian), based on the presence of the graptolites *Monograptus* sp. cf. *M. priodon* and *Monoclimacis* sp. cf. *M. vomerina* below B-MOTH, and isolated scales of the thelodont *Thelodus laevis* and *Paralogania martinssoni* in the B-MOTH fish layer.

Thesis goals and rationale

The purpose of this study is to provide a comprehensive examination of the ischnacanthiform fossils recovered from the fossil fish layers of the Man On The Hill locality. In doing so, it contributes significantly to our understanding of Silurian and Early Devonian gnathostome diversity, ecology, and evolutionary history and relationships. As Ischnacanthiformes likely represent a sister group to the crown Chondrichthyes, crown Osteichthyes, or crown Gnathostomata, knowledge gained about Ischnacanthiformes will elucidate the origins and early evolution of these groups. This study comprises several research questions, which are organized into three parts:

Questions relating to ischnacanthiform diversity: Do the ischnacanthiform fossils from MOTH represent more than one taxon? Do any of the ischnacanthiform fossils from MOTH represent previously undescribed species? Do these fossils provide any insight into the evolutionary trends within the group that might assist in polarizing characters within Ischnacanthiformes?

Questions regarding ischnacanthiform ecology: If the various jaw and tooth forms that seem to be present among ischnanthiform acanthodian specimens from MOTH correspond to different species, is there any evidence to support the hypothesis that these species coexisted by trophic niche partitioning, i.e., the exploitation of different food sources?

Questions about the homology of features in ischnacanthiforms, in particular regarding the evolutionary origin of vertebrate teeth: Are there any characteristics of the jaws and teeth that could be comparable with possibly homologous features in other gnathostome groups, or indicate potential homologies? As representatives of one of the oldest fossil groups with teeth, can ischnacanthiform fossils provide any insight into the hypothetical origins of gnathostome teeth? With the phylogenetic position of the Ischnacanthiformes no longer providing a parsimony-based argument for non-homology of ischnacanthiform jaw bones, is there morphological or histological evidence from MOTH specimens to support Ørvig's (1973) hypothesis for a unique mode of jaw bone growth and tooth attachment in ischnacanthiforms? Is it possible that the jaw bones in ischnacanthiforms are homologous with jaw bones in other gnathostome groups, and is the mode of tooth attachment comparable?

By attempting to address these questions, this study contributes to the existing body of knowledge in the field by: identifying, naming, and describing new species, increasing our estimate of the taxonomic diversity of the time; providing a novel methodology to test for trophic niche differentiation in fossil taxa with a statodont dentition where direct fossil evidence is unavailable, and providing insight into specialized feeding mechanisms in early vertebrates; describing new features in Early Devonian gnathostomes that elucidate the connection between scales and teeth; and providing a new evidence-based hypothesis for jaw bone growth and tooth attachment in Ischnacanthiformes, with comments on the possible homologies of these structures among gnathostome taxa. It is my hope that this information may be useful in future phylogenetic studies, and especially that it may help to clarify the phylogenetic position of the Ischnacanthiformes. These animals lived during a time that is near the first appearance of teeth in the fossil record, and it is likely that they retained at least some characteristics of teeth in their ‘original’ form within vertebrates. Studying these ancient specimens can provide valuable information on the morphology, function, and homology of the earliest and most primitive forms of teeth.

FIGURES

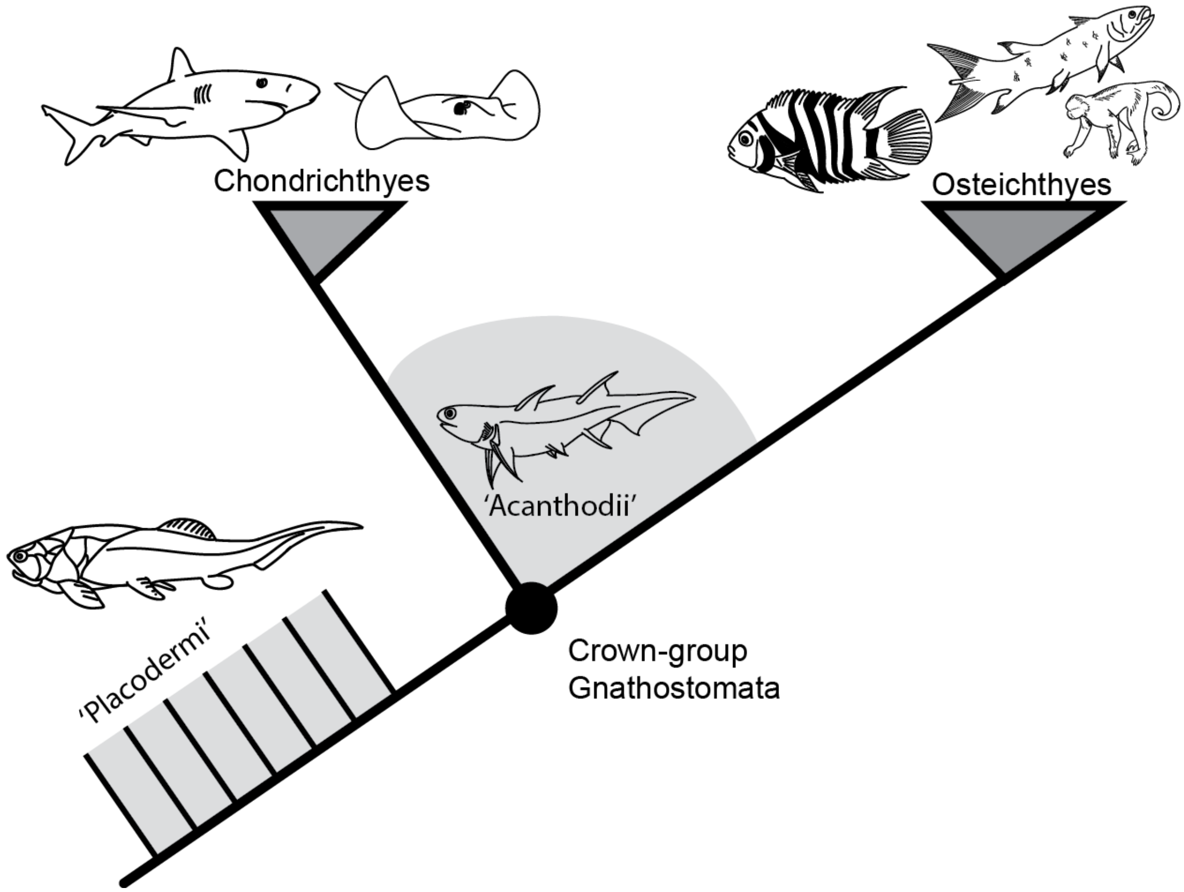

FIGURE 1.1. General phylogenetic relationships of crown-group gnathostomes and placoderms. Chondrichthyes and Osteichthyes are represented by extant members. Grey shading indicates the uncertain interpretation of the phylogenetic positions of placoderms and acanthodians.

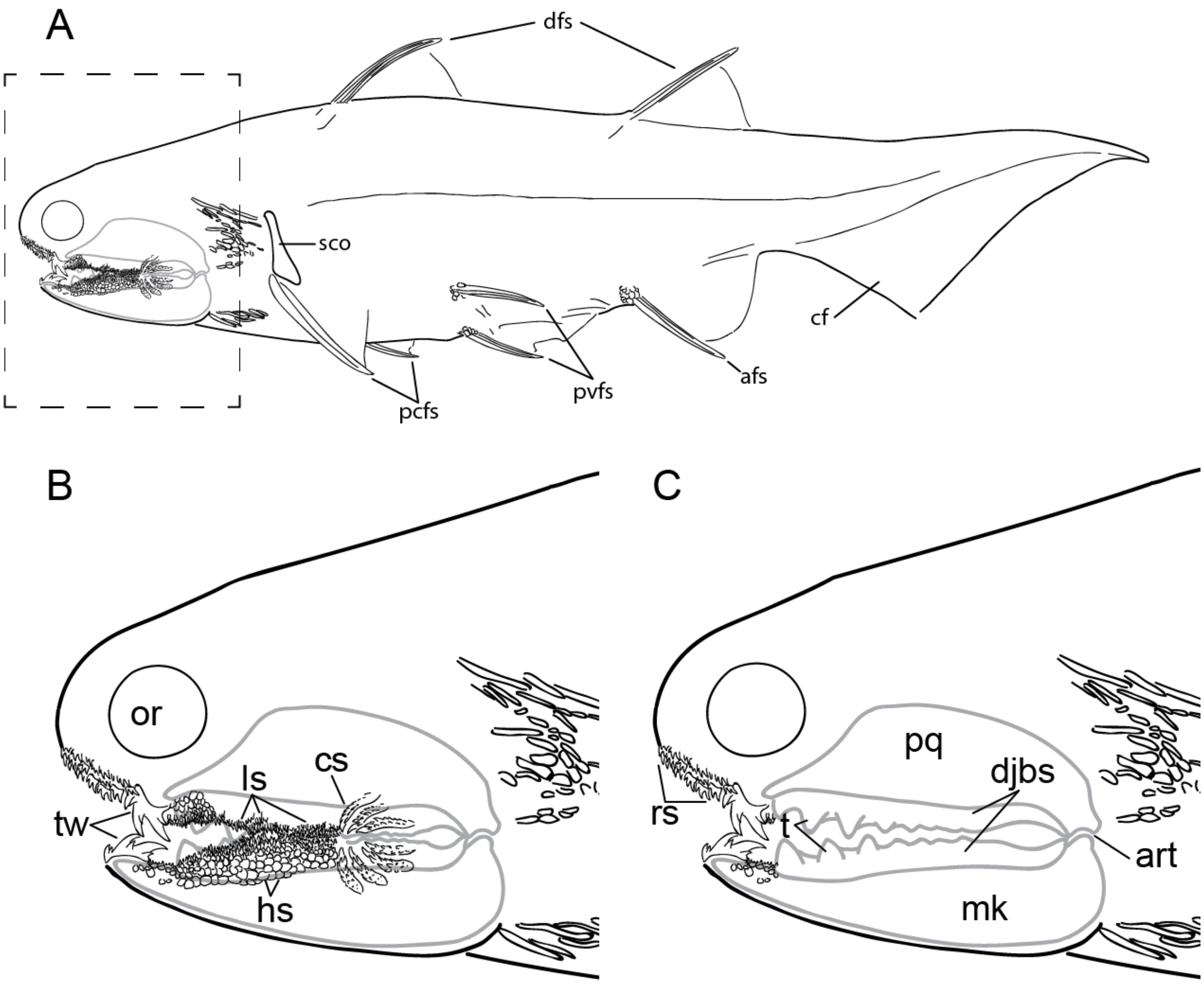

FIGURE 1.2. Illustration of general ischnacanthiform acanthodian anatomy. **A**, complete fish; **B**, detail of the head (dashed box in A) including scale cover; **C**, detail of the head (dashed box in A) with scale cover excluded. **Abbreviations**: **afs**, anal fin spine; **art**, articulation of the jaw cartilages; **cf**, caudal fin; **cs**, cheek scale; **djbs**, dentigerous jaw bones; **dfs**, dorsal fin spine; **hs**, head scales; **ls**, lip scales; **mk**, Meckel's cartilage; **or**, orbit; **pcfs**, pectoral fin spine; **pq**, palatoquadrate cartilage; **pvfs**, pelvic fin spine; **rs**, rostral scales; **sco**, scapulocoracoid; **t**, tooth; **tw**, tooth whorl.

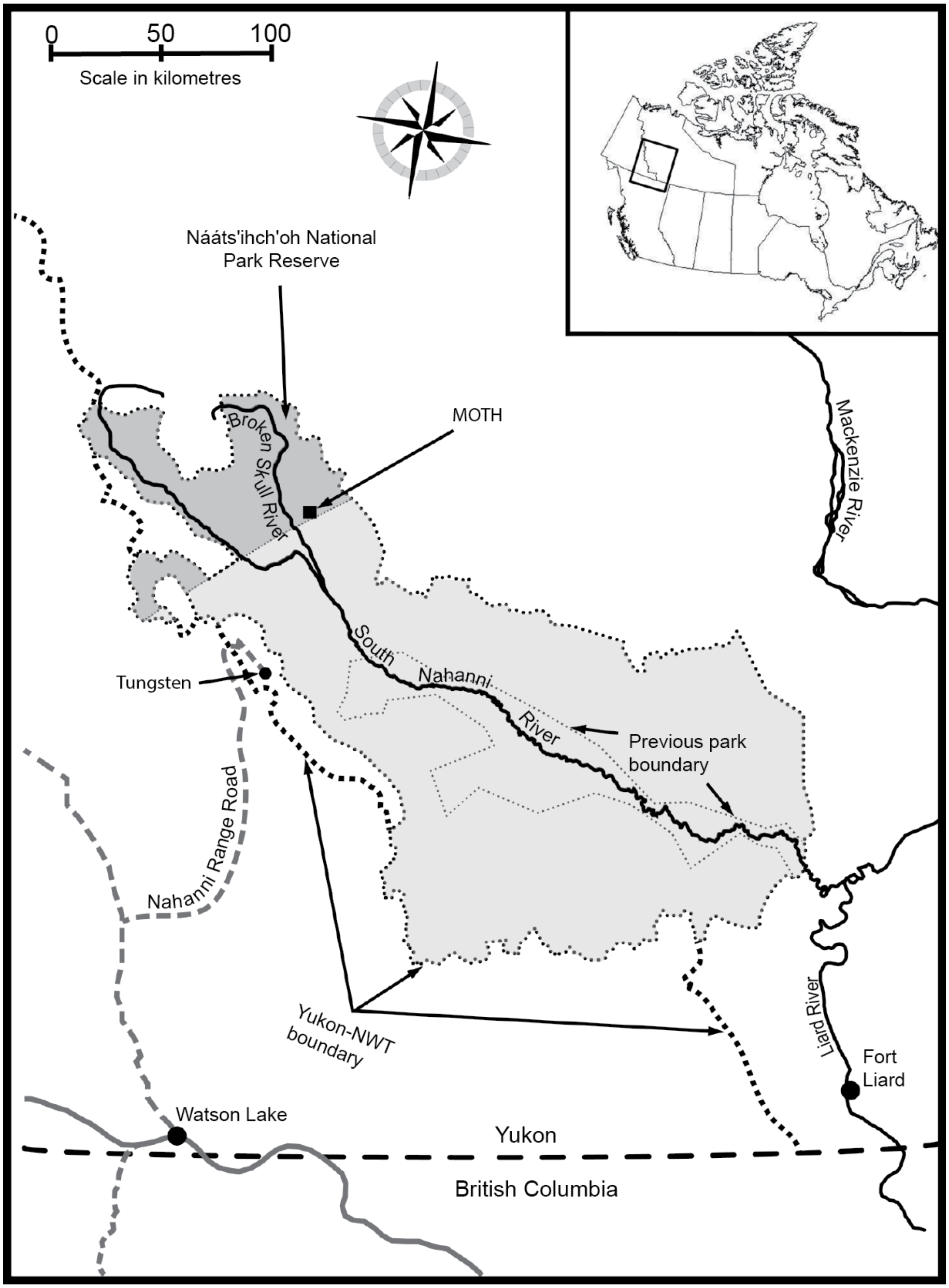

Figure 1.3. Map showing the location of the MOTH locality, Northwest Territories, Canada. Light grey shading indicates Nahanni National Park Reserve. Dark grey shading indicates Nááts'ihch'oh National Park Reserve.

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CHAPTER 2

FOUR NEW EARLY DEVONIAN ISCHNACANTHID ACANTHODIANS FROM THE MACKENZIE MOUNTAINS, NORTHWEST TERRITORIES, CANADA: AN EARLY EXPERIMENT IN DENTAL DIVERSITY.

A nearly identical version of this chapter was published as: Blais, S. A., C. R. Hermus, and M. V. H. Wilson. 2015. Four new Early Devonian ischnacanthid acanthodians from the Mackenzie Mountains, Northwest Territories, Canada: an early experiment in dental diversity. Journal of Vertebrate Paleontology 35: e948546 (13 pages). This study built upon the M.Sc. project of CRH, in which she identified four new species of *Ischnacanthus* from MOTH. I re-evaluated her descriptions and retained three of her specific epithets, but synonymized two of her species and erected three new genera, with new diagnoses, descriptions, and remarks. I was responsible for the examination of the material included in this manuscript, as well as for the composition of the manuscript itself and creation of all figures. MVHW contributed supervisory and funding support, as well as editing of the manuscript.

ABSTRACT

The Early Devonian (Lochkovian) Man On The Hill (MOTH) locality in the Northwest Territories has yielded hundreds of exquisitely preserved specimens of over 72 different species of early vertebrates, greatly increasing our understanding of the diversity of this period. In this chapter, I describe three new genera comprising four new species of ischnacanthid acanthodians, based on their dentigerous jaw bones and teeth. This taxonomic diversity reflects some of the diversity of dentition found among ischnacanthiform acanthodians at the MOTH locality, in contrast to their highly conservative body forms. This high diversity of related forms suggests an early radiation in jaw and tooth morphology in Early Devonian ischnacanthiform acanthodians in this region. All ischnacanthiform specimens from MOTH were originally assigned to *Ischnacanthus gracilis*. However, study of the unique jaw and tooth morphology of MOTH ischnacanthiform specimens indicates it is unlikely that *Ischnacanthus* was present at the MOTH locality.

INTRODUCTION

Acanthodians are an enigmatic group of fossil fishes whose systematic relationships remain obscure after decades of research. Recently, Brazeau (2009) suggested that both major clades of extinct jawed vertebrates, Placodermi and Acanthodii, are paraphyletic groups. This has been contested for both groups (Burrow and Turner, 2010; Young, 2010; Burrow, 2011). Brazeau's (2009) analysis confirmed an idea that had been suggested for decades, that the traditional taxon 'Climatiiformes' is almost certainly not a valid clade (Janvier, 1996; Hanke and Wilson, 2004). In both Brazeau's (2009) and Burrow and Turner's (2010) analysis, 'Climatiiformes' as a clade had no support, but there was strong support for both Ischnacanthiformes and Acanthodiformes as valid clades. In Brazeau's (2009) analysis, Ischnacanthiformes and Acanthodiformes resolved as monophyletic sister taxa, together forming the sister taxon to Osteichthyes, the traditional phylogenetic position of the Acanthodii. Burrow and Turner (2010) supported monophyly of the taxon composed of Ischnacanthiformes, Diplacanthiformes, Acanthodiformes, and *Paucicanthus*, and paraphyly of the 'climatiiforms'. Davis et al. (2012) also resolved Ischnacanthiformes and Acanthodiformes as monophyletic groups, but with Ischnacanthiformes forming the sister group to Osteichthyes, and Acanthodiformes as the sister group to Ischnacanthiformes + Osteichthyes. Zhu et al. (2013) resolved all acanthodians as stem-chondrichthyans, with Chondrichthyes (including acanthodians) as the sister group to Osteichthyes. In this analysis, Ischnacanthiformes and Acanthodiformes form monophyletic groups within a large polytomy on the chondrichthyan stem. Most recently, Brazeau and Friedman (2014) supported the hypotheses postulated by Brazeau (2009) and Zhu et al. (2013) equally. In all cases, Ischnacanthiformes and Acanthodiformes were resolved as monophyletic, closely related taxa, but their relationship to each other, to the 'climatiiform' acanthodians, and to the clades of extant gnathostomes remains ambiguous.

Despite the uncertainty surrounding their phylogenetic position, acanthodian fossils are a valuable source of information about the early evolution of jawed (and toothed) vertebrates. Known putatively from microremains from the Ordovician (Sansom et al., 2001), and definitively from isolated dentigerous jaw bones, scales, and tooth whorls from the Early Silurian (Hanke et al., 2001a; Burrow, 2003a; Karatajute-Talimaa and Smith, 2003) and articulated specimens from the Upper Silurian to the Permian (Denison, 1979; Janvier, 1996; Hanke and Wilson, 2004; Burrow, 2011), they are among the oldest vertebrates with teeth. Acanthodians possessed several different forms of dentition, including tooth-like scales, tooth whorls, crushing plates, isolated teeth, and, in the case of the ischnacanthiform acanthodians, dermal dentigerous jaw bones. The morphology of the teeth fused to these jaw bones is often the only method used to distinguish different species of ischnacanthid acanthodian, as they were characterized by a conservative body plan and diverse dentition. Many of the ischnacanthiform species currently known have been described based on isolated jaw bones, rarely with attached jaw cartilages, and even more rarely as articulated specimens (Burrow, 2004a, 2011).

Vertebrate fossil specimens from the Early Devonian (Lochkovian) locality in the Northwest Territories known as MOTH, or Man On The Hill (Fig. 2.1), offer a unique opportunity to study well-preserved, articulated specimens of acanthodians and other early vertebrates. Specimens from this locality were first described by Dineley and Loeffler (1976) and Bernacsek and Dineley (1977), including several acanthodian taxa based primarily on poorly preserved specimens. Since that time, extensive collecting efforts by B. D. E. Chatterton, Mark V. H. Wilson, and their field parties, including G. F. Hanke, L. A. Lindoe, T. Märss, and H.-P. Schultze in 1983, 1990, 1996, 1998, and 2013 have yielded many more specimens of exquisite quality.

Currently, more than 72 vertebrate species are known from the MOTH locality, approximately half of which have yet to be formally described; the fossil assemblage includes heterostracans, thelodonts, osteostracans, placoderms, chondrichthyans, and acanthodians, as well as enigmatic taxa that are not readily assignable to a specific group. Many of these taxa are represented by articulated specimens, some of which are complete or nearly complete (Wilson et al., 2000, 2011) (Fig. 2.2). Many ischnacanthiform acanthodians from MOTH are represented not only by isolated dentigerous jaw bones as is usual, but by articulated upper and lower dentigerous jaw bones and their associated cartilages, offering rare insight into the occlusion and mechanics of their jaws. Improvement in specimen preparation since the 1980s as well as the discovery of better-preserved fossils has allowed for the redescription of several acanthodian fishes as well as the description of new taxa (Gagnier and Wilson, 1995, 1996a, 1996b; Gagnier et al., 1999; Hanke et al., 2001a, 2001b; Hanke, 2002, 2008; Hanke and Wilson, 2010, 2004, 2006; Hanke and Davis, 2008, 2012; Scott and Wilson, 2012).

Among the acanthodians described by Bernacsek and Dineley (1977) were several specimens of ischnacanthiform acanthodians referred to *Ischnacanthus gracilis* (Egerton, 1861) based on similarities of the body scales, fin spines, and shoulder girdle, although they suggested there were a few differences between MOTH ischnacanthids and *I. gracilis*. The MOTH specimens are smaller than those from the Old Red Sandstone (ORS), with an estimated total body length of the largest MOTH specimen of 131.5 mm, compared with a body length of 250 mm for large Scottish specimens. They also recorded the presence of an “atypical” dentigerous jaw bone (Bernacsek and Dineley, 1977, text-fig. 11, p. 13) and suggested that Canadian assemblages of *Ischnacanthus gracilis* possessed greater variation in their dentition than Scottish material had indicated.

New, more numerous, and better-preserved specimens have since revealed an assortment of jaw bone and tooth forms in the ischnacanthiform acanthodians from

MOTH, none of which corresponds to those of *Ischnacanthus gracilis*. It is thus unlikely that *I. gracilis* was present in the Early Devonian locality represented by the MOTH assemblage, which is even more diverse than previously thought. In addition, these new specimens indicate that some MOTH ischnacanthiforms possessed scales lining the inside of the oral cavity that are more denticle-like proximal to the main tooth rows. Internal scales with this morphology have not been previously described in ischnacanthiform acanthodians. They may be unique to ischnacanthiforms from MOTH, although it seems more likely that they have simply not been preserved in ischnacanthiforms from other localities. Here, I describe three new genera and four new species of ischnacanthiform acanthodians based on this variety in jaw bone and tooth morphology.

LOCALITY AND AGE

All specimens described in this paper are from the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) locality 129, thought to be equivalent to Geological Society of Canada (GSC) locality 69014, in section 43 of Gabrielse et al. (1973), in the central Mackenzie Mountains in the Northwest Territories of Canada (Fig. 2.1). The locality is approximately 70 km north northeast of Tungsten, on the southwest limb of the Grizzly Bear Anticline. The fossils are found in finely interlaminated argillaceous limestone and calcareous shale, within rocks that are considered to be intermediate between basinal Road River Formation rocks and more proximal rocks of the upper part of the Delorme Group and Camsell Formation (Adrain and Wilson, 1994). Adrain and Wilson (1994) used the presence of *Waengsjoeaspis*, a Lochkovian osteostracan, *Canadapteraspis*, a pteraspidid heterostracan, and the placoderm

Romundina to infer a Lochkovian age for the MOTH succession. Hanke (2001) confirmed a middle Lochkovian age based on the presence of the putative chondrichthyans *Altholepis composita*, *Polymerolepis whitei*, and *Seretolepis elegans*, taxa that were erected for isolated scales found elsewhere. Zorn et al. (2005) most recently analysed the lithology of the site and interpreted the depositional environment of the MOTH fish layer to be a hypoxic intra-shelf topographic low below storm wave base, on the outer margin of a carbonate platform.

METHODS

Fish fossils recovered from the MOTH locality are preserved in argillaceous limestone. The overlying calcareous matrix was removed using dilute acetic acid solution. Finer-scale removal of matrix was accomplished using soft brushes, rinsing with water to remove excess matrix; any remaining acid and acetate buffer were also rinsed away. A 5% solution of Glyptal™ cement in acetone was used to stabilize the specimens. The specimens were whitened using ammonium chloride sublimate and photographed using a Zeiss Discovery V8 stereomicroscope and Nikon NIS-Elements F 2.20 imaging software. Specimens described in this study are housed in the UALVP collections. The specimens originally described by Bernacsek and Dineley (1977) are housed at the Canadian Museum of Nature (NMC) in Ottawa.

All specimens described in this paper are distinguishable from each other only by differences in the jaw bones and teeth. All descriptions are thus focused on the jaws and teeth only, particularly on the lingual surfaces of the jaws, where most of the diagnostic features are located. Descriptions of the body specimens of ischnacanthids from MOTH were provided by Hanke (2001) and Hermus (2003). The relationships between the full-body specimens and the species described based on jaw characteristics are currently under study. The extraordinary preservation of MOTH specimens is such that in well-preserved specimens of complete or nearly complete fish, the details of the jaws and teeth are obscured by scale cover (Fig. 2.2). Some of this scale cover, particularly the lip and cheek scales (Blais et al., 2011) may be species-specific; this is also under study.

SYSTEMATIC PALEONTOLOGY

GNATHOSTOMATA Gegenbaur, 1874

ISCHNACANTHIFORMES Berg, 1940

ISCHNACANTHIDAE Woodward, 1891

Remarks— All of the new genera described in this paper are provisionally assigned to Ischnacanthidae based on the circular parabasal sections of their lateral teeth, pending SEM studies of the scales once more complete specimens can be readily assigned to species based on jaw morphology.

EURYACANTHUS RUGOSUS, gen. et sp. nov.

(Fig. 2.3)

Diagnosis—Ischnacanthid acanthodian with small- to medium-sized dentigerous jaw bones approximately half the depth of the height of the largest tooth, dentigerous jaw bones deeper posteriorly, becoming wider and flatter anteriorly, bearing one lateral row of 9–10 large, broad, conical, caniniform teeth which are circular or subcircular in parabasal section, with conspicuous vertical striations on the lingual surfaces; lateral teeth with a small anterolabial flange and a well-developed, denticulated posterolabial flange; dentigerous jaw bones with a shallow furrow medial to the main tooth row separating it from a lingual ridge which bears a patch of small, tricuspid denticles.

Etymology— Greek, *eurys*, broad, *akanthias*, prickly, in reference to the broad lateral teeth and the presence of many fin spines on all ischnacanthiform acanthodian specimens from MOTH in which the body is preserved; Latin, *rugosus*, wrinkled, referring to vertical striations on the lingual surfaces of the main teeth, imparting a wrinkly appearance.

Holotype—UALVP 45648, articulated large right upper and lower jaw bones and partial associated cartilages in lingual view.

Referred Material—UALVP 41650, anterior half of a lower right jaw bone and Meckel’s cartilage in lingual view; UALVP 42023, right upper dentigerous jaw bone and palatoquadrate cartilage in lingual view; UALVP 42025, left upper dentigerous jaw bone and palatoquadrate cartilage in lingual view; UALVP 45040, right upper dentigerous jaw bone and palatoquadrate cartilage in lingual view; and UALVP 45076, partial lower left jaw bone and Meckel’s cartilage in lingual view.

Locality and Age—All specimens known to date come from the Early Devonian (Lochkovian) MOTH fish layer, UALVP Locality 129, GSC locality 69014, or Unit 10 of Section 43 of Gabrielse et al. (1973). The fish-bearing strata, from 430 to 435 m in the

MOTH section as measured in 1996 (Hanke, 2001) are composed of dark grey argillaceous limestone.

Description—The six known specimens of *Euryacanthus rugosus* are large in comparison with specimens of other ischnacanthid species from MOTH, ranging in jaw bone length from 15.7–25.9 mm. Compared to larger ischnacanthiform species with jaw bones up to or in excess of 10 cm in length, such as *Xylacanthus grandis* Ørvig, 1967, *Xylacanthus kenstewarti* Hanke, Wilson and Lindoe, 2001, and *Grenfellacanthus zerinae* Long, Burrow, and Ritchie, 2004, *Euryacanthus rugosus* was not a large fish. The palatoquadrate and Meckel's cartilages of all MOTH ischnacanthid acanthodians closely resemble each other and those of other acanthodian species. The palatoquadrate is roughly b-shaped and the Meckel's cartilage is shallow and wedge-shaped, as are those of chondrichthyans.

The palatoquadrate cartilage of *Euryacanthus rugosus* has an irregular, somewhat wedge-shaped knob of cartilage at its anteroventral margin (Fig. 2.3D). The lingual face of the palatoquadrate bears a low arcing ridge that runs from near the anterior edge of the dermal jaw bone in a dorsoposterior direction and curves again ventrally to the posterior edge of the jaw bone. A deep furrow beginning at the posteroventral corner of the jaw bone and tracing the posterior border of the cartilage anteriorly marks the lingual face of the palatoquadrate. As the furrow proceeds anteriorly, it angles towards the center of the cartilaginous element, shallowing until it disappears near the anterior border (Fig. 2.3D).

The Meckel's cartilage also bears a posterior furrow on its lingual face similar to that of the palatoquadrate, except that this furrow tapers out at approximately the level of the posteriormost teeth. The Meckel's cartilage extends anteriorly past the first tooth in a long projection. The anterior border of this projection is smooth and u-shaped, and the cartilage is thickest at its edge.

The dentigerous jaw bones are shaped like elongated shallow wedges. Posteriorly, the upper and lower dentigerous jaw bones are deep, and proceeding anteriorly, the jaw bones become progressively flatter, the surface topography diverging into a lateral tooth row and a lingual ridge separated by a shallow furrow.

A series of vertical striations covers the lingual surfaces of the teeth of both the upper and lower jaws of *Euryacanthus rugosus*. These striations stop just short of the tooth tip in most cases (Fig. 2.3). The teeth are large, high, and broadly caniniform. Each tooth consists of one large central cusp and one small, pustulose cusp at lingual base of the central cusp (Fig. 2.3C). Each tooth possesses a small anterolabial flange, or set of fused denticles, and a well-developed posterolabial flange nearly half the height of each tooth. The anterior flange has one or two denticle cusps anterior to the main tooth. The posterior flange has two to three denticle cusps just posterior to the main tooth cusp. These denticles are visible on the flanges of the anteriormost teeth, but they appear to be worn smooth on more posterior teeth (Fig 2.3B, C). The posterior denticles of each tooth are lateral to, and slightly overlap, the anterior denticles of the following tooth as described in Burrow (2004a). The largest tooth may be in any of the anteriormost four tooth positions, and the teeth decrease in size anteriorly and posteriorly from this largest tooth.

A denticle patch comprising at least four long, parallel rows of small, tricuspid, pustulose denticles covers the posterior section of the jaw bone’s lingual ridge, as seen in UALVP 45658 (Fig. 2.3A, C). These denticles are organized in rows from the posteriormost point of the jaw bone to a point level with the middle of the lateral tooth row.

An interesting feature of MOTH ischnacanthiform jaws is that the area of attachment of each tooth to the jaw bone is often visible; this is especially true in the larger specimens, including those of *Euryacanthus rugosus*. Each tooth is composed of a main cusp and posterior denticulated flange as described, with all of these components attached to a thin, rounded base that is ankylosed to the lingual surface of the jaw. These tooth bases are especially visible on the anteriormost teeth (Fig. 2.3B).

Remarks—All of the ischnacanthid specimens from MOTH have lateral teeth that are circular in parabasal section, known as "*Gomphonchus*-type" dentigerous jaw bones (Burrow, 2004a). Of the *Gomphonchus*-type ischnacanthid acanthodians with only one row of teeth known from the Early Devonian, *Euryacanthus rugosus* gen. et sp. nov. is most similar to *Ischnacanthus gracilis* (Egerton, 1861). Similarities include the overall form of the dentigerous jaw bones, jaw cartilages, occlusal pattern, and lateral tooth profile. In addition to the similarity of the MOTH body fossils to the articulated specimens of *Ischnacanthus gracilis*, these similarities are likely due to the conservative forms of these features in all ischnacanthiform acanthodians, and are not uniquely shared among *Ischnacanthus* and the MOTH taxa described here.

Ischnacanthus gracilis lacks medial vertical ridges on its teeth, lacks a denticulated lingual ridge on its jaw bones, and has well-developed anterolabial and posterolabial flanges on its teeth. These flanges are more denticulated and are nearly even in height as opposed to the sloping posterolabial flanges in *Euryacanthus*. The teeth in *Ischnacanthus gracilis* are also more slender and slightly curved posteriorly, unlike the stout, conical teeth in *Euryacanthus*, which are relatively straight, although the sloping posterolabial flanges may contribute to a curved appearance.

Cavanacanthus Lindley, 2000 may be a synonym of *Taemasacanthus* Long, 1986 (Burrow, 2002; Voichyshyn and Szaniawski, 2012), which has two rows of teeth. If *Cavanacanthus* is considered a possibly valid species, *Euryacanthus rugosus* may be distinguished from *Cavanacanthus* by having a more well-developed posterolabial flange on each lateral tooth than does *Cavanacanthus*. *Euryacathus* also has a denticle patch composed of several rows of tricuspid denticles that are much smaller than the monocuspid denticles of *Cavanacanthus*, and these denticles cover the mesial and occlusal surfaces of the lingual ridge in *Euryacanthus* and only on the occlusal surface in *Cavanacanthus*. In addition, *Cavanacanthus* has larger teeth relative to the length of the jaw bones than does *Euryacanthus*, its dentigerous jaw bones are much thicker and more robust than those of *Euryacanthus*, and unlike in any of the MOTH ischnacanthiform species, each of the lateral teeth in *Cavanacanthus* is ornamented with vertical rows of denticles.

The first type of ischnacanthid dentigerous jaw bone fragment described by Hairapetian et al. (2006) is a (presumably) lateral tooth that is much broader-based and laterally compressed than those of *Euryacanthus*, with more well-developed anterior denticulated flange and two posterior denticulated flanges. The base of the tooth also appears to be parallel to the dentigerous jaw bone, unlike the rounded bases of the lateral teeth in *Euryacanthus. Cacheacanthus* Burrow, 2007 may be distinguished from *Euryacanthus* by its deep, robust dentigerous jaw bones, lack of a lingual ridge, and lateral teeth which are D-shaped in parabasal section. *Podoliacanthus* is significantly smaller than all MOTH ischnacanthid species described here; in addition, it has relatively deeper jaw bones than does *Euryacanthus*, and they do not appear to flatten anteriorly as they do in *Euryacanthus*.

Some of the dentigerous jaw bones assigned to *Podoliacanthus zychi* Voichyshyn and Szaniawski, 2012 are lacking a medial furrow between its lateral tooth row and lingual denticle row; although there is a medial furrow in others, it does not appear to be as well-developed as that of *Euryacanthus* (Voichyshyn and Szaniawski, 2012, text-fig. 3, p. 886). The lingual denticles in *Euryacanthus* are much smaller relative to the lateral teeth than are the groups of more tooth-like denticles on the lingual row in *Podoliacanthus*. The denticles in *Podoliacanthus* are grouped in sets of three distinct denticles on a common elongate base surrounded by vascular pores, unlike those in *Euryacanthus*, which have three cusps on a single denticle, and no elongate base. The lateral teeth in *Podoliacanthus* appear to be relatively high and slender, unlike the stouter, broader teeth in *Euryacanthus*. The lateral flanges on the teeth in *Podoliacanthus* are also narrow and distinct from the inter-tooth denticle groups, whereas they form a continuous broad posterior flange in *Euryacanthus*.

ERYMNACANTHUS CLIVUS, gen. et sp. nov.

(Fig. 2.4)

Diagnosis—Ischnacanthiform with small- to medium-sized jaw bones approximately twice the depth of the length of the largest tooth, which bear a single row of 13–14 small, caniniform teeth with 1–2 prominent lingual cuspules; distinct anterior and posterior denticles on each lateral tooth; jaw bones thick along their entire length rather than tapering anteriorly, lacking a ridge or furrow medial to the lateral tooth row.

Etymology—Greek, *erymnos*, fortified, strong, *akanthias*, prickly, referring to the unusual thickness of the jaw bones and the presence of many fin spines on all ischnacanthiform acanthodian specimens from MOTH in which the body is preserved; Latin, *clivus*, the sloping side of a hill, in reference to the medially sloping jaw bones lacking a lingual furrow or ridge.

Holotype—UALVP 42666, set of dentigerous jaw bones: nearly complete right upper dentigerous jaw bone and palatoquadrate cartilage in lateral view, complete left and right lower dentigerous jaw bones and Meckel's cartilages preserved in lingual view.

Referred Material—UALVP 42198 and UALVP 45077, upper left dentigerous jaw bones and palatoquadrate cartilages in lingual view; UALVP 45097, partially disarticulated jaws and neural and haemal arches, preserved in right lateral view; UALVP 47234, partial upper right dentigerous jaw bone and palatoquadrate cartilage in lingual view.

Locality and Age—As for *Euryacanthus rugosus*.

Description—*Erymnacanthus clivus*, gen. et sp. nov., (Fig. 2.4) is a moderate-sized ischnacanthiform and like *Euryacanthus rugosus*, it contains some of the largest acanthodian specimens collected from the MOTH fish layer. Upper jaw bones range in length from 21.6 mm to 23 mm, and lower jaw bones from 24.6 mm to 25.1 mm. The morphology of the palatoquadrate cartilage is very similar to that of *Euryacanthus rugosus*. Like *Euryacanthus rugosus*, a deep posterior furrow tracing the outer border on the lingual face characterizes the palatoquadrate cartilage. The primary difference between the palatoquadrate cartilages of the two genera is that the raised arc of cartilage on the lingual face is more evident on those of *Euryacanthus rugosus*. The Meckel's element of *Erymnacanthus clivus* is also nearly identical to that of *Euryacanthus rugosus*, the only difference being that the posteroventral furrow extends farther forward, as far as the middle of the tooth row.

Lateral views of both palatoquadrate and Meckel's cartilages are preserved together with lingual views in several specimens (Fig. 2.4A). Both cartilages have shallow depressions in their lateral surfaces, presumably for muscle attachment. The Meckel's cartilage has a thickening of the dorsal and ventral borders of the anterior projection on the lateral surface as well as on the lingual one, forming a depression between these two thickened areas.

The dentigerous bones of *Erymnacanthus clivus* are much higher and thicker than those of any other MOTH ischnacanthid described here. Another feature that separates *Erymnacanthus clivus* from the other MOTH ischnacanthids is that the jaw bones do not possess a medial furrow or lingual ridge. Only a single lateral tooth row is present, with the rest of the jaw bone curving smoothly medially. *Erymnacanthus clivus* is also the only ischnacanthid species from MOTH to lack denticles on the lingual surfaces of the jaw bones, although it does possess internal scales on these surfaces (Fig. 2.4B). These scales are small, flat, and plate-like, and are superimposed over the lingual surface of the jaw bones. The scales lingual to the posteriormost teeth are very small and more rounded than the scales lingual to the anterior teeth; the scales increase in size and become more flattened lingual to the anteriormost teeth.

Specimens of *Erymnacanthus clivus* bear many small, broad based teeth in each jaw bone. The teeth are smooth and pointed, curving slightly medially. Each tooth possesses one or two conspicuous cuspules at the base of its lingual surface, larger than those in *Euryacanthus rugosus*. These cuspules are connected by ridges to the top of the tooth crown in the anteriormost teeth. The anteriormost teeth each have two associated cuspules, while the posterior teeth each have one. The anterior and posterior denticles associated with each lateral tooth do not connect to form a flange on all the teeth as in *Euryacanthus rugosus*, but project outward away from the tooth base and are only connected in the most posterior teeth.

It is difficult to tell which tooth is the largest in each jaw as many of the teeth are broken due to erosion or preparation, or the anterior portion of the jaw is missing or covered by other fossil material. As well, the teeth of *Erymnacanthus clivus* are much more similar in size along the tooth row within a jaw than are teeth in the jaws of other species. It appears, however, that the second or third tooth from the front is usually the largest tooth, with the tooth size decreasing posteriorly and anteriorly from the largest tooth.

Remarks— *Erymnacanthus clivus* resembles *Euryacanthus rugosus* and *Ischnacanthus gracilis* in size. However, *Erymnacanthus clivus* specimens are unique in possessing a single row of many small teeth bearing conspicuous lingual, anterior, and posterior denticles borne on uniquely robust dentigerous jaw bones that lack a medial furrow and ridge and are of a consistent height and thickness for the entire length of the jaw. *Euryacanthus rugosus*, *Ischnacanthus gracilis*, and *Cavanacanthus* specimens have fewer, larger, caniniform teeth and a distinct medial ridge and furrow on the tooth bearing bones. *Xylacanthus minutus* Gagnier and Goujet, 1997 is much larger than *Erymnacanthus*, and it has a lingual furrow and denticle-bearing lingual ridge. *Erymnacanthus clivus* is also the only species of ischnacanthid acanthodian from MOTH that lacks any denticulation on the medial surface of the jaw bones, although it does possess internal oral scales.

TRICUSPICANTHUS, gen. nov.

(Fig. 2.5, 2.6, 2.7)

Type species—*Tricuspicanthus gannitus*, sp. nov.

Diagnosis—Small ischnacanthid acanthodians with jaw bones carrying one lateral row of 10-12 long, caniniform teeth, and one or more rows of tricuspid teeth on the pronounced lingual ridge of the jaw bones.

Etymology—Latin, *tres*, three, *cuspis*, point, *acanthias*, prickly, referring to the tricuspid teeth on the lingual ridge of the jaw bones and the presence of many fin spines on all ischnacanthiform acanthodian specimens from MOTH in which the body is preserved.

TRICUSPICANTHUS GANNITUS, sp. nov.

(Fig. 2.5, 2.6)

Diagnosis—Small ischnacanthid acanthodian with jaw bones approximately half the depth of the length of the largest tooth in the lateral row; jaw bones bear one row of 10-12 caniniform teeth; teeth very long relative to the length of the jaw bones; lingual ridge on the jaw bears two rows of short, rounded, robust tricuspid teeth.

Etymology—Latin, *gannitus*, snarling, in reference to the very long, fang-like lateral teeth.

Holotype—UALVP 45078, articulated upper and lower left dentigerous jaw bones and cartilages preserved in lingual view.

Referred Material—UALVP 23294, lower left dentigerous jaw bone and Meckel's cartilage preserved in lingual view; UALVP 32443, left upper dentigerous jaw bone and palatoquadrate cartilage in lingual view; UALVP 41527, left upper (or right lower) dentigerous jaw bone in lingual view, without associated cartilage; UALVP 41663, small right and left upper dentigerous jaw bones and palatoquadrate cartilages in lingual view; UALVP 41920, articulated right upper and lower dentigerous jaw bones and cartilages (palatoquadrate and Meckel's cartilages, respectively) in lingual view; UALVP 42015, right upper jaw bone and partial palatoquadrate cartilage in lingual view; UALVP 42062, left lower dentigerous jaw bone with Meckel's cartilage in lingual view; UALVP 42143, right lower dentigerous jaw bone with Meckel's cartilage in lingual view; UALVP 42199, complete left and right upper dentigerous jaw bones and palatoquadrate cartilages preserved in lingual view, complete right lower dentigerous jaw bone and Meckel's cartilage in lingual view, left lower dentigerous jaw bone in lingual view, missing Meckel's cartilage and teeth; UALVP 45649, right upper and lower jaw bones and associated cartilages in lingual view; UALVP 45650, right upper jaw bone and partial palatoquadrate cartilage in lingual view; UALVP 42658, left upper dentigerous jaw bone and palatoquadrate cartilage in lingual view; UALVP 42659, anterior portion of mid-sized fish with right lower dentigerous jaw bone and Meckel's cartilage visible in lingual view; UALVP 42660, head of mid-sized fish preserved in right lateral view; UALVP 45074, lower left dentigerous jawbones and Meckel's cartilages in lingual view; UALVP 45075, left upper dentigerous jaw bones and palatoquadrate cartilages in lingual view.

Locality and Age—As for *Euryacanthus rugosus*.

Description—*Tricuspicanthus gannitus* is the most abundant ischnacanthid in the MOTH collection, as well as one of the smallest, with jawbones ranging in length from 8.4–12.6 mm. The palatoquadrate and Meckel's cartilages are similar in form to those of *E. rugosus*. The arcing ridge in the centre of the medial surface of the palatoquadrate in *Euryacanthus* and *Erymnacanthus* is either not visible or very shallow on the specimens assigned to this species. In addition, the palatoquadrate cartilage of *T. gannitus* has a shorter posterodorsal margin than that of other ischnacanthid species from MOTH, coming to a sharp point dorsal to the anterior end of the upper dentigerous jaw bone (Fig. 2.5A).

Most *T. gannitus* specimens possess a robust dentition. The main teeth are quite large compared to the overall size of the jawbone, and are smooth, curved and pointed. As in the other MOTH ischnacanthiforms, a large lingual cuspule is present at the base of each tooth (Fig. 2.5, Fig. 2.6). In some specimens, this cuspule is joined with the top of the tooth crown by a pronounced lingual ridge, which makes the teeth in these specimens seem anteroposterially compressed or triangular in parabasal section. Occasionally specimens bear other small cuspules on the lingual surface of the main tooth, usually an anteromedial cuspule, a posteromedial cuspule, or both. The anterior and posterior denticles associated with each lateral tooth cusp are joined to form denticulated flanges, which are most clearly visible in the anteriormost teeth (Fig. 2.6A).

The most striking feature of *T. gannitus* is its medial dentition: its jaw bones bear large, blunt, tricuspid teeth on their lingual ridges (Fig. 2.5, Fig. 2.6). The first medial tooth row begins posterior to the posteriormost tooth in the lateral tooth row, and it extends anteriorly to a point lingual to the third or fourth lateral tooth from the front. The central cusp on these medial teeth is much larger than the two lateral cusps, and the teeth are imbricated, slightly overlapping within the row. They are so closely spaced that they may appear to touch. Lingual to this tooth row, there is a second tooth row composed of much smaller teeth of similar shape and alignment to the first row. This smaller row begins just anterior to the posteriormost tooth in the first medial tooth row and extends anteriorly to the position of the fourth or fifth tooth of that row. Teeth increase in size anteriorly in their row.

In addition to medial tooth rows, *Tricuspicanthus gannitus* possesses well-developed internal oral scales. UALVP 42660 is preserved in such a way that the lingual surface of the lower left jaw is visible as well as the lateral surface of the upper and lower right jaws (Fig. 2.6A). Because of this, both the internal oral scale cover and the external scale cover may be compared for the same fish. Superimposed over the right jaw cartilages is a dermal covering that is typical of ischnacanthid acanthodian heads: large, flat, plate-like tesserae, which overlap slightly and in which concentric growth lines may be observed. The internal oral scales, which point inward into the mouth cavity and which must have been embedded in skin covering the lingual surfaces of the jaw cartilages and dentigerous jaw bones, are much smaller, thinner, and asymmetrical. They appear to be organized into imbricated rows, projecting away from the jaw surface and pointing toward the occlusal margin of the jaws, suggesting they projected out of the skin lining the oral cavity and into the mouth.

UALVP 42660 also reveals that *Tricuspicanthus gannitus* body scales are typical of ischnacanthid acanthodians. The scales are smaller than the head tesserae and have flat, diamond-shaped crowns, which overlap slightly (Fig. 2.6A). The orbit is large, as in most acanthodians, with no evidence of a sclerotic ring, and there is a large deposit of otic material just posterior to the orbit. The rostral scales are not well-preserved, but they appear to be similar to the rostral scales present in acanthodians with Type B lip and cheek scales (Blais et al., 2011), as are the labial scales lining the mouth margins (Fig. 2.6B). These are modified from the typical head scale form to one that is slender, needle-like, and asymmetrical, pointing toward the occlusal margin of the jaws. The cheek scales are not well-preserved in UALVP 42660, but there are four curved ridges arcing inward toward a convergence point. These likely represent the bases of the tooth whorl-like cheek scales as described in Blais et al. (2011).

Along the ventral margin of the Meckel's cartilage, the scales are enlarged and elongated, likely indicative of the position of the mandibular canal (Fig. 2.6C). There is another row of raised scales dorsal and posterior to the palatoquadrate cartilage, which may indicate the position of another canal. The scapulocoracoid (Fig. 2.6A) is poorly preserved in UALVP 42660, but it is smooth and unornamented, suggesting it is perichondrally ossified.

The visible portion of the left palatoquadrate cartilage includes a deep, cup-like articular cotylus, which articulates with the condyle visible on the left Meckel's cartilage (Fig. 2.6A, C). The left lower dentigerous jaw bone also appears to support several long, slender, needle-like teeth, which do not appear to have been anchored to the jaw bones, but which are regularly spaced and not likely to have been displaced. These "basibranchial teeth" may have been connected to soft tissue in the floor of the mouth, and are preserved curving over the lingual surface of the lower dentigerous jaw bone (Fig. 2.6C).

Remarks—*Tricuspicanthus gannitus* gen. et sp. nov. is unique among ischnacanthid acanthodians in having medial rows of large, well-developed tricuspid teeth as well as a lateral row of large conical teeth. The only other ischnacanthiform acanthodians with similar denticles are *Podoliacanthus* and *Euryacanthus*. *Podoliacanthus* Voichyshyn and Szaniawski, 2012, has separate and distinct denticles grouped in sets of three on an elongate base, unlike the lingual teeth in *Tricuspicanthus*, which are much larger relative to the lateral teeth than the denticles in *Podoliacanthus* and have three cusps on a single tooth, with no separation of their bases. The dentigerous jaw bones in *Podoliacanthus* also do not appear to flatten anteriorly as they do in *Tricuspicanthus*.

Tricuspicanthus is smaller than *Euryacanthus*, its lingual teeth are much larger relative to the lateral teeth than are the lingual denticles in *Euryacanthus*, and it has higher, more fang-like lateral teeth, compared to the broader striated teeth in *Euryacanthus*. It is smaller than *Ischnacanthus gracilis* and *Erymnacanthus*, which both have only one tooth row. It has a relatively shorter posterodorsal margin on its palatoquadrate cartilage than any other MOTH ischnacanthid. *Tricuspicanthus* may be distinguished on the basis of its small size from *Taemasacanthus* Long, 1986, and *Atopacanthus* Hussakof and Bryant, 1918, which also have large teeth on the lingual ridge. *Tricuspicanthus* also differs from these in that it lacks any ornamentation such as vertical denticle rows or grooves on its lateral teeth, and it lacks a prominent ridge between its tooth rows. *Atopacanthus* as redescribed by Burrow (2004b) and *Taemasacanthus* dentigerous jaw bones also do not appear to flatten anteriorly as do those of *Tricuspicanthus*.

TRICUSPICANTHUS PISCICULUS, sp. nov.

(Fig. 2.7)

Diagnosis—Very small ischnacanthid acanthodian with jaw bones bearing a single lateral row of long, thin, caniniform teeth; lingual ridge of jaw bone bearing single row of small, pointed, tricuspid teeth.

Etymology—Latin, *pisciculus*, little fish, in reference to the unusually small size of the jaw bones and the inferred small size of the fish.

Holotype—UALVP 45072, a small left upper dentigerous jawbone and palatoquadrate cartilage preserved in lingual view.

Referred Material—UALVP 45620, a small left upper dentigerous jawbone and palatoquadrate cartilage preserved in lingual view.

Locality and Age—As for *Euryacanthus rugosus*.

Description—Only two left upper dentigerous jawbones and palatoquadrate cartilages have been assigned to *Tricuspicanthus pisciculus*. Both are very small, 7 and 7.4 mm long, and are preserved in lingual view. The palatoquadrate cartilages and the dentigerous jaw bones are similar in form to those of *Euryacanthus rugosus* and *Tricuspicanthus gannitus*, although much smaller. Although it is poorly preserved, the dorsal profile of the palatoquadrate cartilage in *T. pisciculus* appears to be more symmetrical than that of *T. gannitus*. Similarly to *T. gannitus*, *T. pisciculus* lacks the arcing ridge on the medial surface of the palatoquadrate that is present in *Euryacanthus*.

The lateral tooth row of *T. pisciculus* consists of 10-11 long, caniniform, slightly recurved teeth, which are more slender and columnar than the broader-based, conical teeth of other MOTH ischnacanthids. At the base of each tooth is a conspicuous medial cuspule (Fig. 2.7).

The morphology of the medial tooth row is unusual in *T. pisciculus*. Because of their very small size and because there are few specimens, it is difficult to determine if these are true teeth or enlarged denticles. They are large in comparison to the jaw bone and lateral tooth row and in comparison to the relative size of the denticles in *Euryacanthus rugosus*, and I will refer to them here as teeth to distinguish them from the denticles present in *Euryacanthus rugosus*, pending histological analysis. The medial tooth row begins just posterior to the lateral tooth row and continues anterior to approximately the third tooth position. The medial teeth are tricuspid as in *T. gannitus*, but much smaller, sharper-edged, and more widely spaced.

The dentigerous jaw bones in *T. pisciculus* specimens appear to be more curved dorsoventrally than in specimens belonging to other species of ischnacanthid acanthodians at MOTH. However, with only two specimens, it is difficult to determine whether this is an artefact of preservation or indicative of its shape during the life of the animal.

Remarks—*Tricuspicanthus pisciculus* may be distinguished from *Tricuspicanthus gannitus* by its size, and also by the unique morphology of its long, slender lateral teeth, which are much more delicate and needle-like than the more robust, conical fang-like teeth of *T. gannitus* or any other MOTH species. Both species have a similar number of teeth in the lateral row, suggesting the difference in size is not due to ontogeny. In addition, *T. pisciculus* jaw bones appear to have been more curved than those of *T. gannitus* and the other MOTH ischnacanthids, and the posterodorsal margin of the palatoquadrate in *T. pisciculus* is relatively longer than that of *T. gannitus.*

DISCUSSION

Based on the dental anatomy of the specimens of ischnacanthid acanthodians from MOTH, it is unlikely that *Ischnacanthus gracilis* (Egerton, 1861) was present at this locality as suggested by Bernacsek and Dineley (1977). Material that they used for comparison consisted of poorly preserved split slabs (part and counterpart) of sandstone, with many features obscured. The overall morphology of the jaws and teeth suggests that there have been no specimens of *I. gracilis* found from the Mackenzie Mountains. *Ischnacanthus gracilis* jaws resemble those of *Euryacanthus rugosus* in their gross morphology, but lack the vertical striae on the lingual surfaces of the main teeth that characterize the latter species. The teeth of *Ischnacanthus* are long and fang-like, with sharp cusps on the anterolabial and posterolabial flanges, and *I. gracilis* lacks any denticle- or tooth-bearing ridges on the lingual surfaces of the jaw bones (Burrow, 2013). In addition, *I. gracilis* lacks medial cuspules on the lateral teeth, a feature that all MOTH ischnacanthids possess.

Ischnacanthus gracilis has only been found in freshwater deposits (Trewin and Davidson, 1996), whereas MOTH specimens are preserved in marine sediments (Gabrielse et al. 1973; Dineley and Loeffler 1976; Adrain and Wilson 1994; Hanke, 2001; Hanke et al., 2001a; Zorn et al., 2005). This further supports the hypothesis that *Ischnacanthus gracilis* was unlikely to have lived at the MOTH locality during the Early Devonian.

The variety of dental features in incomplete specimens of ischnacanthid acanthodians originally assigned to *Ischnacanthus gracilis* suggests that *I. gracilis* may consist of more than one species, differentiable by close examination of the jaws and teeth. Only a few poorly preserved specimens of *I. gracilis* were available for comparison in this study. A more in-depth investigation could reveal differences in the dental anatomy among the hundreds of existing specimens of *I. gracilis*.

In modern habitats, competition for resources may preclude high numbers of closely-related species inhabiting the same environment. The presence of at least four species of ischnacanthids in one small geographic area is thus enigmatic. It is possible that the different species come from different fossil horizons at the MOTH locality, as specimens are collected from a talus slope and typically only one species is found on each slab of rock. They may also have inhabited different parts of the water column. It is unlikely that acanthodians were benthic animals, based on their fusiform bodies and large eyes; perhaps they operated at different depths. There are cases, however, such as in species flocks, where closely related species can coexist in a small area. Amongst modern cichlids in African rift lakes, a genus can consist of many species that are distinguished mainly by their tooth morphology (Fryer and Iles, 1972; McCune, 1987). These differences in tooth morphology are reflected in the trophic niches occupied by the different cichlid species. Each species is specialized for eating fish scales, scraping algae from rocks, crushing molluscs, eating other fishes, or one of a myriad of other possibilities.

The MOTH ischnacanthid species represent an early experiment in jaw and tooth morphology. The differences in the dentitions exhibited by the new species named herein are at least equally significant to those among species in a modern cichlid species flock. Ischnacanthid species in the Early Devonian shallow sea that is now part of the Mackenzie Mountains may have also exploited different food sources, as evidenced by their different tooth morphologies, although it remains unclear what they were eating, as stomach contents in MOTH ischnacanthiform specimens have not been found.

Specimens from MOTH, thanks to their extraordinary preservation, have allowed us to identify previously unknown features in several groups (e.g., Greeniaus and Wilson, 2003; Hanke and Wilson, 2006; Blais et al., 2011, among others). An example of another previously unknown feature is the presence of internal oral scales described here. These scales likely lined the inside of the oral cavity, projecting up out of a layer of skin covering the lingual surfaces of the jaw cartilages and dentigerous jaw bones. These internal scales are morphologically distinct from the dermal covering on the external surfaces of the jaws. They are very small and appear to be delicate, so it is unlikely they were used in prey capture, but they could have contributed to the gripping and processing of food inside the mouth prior to swallowing. The presence of intermeshing tooth-like scales covering the posteriormost region of the jaws suggested ischnacanthid acanthodians from MOTH had cheeks (Blais et al., 2011), and it would have been a significant advantage to be able to more efficiently grip or process food once captured.

CONCLUSIONS

Four new ischnacanthid species in three new genera are described from isolated jaw elements. A current study is under way to try to identify diagnostic characters aside from those on the lingual surfaces of the jaws and teeth; for the purposes of this study, only the lingual sides of the jaws and teeth provide diagnostic information. Many nearly complete, articulated, well-preserved body fossil specimens from MOTH could not yet be assigned to species as their jaws were preserved closed or obscured by scale cover.

Body fossils of MOTH ischnacanthids strongly resemble *Ischnacanthus gracilis* (Egerton, 1861) (Hanke, 2001; Hermus, 2003). Comparison of the jaw bones and teeth has revealed several features of MOTH specimens that are different from those of *I. gracilis*. The presence of medial cuspules on the lateral teeth of MOTH species, the presence of denticles on their jaw bones and teeth, and the general form of the teeth and jaw bones distinguish the MOTH specimens from those of *I. gracilis*.

The presence at the MOTH locality of three genera and four species of ischnacanthid acanthodians, apparently differing only in their dentition, is surprising, as competitive exclusion usually prevents closely related species from inhabiting the same geographic range. The differences in jaw and tooth morphology suggest that the ischnacanthid species may have been adapted to different food sources, enabling them to occupy different trophic niches in the MOTH environment during the Early Devonian.

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FIGURES

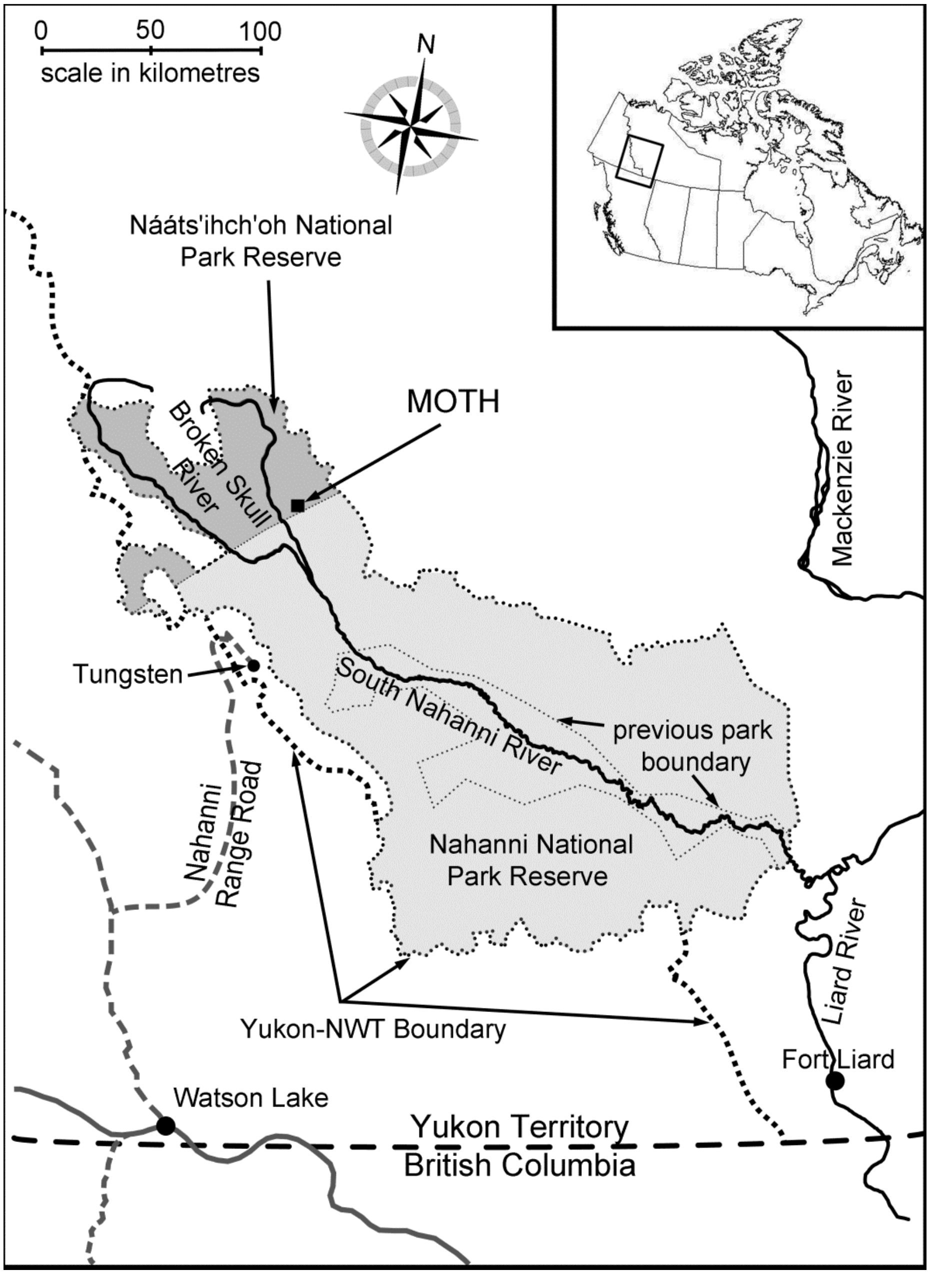

FIGURE 2.1. Map showing the location of the MOTH (Man on the Hill) section (section 43 of Gabrielse et al. (1973)) that contains UALVP Locality 129 (= GSC locality 69014), southern Mackenzie Mountains, Northwest Territories, within Nááts'ihch'oh National Park Reserve.

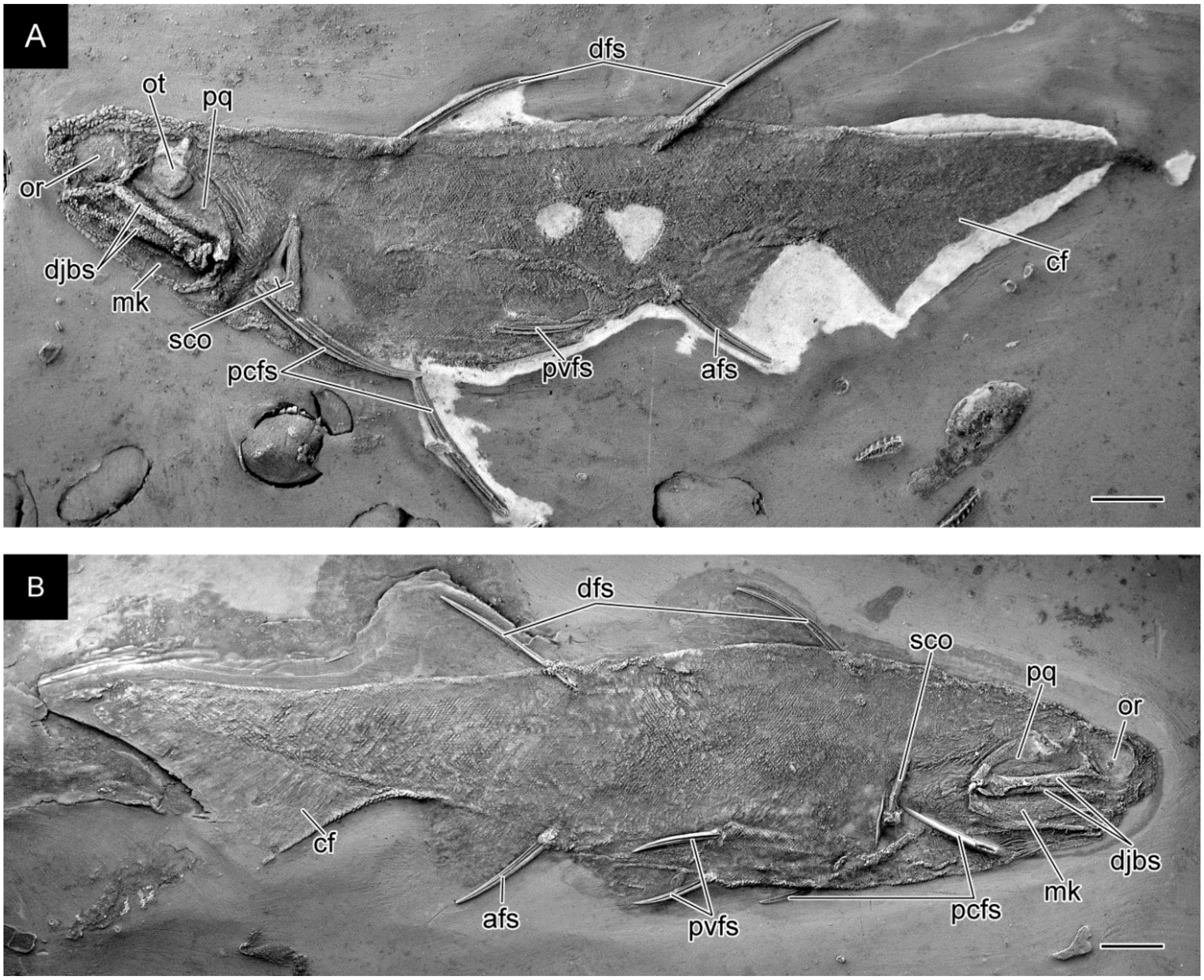

FIGURE 2.2. Articulated specimens of near-complete ischnacanthid acanthodians from the MOTH locality. **A**, UALVP 43245, preserved in left lateral view; **B**, UALVP 45014, right lateral view. **Abbreviations**: **afs**, anal fin spine; **cf**, caudal fin; **dfs**, dorsal fin spine; **djbs**, dentigerous jaw bones; **mk**, Meckel's cartilage; **or**, orbit; **ot**, otic material; **pcfs**, pectoral fin spine; **pq**, palatoquadrate; **pvfs**, pelvic fin spine; **sco**, scapulocoracoid. Scale bars equal 5mm.

FIGURE 2.3 (following page). *Euryacanthus rugosus*, gen. et sp. nov., from the MOTH locality, Northwest Territories, Canada. **A**–**C**, holotype specimen UALVP 45648, articulated upper and lower dentigerous jaw bones and associated cartilages, right lingual view; **A**, full specimen; **B**, close-up of anterior teeth; **C**, close-up of lingual denticles and posterior teeth; **D**, UALVP 45040, upper right dentigerous jaw bone and associated palatoquadrate cartilage, right lingual view. **Abbreviations**: **art**, articulation of the jaw cartilages; **ldjb**, lower dentigerous jaw bone; **ldp**, lower denticle patch; **lpqf**, lingual palatoquadrate furrow; **lpqr**, lingual palatoquadrate ridge; **lr**, longitudinal ridges on lateral teeth; **lt**, lateral tooth; **ltrs**, lateral tooth rows; **mc**, medial cusp; **mk**, Meckel's cartilage; **pq**, palatoquadrate cartilage; **tcd**, tricuspid denticles; **udjb**, upper dentigerous jaw bone; **udp**, upper denticle patch. Scale bars for A and D equal 5 mm; scale bars for B and C equal 1 mm.

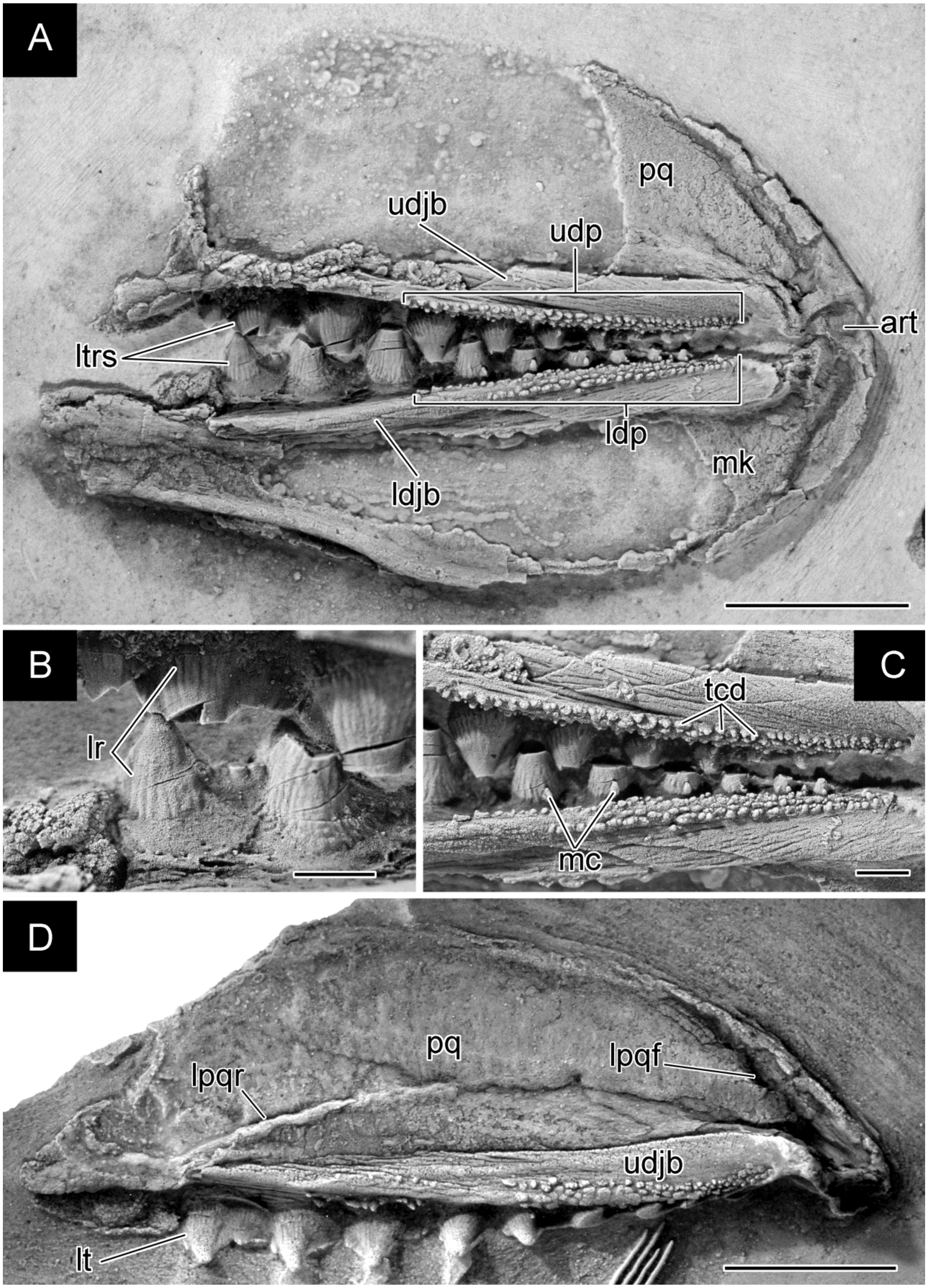
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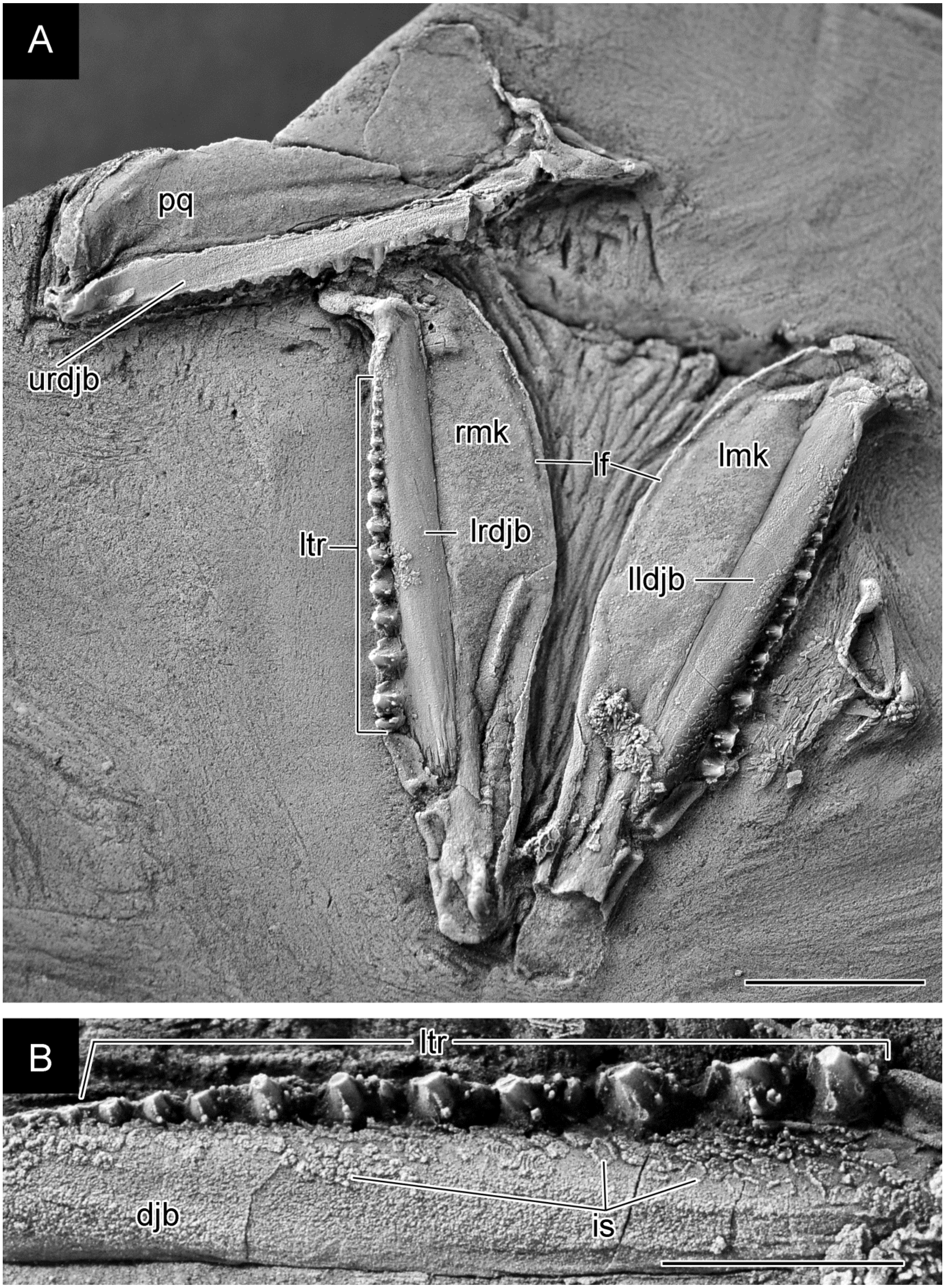
FIGURE 2.4 (following page). *Erymnacanthus clivus*, gen. et sp. nov., holotype specimen UALVP 42666 from the MOTH locality, Northwest Territories, Canada. **A**, upper dentigerous jaw bone and palatoquadrate cartilage in right lateral view and right and left lower dentigerous jaw bones and cartilages in lingual view; **B**, close-up of left lower jaw, lingual view. **Abbreviations**: **djb**, dentigerous jaw bone; **is**, internal scales; **lf**, lingual furrow; **lldjb**, lower left dentigerous jaw bone; **lmk**, left Meckel's cartilage; **lrdjb**, lower right dentigerous jaw bone; **ltr**, lateral tooth row; **pq**, palatoquadrate cartilage; **rmk**, right Meckel's cartilage; **urdjb**, upper right dentigerous jaw bone. Scale bar for A equals 5 mm; scale bar for B equals 2.5 mm.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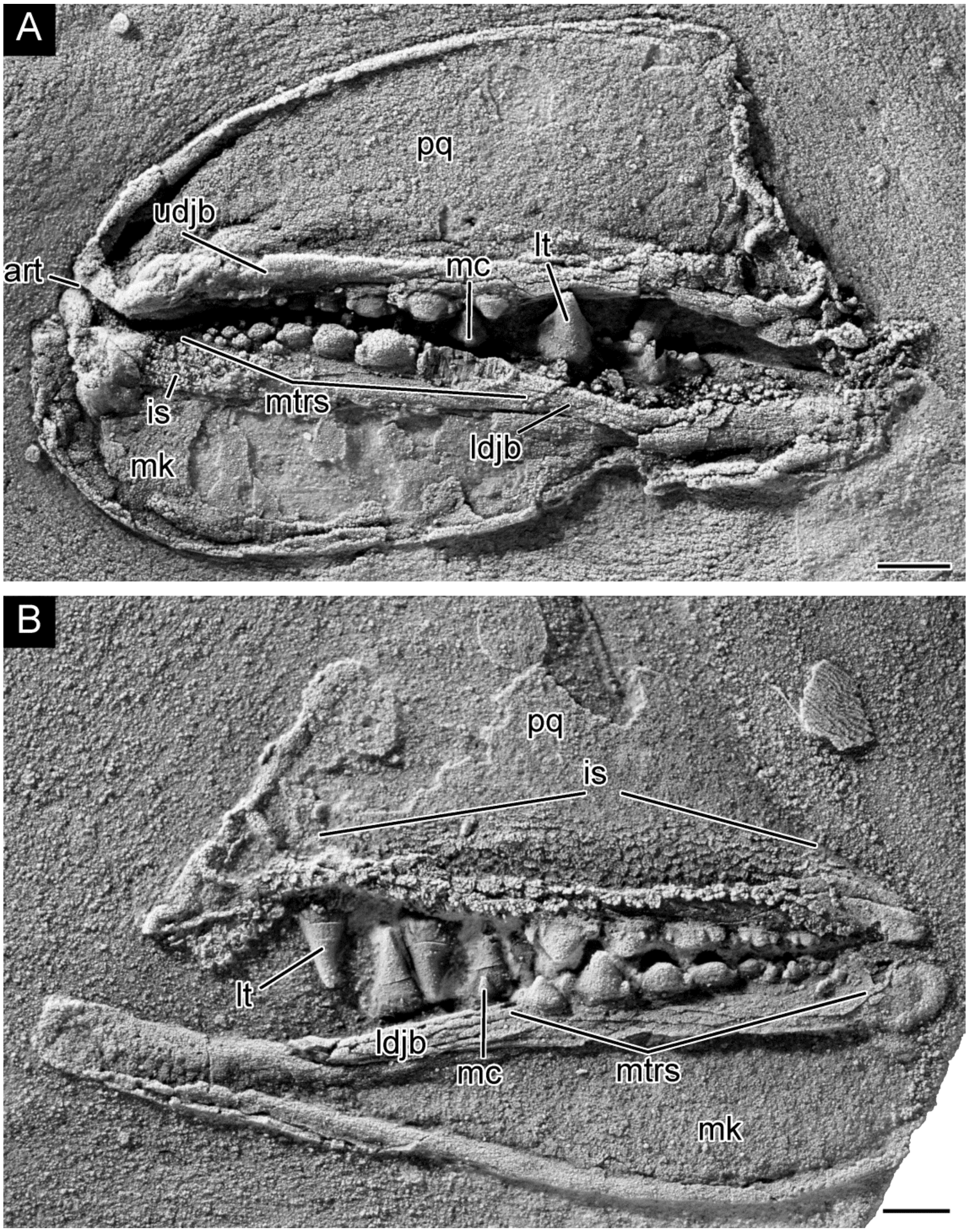
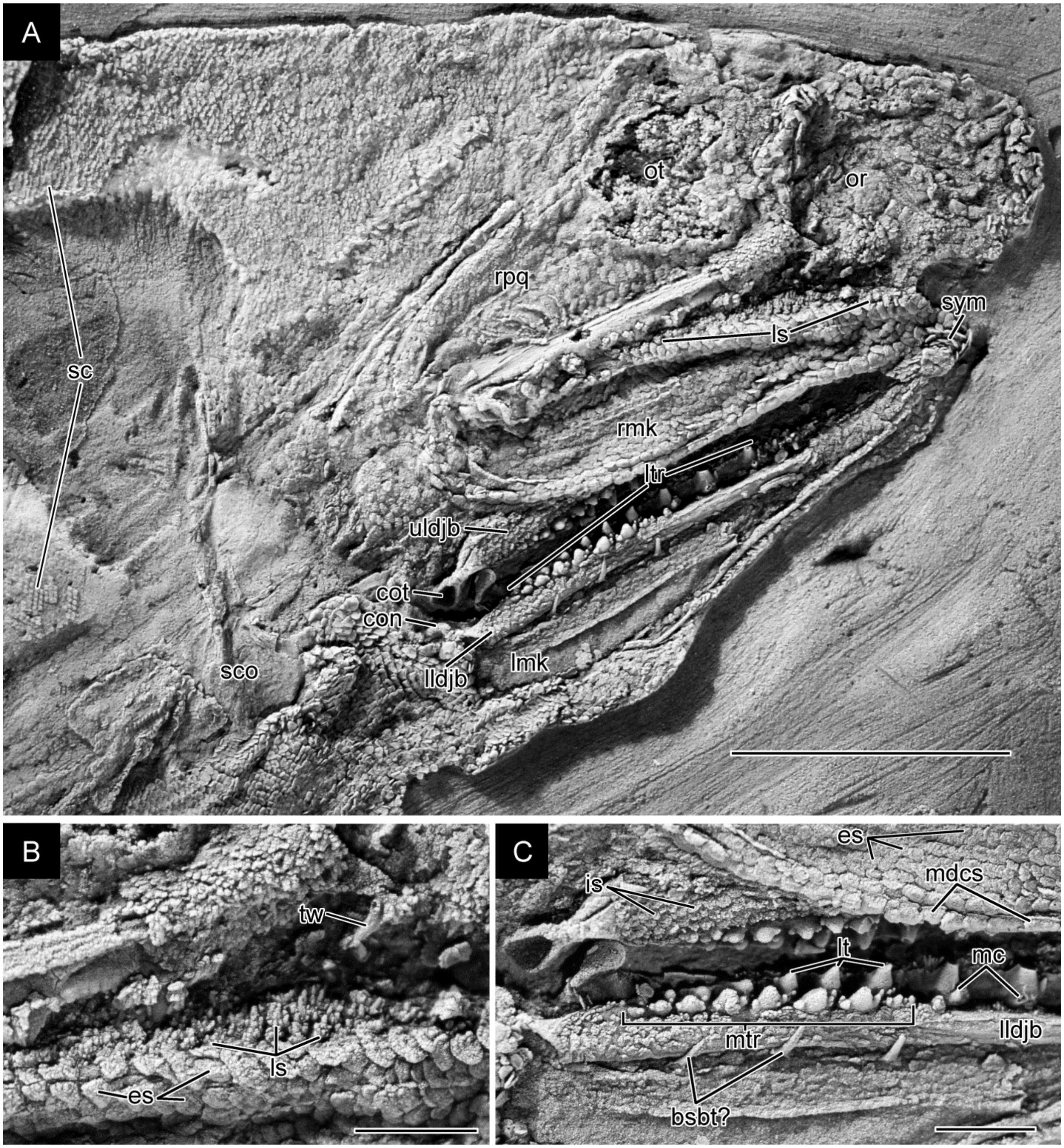


FIGURE 2.5. Articulated upper and lower jaws of *Tricuspicanthus gannitus*, gen. et sp. nov., from the MOTH locality, Northwest Territories, Canada. **A**, holotype specimen UALVP 45078, left lingual view; **B**, UALVP 41920, right lingual view. **Abbreviations**: **art**, articulation of jaw cartilages; **is**, internal scales; **ldjb**, lower dentigerous jaw bone; **lt**, lateral tooth; **mc**, medial cusp; **mk**, Meckel's cartilage; **mtrs**, medial tooth rows; **pq**, palatoquadrate cartilage; **udjb**, upper dentigerous jaw bone. Scale bars equal 1 mm.

FIGURE 2.6 (following page). Articulated head of *Tricuspicanthus gannitus*, gen. et sp. nov., specimen UALVP 42660 from the MOTH locality, Northwest Territories, Canada, right lateral view. **A**, head preserved in right lateral view, lingual view of left jaws exposed below and posterior to right jaws; **B**, close-up of anterior part of right jaws, lateral view; **C**, close-up of posterior half of left upper and lower jaws, lingual view. **Abbreviations**: **bsbt?**, possible basibranchial teeth; **con**, articular condyle; **cot**, articular cotylus; **es**, external scales; **is**, internal scales; **lldjb**, lower left dentigerous jaw bone; **lmk**, left Meckel's cartilage; **ls**, lip scales; **lt**, lateral tooth; **ltr**, lateral tooth row; **mc**, medial cusp; **mdcs**, mandibular canal scales; **mtr**, medial tooth rows; **or**, orbit; **ot**, otic material; **rmk**, right Meckel's cartilage; **rpq**, right palatoquadrate cartilage; **sc**, body scales; **sco**, scapulocoracoid; **sym**, location of lower jaw symphysis; **tw**, tooth whorl; **uldjb**, upper left dentigerous jaw bone. Scale bar for A equals 5 mm, scale bars for B and C equal 1 mm.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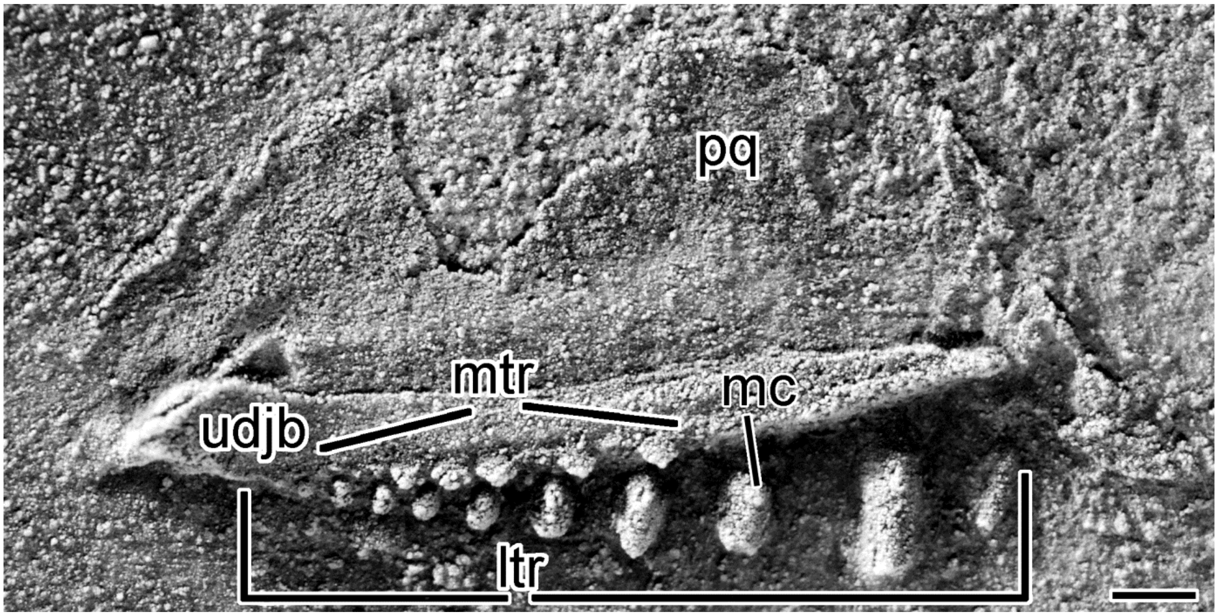

FIGURE 2.7. *Tricuspicanthus pisciculus*, gen. et sp. nov., holotype specimen UALVP 45072, left upper dentigerous jaw bone and palatoquadrate cartilage in lingual view. **Abbreviations**: **ltr**, lateral tooth row; **mc**, medial cuspule; **mtr**, medial tooth row; **pq**, palatoquadrate cartilage; **udjb**, upper dentigerous jaw bone. Scale bar equals 0.5 mm.

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CHAPTER 3

TWO NEW SILURIAN ISCHNACANTHIFORMS FROM THE NORTHWEST TERRITORIES, CANADA

ABSTRACT

Two new ischnacanthiform acanthodians are described from the Silurian (Wenlock or Ludlow) fish layer from the Man On The Hill (MOTH) locality, known as B-MOTH. *Euryacanthus serratus*, sp. nov., is based on a nearly complete upper dentigerous jaw bone and associated palatoquadrate cartilage, and *Oroichthys theobromodon*, gen. et sp. nov., is based on a fragmentary dentigerous jaw bone and teeth. These add to our understanding of the diversity of Silurian ischnacanthiform acanthodians, particularly from the MOTH locality, where they were previously represented only by *Xylacanthus kenstewarti* and *Granulacanthus joenelsoni*. The two species show signs of differing patterns of tooth wear, suggesting they may have coexisted by employing varied feeding strategies and exploiting different food sources. Both of these species as well as *Xylacanthus kenstewarti* and other Silurian forms have a single row of lateral teeth and a denticulated lingual ridge, suggesting this may be the plesiomorphic condition for ischnacanthiforms, as opposed to later Devonian forms with multiple tooth rows, or lacking denticulated ridges.

INTRODUCTION

Since the first description of vertebrate fossils from the Early Devonian Man On The Hill (MOTH) locality (Dineley and Loeffler, 1976; Bernacsek and Dineley, 1977), this fossil site has proven to be an extraordinary resource for the study of early vertebrates. Beautifully preserved fossils of ancient jawless and jawed fishes have revealed new insight into their modes of growth, diversity of form, and the homology and evolution of their features (Adrain and Wilson, 1994; Gagnier and Wilson, 1995; Wilson and Caldwell, 1998; Hanke et al., 2001b; Sahney and Wilson, 2001; Hanke, 2002; Greeniaus and Wilson, 2003; Hanke and Wilson, 2006; Hawthorn et al., 2008; Blais et al., 2011; Scott and Wilson, 2012; Hanke and Davis, 2012).

In particular, the MOTH locality is one of the best sources of acanthodian fossils in the world. These small, spiny fishes have been interpreted as a monophyletic, paraphyletic, or polyphyletic assemblage according to several recent phylogenetic analyses (Brazeau, 2009; Burrow and Turner, 2010; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015; Long et al., 2015a), distributed on the gnathostome, chondrichthyan, or osteichthyan stem, or on some combination of the three. All of these phylogenetic analyses, however, resulted in hundreds of thousands of shortest trees and low support values, making it difficult to draw any reliable conclusion about the distribution of acanthodian taxa around the crown-group gnathostome node. Although their phylogenetic position remains ambiguous, at least some acanthodians likely formed the sister group to either one or both clades of living gnathostomes (or the sister group to all crown-group gnathostomes), and the conditions in acanthodians may represent the ancestral conditions for extant chondrichthyans or osteichthyans, or for both. It has therefore become increasingly important to add to the existing body of knowledge concerning acanthodians, in an attempt to discover new means of comparison among these poorly-understood animals.

Little is known of the earliest members of the group, making it difficult to determine the plesiomorphic state of acanthodian characters. Although disarticulated acanthodian scales and spines are fairly common from as early as the Ordovician

(Denison, 1979), other specimens of pre-Early Devonian acanthodians are rare. Acanthodians belonging to the order Ischnacanthiformes, in particular, are represented almost entirely by a few isolated tooth-bearing jaw bones. The oldest of these represent the Silurian (Wenlock or Ludlow) species *Xylacanthus kenstewarti* Hanke, Wilson, and Lindoe, 2001. These fossils were recovered from an older fossiliferous layer that occurs approximately 200 metres below the MOTH fish layer, in the Mackenzie Mountains of the Northwest Territories, Canada (Fig. 3.1). This Silurian fish layer is known informally as B-MOTH. The B-MOTH layer is rich in vertebrate remains, particularly heterostracan scales and shields (Soehn et al., 2000), as well as the three acanthodian jaws collected by T. Märss and G. F. Hanke in 1996 and 1998 (Hanke et al., 2001a). In 2013, M. V. H. Wilson and T. D. Cook led the most recent field party to the MOTH locality, with A. L. Lindoe, B. R. Scott, L. A. MacKenzie, and myself. Among our findings were the two acanthodian jaws from the B-MOTH fish layer described here, offering us a rare insight into the diversity of these enigmatic fishes during the Silurian and the first evidence for trophic niche differentiation in a related group of Silurian gnathostomes.

LOCALITY AND AGE

The specimens described in this paper are from the MOTH locality (referred to as section 43 in Gabrielse et al. (1973), in the Mackenzie Mountains of Canada (Fig. 3.1). Although vertebrate fossils from the locality were first described by Dineley and Loeffler (1976), the Silurian B-MOTH layer was not discovered until 1990, when it was found by Jonathan Adrain (Hanke et al., 2001). The specimens were recovered from talus, but their lithic composition and the location of their discovery makes it clear that they eroded out of the B-MOTH fish layer, rather than the younger MOTH layer.

The B-MOTH rocks are composed of dark grey limestone with clay inclusions, interpreted by Hanke et al. (2001) as rip-up clasts. Common fossils from this layer include disarticulated fragments of bryozoans, brachiopods, crinoid ossicles, and broken, disarticulated heterostracan shields. The presence of iron minerals, including pyrite, suggests the sediments were hypoxic or anoxic. No articulated vertebrate fossils have been recovered from the B-MOTH layer. Hanke et al. (2001) used the presence of the graptolites *Monograptus* sp. cf. *M. priodon* and *Monoclimacis* sp. cf. *M. vomerina* below B-MOTH, and isolated scales of the thelodont *Thelodus laevis* and *Paralogania martinssoni* in the B-MOTH fish layer to constrain its age to late Wenklockian (Homerian) or early Ludlovian (Gorstian).

METHODS

A dilute acetic acid solution was used to dissolve the calcareous matrix overlying the specimens, with finer-scale removal of the remaining residue accomplished through the use of soft brushes. A 5% solution of Glyptal cement in acetone was used to stabilize the specimens after the excess matrix, remaining acid, and acetate buffer were rinsed away. The specimens were whitened using ammonium chloride sublimate and photographed using a Zeiss Discovery V8 stereomicroscope and Nikon NIS-Elements F 2.20 imaging software. Specimens described in this study are housed in the UALVP collections.

SYSTEMATIC PALEONTOLOGY

GNATHOSTOMATA Gegenbaur, 1874

ISCHNACANTHIFORMES Berg, 1940

ISCHNACANTHIDAE Woodward, 1891

Remarks—The new species described in this paper are provisionally assigned to Ischnacanthidae based on the circular or subcircular parabasal sections of their lateral teeth, pending SEM studies of scales if more complete specimens are found.

EURYACANTHUS Blais, Hermus, & Wilson, 2015

Type Species—*Euryacanthus rugosus* Blais, Hermus, & Wilson, 2015

EURYACANTHUS SERRATUS, sp. nov.

(Fig. 3.2)

Diagnosis—Ischnacanthid acanthodian with medium-sized dentigerous jaw bones approximately half to two-thirds the depth of the height of the largest tooth; dentigerous jaw bones deeper posteriorly, becoming wider and flatter anteriorly, bearing one lateral row of 12 teeth, each composed of a large central cusp that is circular or subcircular in parabasal section, and several smaller labial denticles that are laterally compressed; lateral tooth cusps large, caniniform, and slightly recurved, bearing one large lingual cuspule; lateral tooth cusps, labial denticles, and lingual cuspules bearing fine longitudinal ridges; dentigerous jaw bones with a deep furrow or groove medial to the main tooth row, separating it from a lingual ridge which bears an elongate patch of small, low, round denticles.

Etymology—Latin, *'serratus*', serrated, in reference to saw-like lateral tooth row, with large main tooth cusps and sharply defined labial denticles.

Holotype—UALVP catalogue number not yet assigned, isolated right upper dentigerous jaw bone and accompanying palatoquadrate cartilage, preserved in medial view.

Locality and Age—UALVP Locality 970, Silurian (late Wenlock (Homerian) or early Ludlow (Gorstian)) of Section 43 of Gabrielse et al. (1973). The strata of the B-MOTH fish layer, at 235 m in the MOTH section as measured in 1996 (Hanke et al., 2001a) are composed of dark grey limestone with clay inclusions.

Description—The holotype and only specimen representing *Euryacanthus serratus* is a nearly complete upper jaw, with a jaw bone length of 39.5 mm and a total length of 51 mm, including the palatoquadrate cartilage (Fig. 3.2). The overall shape of the jaw bone and palatoquadrate cartilage is very similar to that of the same elements in *Euryacanthus rugosus* and the other ischnacanthiforms from the MOTH locality (Blais et al., 2015). The palatoquadrate is roughly cleaver-shaped, as is the palatoquadrate in most ischnacanthiform acanthodians. There is an irregular wedge of folded and convoluted cartilage at the anteroventral margin of the jaw, and a thickened ridge of cartilage at the posterior margin leading to the shallow hollow that forms the articular cotylus. The central portion of the palatoquadrate is not preserved in this specimen. The anteroventral part of the palatoquadrate appears to wrap around the anterior end of the jaw bone, giving the jaw the appearance of a sharp ventral bend at its anteriormost margin.

The dentigerous jaw bone is shaped like an elongate shallow wedge, deep posteriorly and shallow anteriorly. Posteriorly, the dentigerous jaw bone is massive, diverging anteriorly into a lingual ridge and lateral tooth row, separated by a groove. A patch of very small, low, rounded denticles covers approximately 40% of the lingual ridge of the jaw bone, extending anteriorly to the posterior edge of the fifth tooth from the front, and posteriorly to a flat area that corresponds to the area on the jaw bone referred to by Hanke et al. (2001) as the fossa for the adductor mandibulae. The denticles are organized into rows near the crest of the lingual ridge, but the rows are more irregular dorsally on the lingual surface of the jaw bone. The surface of the dentigerous jaw bone bears a series of very fine grooves anteriorly, which roughly parallel the slope of the lingual ridge.

The lateral teeth are composed of a large, caniniform central cusp, with 1-2 smaller secondary cusps anterior to the main cusp and 2-3 secondary cusps posterior to the main cusp. These secondary cusps are distinct for all but the posteriormost teeth, where they form a continuous labial flange anterior and posterior to the main tooth cusp. In addition to the secondary cusps, each tooth also possesses an accompanying, large secondary cusp located at the center of the lingual base of the main tooth cusp; this cusp is referred to here as a lingual denticle to distinguish it from the secondary cusps anterior and posterior to the main tooth cusp. This lingual denticle is very distinct in the anteriormost teeth, but is connected to the main tooth cusp by a ridge in the more posterior teeth, giving these teeth a more triangular appearance. The lingual surfaces of the main tooth cusp, the lingual denticle, and the secondary cusps are covered with very fine vertical striations that stop just short of the tip of the tooth or denticle. The largest tooth is in tooth position 4, with the teeth decreasing in size anteriorly and posteriorly from the largest tooth (Fig. 3.2).

The groove between the lingual ridge of the jaw bone and the lateral tooth row appears to be mostly composed of the attachment bone associated with the base of each lateral tooth; it is pocked with nutrient foramina, particularly at its anterior end. The area of attachment of the tooth to the jaw bone is also most clearly delineated in the anteriormost teeth. The area of attachment for the second tooth from the front slightly overlaps the secondary cusps of the third tooth, and appears to be only loosely attached to the jaw bone. The anteriormost tooth is small, with very small secondary cusps, and the vascular canals at its base are clearly visible, suggesting it is only loosely attached.

Remarks—All of the ischnacanthiform specimens from MOTH and B-MOTH have lateral tooth cusps that are circular or subcircular in parabasal section, otherwise known as "*Gomphonchus*-type" dentigerous jaw bones (Burrow, 2004a). These are typical of ischnacanthid ischnacanthiforms, as opposed to the triangular parabasal sections found in typical poracanthodid ischnacanthiform jaw bones, known as "*Nostolepis*-type". Histological studies of the scales are required to determine whether the ischnacanthiforms from MOTH and B-MOTH can be confidently assigned to the Ischnacanthidae or Poracanthodidae, but in the absence of scales they are provisionally assigned to the Ischnacanthidae based on the circular parabasal sections of their teeth.

Of the ischnacanthiform acanthodians with *Gomphonchus*-type dentigerous jaw bones with only a single lateral tooth row, *Euryacanthus serratus*, sp. nov., is most similar to *Euryacanthus rugosus*. The two species are very similar in terms of the overall form of their dentigerous jaw bones and palatoquadrate cartilages, particularly in the wedge shape of the jaw bone and the relatively deep groove between the lingual ridge and lateral tooth row. Both share a single large lingual denticle at the center of the base of each main tooth cusp, vertical striations on the lingual surfaces of the teeth, and a denticle patch on the lingual ridge of the jaw bone.

Although *Euryacanthus serratus*, sp. nov., is very similar to *Euryacanthus rugosus* in terms of the morphology of at least its upper jaw bones, the two species can be distinguished based on morphology of the teeth and denticles: *Euryacanthus rugosus* has broader, stouter tooth cusps, bearing smooth anterior and posterior labial flanges with no secondary cusps. *Euryacanthus serratus* has comparatively more fang-like lateral teeth with pronounced secondary cusps; it also has 12 lateral teeth, compared to approximately 10 lateral teeth in *Euryacanthus rugosus*. *Euryacanthus rugosus* has a large lingual denticle at the base of each tooth cusp, but this denticle is absent in the anteriormost teeth and prominent in the posteriormost teeth; this is the opposite of the pattern observed in *Euryacanthus serratus*, in which the lingual denticle is largest and most prominent in the anteriormost teeth and forms part of a central lingual ridge in the posteriormost teeth. *Euryacanthus serratus* also has a lingual denticle patch composed of small, low, round denticles that are less organized than the orderly rows of relatively larger, sharp, tricuspid denticles in *Euryacanthus rugosus*. *Euryacanthus serratus* is older compared to the Lochkovian *Euryacanthus rugosus*, and much larger, with a jaw length of 51 mm compared to a maximum observed jaw length of 25.9 mm for *Euryacanthus rugosus* (Fig. 3.2).

Euryacanthus serratus also bears some resemblance to the first described ischnacanthiform species from B-MOTH, *Xylacanthus kenstewarti*, but differs from this species in several respects. *Xylacanthus kenstewarti* is approximately twice the size of *Euryacanthus serratus*. The jaw bones in *X. kenstewarti* do diverge anteriorly into a lateral tooth row and lingual ridge, but they do not flatten anteriorly as do those of both species of *Euryacanthus*, instead maintaining a relatively uniform height throughout the length of the jaw. The lingual ridge in *X. kenstewarti* is wider and less acute, and the groove between the ridge and tooth row is shallower than in *Euryacanthus serratus*. The posterior end of the jaw bone in *Xylacanthus kenstewarti* is also expanded dorsoventrally, unlike that of *E. serratus*. In addition to these differences in jaw bone morphology, *Xylacanthus kenstewarti* lacks the large lingual denticle located at the base of each tooth cusp in *Euryacanthus serratus*, its teeth are more stout and conical than caniniform, and the vertical ridges ornamenting the tooth surfaces are much coarser than those of *Euryacanthus serratus*.

Euryacanthus serratus is also distinguishable from the other two species of the genus *Xylacanthus*; the jaws of *Xylacanthus minutus* are similar in size to those of *Xylacanthus kenstewarti* and thus much larger than those of *Euryacanthus serratus. Xylacanthus minutus* also has lateral teeth that are triangular in parabasal section (Hanke et al., 2001a) and should probably be assigned to a different genus as this type of tooth morphology is usually indicative of poracanthodid ischnacanthiforms. *Xylacanthus grandis* is the largest known ischnacanthiform, with jaws estimated at 350 mm long (Ørvig, 1967; Denison, 1979); it is geologically younger than the B-MOTH species, and it lacks a denticulated lingual ridge on its jaw bones.

Of the other Silurian–Early Devonian ischnacanthiform acanthodians with *Gomphonchus*-type jaw bones bearing only a single lateral row of teeth, the jaw bone of *Euryacanthus serratus* is most comparable to those of *Ischnacanthus*. *Euryacanthus serratus* may be distinguished from the species belonging to this genus by its possession of a denticulated lingual ridge on the jaw bone, and by the secondary cusps and lingual denticle associated with each tooth cusp. Although *Ischnacanthus wickhami* was described by White (1961) as having an irregular series of denticles medial to the main tooth row, Hanke et al. (2001) confirmed that *Ischnacanthus wickhami* lacked medial ridge denticles, as do all species of *Ischnacanthus* (Burrow, 2004a).

According to Burrow (2002), *Cavanacanthus* Lindley, 2000, is a synonym of *Taemasacanthus* Long, 1986, which has two robust tooth rows. If *Cavanacanthus* is a valid taxon, it may be distinguished from *Euryacanthus* based on its extremely thick and robust jaw bones, large, stout lateral teeth ornamented by vertical rows of denticles, and relatively large denticles organized into only two rows on the lingual ridge of the jaw bone. *Cacheacanthus* Burrow, 2007, and *Erymnacanthus* Blais et al., 2015, are two other ischnacanthiform genera with much deeper and more robust jaw bones than those of *Euryacanthus*; these genera also lack a lingual ridge and mesial denticles. The lingual ridge of the jaw bones in *Podoliacanthus* Voichyshyn and Szaniawski, 2012, bears denticles, but these are organized into groups of three, and the denticles are larger relative to the jaw bones and teeth than those in *Euryacanthus*. In addition, *Podoliacanthus* is much smaller than *Euryacanthus serratus*, with jaw bones up to 7 mm in length, and *Podoliacanthus* lacks a groove between the lateral tooth row and the lingual ridge on the jaw bones, with the lateral tooth bases in direct contact with the lingual ridge.

OROICHTHYS THEOBROMODON, gen. et sp. nov.

(Fig. 3.3, Fig. 3.4)

Diagnosis—Medium-sized ischnacanthiform with jaw bones bearing a single lateral row of large, pointed, caniniform teeth with very prominent flutes and grooves on the lingual surfaces of the teeth; lateral teeth lacking any secondary denticles or cusps lingually or labially between the teeth; lateral teeth flat and slightly concave labially, and subcircular or D-shaped in parabasal section; jaw bones shallow anteriorly, bearing a prominent lingual ridge and a wide, shallow groove between the lingual ridge and the lateral tooth row; lingual ridge of the jaw bone bearing a patch of relatively large denticles, very similar in shape to the lateral teeth and also characterized by prominent fluting of the denticle surface, organized into alternating rows, with the central row bearing the largest denticles and the denticles decreasing in size from this central row.

Etymology—Greek, ‘*oros*’, mountain, and ‘*ichthys*’, fish, referring to the lateral tooth row resembling mountain peaks, and also to the Mackenzie Mountains whence it came; Greek, ‘*theobroma*’, chocolate (literally ‘food of the gods’), ‘*odon*’, tooth, referring to the prominent, sharp-edged flutes and ridges on the lingual surfaces of the teeth, which give the teeth the appearance of piped frosting or “chocolate buds” candies.

Holotype—UALVP catalogue number not yet assigned, isolated fragment of the anterior part of the jaw bone, bearing four lateral teeth and the anteriormost part of a patch of fluted denticles; the jaw bone is broken posteriorly but intact anteriorly.

Locality and Age—As for *Euryacanthus serratus*.

Description—Based on the fragment of the anterior portion of the jaw that is the type and only specimen found to represent this species (Fig. 3.3, Fig. 3.4), *Oroichthys theobromodon*, gen. et sp. nov., was a medium-sized ischnacanthiform acanthodian. Comparing the distance between the three largest teeth to the distance between the corresponding three largest teeth in *Euracanthus serratus* (assuming the proportions are similar) provides an estimated total length for the jaw of ~68 mm including the cartilage, and ~53 mm including only the jaw bone. It is therefore likely to have been a larger fish than *Euryacanthus serratus*, but not as large as the ischnacanthiforms belonging to the genus *Xylacanthus*.

Based on this fragmentary fossil, *Oroichthys theobromodon* had very long lateral teeth relative to the height of its jaw bones, although this is probably exaggerated if the jaw bone is at its shallowest at its anterior end, as is the case for *Euryacanthus*. The jaw bone is nevertheless extremely shallow as far posteriorly as the fourth tooth and the anteriormost edge of the lingual ridge, and the lingual ridge and lateral tooth row are roughly parallel to each other. The lingual ridge and lateral tooth row are separated by a wide, shallow groove that appears to be composed mainly of the attachment bone associated with the lateral teeth (Fig. 3.3, 3.4B). This tissue is pocked with nutrient foramina, particularly at the base of the anteriormost tooth, which overlaps the second tooth lingually. The anteriormost tip of the lingual ridge of the jaw bone is smooth and rounded, whereas the anteriormost edge of the lateral tooth row and groove is irregular and appears unfinished. The ventral side of the jaw bone is relatively smooth, bearing fine longitudinal striations, likely representing vascular canals, running roughly parallel to the long axis of the jaw bone and the lingual ridge. At the posterior end of the jaw fragment, beginning lingual to the center of the fourth tooth from the front, is a patch of large, pointed, laterally compressed, fluted denticles similar in overall shape to the lateral teeth. The jaw bone is broken posteriorly to the fourth tooth, but it is nonetheless clear that the denticles are organized into alternating rows, with the central row bearing the largest denticles. The denticles decrease in size with increasing distance from the central row.

The lateral teeth are separated by a wide space between the third and fourth tooth and posteriorly to the fourth tooth, which lacks any denticles or flanges between the teeth. The space between the teeth is narrower between the second and third tooth, and narrower still and more sharply delineated between the first and second tooth. There appears to be a lateral flange between the first and second tooth, two denticles or the remains of a lateral flange between the second and third tooth, and no flange or denticles between the third and fourth tooth. It is difficult to determine whether the difference in the appearance (or lack thereof) of the lateral flange is taphonomic with only one representative specimen. The difference in the spacing of the teeth may be due to ontogeny rather than taphonomy; it is possible that tissue was added between each successive tooth cusp as the new tooth became ankylosed to the jaw bone. It is also possible that the lateral flange between the tooth cusps was removed by wear in all but the youngest tooth pairs, or that it is simply broken in this specimen (Fig. 3.3, 3.4).

The lateral tooth crowns are high relative to the thickness of the jaw bone and caniniform, with sharply pointed cusps that are slightly posteriorly curved. The teeth bear sharp-edged, vertical flutes on their lingual surfaces, giving them an appearance similar to piped frosting or chocolate buds. The teeth are flat or slightly concave labially, with a subcircular, roughly D-shaped parabasal section (Fig. 3.4).

Remarks—*Oroichthys theobromodon* is represented by an incomplete fragment of the jaw bone, but that fragment is sufficiently unique among ischnacanthiform acanthodians to assign it to a new genus and species. The sharply defined flutes on the lingual surfaces of the teeth and lingual ridge denticles, in particular, are unique among ischnacanthiform acanthodians.

In terms of what can be determined about the morphology of the jaw bone, it is most similar to species of *Euryacanthus* in that the anterior jaw bone is very shallow, and the lingual ridge of the jaw bone and the lateral tooth row are separated by a wide, shallow groove. However, it can be distinguished from species of *Euryacanthus* based upon its tooth and denticle morphology. *Euryacanthus rugosus* and *E. serratus*, sp. nov., both possess large denticles or cuspules medial to the base of each lateral tooth as well as anterior and posterior secondary cusps or flanges, all of which are absent in *O. theobromodon*. The teeth in *Oroichthys theobromodon* are longer relative to the jaw bone height than those in species of *Euryacanthus*, and the angle between the long axis of the tooth cusps and the long axis of the jaw bone is more acute in *Oroichthys theobromodon*. The denticles in *Oroichthys theobromodon* are much larger relative to the jaw bone and lateral teeth than those in either species of *Euryacanthus*, and much more similar in their morphology to the lateral teeth. Finally, the teeth of *Euryacanthus serratus* exhibit wear facets that suggest their jaw occlusion was similar to that of *Euryacanthus rugosus* (see Chapter 4 of this thesis) in which the main points of contact are between the anterior and posterior lingual surfaces of each tooth and the labial flanges (or secondary cusps) of the opposing tooth, whereas the teeth in *Oroichthys theobromodon* seem to have wear facets on the posterior edges of the teeth only, possibly extending to the bone attaching the tooth to the jaw bone itself. Based on the results described in Chapter 4 of this thesis, differences in the wear pattern and occlusion of the teeth (presumably reflecting feeding strategies) would also suggest these jaws represent two different species.

Oroichthys theobromodon is also similar in some respects to the coeval *Xylacanthus kenstewarti* and its larger relative *Xylacanthus grandis*, but *Oroichthys theobromodon* is smaller and has much more shallow dentigerous jaw bones with a more prominent lingual ridge. The teeth in *Oroichthys theobromodon* are relatively longer and more caniniform than those of *Xylacanthus* species, and they lack lingual and lateral secondary cusps or flanges. The flutes on the lingual surfaces of the teeth of *Oroichthys theobromodon* are also very different from the coarse ridges on the teeth of *Xylacanthus kenstewarti*. Finally, the lingual denticle patch in *Oroichthys theobromodon* is composed of denticles that more closely resemble the lateral teeth, being much larger than those of *Xylacanthus kenstewarti*, and laterally compressed and sharp instead of low-crowned and rounded. These denticles are also much more organized than the irregular patch in *Xylacanthus kenstewarti*, being arranged into very clearly delineated alternating rows of denticles decreasing in size from the central row.

Oroichthys theobromodon can be distinguished from species of *Ischnacanthus* by its possession of a denticulated lingual ridge, and from *Cacheacanthus, Cavanacanthus,* and *Erymnacanthus* based on its very shallow dentigerous jaw bones.

DISCUSSION & CONCLUSIONS

The two species described here, *Euryacanthus serratus*, sp. nov., and *Oroichthys theobromodon*, gen. et sp. nov., add to the number of known ischnacanthiform genera from the Silurian B-MOTH fish layer from the MOTH locality, previously represented only by *Xylacanthus kenstewarti*. The Silurian *Euryacanthus serratus* extends the temporal range of the genus, and suggests the B-MOTH and MOTH ischnacanthiform assemblages were likely related. The patterns of tooth wear in *E. serratus* and *O. theobromodon* are different, suggesting that their teeth occluded differently and the two species (as well as, presumably, *Xylacanthus kenstewarti*) may have coexisted by exploiting different food sources.

The fossil record of Silurian ischnacanthiforms is relatively poor, but it does suggest the group was fairly diverse as early as the Late Wenlock or Early Ludlow. Silurian forms are most commonly found in North America and Europe, and are comparatively rare in Gondwanan localities (Burrow, 2004). Conversely, Silurian osteichthyans are rare in North America, and they are the only group not represented at all from the Lochkovian MOTH fish layer. Perhaps the ischnacanthiforms were able to diversify in the absence of established osteichthyan groups in the Silurian and Early Devonian of North America and Europe.

Silurian ischnacanthiforms most commonly possessed a single row of lateral teeth and a lingual ridge on the jaw bone, such as that found in both species assigned to *Euryacanthus*, *Xylacanthus kenstewarti*, *Xylacanthus grandis*, *Ischnacanthus kingi*, and *Oroichthys theobromodon*. This may represent the plesiomorphic condition for ischnacanthiforms, with forms bearing multiple rows of teeth appearing later, in the

Devonian. This would undoubtedly be useful to add to future phylogenetic analyses of the group; such analyses have in the past represented Ischnacanthiformes with only one or two taxa, and these ancient fishes may be central to our understanding of the diversification and evolution of crown-group gnathostomes.

FIGURES

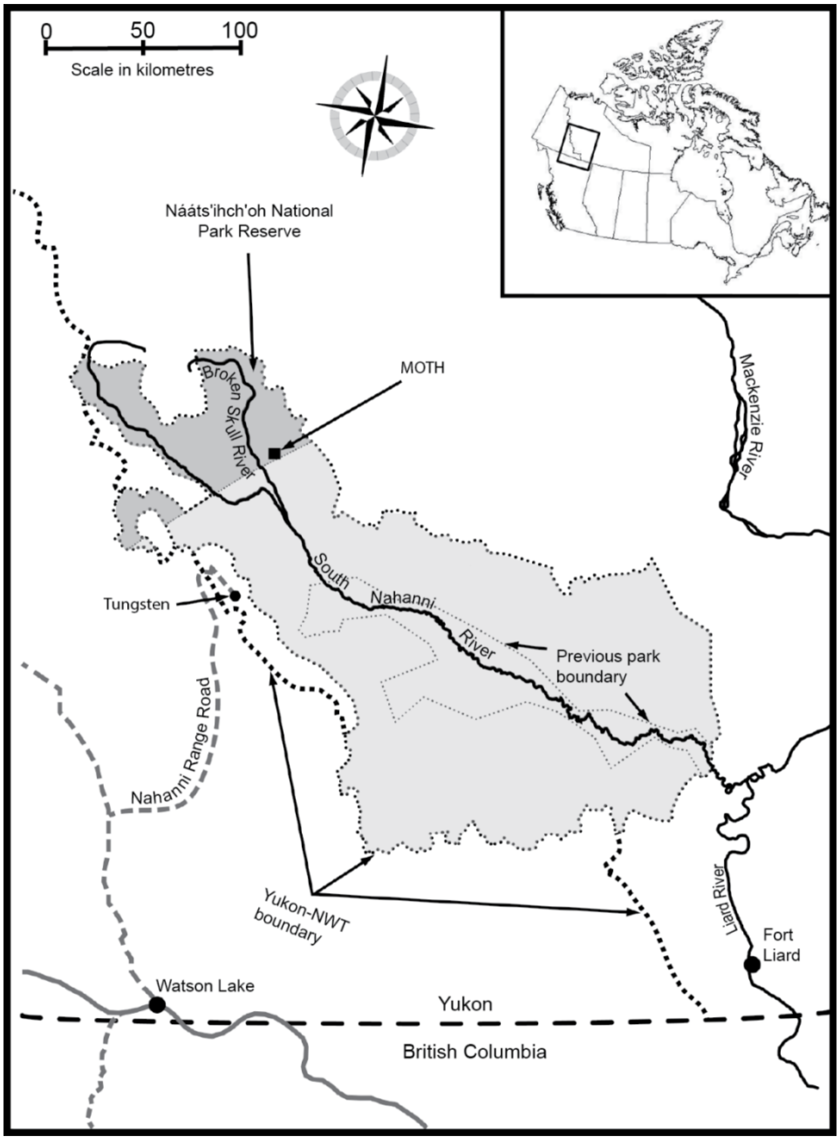
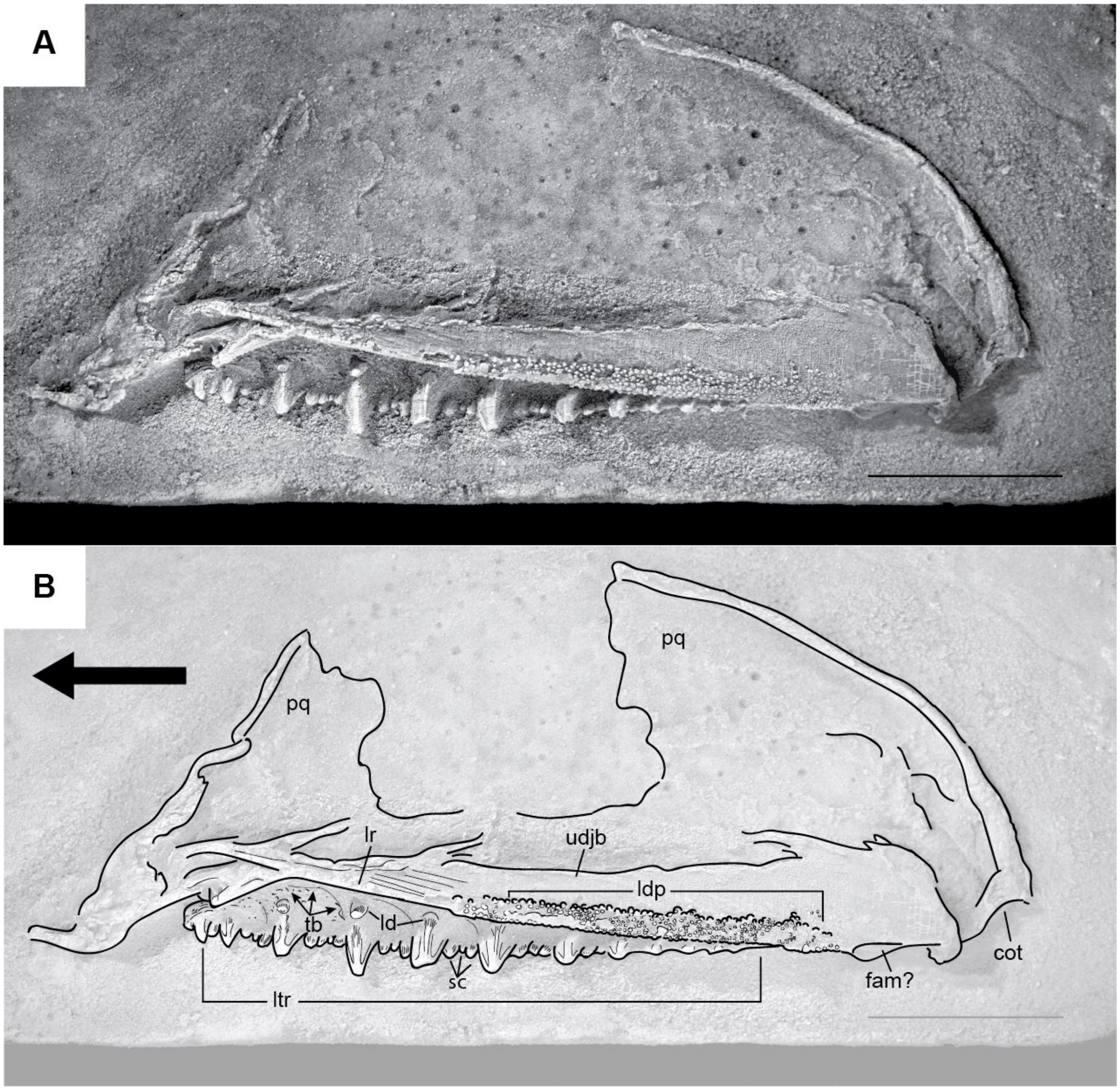


FIGURE 3.1. Map showing the location of the MOTH (Man on the Hill) locality (section 43 of Gabrielse et al. (1973)) (= GSC locality 69014), directly below which is the Silurian (Homerian or Gorstian) B-MOTH fish layer UALVP Locality 970, southern Mackenzie Mountains, Northwest Territories, within Nááts'ihch'oh National Park Reserve.

FIGURE 3.2 (following page). *Euryacanthus serratus*, sp. nov., from the B-MOTH fish layer of the MOTH locality, Northwest Territories, Canada. **A**, **B**, holotype specimen (UALVP number not yet assigned), complete upper right dentigerous jaw bone and associated palatoquadrate cartilage, right lingual view; **A**, full specimen; **B**, labelled trace of specimen. **Abbreviations**: **cot**, articular cotylus; **fam?**, fossa for the adductor mandibulae; **ld**, lingual denticle; **ldp**, lingual denticle patch; **lr**, lingual ridge; **ltr**, lateral tooth row; **pq**, palatoquadrate cartilage; **sc**, secondary cusps; **tb**, tooth base; **udjb**, upper dentigerous jaw bone. Arrow indicates anterior. Scale bar equals 1 cm.


A
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pq
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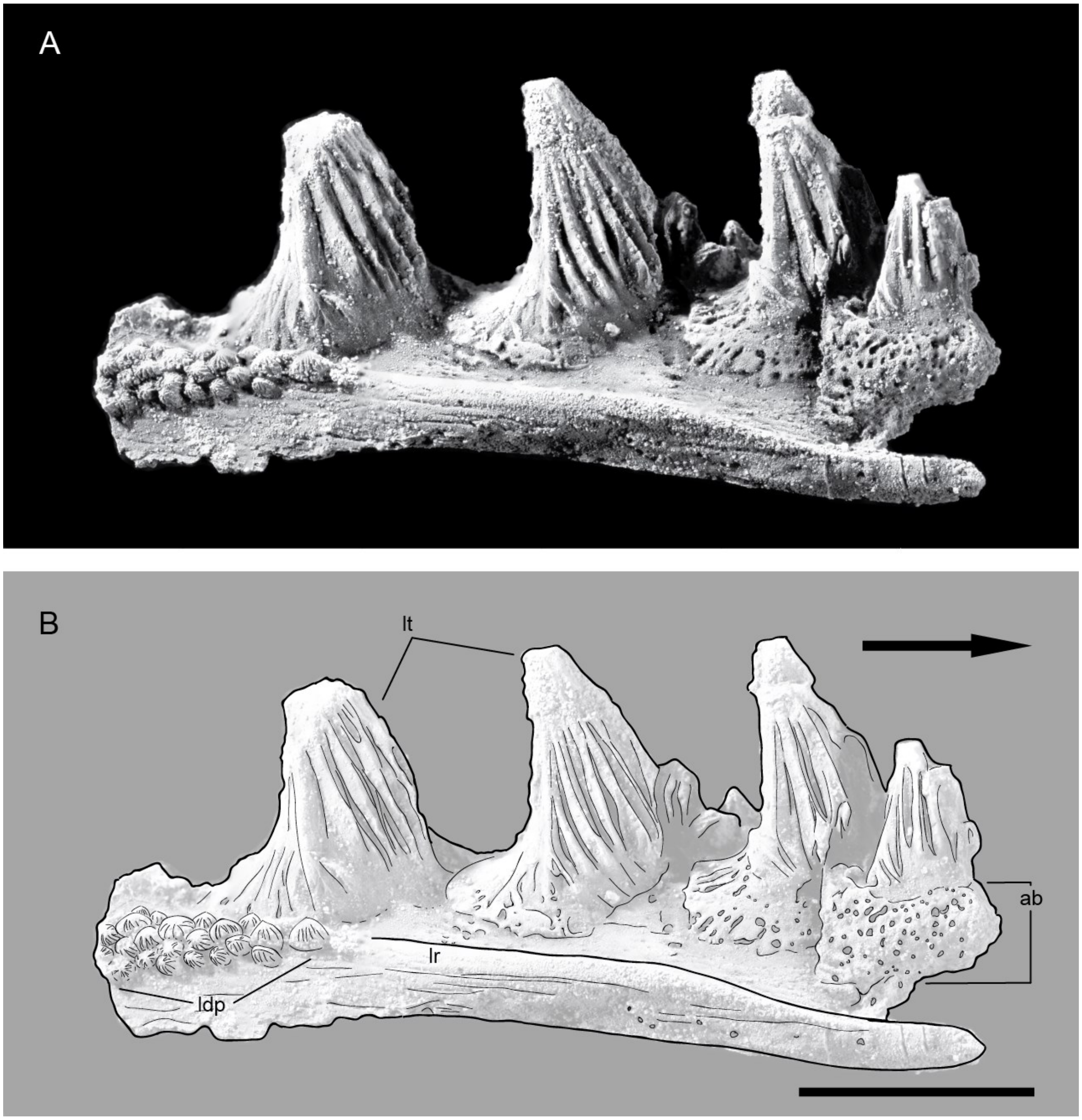

FIGURE 3.3 *Oroichthys theobromodon*, gen. et sp. nov., from the B-MOTH fish layer of the MOTH locality, Northwest Territories, Canada. **A**, **B**, holotype specimen (UALVP number not yet assigned), partial dentigerous jaw bone, lingual view; **A**, full specimen; **B**, labelled trace of specimen. **Abbreviations**: **ab**, attachment bone; **ldp**, lingual denticle patch; **lr**, lingual ridge; **lt**, lateral tooth. Arrow indicates anterior. Scale bar equals 5 mm.

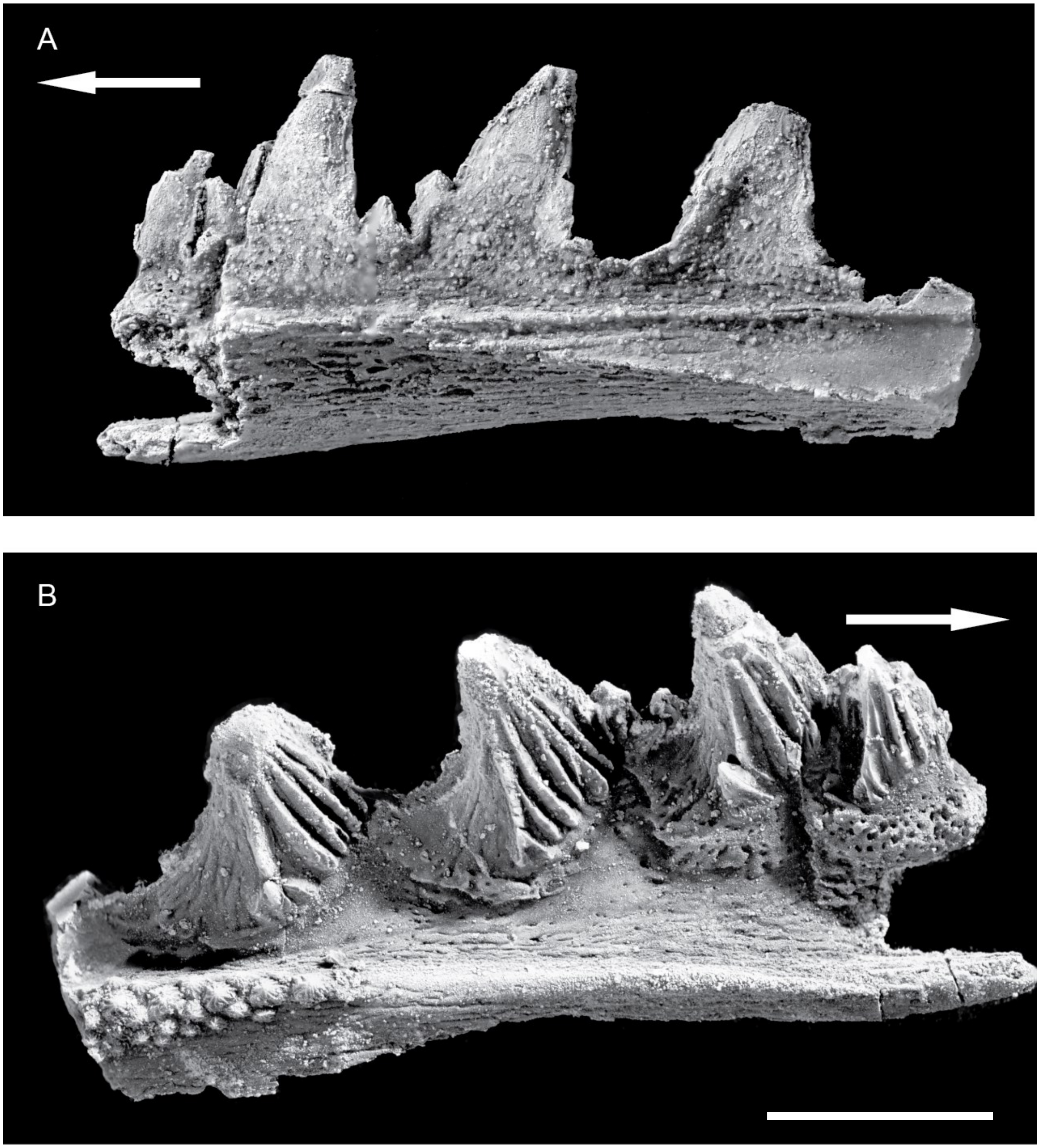

FIGURE 3.4. *Oroichthys theobromodon*, gen. et sp. nov., from the B-MOTH fish layer of the MOTH locality, Northwest Territories, Canada. **A**, **B**, holotype specimen (UALVP number not yet assigned), partial dentigerous jaw bone; **A**, labial view; **B**, occlusal view. Arrows indicate anterior. Scale bar equals 5 mm.

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CHAPTER 4

TOOTH OCCLUSION AND TROPHIC NICHE DIFFERENTIATION IN EARLY DEVONIAN ISCHNACANTHIFORMES

ABSTRACT

Acanthodians have recently become the focus of several phylogenetic analyses, as they may represent a paraphyletic assemblage of early chondrichthyans, osteichthyans, stem gnathostomes, or some combination of the three. One of the difficulties in determining the phylogenetic affinities of this group of small, spiny fishes is that several subgroups of acanthodians are represented by relatively little information in the fossil record. It is becoming increasingly apparent that in order to understand the evolution of gnathostomes, we must understand more about acanthodians. This study uses micro-Computed Tomography to test previously uncontested hypotheses about acanthodian jaw function, and in doing so provides valuable insight into the form, function, and ecological role of ischnacanthiform acanthodian jaws and teeth from an extraordinary Early Devonian fossil locality in the Northwest Territories of Canada. The results of this study suggest that ischnacanthiform acanthodians coexisted by trophic niche differentiation, employing specialized, complex feeding strategies during the Early Devonian.

INTRODUCTION

Acanthodians were generally small, spiny fishes that are represented in the fossil record from the Early Silurian (Hanke et al., 2001a; Karatajute-Talimaa et al., 2002; Burrow, 2003a) to the Permian (Denison, 1979) by mostly disarticulated scales, fin spines, and teeth. Recently, several phylogenetic analyses have suggested that acanthodians as a group are most likely paraphyletic and possibly polyphyletic, branching off either the chondrichthyan stem, the osteichthyan stem, the gnathostome stem, or some combination of the three (Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015; Long et al., 2015a). It has become increasingly clear that understanding acanthodians is integral to our understanding of early gnathostome phylogenetic relationships, and that conditions in acanthodians may reflect the primitive conditions for at least some crown group gnathostomes.

Compounding the problem of acanthodian interrelationships is the relative dearth of fossil material and lack of comparable characters among acanthodians and between acanthodians and other gnathostome groups. Articulated acanthodian specimens are rare, particularly ischnacanthiform acanthodians (Burrow, 2004a; Burrow and Rudkin, 2014). The vast majority of ischnacanthiform acanthodian specimens are disarticulated dermal tooth-bearing elements, or dentigerous jaw bones (Long, 1986; Hanke et al., 2001a; Burrow, 2004a, 2007; Hairapetian et al., 2006; Voichyshyn and Szaniawski, 2012), the synapomorphy of the group. These dentigerous jaw bones are often found singly, and represent the only source of information upon which to base diagnosis and description of new species. Although the dentition is used to describe and differentiate new species of ischnacanthiform, very few studies have focussed on comparing dental characters among gnathostome groups, or attempting to use the dentition to provide insight into ischnacanthiform acanthodian ecology or biological role. As a result, we understand relatively little about how ischnacanthiform acanthodians interacted with each other or the other organisms inhabiting their environment; we know what their jaw bones looked like, but are of necessity less confident in interpreting how they may have functioned.

Understanding feeding mechanics in these very early jawed vertebrates is integral to our understanding of the ecosystems in which they lived. Feeding mechanisms in extant fishes are often highly variable among species, and jaws and teeth provide valuable information about their ecological and biological roles (Darras, 2012; Bellwood et al., 2014; Gibson, 2015). Despite the relatively poor fossil record, paleontologists have made attempts to characterize jaw occlusion and feeding mechanics in ischnacanthiform acanthodians. The eminent paleohistologist Tor Ørvig, in his work on acanthodian dentitions (Ørvig, 1973), described the jaw occlusion in ischnacanthiforms as interlocking, with the tooth cusps on one jaw bone coming into contact with the inter-tooth pit on the medial side of the opposing jaw bone. Ørvig (1973) suggested this type of occlusion also explained the type of tooth wear exhibited in ischnacanthiforms, in which the posteriormost teeth were worn down to 'stumps' by striking against this opposing inter-tooth pit. Burrow (2004), in her review of acanthodians with dentigerous jaw bones, suggested that the jaws of Silurian–Early Devonian ischnacanthiforms occluded in dorsoventral cog-like action, and agreed with Ørvig's (1973) interpretation of the tooth wear. According to these interpretations, the teeth were blunted by occluding with the inter-tooth pit of the opposing jaw bone. The older, posteriormost teeth were thus worn down from this contact, explaining why the posterior teeth in most ischnacanthiform acanthodians are short and blunt, as opposed to the longer, more fang-like teeth at the anterior end of the jaw bones. The jaws of Middle–Late Devonian forms, according to Burrow (2004), occluded in a more complex shearing action that sharpened, rather than blunted, the teeth. The later ischnacanthiformes were interpreted to employ more sophisticated feeding strategies than their Silurian–Early Devonian predecessors.

Both of these studies were based primarily on observations of isolated dentigerous jaw bones, and the majority of these had been taphonomically distorted and flattened. In this study, I use well-preserved fossils from the Northwest Territories of Canada to reconstruct ischnacanthiform acanthodian jaws to attempt to provide insight into their life position and occlusion. Fossils from the Early Devonian Man On The Hill (MOTH) locality present a unique opportunity to observe early vertebrates in exquisite anatomical detail. Extraordinarily well-preserved fossils of acanthodians and stem-chondrichthyans, as well as of many agnathan taxa, have been recovered (Wilson and Caldwell, 1998; Hanke et al., 2001a, 2001b; Hanke, 2002; Hanke and Wilson, 2004, 2006; Blais et al., 2011, 2015; Scott and Wilson, 2012), including nearly complete articulated specimens of ischnacanthiform acanthodians (Fig. 4.1). Specimens of ischnacanthiform acanthodians from MOTH, when articulated, are commonly preserved with their mouths tightly closed and the lateral surfaces of their jaws either exposed or covered by superimposed scales. When the teeth are visible, they appear to occlude in a tightly interlocking fashion, with each tooth cusp medial to and hidden from view by the lateral anteroposterior flanges of the opposing teeth (Fig. 4.1B, C). These specimens do not appear upon first observation to fit the pattern for Silurian-Early Devonian ischnacanthiforms proposed by Burrow (2004), although they do seem to closely match the interlocking occlusion proposed by Ørvig (1973).

In addition to articulated specimens, disarticulated ischnacanthiform jaws are also relatively abundant at the MOTH locality (Fig. 4.2). These are, unusually, often preserved with their associated mineralized cartilages, allowing them to be readily identifiable as upper or lower jaws. In addition, several specimens have been recovered comprising articulated pairs of upper and lower jaws, with their associated cartilages.

These articulated jaws offer an unprecedented opportunity to more accurately reconstruct the position and occlusion of the jaws as it may have been in life.

These articulated jaws also provide the opportunity to indirectly test hypotheses about the possible ecology of these animals. Based on the relationship between species coexistence and trophic niche partitioning in analogous extant and extinct taxa (Purnell et al., 2006, 2012; Knickle and Rose, 2013; Polačik et al., 2013), such closely related coexisting animals as have been described from the MOTH locality would be expected to have exploited different food sources. Due to the lack of direct fossil evidence such as stomach contents or coprolites, this hypothesis has not previously been tested the MOTH ischnacanthiforms.

To determine whether the jaw occlusion of different MOTH ischnacanthiforms suggested they could have exploited different food sources, specimens of articulated pairs of upper and lower jaws from two different species of ischnacanthiform from the MOTH locality, *Euryacanthus rugosus* and *Tricuspicanthus gannitus* (Fig. 4.2), were isolated from the surrounding matrix and scanned using micro-computed tomography (μCT) to create three-dimensional reconstructions. Once reconstructed, the jaws were manipulated digitally in order to gain a better understanding of how they could have occluded in life.

METHODS

Specimen preparation and photography

Specimens described in this study are housed in the UALVP collections. The calcareous matrix of argillaceous limestone in which fossils from MOTH are preserved was removed from the fossils using a solution of dilute acetic acid and soft brushes;

fossils were stabilized using a 5% solution of Glyptal cement in acetone. The specimens were whitened using ammonium chloride sublimate and photographed using a Zeiss Discovery V8 stereomicroscope and Nikon NIS-Elements F 2.20 imaging software. With the exception of holotype specimens, the fossils were then embedded in Buehler EpoThin Low Viscosity Resin and Hardener and prepared from the buried side in order to remove the remaining matrix, separating the fossil entirely from the matrix to facilitate CT scanning.

X-Ray Computed Tomography and reconstruction

Specimens UALVP 45648 and 48487, representing the ischnacanthiform species *Euryacanthus rugosus* and *Tricuspicanthus gannitus,* respectively (Fig. 4.2), were scanned using a SkyScan 1172 μCT scanner. Slice data were analysed using OsiriX, Mimics and Avizo 6.3. A stereolithography (STL) surface mesh of the three-dimensional geometry was created in Mimics from the stacked DICOM (Digital Imaging and Communications in Medicine format) images acquired by the CT scanner. Each STL was then imported into Geomagic Studio 6 software. Geomagic was used to reconstruct broken or missing teeth, using intact specimens of the same species for reference, and was used to fill in the labial side of UALVP 45648, which was not embedded and prepared out of the matrix due to its stature as holotype for the species (it was reconstructed on the lingual side only). Three-dimensional surface meshes were created for the flattened specimens and manipulated to determine their occlusion. The surface meshes were then retrodeformed using Geomagic until the curvature of the ischnacanthiform jaws more closely resembled the curvature of the jaws in related

Devonian fossil specimens (Fig. 4.3), including *Ptomacanthus anglicus* Miles, 1973, redescribed by Brazeau (2009), *Doliodus problematicus* (Woodward, 1982) based on CT data presented by Maisey et al. (2009, 2014), and *Gogoselachus lynbeazleyae* Long et al., 2015. The curved reconstructions were then re-examined to determine whether the interpretation of their occlusal style was significantly affected by their taphonomic deformation. CT scans are reposited at the University of Alberta.

RESULTS

The three-dimensional surface meshes created from the μCT slice data for the flattened specimens revealed different occlusal styles for the two different species. Neither species exhibited a simple up-and-down cog-like style of occlusion in which each cusp proceeded unobstructed to the opposing inter-tooth pit. The occlusion of the teeth was restricted by the anterior and posterior lateral flanges associated with each lateral tooth cusp in *Euryacanthus rugosus*, and by the flanges and posterior teeth in *Tricuspicanthus gannitus*. In the flattened models created for both species (Fig. 4.4), the teeth curve slightly medially and interlock, with each tooth cusp being stopped short of and slightly medially to the opposing inter-tooth pit of the opposing jaw as its anteroposterior flanges contact the flanges associated with the opposing teeth on the opposite ramus of the jaw. The main points of contact are between the anterior and posterior surfaces of each tooth cusp, not between the tip of the tooth cusp and the opposing jaw bone. Regardless of the relative positions of each jaw or the distance between the articular cotylus and condyle of the associated jaw cartilages, this interlocking occlusion is the only way the teeth fit together.

When the surface mesh models were subsequently deformed to reflect the curvature of the jaw elements in related Devonian species (Fig. 4.3, 4.5, 4.6), the teeth fit more closely together than in the flat models. Re-orienting the jaw cartilages 'corrected' the medial curve of the teeth and they occluded more vertically, but the anteroposterior flanges of opposing teeth continued to come into contact with each other before each tooth cusp contacted the inter-tooth pit on the opposing jaw. The teeth still interlock tightly together with the tooth cusps remaining slightly medial to the lateral flanges of the opposing teeth. The main points of contact remain the anterior and posterior surfaces of each tooth cusp. The tooth cusps in both species are unable to contact the inter-tooth pits on the opposing jaws, regardless of the orientation of the jaws.

Euryacanthus rugosus

The anteroposterior flanges are well developed in *Euryacanthus rugosus*, and the teeth occlude tightly together in this species (Fig. 4.4, 4.5). The large lateral teeth curve slightly medially, even in the retrodeformed models. When the anteroposterior flanges of opposing teeth are in contact with each other, each tooth cusp is slightly 'above' (either dorsal or ventral to) and medial to the opposing inter-tooth pit. When the teeth are in contact with each other in the central and anterior part of the jaw as in the articulated specimens, there is very little open space left between each pair of opposing teeth. The smaller teeth at the anterior and posterior ends of the jaw bones do not contact each other. The anteroposterior flanges form an almost continuous surface when the jaws are tightly closed, coming together like scissor blades. The jaw bones themselves are curved dorsoventrally, so that at the anterior end of the jaws the distance between the upper and lower jaw bone is greatest. Based on articulated ischnacanthiform specimens, this space was probably occupied by large tooth whorls anterior to both the palatoquadrates and Meckel's cartilages.

The lateral teeth are broad, with longer posterior flanges than anterior flanges, and slightly recurved. When the lower jaw is moved relative to the upper jaw to close the jaws, the teeth occlude in a shearing motion. Each upper tooth cusp contacts and shears down the posterior surface of the opposing lower tooth until the posterior flanges contact each other.

Tricuspicanthus gannitus

The lateral teeth in *Tricuspicanthus gannitus* are less broad than the teeth in *Euryacanthus rugosus*, with smaller anterior and posterior labial flanges. The teeth are also larger relative to the overall size of the jaws and more widely spaced than those in *E. rugosus*. Because of this, the anteriormost teeth do not occlude as closely together, and there is space left between the opposing anteriormost teeth when the jaws are closed (Fig. 4.4, 4.6). The teeth near the centre of the jaws occlude tightly, but the posteriormost teeth do not contact the posteriormost teeth on the opposing jaw. The anteriormost and the largest tooth cusps are prevented from contacting the inter-tooth pits on the opposing jaw bone by their associated anterior and posterior labial flanges, which come into contact with the base of the opposing tooth. If the jaw joint is disarticulated, the space between the anteriormost teeth is reduced, but the teeth still do not contact the opposing inter-tooth pits. The main points of contact on the anteriormost teeth appear to be the lower half of each tooth cusp with the anteroposterior labial flanges of the opposing teeth. The teeth in *T. gannitus* also appear to occlude via a more vertical motion than the teeth in *E. rugosus*, but there is still an element of shear in the anteriormost teeth. There is also less distance between the anterior ends of the upper and lower jaws than in *E. rugosus*, which is likely related to the smaller tooth whorls in this species.

Interestingly, the robust medial teeth in *Tricuspicanthus gannitus* never come into contact with the medial teeth of the opposing jaw, regardless of how the jaws are manipulated. If the lateral teeth occlude in the interlocking manner indicated by the articulated specimens, the medial teeth cannot occlude. Instead, they project 'up' (either dorsally or ventrally) and slightly medially into the mouth cavity (Fig. 4.6).

DISCUSSION

Trophic niche differentiation

The three-dimensional models created for the two species in this study reveal two different and distinct styles of jaw and tooth occlusion. As these species were coeval, the hypothesis that ischnacanthiforms can be grouped chronologically based on their jaw occlusion types (Burrow, 2004) must therefore be rejected. Although the occlusion in *T. gannitus* is closer to the cog-like vertical tooth closure suggested by Burrow (2004) than is the occlusion in *E. rugosus*, neither species fits the model proposed for Silurian-Middle Devonian ischnacanthiformes. The teeth in both species occlude in an interlocking fashion similar to that proposed by Ørvig (1973), with a precision unusual for fishes. Because these animals retained their teeth throughout their lives without replacing them, very precisely aligning teeth may have been advantageous. Conversely, if a single tooth was out of alignment with the rest of the teeth in the jaw, the animal's ability to bite effectively would likely have been greatly impacted. In this sense, tooth occlusion in ischnacanthiform acanthodians may be more comparable to that in most mammals and some other tooth-retaining tetrapods than to that in polyphyodont taxa like chondrichthyans and most bony fishes.

Similarly to the condition in mammals, it is possible that the differences in the tooth morphology and occlusion between the two species of ischnacanthiforms reflect differences in biting and feeding strategies, which were evidently more varied than expected in at least some Early Devonian ischnacanthiforms. The employment of different biting or chewing strategies by coeval ischnacanthiforms at the MOTH localtity provides support for the hypothesis that these two species could possibly have coexisted by partitioning of trophic niches and specialization in prey sources. This also supports the hypothesis proposed by Choo et al. (2014) that early gnathostomes had likely undergone significant trophic niche differentiation by the Devonian.

In addition to the indication that the two species of ischnacanthiforms could have specialized in different food sources, the three-dimensional models also provide some insight into the possible ecological role of each species. The shearing, interlocking occlusion, fang-like curved tooth cusps and sharp, smooth anteroposterior tooth flanges present in *Euryacanthus rugosus* (Fig. 4.5) suggest that it could have been an effective predator of large prey (relative to its body size), including soft-bodied animals. Tightly interlocking teeth have been suggested as an indicator of macrophagy in crocodylians (Young et al., 2012), and the anteroposterior flanges would have formed an almost continuous slicing or cutting surface. The teeth in *E. rugosus* also have longitudinal ridges (Blais et al., 2015), which in other taxa have been suggested to indicate the presence of plicidentine (Meunier et al., 2014). A histological analysis of the teeth would be required to confirm this in *Euryacanthus*. Plicidentine has been hypothesized to strengthen the attachment of the teeth to the tooth-bearing element of the jaw, particularly in active predators (Scanlon and Lee, 2002; Modesto and Reisz, 2008; Maxwell et al., 2011a, 2011b; Meunier et al., 2014). *Euryacanthus rugosus* was also one of the largest ischnacanthiform acanthodians from the Early Devonian MOTH locality, although compared to ischnacanthiforms from other localities and ages, it was still rather small. Taken together, the relative size, jaw occlusion, and tooth morphology including the possible presence of plicidentine suggest an actively predatory ecological role for *E. rugosus*.

Because *Euryacanthus rugosus* has a single row of teeth on each jaw bone, the tooth occlusion in this species is relatively simple compared to that of *Tricuspicanthus gannitus*. *Tricuspicanthus gannitus* has multiple rows of teeth on each jaw bone and is monognathically heterodont, with striking differences in tooth morphology and occlusion between its lateral and medial dentition (Fig. 4.4, 4.6). The lateral teeth in *T. gannitus* are long, widely spaced, and caniniform, typical of the 'piercing graspers' of Bellwood et al. (2014). These teeth could have been well suited to puncturing soft prey. The medial teeth, however, are blunt, robust, and low-crowned, typical of animals interpreted to be durophagous (Pregill, 1984; Motani, 2005; Choo et al., 2014; Crofts and Summers, 2014). Two very different forms of teeth on the same tooth-bearing element in the jaw could be indicative of several possible feeding strategies. Perhaps *Tricuspicanthus gannitus* exploited a wide range of food sources, using its lateral dentition to puncture softer prey and using its robust medial teeth to crush hard-shelled animals such as bivalves or arthropods, certainly present at the MOTH locality during the Early Devonian. Alternatively, it may have specialized in hard-shelled prey, grasping with its lateral teeth and crushing with its medial teeth. This type of strategy has been proposed for *Megamastax amblyodus* Choo et al., 2014, and could have also been employed by *Tricuspicanthus gannitus*.

It is interesting to note, however, that the medial teeth of the upper and lower jaws in this species cannot come into contact with each other, indicating that *Tricuspicanthus gannitus* would have only been able to effectively crush shelled prey that was larger than the gap between the upper and lower medial tooth rows. This suggests that not only might *T. gannitus* have specialized in hard-shelled prey, but specifically in large hard shelled prey ("large" being relative to the size of *T. gannitus*, one of the smallest ischnacanthiforms from MOTH). Of the possible candidates for such prey known from the MOTH locality, eurypterids and molluscs seem the most likely. It is also possible that *T. gannitus* could have ingested small, subadult heterostracans or osteostracans, fossils of which have been recovered from the MOTH locality (Greeniaus and Wilson, 2003; Hawthorn et al., 2008). One other possibility is that *Tricuspicanthus gannitus* specialized in hard-shelled prey until it reached a certain size; perhaps while its lateral dentition remained relatively small, its medial dentition could have been more effective on smaller prey such as ostracods, also relatively abundant at the MOTH locality (Zorn et al., 2005). Judging from the relative abundance of specimens of *T. gannitus* compared to the other ischnacanthiform species from MOTH (Blais et al., 2015), whatever feeding strategy it employed seems to have been a successful one.

Tricuspicanthus gannitus has very tightly packed, needle-like lip scales that cover the posterior half of the jaws in articulated specimens (Blais et al., 2011). These lip scales appear to form a continuous cover, intermeshing with no obvious diving line between the posterior part of the upper and lower halves of the jaws (Fig. 4.7). This indicates that the posterior region of the mouth in these animals was enveloped by a layer of skin, which would have supported the scales. Effectively, *Tricuspicanthus gannitus* may have had cheeks. They also possessed tiny, sharp scales lining the inside of the oral cavity (Blais et al., 2015). If these ischnacanthiforms were eating soft-bodied prey or separating the soft parts from hard-shelled prey, perhaps the combination of a membranous cheek and sandpaper-like roughened internal oral surface combined to prevent the prey tissue from sliding out of the mouth during processing and position is more precisely for chewing. Taken together, these features suggest that complex feeding habits, including post-capture processing of prey, were present in *Tricuspicanthus gannitus.*

Tooth wear in ischnacanthiforms

According to the hypotheses posited by Ørvig (1973) and Burrow (2004), the posterior tooth cusps in Early to Middle Devonian ischnacanthiform acanthodians were worn down to “stumps” by regularly coming into contact with the inter-tooth pit on the occlusal surface of the opposing jaw bone. If the tips of the posterior tooth cusps were being ground away by such contact, one would expect the orthodentine layer of the apices of the posteriormost tooth cusps to be truncated and worn away, exposing the pulp cavities. Thin sections of ischnacanthiform dentigerous jaw bones from the Man On The Hill locality have revealed that this is not the case, and that the orthodentine layer covering the posteriormost teeth is continuous with that covering the anteriormost teeth (MacKenzie, 2008). The posteriormost tooth cusps do not appear to be significantly worn relative to the anteriormost tooth cusps, and the pulp cavities in the posteriormost teeth are not exposed.

This lack of significant wear on the posteriormost tooth cusps relative to the anteriormost tooth cusps can be explained using the model of jaw and tooth occlusion proposed in this study. The main points of contact between teeth according to the three-dimensional models of *T. gannitus* and *E. rugosus* jaws were not the apices of the tooth cusps, but the anterior and posterior medial surfaces of the tooth cusps. These surfaces are smooth in most ischnacanthiforms from the MOTH locality; in species with medial denticles or cuspules associated with each tooth cusp, these are medial to the center of the tooth cusp, with smooth unornamented regions on the anterior and posterior surfaces. A newly discovered specimen of Silurian ischnacanthiform from the MOTH locality (described in Chapter 3 of this thesis; Fig. 3.2) provides the first unequivocal evidence of tooth-on-tooth wear in these animals. Though not a member of one of the species for which the three-dimensional models were created, it was likely closely related, based on similar tooth and jaw morphology. It is likely that its jaws could have occluded in an interlocking, shearing manner similar to that of *E. rugosus*. It has prominent wear facets on the anterior and posterior lingual surfaces of its lateral tooth cusps that do not extend to the apex of the tooth cusp. This wear pattern supports the manner of occlusion proposed here, in which the teeth interlock and the tooth cusps do not come into contact with the inter-tooth pits of the opposing jaw bone. This evidence of interlocking tooth-tooth contact also supports the hypothesis that these fishes were likely active predators consuming relatively large prey, and that acanthodians were specialized, predatory feeders by the Late Silurian.

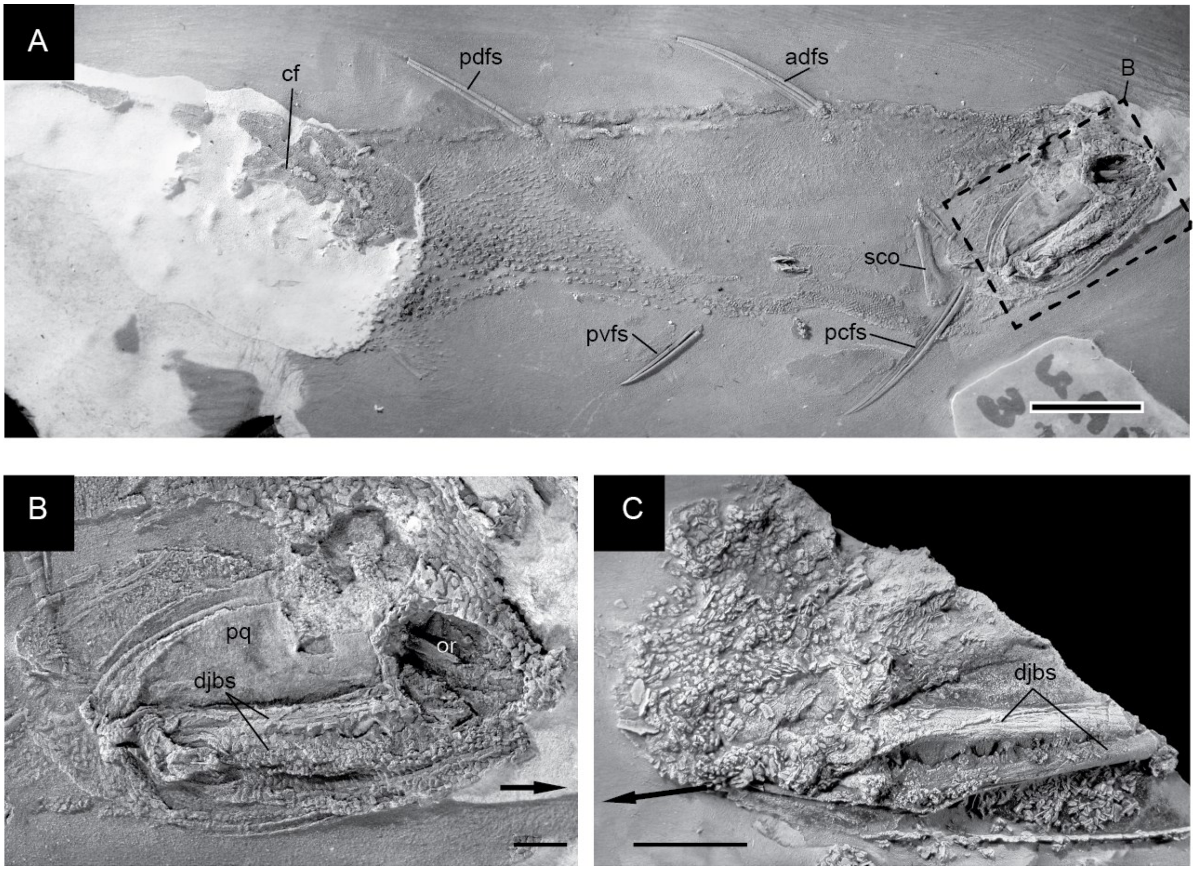
CONCLUSIONS

The use of micro-CT scanning and three-dimensional reconstructions of articulated upper and lower ischnacanthiform jaws has proven to be an effective tool in understanding ischnacanthiform bite mechanics and inferring possible ecological roles for these fishes. Reconstruction of the jaws in a more true-to-life position allowed their occlusion to be more accurately assessed. This study provides valuable insight into the feeding mechanics and ecology of ischnacanthiform acanthodians from the MOTH locality. It also presents a novel application of computed tomography and three-dimensional reconstructions of fossil materials. This method may be useful for interpreting the ecology of similar groups of closely related taxa if more direct means of inferring trophic niche, such as stomach contents or coprolites, are unavailable.

Ischnacanthiforms representing two distinct coeval species, *Euryacanthus rugosus* and *Tricuspicanthus gannitus*, exhibit differing styles of jaw and tooth occlusion. This suggests that these species captured and processed prey differently. This method thus provides support for a hypothesis of trophic niche differentiation and insight into specialized, complex feeding strategies among these ancient vertebrate predators from the Early Devonian MOTH locality.

FIGURES

FIGURE 4.1 (following page). Articulated specimens of ischnacanthiform acanthodians from the Early Devonian MOTH locality. **A**, UALVP 32401, articulated, nearly complete specimen, preserved in right lateral view; **B**, close-up of area outlined by the dashed rectangle in **A**, **C**, UALVP 42055, articulated specimen of the anterior part of the head of an ischnacanthiform acanthodian, preserved in left lateral view. **Abbreviations**: **adfs**, anterior dorsal fin spine; **cf**, caudal fin; **djbs**, dentigerous jaw bones; **or**, orbit; **pcfs**, pectoral fin spine; **pdfs**, posterior dorsal fin spine; **pq**, palatoquadrate cartilage; **pvfs**, pelvic fin spine; **sco**, scapulocoracoid. Arrows indicate anterior in **B** and **C**. Scale bar for **A** and **C** equals 5 mm; scale bar for **B** equals 1 mm.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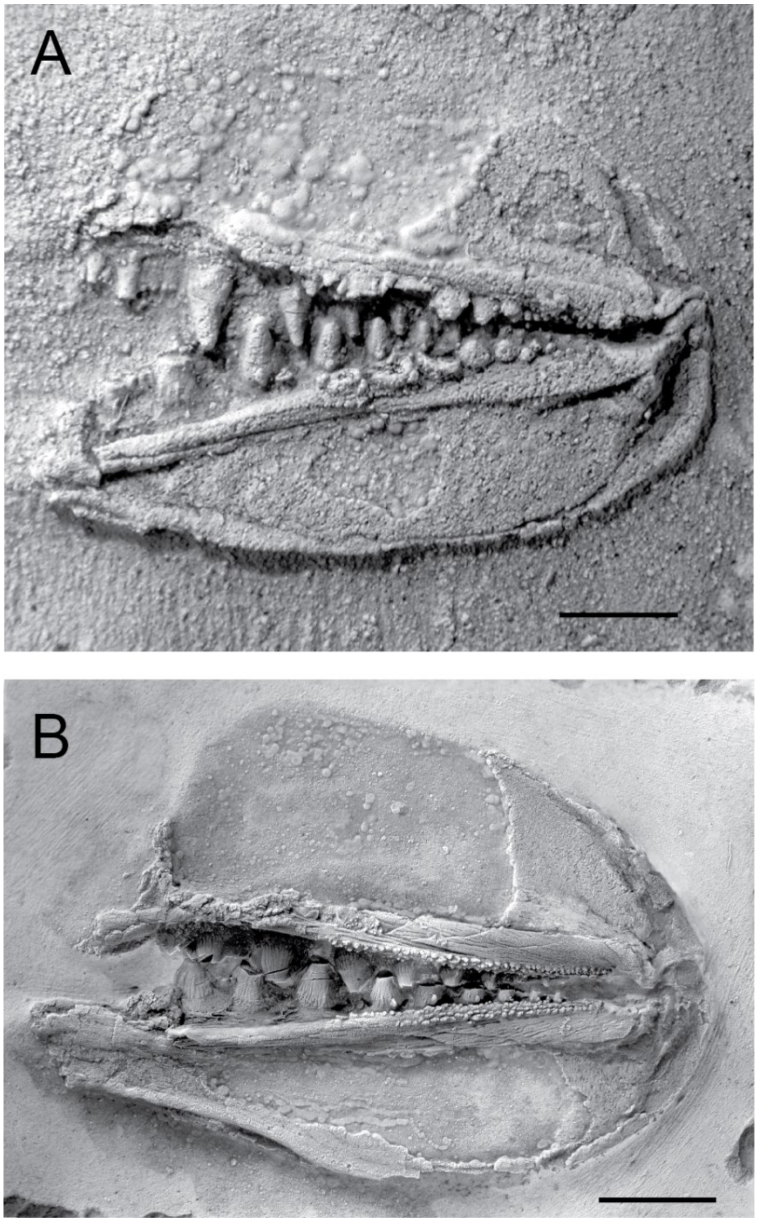

FIGURE 4.2. Articulated upper and lower dentigerous jaw bones and associated cartilages used to create the three-dimensional reconstructions in this study. **A**, UALVP 48487, right upper and lower jaws of *Tricuspicanthus gannitus*, preserved in lingual view; **B**, UALVP 45648; right upper and lower jaws of *Euryacanthus rugosus*, preserved in lingual view. Anterior is to the left. Scale bar for **A** equals 1 mm; scale bar for **B** equals 5 mm.

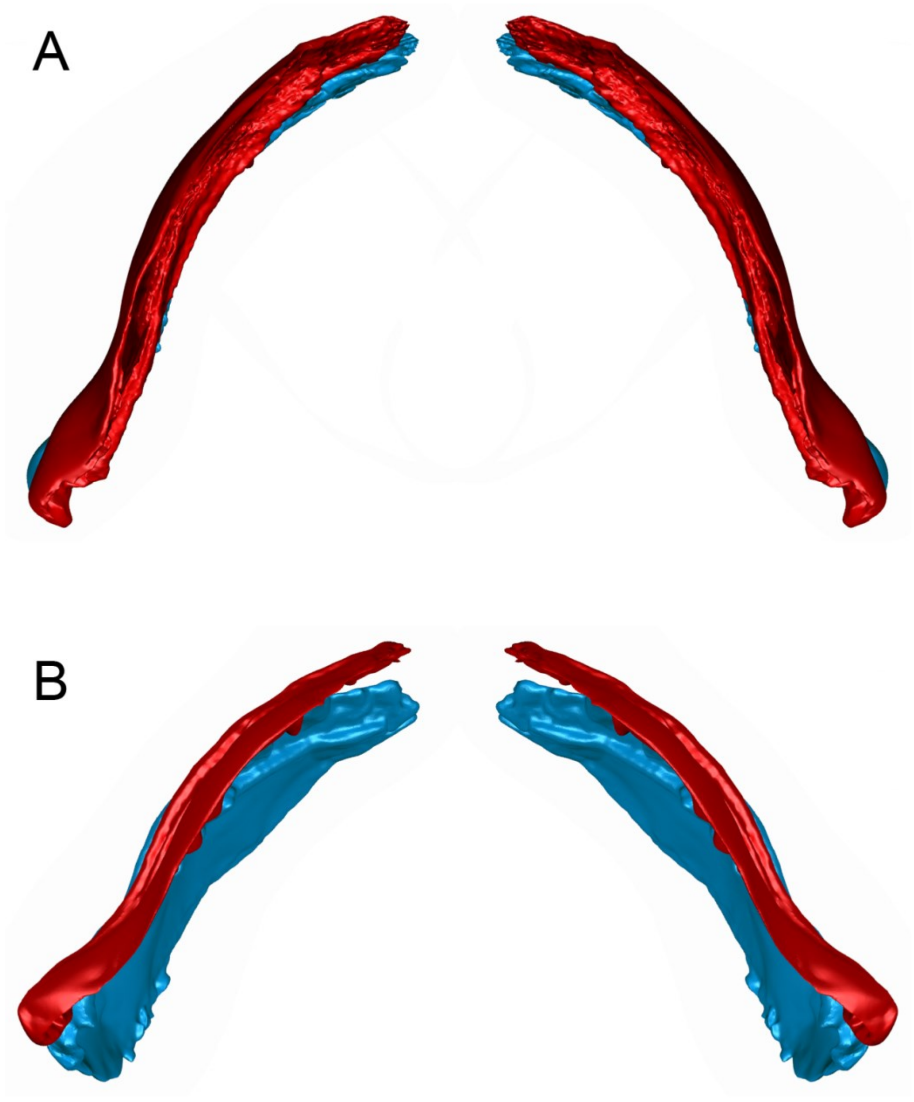

FIGURE 4.3. Three-dimensionally reconstructed ischnacanthiform jaws, retrodeformed to approximate a similar curvature to that of related fossil taxa preserved dorsoventrally or in three dimensions. **A**, reconstructed jaws of *Euryacanthus rugosus*, in dorsal view; **B**, reconstructed jaws of *Tricuspicanthus gannitus*, in dorsal view. The palatoquadrate and upper dentigerous jaw bone are rendered in red, while the Meckel's cartilage and lower dentigerous jaw bone are rendered in blue.

FIGURE 4.4 (following page): Three-dimensional reconstructions of flattened specimens of ischnacanthiform jaws, as preserved at the MOTH locality. **A-B**, reconstruction based on UALVP 45648, holotype of *Euryacanthus rugosus*; **C-F**, reconstruction based on UALVP 48487, *Tricuspicanthus gannitus*. **A**, reconstruction of the jaw of *Euryacanthus rugosus* based on UALVP 45648, lingual view; anterior is to the right; **B**, reconstruction of *Euryacanthus rugosus* in anterior view; **C**, reconstruction of the jaw of *Tricuspicanthus gannitus* based on UALVP 48487, lingual view; anterior is to the left; **D**, reconstruction of *Tricuspicanthus gannitus* in anterior view; **E**, reconstruction of *Tricuspicanthus gannitus* in posterior view; **F**, reconstruction of *Tricuspicanthus gannitus* in lateral view; anterior is to the right. Upper dentigerous jaw bones and palatoquadrate cartilages are rendered in orange; lower dentigerous jaw bones and Meckel's cartilages are rendered in green.

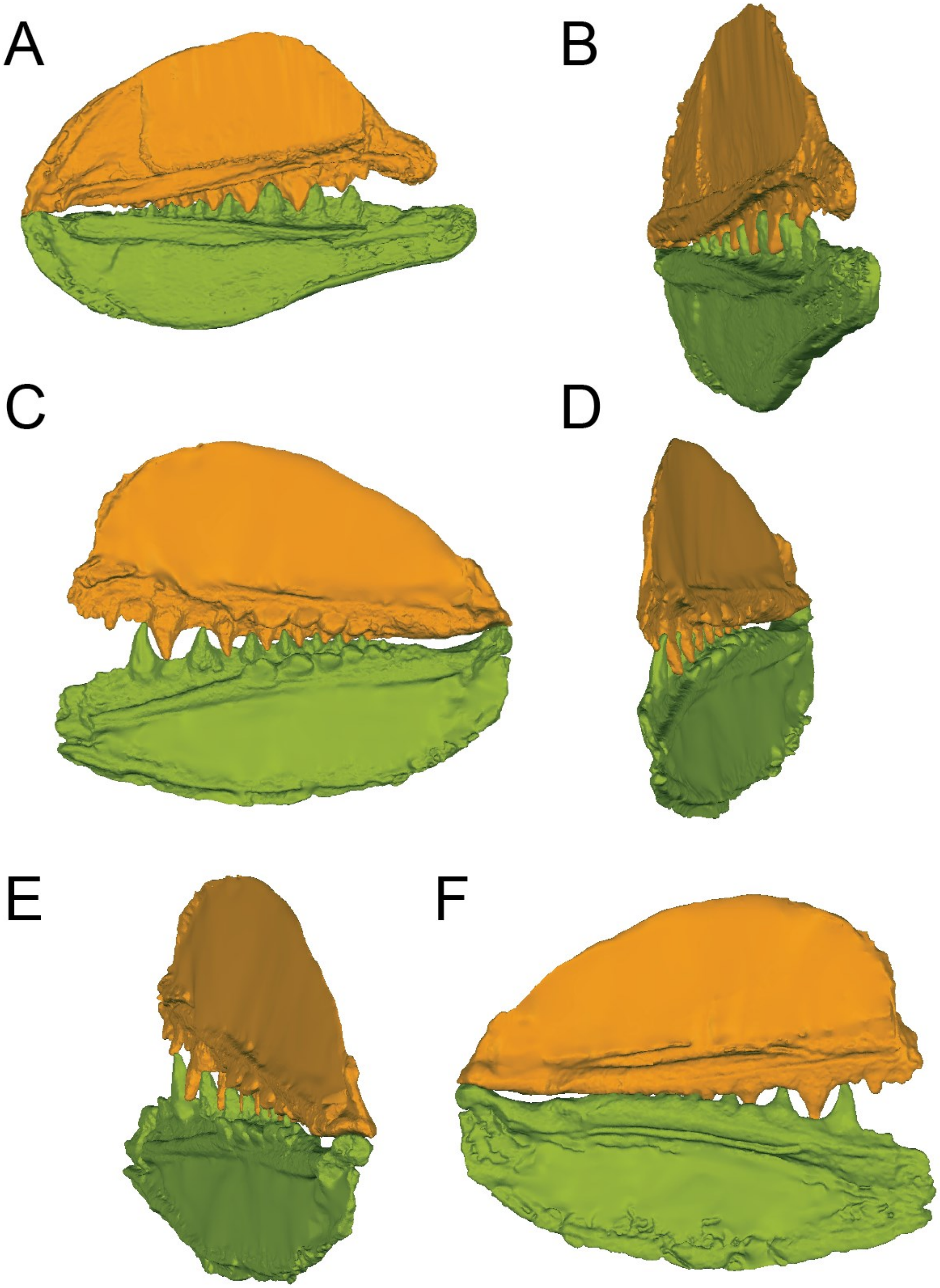
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FIGURE 4.5 (following page): Retrodeformed three-dimensional reconstruction of the jaws of *Euryacanthus rugosus*. **A**, reconstructed jaws in lingual view; anterior is to the right; **B**, reconstructed jaws in anterior view; lingual is to the left. The upper dentigerous jaw bone and palatoquadrate cartilage are rendered in red. The lower dentigerous jaw bone and Meckel’s cartilage are rendered in blue.

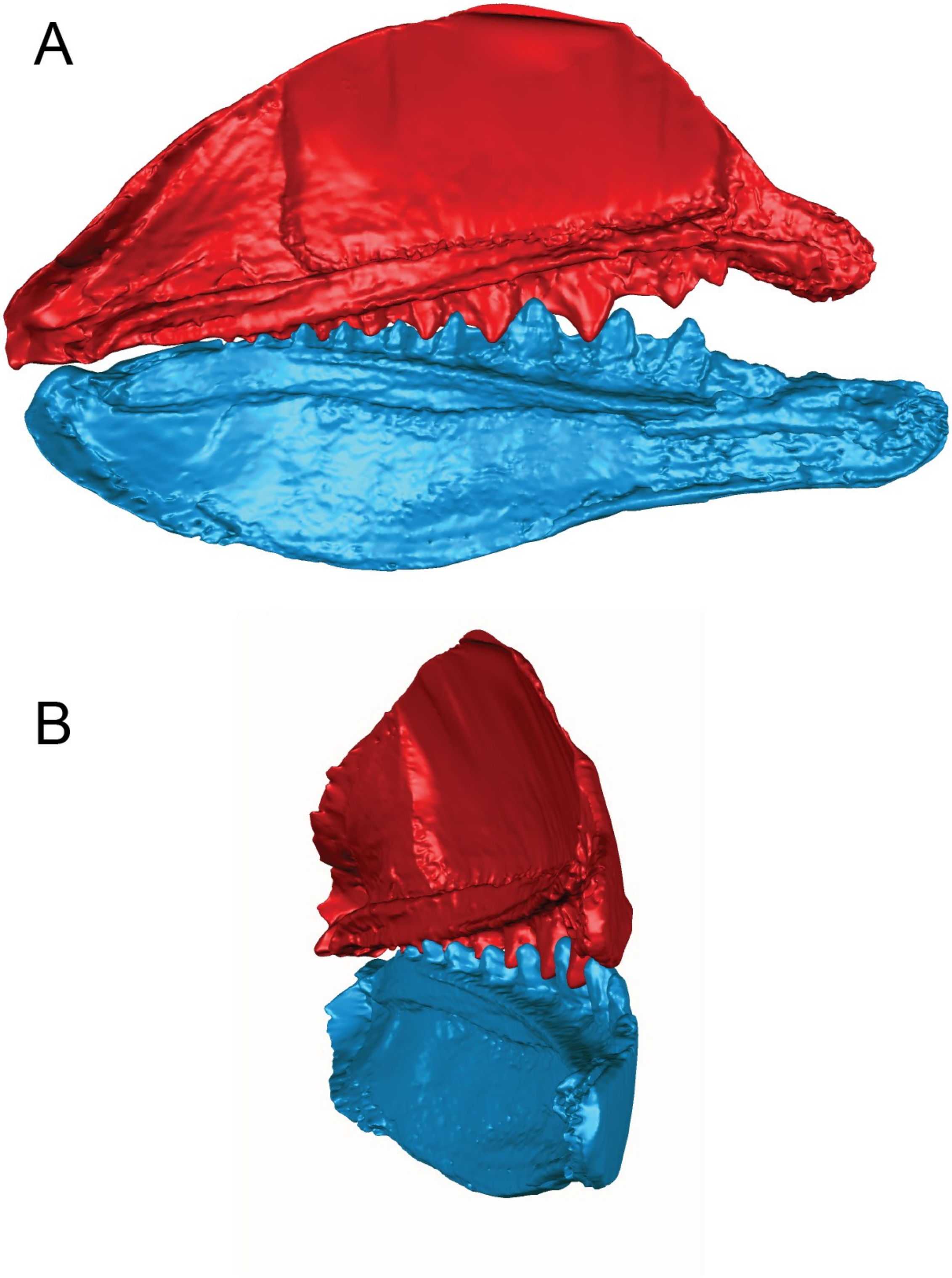
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FIGURE 4.6 (following page): Retrodeformed three-dimensional reconstruction of the jaws of *Tricuspicanthus gannitus*. **A**, reconstructed jaws in lingual view; anterior is to the left; **B**, reconstructed jaws in anterior view; lingual is to the right. The upper dentigerous jaw bone and palatoquadrate cartilage are rendered in red. The lower dentigerous jaw bone and Meckel's cartilage are rendered in blue.

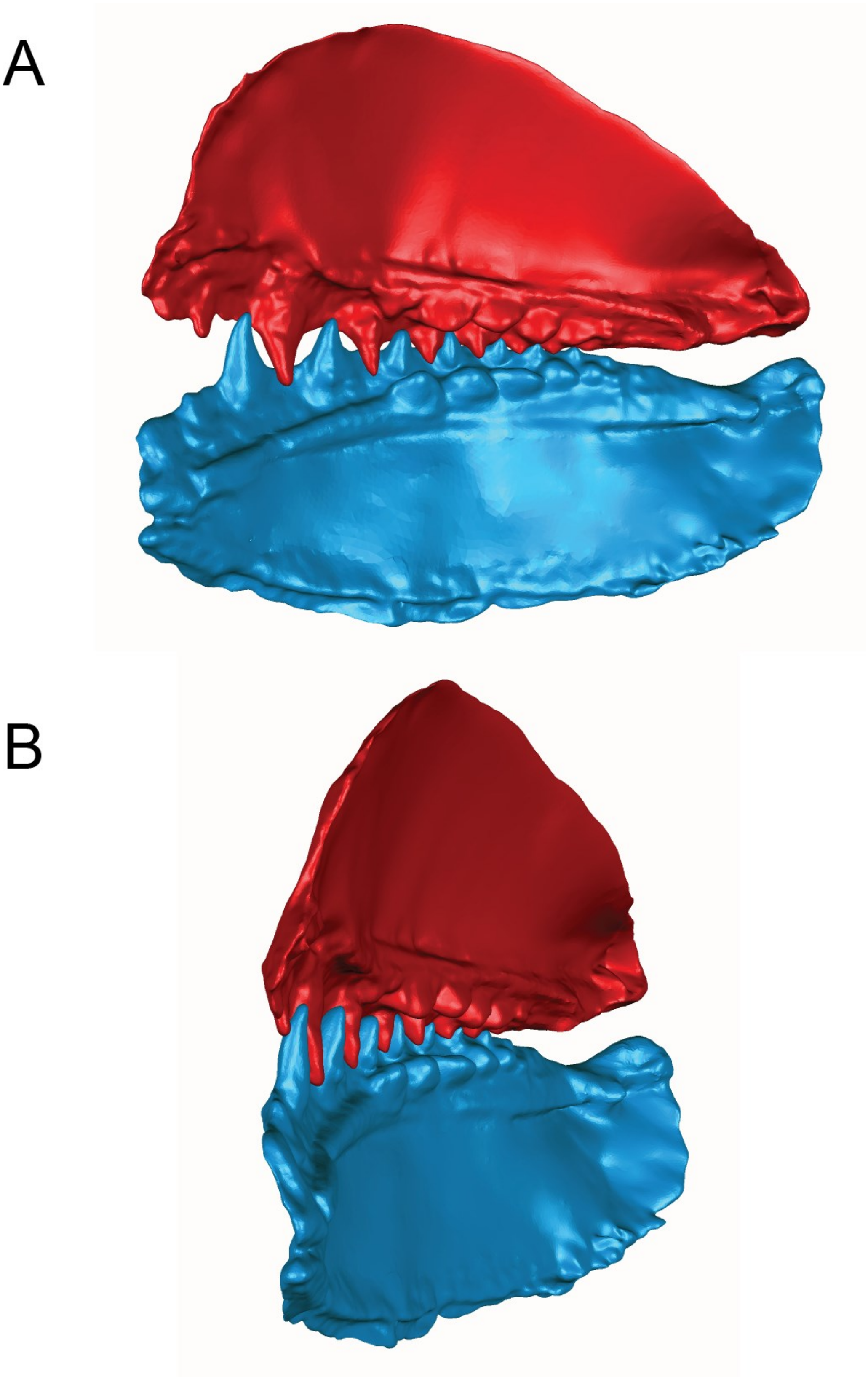
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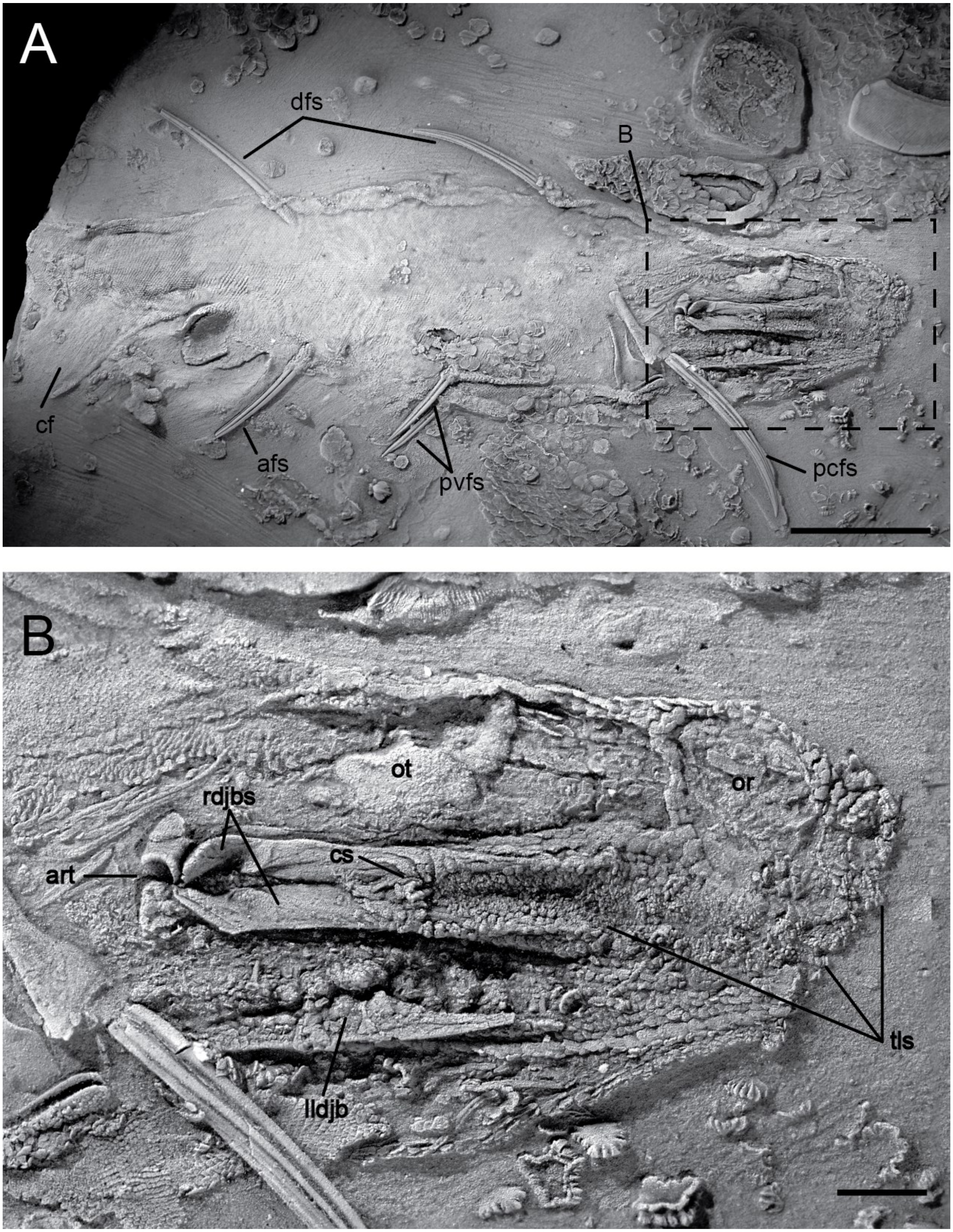
FIGURE 4.7 (following page): Articulated nearly complete specimen of *Tricuspicanthus gannitus*, UALVP 32405. **A**, complete specimen preserved in right lateral view; anterior is to the right; **B**, close-up of area outlined by the dashed rectangle in **A**. **Abbreviations**: **afs**, anal fin spine; **art**, articulation of the palatoquadrate and Meckel's cartilages; **cf**, caudal fin; **cs**, cheek scales; **dfs**, dorsal fin spine; **lldjb**, lower left dentigerous jaw bone; **or**, orbit; **ot**, otic material; **pcfs**, pectoral fin spine; **pvfs**, pelvic fin spine; **rdjbs**, right dentigerous jaw bones; **tls**, tooth-like scales. Scale bar for **A** equals 5 mm; scale bar for **B** equals 1 mm.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CHAPTER 5

TOOTH-LIKE SCALES IN EARLY DEVONIAN EUGNATHOSTOMES AND THE ‘OUTSIDE-IN’ HYPOTHESIS FOR THE ORIGINS OF TEETH IN VERTEBRATES

A nearly identical version of this chapter was published as: Blais, S. A., L. A. MacKenzie, and M. V. H. Wilson. 2011. Tooth-like scales in Early Devonian eugnathostomes and the ‘outside-in’ hypothesis for the origins of teeth in vertebrates. Journal of Vertebrate Paleontology 31:1189-1199. I was responsible for the examination of the material included in this manuscript, as well as for the composition of the manuscript itself and creation of all figures. This chapter builds on part of the M. Sc. project of LAM, in which she described lip scales in *Obtusacanthus* and UALVP 32520 and suggested their connection to the origins of teeth. LAM also contributed the SEM images used in Figure 5.6. MVHW contributed supervisory and funding support, as well as editing of the manuscript.

ABSTRACT

Although teeth are considered one of the most important steps in vertebrate evolution, details of their origins are obscure. Two prominent and opposing theories for the evolution of the vertebrate dentition are current: the ‘outside-in’ hypothesis and the ‘inside-out’ hypothesis. One of the main arguments against the ‘outside-in’ hypothesis is that, although similarities between teeth and scales have been observed, there is little fossil evidence of transitional forms between the two structures. Specimens of ischnacanthid acanthodians from the Man On The Hill (MOTH) locality in the Mackenzie Mountains of Canada provide the first unequivocal example of such transitional forms in an Early Devonian (Lochkovian) vertebrate assemblage. The head scales of these specimens are modified with proximity to the mouth to be extremely tooth-like. Three distinct morphotypes of modified cheek and lip scales are described. Their detailed similarity to teeth suggests they are a result of the same developmental processes, and also suggests the existence of a field of gene expression near the mouth margin in which scales could be transformed into teeth. These transitional forms remove one of the chief objections to the ‘outside-in’ hypothesis for the origins of teeth in vertebrates.

INTRODUCTION

Teeth, defined by Reif (1982) as elements of dentition formed from an odontode in a dental lamina, with replacement teeth forming before the functional tooth is shed, are traditionally considered to be one of the key synapomorphies of Eugnathostomata

(DeIuliis and Pulerà, 2007), or crown-group gnathostomes, comprising all jawed vertebrates except placoderms (Donoghue and Sansom, 2002). Even after decades of study, the evolutionary origins of teeth in vertebrates remain controversial. At present, two prominent opposing hypotheses on the origins of teeth dominate the field. The classical, 'outside-in' hypothesis (Fig. 5.1A) states that teeth originated as dermal denticles at the margin of the jaws that became secondarily specialized as feeding structures upon migration into the oral cavity (Hertwig, 1874). Support for this hypothesis includes the morphological similarity between teeth and the placoid scales of sharks, even including descriptions of 'transitional' scales in modern sharks (Daniel, 1934). An argument often cited against the 'outside-in' hypothesis is that there is no unequivocal example of a continuous, gradual transition between these two structures in the fossil record (Reif, 1980; Smith and Coates, 2001). However, suggestions of a transition between scales and teeth have been observed in early osteichthyans (Botella et al., 2007) and primitive chondrichthyans (Miller et al., 2003).

Recent research has emphasized the similarities between teeth and external tooth-like structures such as denticles or 'extra-oral teeth' in certain taxa, as well as the broader homology among odontodes, teeth, and denticles (Sire and Huysseune, 2003; Huysseune et al., 2010). The odontode is generally considered to be the main building block of the dermal skeleton (Janvier, 1996) as well as the structural unit of the vertebrate tooth. Individual odontodes form the scales of thelodonts and the placoid scales of modern chondrichthyans, and may accrete or fuse to dermal bone to form larger units, including polyodontode scales, such as those of acanthodians and primitive chondrichthyans, or dermal plates (Reif, 1982). This accretion of odontodes to form dermoskeletal elements has also been demonstrated to have occurred throughout ontogeny in specimens of two species of heterostracan agnathans from the Early Devonian (Greeniaus and Wilson, 2003). Dentine ridges on the external dermal plates of heterostracans show a gradual morphological transition into organized denticles on the oral plates (Purnell, 2002), indicating a relationship between these structures. A similar ontogenetic process occurred in the osteostracan agnathan *Superciliaspis* (Hawthorn et al., 2008).

An alternative, ‘inside-out’ hypothesis (Fig. 5.1B) has been proposed (Smith and Coates, 1998, 2000, 2001), which states that organized tooth families evolved from sets of putatively endodermally-derived pharyngeal denticles, as observed in specimens of the thelodont *Loganellia scotica,* independently of and preceding the evolution of jaws. It also states that internal (oro-pharyngeal) and external denticles possessed divergent evolutionary histories, citing conodonts as the first vertebrate group to show mineralization of the skeleton, which was restricted to the oro-pharyngeal cavity and inferred to be endodermal in origin. Smith and Coates (2001) suggested that the organized pharyngeal denticles were produced by the same developmental processes that produced replacement tooth families in the jaws, and cited evidence for this including the morphological similarity between the pharyngeal denticle sets of *L. scotica* and denticle spirals on the gill bars of sharks. Smith and Johanson (2003a) further suggested that teeth evolved independently within certain derived placoderms, and that these ‘teeth’ and pharyngeal denticles acquired their pattern information from the endoderm, unlike dermal denticles (Smith and Johanson, 2003b). This has prompted discussion on the definition of a ‘true’ tooth as opposed to an odontode or denticle, and the claim that placoderms possessed true teeth has been contested (Burrow, 2003b; Young, 2003, 2009, 2010).

Huysseune et al. (2009) reviewed several cases of tooth development in the absence of a dental lamina, and it has been suggested that the only distinction between a tooth and a denticle is that of topology, such that teeth are found inside the mouth and denticles are external to the oral cavity (Donoghue and Aldridge, 2001). In addition, the homologies between teeth in chondrichthyans and teleostomes, while long assumed, have not been formally defined. These issues remain a matter of debate (Donoghue and Sansom, 2002; Burrow, 2003b; Johanson and Smith, 2003, 2005; Smith, 2003; Smith and Johanson, 2003a, 2003b; Young, 2003, 2009, 2010).

One of the main arguments against the ‘inside-out’ hypothesis is that there is no phylogenetic support for homology between the teeth of crown-group gnathostomes and the oral skeleton of thelodonts. *Loganellia scotica* occupies a derived position within the Thelodonti (Donoghue and Smith, 2001; Wilson and Märss, 2004, 2009), indicating that any morphological similarity between the denticle ‘whorls’ of *Loganellia* and the tooth whorls of eugnathostomes is the result of convergence rather than homology. In addition, the ‘vertebrate’ status of conodonts has been contested, and it is unlikely that they represent the earliest vertebrate group to show skeletal mineralization (Blieck et al., 2010; Turner et al., 2010). Other jawless vertebrates, including anaspids and heterostracans, lack teeth, and osteostracans, considered the sister group of all jawed vertebrates, possess neither teeth nor oropharyngeal denticles.

Recently proposed modifications of the two main hypotheses rely primarily on developmental and molecular data. A hypothesis for a dual epithelial origin of teeth (Soukup et al., 2008) suggests the developmental machinery to produce teeth evolved once and that endodermal and ectodermal teeth are essentially the same. A ‘modified outside-in' hypothesis (Huysseune et al., 2010) suggests skin denticles and teeth are homologous, and tooth-forming competence was secondarily transferred to endoderm through contact with ectoderm that migrated into the oropharyngeal cavity through the gill slits, though the presence of ectoderm remained necessary to produce teeth. An 'inside and out' model (Fraser et al., 2010) suggests that all odontodes are homologous, and that odontode development is dependent on interactions between neural crest-derived and epithelial ectomesenchymal gene networks, independent of germ layer distribution.

Developmental and molecular data are valuable and necessary to establish the origins of the developmental processes and genetic potential for the production of structures such as teeth. However, the groups in which the first teeth evolved are long extinct, so fossil evidence provides the only physical evidence of the existence of the structures themselves. Homology can be suggested through detailed morphological similarity between teeth and tooth-like structures, as well as through transitional or linking forms which exhibit detailed morphological similarity to both teeth and other structures. Specimens of organisms that lived at a time near the origins of teeth are likely to have retained teeth in their original form, with the original developmental machinery intact. Studying these fossil specimens can provide valuable information on the morphology, development, and homology of the earliest and most primitive forms of teeth.

The oldest vertebrate group to undoubtedly possess 'true' teeth (i.e., formed from an odontode in a dental lamina), acanthodians are doubtfully known as microremains from the Ordovician (Sansom et al., 2001), from isolated dentigerous jaw bones and tooth whorls from the Early Silurian (Hanke et al., 2001a; Burrow, 2003a), and as articulated specimens from the Lower Silurian to the Permian (Denison, 1979; Janvier, 1996; Hanke and Wilson, 2004). Acanthodians may possess one or several types of dentition, including tooth whorls, isolated teeth, teeth ankylosed to dermal jaw bones (also known as dentigerous jaw bones, and unique to ischnacanthid acanthodians) overlying the Meckel's and palatoquadrate cartilages, pharyngeal denticles and denticulated cones, crushing plates, 'gill rakers', and lip and cheek scales (Watson, 1937; Gross, 1971; Ørvig, 1973; Valiukevičius, 1992; Gagnier, 1996; Burrow, 2004a; MacKenzie, 2008). The lip and cheek scales, discussed in this paper in acanthodians and a putative chondrichthyan, are head scales that are modified to become tooth-like in form with proximity to the mouth, with an observable transition back to 'typical' head scale form away from the mouth margins. These scales provide an unequivocal example of a transitional form between teeth and scales in specimens from a time close to the appearance of teeth in the fossil record, exhibiting detailed similarity between teeth and head scales. The individuals that possessed these cheek and lip scales are more likely to have retained the primitive dental characteristics of their first toothed ancestors than extant specimens, and can provide insight into the developmental machinery operating in the earliest toothed animals.

LOCALITY

The MOTH locality, situated in the central Mackenzie Mountains, N. W. T., Canada, has produced a diverse assemblage of extraordinarily well-preserved agnathan and early jawed vertebrates of Lower Devonian (Lochkovian) age (Wilson et al., 2000). Vertebrate specimens from MOTH were first described by Dineley and Loeffler (1976) and Bernacsek and Dineley (1977), who identified all ischnacanthid specimens from MOTH as *Ischnacanthus gracilis*. The fossils are found in interlaminated calcareous shale and argillaceous limestone between the basinal Road River Formation and more proximal Delorme Group and Camsell Formation strata. Zorn et al. (2005) most recently described the geology of the site and interpreted the depositional environment for the fossil-bearing beds as a hypoxic intra-shelf topographic low, below storm wave base, on the outer margin of a carbonate platform. Fossils have been collected by Dr. Brian D. E. Chatterton and Dr. Mark V. H. Wilson and their field parties in 1983, 1990, 1996, and 1998. These have been the subject of much systematic research on acanthodians (Gagnier and Wilson, 1995, 1996a, 1996b; Gagnier et al., 1999; Hanke et al., 2001b; Hanke and Wilson, 2004, 2006) as well as on the other taxa represented at this locality, including heterostracans, furcacaudiform thelodonts, osteostracans, placoderms, and chondrichthyans (Wilson et al., 2000).

MATERIALS AND METHODS

Fish fossils recovered from the MOTH locality, preserved in argillaceous limestone, were prepared using a dilute acetic acid solution to remove overlying calcareous matrix. Finer-scale removal of matrix was accomplished using soft brushes, rinsing with water. Any remaining acid and acetate buffer were rinsed away after removal of excess matrix was completed. A 5% solution of Glyptal™ cement in acetone was used to stabilize the specimens. The specimens were whitened using ammonium chloride sublimate and photographed using a Zeiss Discovery V8 stereomicroscope and Nikon NIS-Elements F 2.20 imaging software.

Referred Specimens

Those specimens that can be readily assigned to a scale morphotype are referred to here. Those specimens that cannot are here listed as ‘scale type indet.’. All of the specimens discussed in this paper are housed in the University of Alberta Laboratory for Vertebrate Paleontology collections, and all catalogue numbers listed below are prefixed by UALVP.

Type A Scales—42660, 43245, 43994, 45014, 45034, 45087.

Type B Scales—19267, 32401, 32405, 39063, 39086, 42201, 42664, 43245, 45548.

Type C Scales—32520, 45039.

Scale Type Indet.—19261, 32470, 42203, 42520, 42659, 42668, 45035, 45036, 45082, 45553.

DESCRIPTION

Several species of ischnacanthid acanthodians were present at the MOTH locality (Hermus, 2003; Chapters 2 and 3 of this thesis). Their overall body form and scales are virtually identical, but the different species are identifiable based on characteristics of the ossified palatoquadrate and Meckel’s cartilages, their overlying dentigerous jaw bones, and the teeth fused to the jaw bones. Modified scales close to the margins of the mouth also appear to vary among species, and may correlate with characteristics of the teeth and jaws to provide another means of species identification. For the purposes of this paper, I will refer to the different scale types as A, B, and C.

Though the morphology of the cheek and lip scales is different for each type, they all follow a general pattern (Fig. 5.2A, B). They have, to the authors' knowledge, not been described previously and they are likely present in MOTH specimens thanks to the extraordinary preservational quality of this locality. Cheek and lip scales are rare even in MOTH specimens, and are lost if the jaws have been disturbed during decay, burial, or diagenesis. The scales are most readily preserved in specimens that are laterally compressed. They are superimposed over the labial surfaces of the palatoquadrate and Meckel's cartilages, as well as over the labial surfaces of the dentigerous jaw bones and teeth.

The recess for the adductor mandibulae (see Gagnier and Wilson, 1995) anterior to the articulation of the jaw cartilages is clearly visible in most of these specimens, and in several cases the phosphatized tendon, which would have been embedded in the jaw musculature, is also preserved (Fig. 5.2A). The lip and cheek scales are preserved superimposed over the labial surface of the phosphatized tendon as well as over the labial surfaces of the jaw cartilages and dentigerous jaw bones, which indicates that the scales were located labial to the jaw musculature. The scales were most likely embedded in the skin of the animal, with the crowns of the scales protruding from the skin surface. The orientation of the scale crowns, which point outward (labially), indicates the scales were embedded in the skin on the external surface of the head, and not in the skin inside the oral cavity. The same type of scales is not present on the lingual surfaces of the jaws. The cheek and lip scales are not always superimposed over the entire extent of the cartilages, but this is likely an effect of preservation, in which some of the scale covering is lost.

Labial to the outer, posterior edges of the palatoquadrate and Meckel's cartilages, the scales, when preserved, are typical of head scales in *Ischnacanthus*, simple and plate-like (Hanke and Wilson, 2004). A complete description of *Ischnacanthus* and in particular its scale morphologies is provided by Hanke (2001). From a point labial to the articulation of the cartilages, the scales arc anterodorsally labial to the palatoquadrate and anteroventrally labial to the Meckel's cartilage, arcing back toward the margins of the jaws at a point approximately halfway between the front of the jaw bones and the articulation of the cartilages (Fig. 5.2B; 5.3A, B; 5.4A, B; 5.5A, B). Three to five well-developed rows of cheek scales on each of the upper and lower jaw cartilages converge labial to the jaw bones, on a point halfway to two thirds of the way down the length of the jaw bones from the front of the mouth. This point, termed here the convergence point (Fig. 5.2B), is where these cheek scales are most highly developed and concentrated. In several specimens, a tooth whorl may be preserved near the convergence point; it is unclear if this whorl is in situ or displaced. The converging rows of cheek scales are similar in appearance to the tooth whorls present at the front of the mouth, although they appear to have lain flat to the surface of the skin and do not have a recurved base (Fig. 5.6A–C). Each cheek scale is composed of a long, arcing, narrow base with multiple rows of cusps, which point toward the mouth. At the end of the cheek scale most distal to the convergence point, there are several small cusps, which, with increasing proximity to the convergence point, transition down the length of the scale to fewer, larger cusps. On each cheek scale proximal to the convergence point, there is generally only one large cusp, similar to the youngest tooth in a tooth whorl, pointing toward the convergence point and the cleft of the mouth.

Just anterior to the convergence point, the scales superimposed over the labial surfaces of the palatoquadrate and Meckel's cartilages are organized into lateral rows parallel to the jaw bones (Fig. 5.2B; 5.3C; 5.4C). The labial surfaces of the jaw bones, thicker than the cartilages they overlie, project outward from the relatively flat cartilage surface, and the scales, superimposed on the labial surface of the jaw bones, curve gently as if draped over the bones' surface. The scales are generally preserved more often superimposed over the jaw bone surface than that of the cartilages; it may be due to this difference in relief. The scales labial to the labial surface of the jaw bones anterior to the convergence point and distal to the cleft of the mouth are modified to become elongated and asymmetrical, with a sharp end pointing inward toward the mouth. Over the space of one or two rows, with increasing proximity to the cleft of the mouth, these scales are further modified to become smaller, more slender, and needle-like, and they point inward toward the mouth. These needle-like lip scales extend from the convergence point of the cheek scales to a point ventral to the orbit, and may extend, in the case of the upper lip scales, to the rostrum. The lip scales in the rostral region and along the jaw margins may be further modified to be very similar to the symphyseal tooth whorls in appearance, though much smaller (Fig. 5.5A, D; 5.6A, D).

Most of the specimens with cheek and lip scales were preserved with closed mouths or with mouths only slightly open. The upper and lower lip scales are easily distinguished from each other in specimens where the jaws are open, at least in the anterior part of the mouth. Closer to the convergence point, the upper and lower lip scales appear to intermesh, and are so finely needle-like that it is difficult to judge where the lips would gape, or if the scales overlap (Fig. 5.4B, C). The cheek scales do not appear to overlap, though the large cusps of separate whorls may touch at the convergence point. It is possible that the skin covering the labial surfaces of the palatoquadrate and Meckel's cartilages, and supporting the cheek and lip scales, extended over the jaw bones at and just anterior to the convergence point, effectively creating cheeks.

The cheek and lip scales from the specimens featured in this study all follow this general pattern (Fig. 5.2B). They all have distinct, flattened whorl-like cheek scales, which converge labial to a point approximately two thirds down the length of the jaw bones from the front of the mouth, and small, pointed lip scales lining the margins of the mouth. The different types of cheek and lip scales can be distinguished based on the shape of the cusps on the cheek scales and of the individual lip scales. The three distinct types of scales are further described in the following section.

Type A Cheek and Lip Scales

Type A lip and cheek scales are relatively short and low-crowned, with rounded edges. The few specimens exhibiting type A cheek and lip scales (Fig. 5.3) are small to medium-sized ischnacanthids. The whorl-like cheek scales of specimens with type A scales are relatively short, and arc toward the convergence point labial to the jaw bones only; the arc of the cheek scales does not extend past the jaw bones and labial to the jaw cartilages. The cheek scales labial to the lower jaw arc slightly, and are arranged almost parallel to the long axis of the jaw bones near the convergence point. The cusps on the whorl-like scales are low-crowned, short, squat, and bulbous, lacking sharp points; even the point of the largest cusp on each whorl, closest to the convergence point, is somewhat rounded.

The lip scales are small and asymmetrical, pointing inward toward the mouth margins, but they are also somewhat rounded and less needle-like than type B or C scales. The rows of small, asymmetrical scales extend dorsally and are superimposed over the ventral half of the palatoquadrate cartilage, where they transition into more typical head scale form. The scales covering the Meckel's cartilage are more typical and the modified asymmetrical lip scales are superimposed over the lower jaw bones only. In one specimen, UALVP 43994 (Fig. 5.3), which is missing the scales covering the posterior part of the jaw bones and appears to be missing some of the whorl-like cheek scales, the lip scales extend posteriorly past the convergence point and are visible along the lip margins inside the curves of the cheek scales. The small, pointed lip scales do not appear to extend farther anteriorly than the jaw cartilages, and the scales on the rostrum are typical head scales, which are not modified to be tooth-like near the opening of the mouth. The symphyseal tooth whorls are small, inconspicuous, and low-crowned, with one large medial row of somewhat rounded teeth and two rows of small lateral cusps on either side of each medial tooth. The specimens themselves are medium-sized, with closed mouths, and the scales cover the labial surfaces of the teeth and jaws, making it difficult to assign them to any particular species of ischnacanthid.

Type B Cheek and Lip Scales

Type B cheek scales are higher crowned than type A cheek scales, with longer cusps, and type B lip scales are much more slender, sharply pointed, and needle-like than type A lip scales. Specimens exhibiting type B scale morphologies (Fig. 5.4) are more numerous in the MOTH collection than those with type A or C scales. They are small to medium-sized, encompassing within their range the sizes of the specimens with type A scales. The whorl-like cheek scales are longer than those in specimens with type A scales, and they arc toward the convergence point labial to the palatoquadrate and Meckel's cartilages, as well as the jaw bones. The angle between the whorl-like scales and the jaw bones is higher than that in type A scales, and the cusps are more prominent. At the convergence point, the cusps are large, conical, and pointed inward toward the mouth. In several specimens, the cusps appear to be worn or missing, but the base of each scale is retained.

The lip scales are very small, sharply pointed, slender, and overall more needle-like in appearance than type A lip scales. They are preserved superimposed over the labial surfaces of the jaw bones and do not extend to cover the surfaces of the jaw cartilages, over which more typical head scales are superimposed. The transition between typical head scale form and modified lip scale form occurs in a single row, close to the margins of the mouth. Each scale in this row appears to bear multiple small, pointed cusps pointing toward the mouth. They intermesh closely near the convergence point of the cheek scales, and it is difficult to distinguish the upper lip scales from the lower lip scales in this region. The upper and lower lip scales are more easily distinguishable where the lips are open, starting approximately halfway between the convergence point and the front of the jaw bones, and extending to the rostrum.

The rostral scales are also modified to be asymmetrical and slender, though not as small or needle-like as the lip scales, and often obscure the tooth whorls. The tooth whorls at the front of the mouth are large relative to the cheek scales, and high-crowned, with one large medial row of long, slender, pointed teeth and two smaller lateral cusps on either side of each medial tooth. The medial tooth crowns are smooth and conical; they are slightly recurved and the youngest, largest teeth, in the most lingual position on the whorl, point into the gape. One specimen, which is preserved so that the lingual side of the left jaw is visible as well as the labial surface of the right jaw, is readily assignable to a yet-unnamed species of ischnacanthid acanthodian based on the form of the ankylosed teeth. It is not currently known whether the other specimens exhibiting the same lip and cheek scale morphologies, which cover the closed jaws and obscure the teeth, belong to the same species. It is possible that this scale form is typical of one ischnacanthid species, but there is currently no evidence to corroborate this hypothesis.

Type C Cheek and Lip Scales

Type C lip and cheek scales are much more similar in appearance to tooth whorls than are type A or type B scales. The cusps of type C scales are much longer, more slender, and higher-crowned, and the lip scales in particular are much more organized into tooth-whorl-like groups, as opposed to the simpler rows of asymmetrical scales characteristic of the other two scale types. The scales superimposed over the jaw cartilages are also modified and much more highly organized than those in specimens with type A or B scales. The two specimens with type C cheek and lip scales from the MOTH collections are not fully preserved. One specimen, UALVP 45039 (Fig. 5.5), comprises the articulated left upper and lower jaws, with the palatoquadrate and Meckel's cartilages, jaw bones, and part of the rostrum, all preserved with superimposed scales. The other specimen, UALVP 32520 (Fig 5.6.), comprises the left and right upper and lower jaw bones, the tooth whorls at the front of the mouth, and the rostral scales, with cheek and lip scales preserved superimposed on the labial surface of the left upper and lower jaw bones. UALVP 45039 is significantly larger than UALVP 32520, suggesting the form of the modified scales is not related to the size, or consequently the age, of the animal. In fact, UALVP 32520 is a small set of ischnacanthid jaws, while UALVP 45039 is one of the largest sets of ischnacanthid jaws in the MOTH collection.

Unlike the typical head scales superimposed on the jaw cartilages of specimens with type A and B scales, the lateral head scales superimposed on the cartilage surface in specimens with type C scales are long, slender, and tapered at both ends, forming an elongate rhomboid shape (Fig. 5.5A, B). These scales are highly ornamented and much more organized than those in specimens with type A or B scales. The lateral head scales are organized in rows that arc from the articulation of the cartilages away from the cleft of the mouth, and back toward the jaw cleft at the convergence point on the jaw bones. Below the ventral surface of the Meckel's cartilage, the scales become more typical and plate-like; the area above the dorsal surface of the palatoquadrate is not well preserved but a few typical head scales in this region suggest the same transition occurs on the rest of the head.

Labial to the jaw bones' surface, the arcing rows of scales become further modified and very tooth-like in appearance. Between one scale and the next, the scales near the convergence point develop rows of small cusp-like projections which, progressing along the elongated scale base toward the margin of the mouth, become larger, more sharply pointed, and higher crowned (Fig. 5.6A–C). Closest to the convergence point, there is a single medial row of very high crowned, tooth-like projecting cusps. Several of the cusps along the length of each cheek scale are broken, revealing a single hollow pulp cavity in the center of each cusp, which is not typical of non-tooth-like head scales in ischnacanthid acanthodians. The type C cheek scales are the largest, most high crowned, and most tooth-whorl-like of the cheek scales in the MOTH specimens.

The lip scales, unlike those in specimens with type A or B scales, are also whorl-like, and large, though not as well-developed as the cheek scales (Fig. 5.5C; 5.6B, C). They extend along the margins of the lips anteriorly, but do not extend dorso-ventrally past the oral margin of the jaw bones. The lip scales are multicuspid and high crowned. Each scale has several small projections on the end distal to the mouth, which transition over the length of a single scale to one row of long, pointed, tooth-like cusps, which point inward toward the mouth margins. Each lip scale is similar to a tooth whorl in appearance, although much smaller, and the bases appear slightly curved. These small tooth-whorl-like lip scales line the margins of the mouth, extending to the symphysis of the lower jaw and to the rostrum, where they are further modified and even more whorl-like (Fig. 5.5D; 5.6D). The rostral scales, which extend from the top of the rostrum to its underside, are superimposed over and around the upper tooth whorls, and are virtually identical to the whorls in morphology, albeit on a much smaller scale. The base of each rostral scale is curved, with the largest, lingual-most cusp pointing inward toward the mouth. There appear to be three to five rows of cusps on each rostral scale: one medial row of large, curved, sharply pointed conical cusps, and one or two lateral rows of smaller, similarly shaped cusps on each side of the medial row. Several cusps have been broken, revealing a single hollow pulp cavity in the center of each cusp.

Each ramus of the upper and lower jaws has a large tooth whorl anterior to it (Fig. 5.6A, D). These tooth whorls were likely parasymphyseal. The tooth whorls are very large, high crowned, and conspicuous, several times larger than the whorl-like rostral, lip, and cheek scales, and easily identified. There are five rows of tooth cusps on each whorl, including one medial row of very large, conical, smooth, high, and slightly recurved cusps, and two lateral rows of smaller, but still long and slender cusps on each side of the medial tooth row. The largest, youngest tooth is in the most lingual position on the whorl, and all of the teeth point into the gape. Each medial tooth cusp has a conspicuous primary cutting edge in the centre of its lateral surface, and this cutting edge curves parallel to the curves of the tooth cusp. Although the labial surfaces of a few teeth attached to the jaw bones are visible, these two specimens have not yet been formally assigned to a particular species of ischnacanthid.

DISCUSSION

The form and structure of the modified scales lining the labial margins of the mouth in the ischnacanthid specimens just described are extremely similar to true teeth. The cheek scales, in particular, are highly organized, whorl-like arrangements of cusps, each with a single pulp cavity, and fused to a bony base. The similarity to the tooth whorls at the front of the mouth of these animals, especially those with type C scales, is such that the only identifiable difference is overall size. This detailed level of similarity in pattern and development strongly suggests that they are the result of the same developmental processes. These scales provide evidence that intermediate morphologies between head scales and true teeth existed in early gnathostomes, and are an example of the effects of proximity to the jaw margins on scale development. The scales are increasingly tooth-like and well developed nearest the margins of the mouth, and gradually assume a form more typical of head scales with increasing distance from the mouth, suggesting they were subject to the same developmental processes that produce teeth. This developmental machinery may not have been limited to the mouth but may have been expressed in a field that included the external margins of the mouth, and acted on the scales in that area.

This modification of scales near the margins of the mouth was not limited to ischnacanthids, nor to acanthodians in general. *Obtusacanthus corroconis*, a species of putative chondrichthyan from MOTH, was described by Hanke and Wilson (2004), and the specialized lip scales of this species were further described by MacKenzie (2008). The head and mouth region of the holotype of this species is very well preserved, and the modified scales that lined the lips of the animal are clearly visible (Fig. 5.7). Near the margins of the front of the mouth, the scales are modified from the rounded, nearly symmetrical stellate morphology typical of the head, to a single row of fan-shaped transitional scales, which are asymmetrical and point toward the mouth. These fan-shaped scales lie between the stellate head scales and the lip scales, which are further modified. The lip scales are elongate, with three to four high ridges, and asymmetrical, with a sharply pointed tip, which is oriented toward the mouth. The scales near the angle of the jaws are not modified and retain the typical stellate head scale form, and the rows of modified lip scales increase anteriorly along the margins of the jaws, with four rows of lip scales at the front of the mouth, ventral to the rostrum.

Obtusacanthus corroconis is one of several species of early vertebrates from MOTH, including acanthodians and putative chondrichthyans, possessing jaws but no teeth. The presence of several toothless groups at MOTH suggests that these taxa either had not yet evolved teeth, although teeth were present in the fossil record at this time, or had secondarily lost them. In the case of *Obtusacanthus*, the latter seems unlikely. Teeth would surely have represented a significant adaptive advantage, especially in predatory species such as *Obtusacanthus corroconis*, and would be expected to be retained. The exquisite quality of these specimens indicates that their lack of teeth is not a result of loss during preparation, as the tooth-like scale structures around the mouth, which would have been embedded in the skin of the animal external to the oral cavity, are preserved in place. These groups may then represent a major transition between groups that possessed jaws but not teeth, and those that possessed both.

It is not certain what the function of the tooth-like lip and cheek scales may have been. Stomach contents of *Obtusacanthus corroconis* indicate that although it possessed no true teeth, it was capable of eating other vertebrates; MacKenzie (2008) identified a cephalaspid and *Lepidaspis*-like osteostracan in the stomach of the specimen of *Obtusacanthus* catalogued as UALVP 19338. It is possible that the asymmetrical lip scales in *Obtusacanthus*, which all point toward the mouth opening, functioned as tooth analogs and may have been used to grasp and engulf prey. The needle-like, asymmetrical lip scales of some ischnacanthid specimens may have functioned similarly, perhaps preventing prey from escaping the mouth, while the larger, true teeth processed food. The possible function of the whorl-like cheek scales is less clear. Their position outside the mouth suggests prey capture was not their primary function, although the more highly developed, larger cusps closest to the mouth margins may have also helped to prevent food from escaping the mouth. It is also possible the scales could have acted as a means of grasping another fish during mating or as a visual cue for recognition. The different types of cheek scales suggests they may have functioned as species identification markers; if a relationship between the cheek scale types and different species can be determined, it would support this hypothesis.

It is not likely that the different scale types are a result of ontogeny, because specimens with type A and B scales are similar in size, and the two specimens with type C scales are of significantly different sizes. It is possible that the scale morphologies may be related to sexual dimorphism, although there are at least three different scale types. It may be that the type A and B specimens represent males and females of the same species, but that does not explain the type C scales, nor the disparity in abundance of specimens of the different types, though that may be due to preservational or collecting bias.

Smith and Coates (1998, 2000, 2001) have suggested that the morphological similarity between pharyngeal denticle 'whorls' of the thelodont *Loganellia scotica* and the denticle spirals on the gill bars of sharks is evidence that tooth precursors may have evolved first in the oropharyngeal cavity of jawless vertebrates, and that teeth and scales did not share a common evolutionary history. The denticle whorls are composed of an elongate patch of denticles of similar size, fused together with secondary bone forming a base under the older part of the whorl, without an increase in size as new denticles were added to the whorl. The lip and cheek scales found in ischnacanthid acanthodian specimens from MOTH are similar to tooth whorls on a more detailed level: the cusps on each whorl-like scale possess a single pulp cavity, are fused to a curved bony base, and increase in size with proximity to the mouth, with cusps pointing into the gape. Based on morphology alone, these scales represent clear evidence for a relationship between scales and teeth supporting the 'outside-in' hypothesis, at least equal to that supporting the 'inside-out' hypothesis. The lip and cheek scales from eugnathostomes from MOTH thus provide convincing evidence of scale-tooth transitional elements in early jawed vertebrates.

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FIGURES

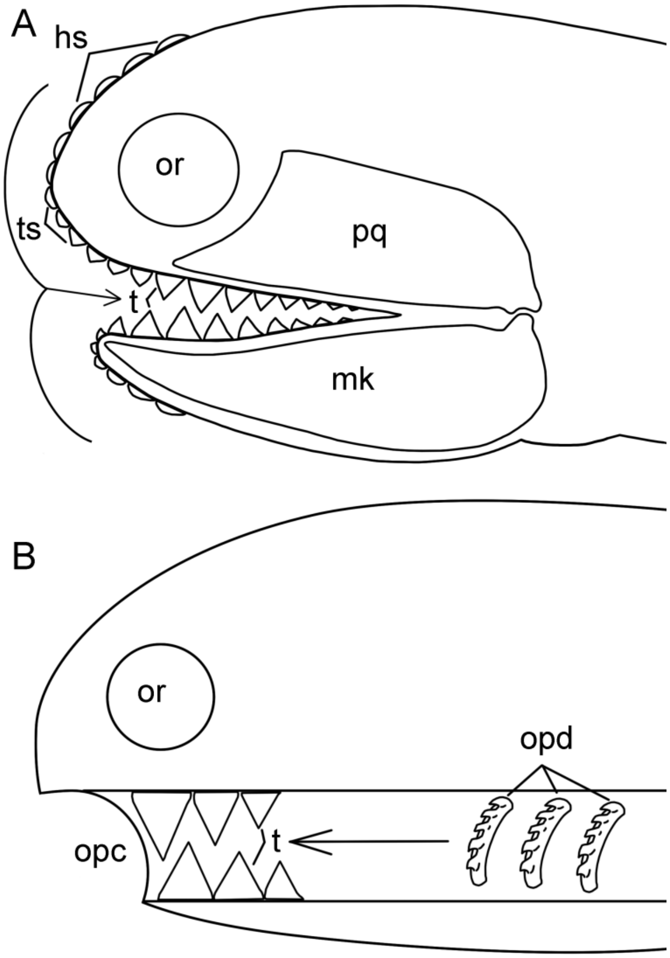
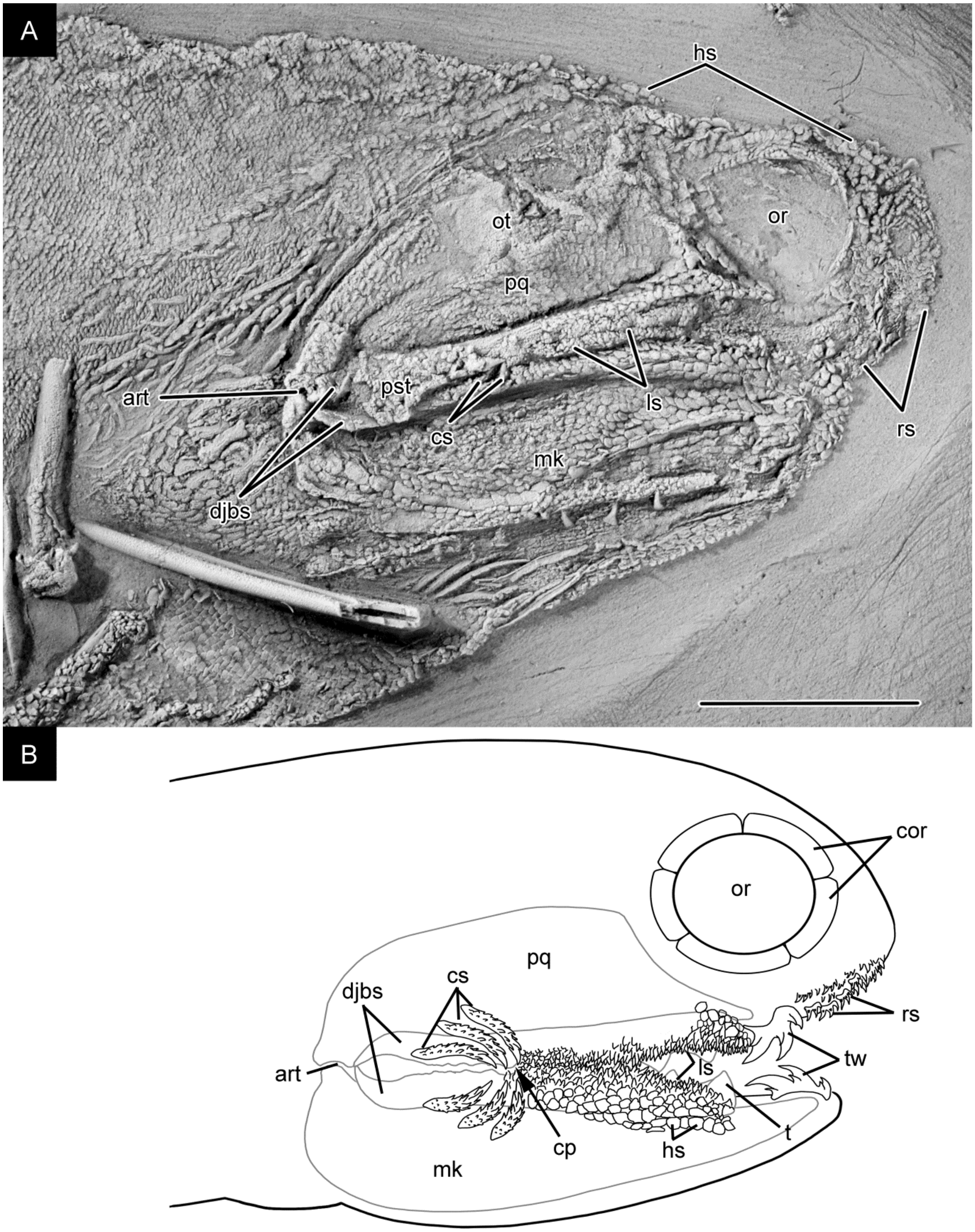


FIGURE 5.1. Diagrammatic representations of the 'outside-in' and 'inside-out' hypotheses for the origins of teeth in vertebrates. **A**, the 'outside-in' hypothesis, depicting migration of head scales into the mouth in a hypothetical early jawed vertebrate; **B**, the 'inside-out' hypothesis, illustrating the co-opting of the developmental processes that formed oropharyngeal denticles in early jawless vertebrates to form teeth. **Abbreviations**: **hs**, head scale; **mk**, Meckel's cartilage; **opc**, oropharyngeal cavity; **opd**, oropharyngeal denticle; **or**, orbit; **pq**, palatoquadrate cartilage; **t**, tooth; **ts**, transitional scale.

FIGURE 5.2 (following page). Cranial elements and dentition of an ischnacanthid from MOTH. **A**, UALVP 45014, right lateral view; **B**, illustration of general layout of modified scales in ischnacanthids from MOTH, left lateral view. The modified scales are preserved superimposed over the lateral surfaces of the jaw cartilages and dentigerous jaw bones, which are outlined in grey. **Abbreviations**: **art**, articulation of the jaw cartilages; **cor**, circumorbital bone; **cp**, convergence point; **cs**, cheek scale; **djbs**, dentigerous jaw bones; **hs**, head scale; **ls**, lip scale; **mk**, Meckel's cartilage; **or**, orbit; **ot**, otic material; **pq**, palatoquadrate cartilage; **pst**, phosphatized tendon; **rs**, rostral scale; **t**, tooth; **tw**, tooth whorl. Scale bar for A equals 5 mm.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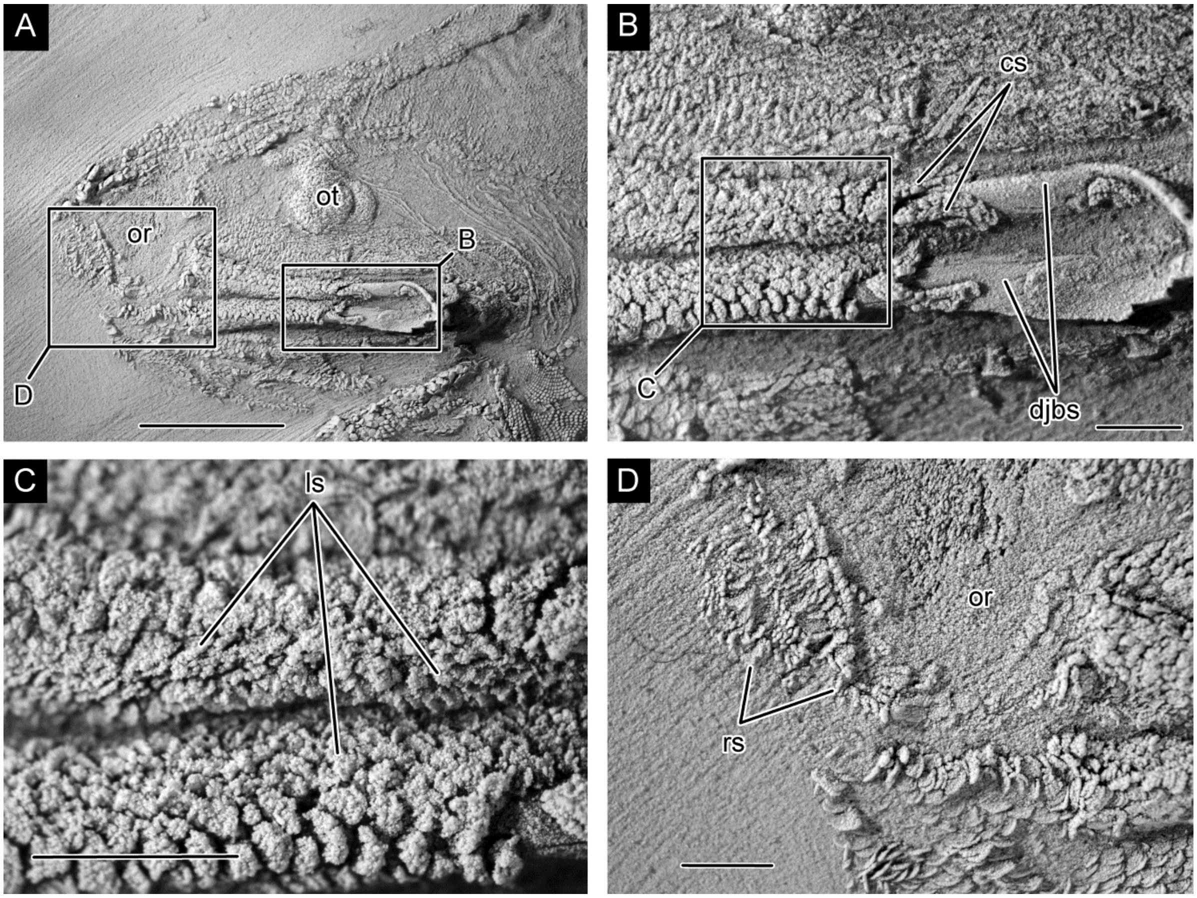

FIGURE 5.3. Type A lip and cheek scales in an ischnacanthid from MOTH, UALVP 43994, left lateral view. **A**, ischnacanthid cranium; **B**, close-up of cheek scales; **C**, close-up of lip scales; **D**, close-up of rostrum. **Abbreviations**: **cs**, cheek scale; **djbs**, dentigerous jaw bones; **ls**, lip scale; **or**, orbit; **ot**, otic material. Scale bar for A equals 5 mm; all other scale bars equal 1 mm.

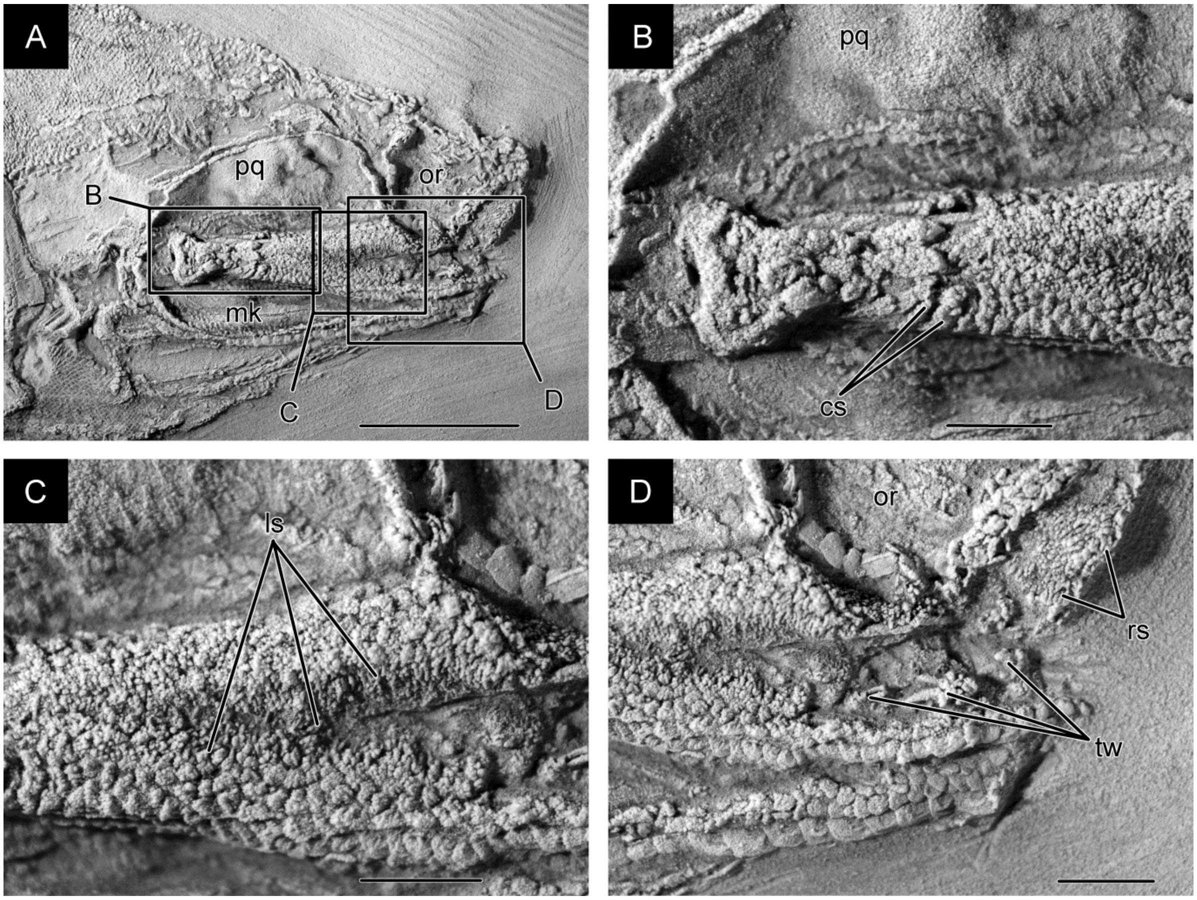

FIGURE 5.4. Type B lip and cheek scales in an ischnacanthid from MOTH, UALVP 42201, right lateral view. **A**, ischnacanthid cranium; **B**, close-up of cheek scales; **C**, close-up of lip scales; **D**, close-up of rostrum and tooth whorls. **Abbreviations**: **cs**, cheek scale; **ls**, lip scale; **mk**, Meckel's cartilage; **or**, orbit; **pq**, palatoquadrate cartilage; **rs**, rostral scale; **tw**, tooth whorl. Scale bar for A equals 5 mm; all other scale bars equal 1 mm.

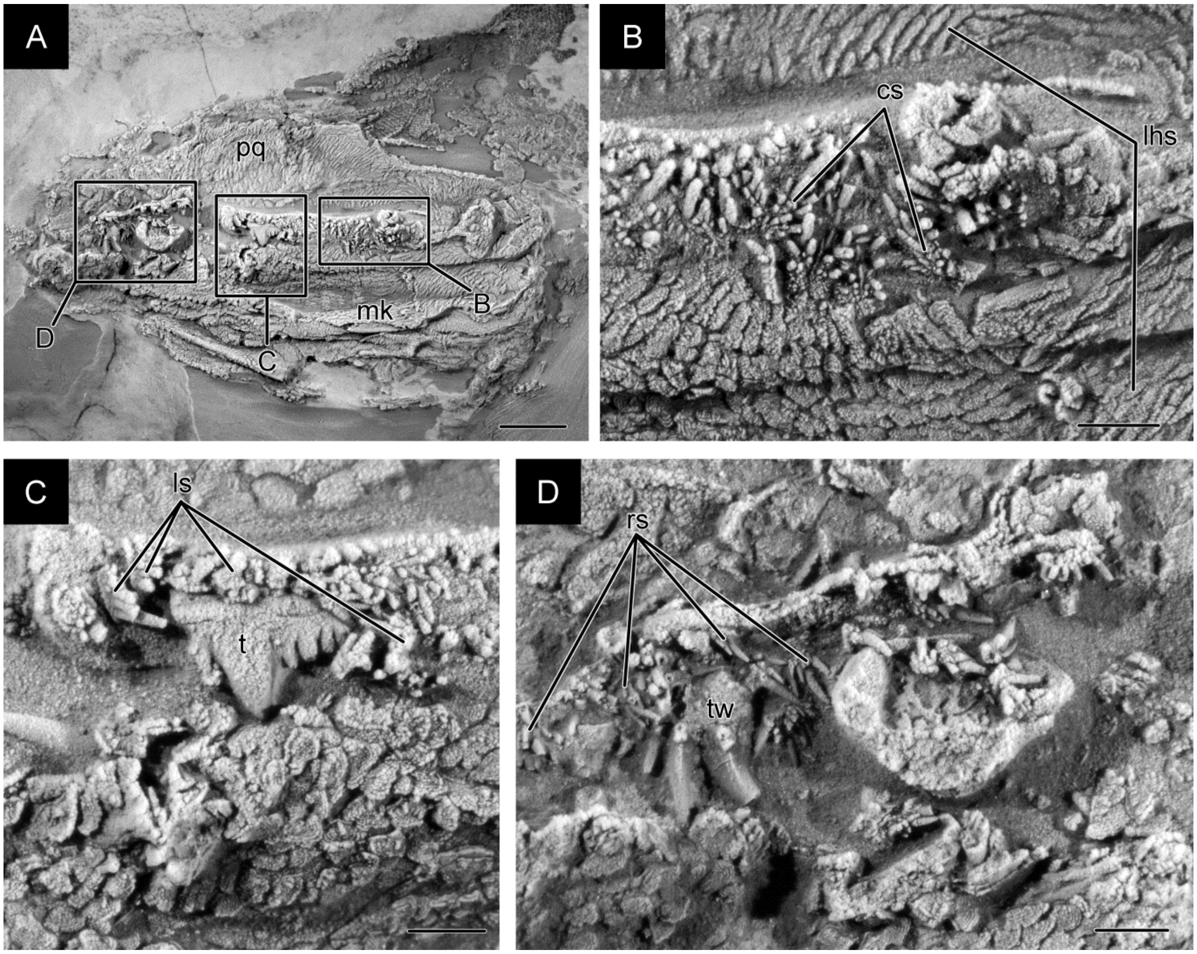

FIGURE 5.5. Type C lip and cheek scales in an ischnacanthid from MOTH, UALVP 45039, left lateral view. **A**, articulated upper and lower jaws of an ischnacanthid; **B**, close-up of cheek scales; **C**, close-up of lip scales; **D**, close-up of tooth whorls and rostral scales. **Abbreviations**: **cs**, cheek scale; **lhs**, lateral head scale; **ls**, lip scale; **mk**, Meckel's cartilage; **pq**, palatoquadrate cartilage; **rs**, rostral scale; **t**, tooth; **tw**, tooth whorl. Scale bar for A equals 5 mm; all other scale bars equal 1 mm.

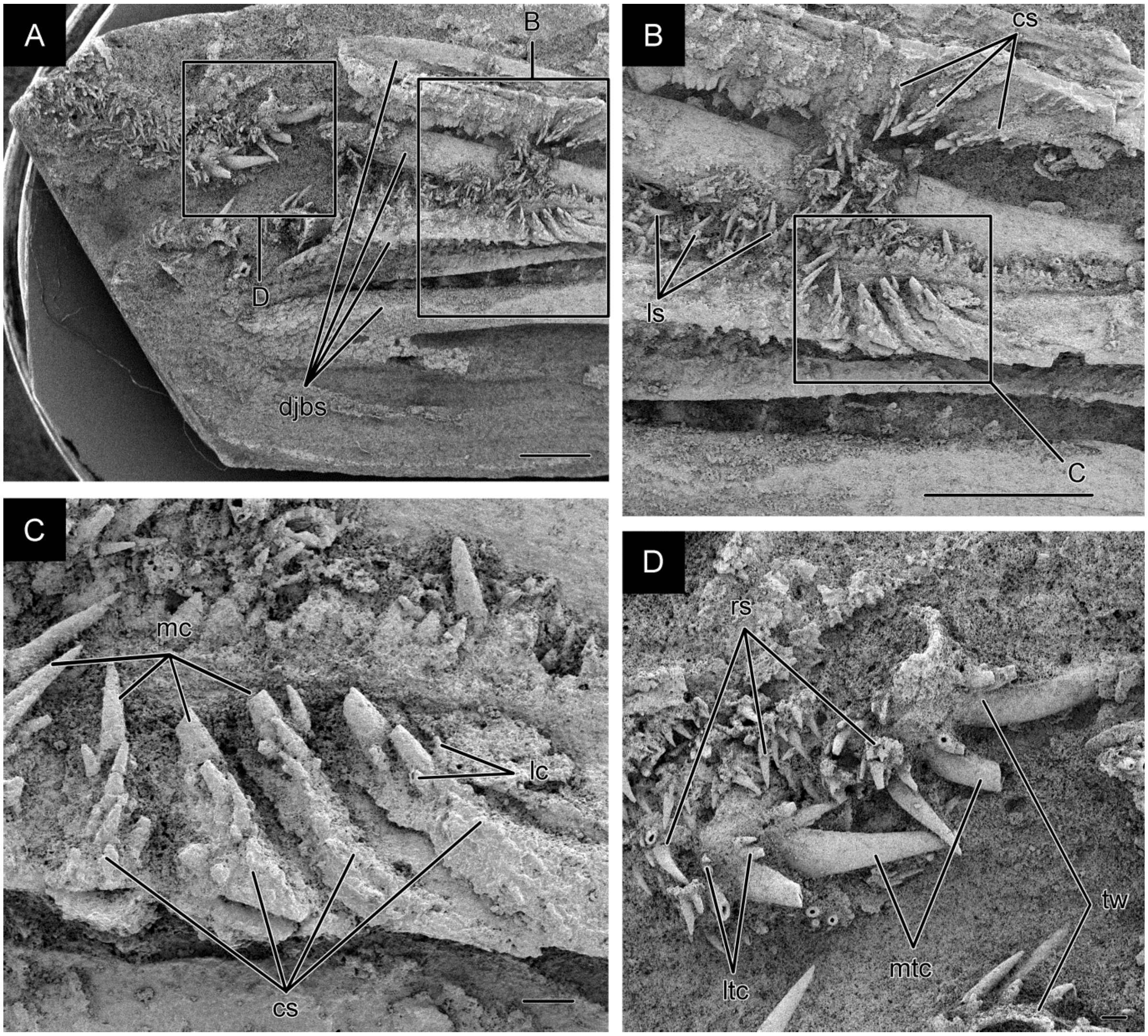

FIGURE 5.6. Type C lip and cheek scales in an ischnacanthid from MOTH, UALVP 32520, left lateral view. **A**, upper and lower dentigerous jaw bones of an ischnacanthid; **B**, close-up of lip scales and cheek scales; **C**, close-up of cheek scales superimposed on lower left dentigerous jaw bone; **D**, close-up of tooth whorls and rostral scales. **Abbreviations**: **cs**, cheek scale; **djbs**, dentigerous jaw bones; **lc**, lateral cusp; **ls**, lip scale; **ltc**, lateral tooth cusp; **mc**, medial cusp; **mtc**, medial tooth cusp; **rs**, rostral scale; **tw**, tooth whorl. Scale bars for A and B equal 1 mm; scale bars for C and D equal 100 μm. SEM images from MacKenzie (2008).

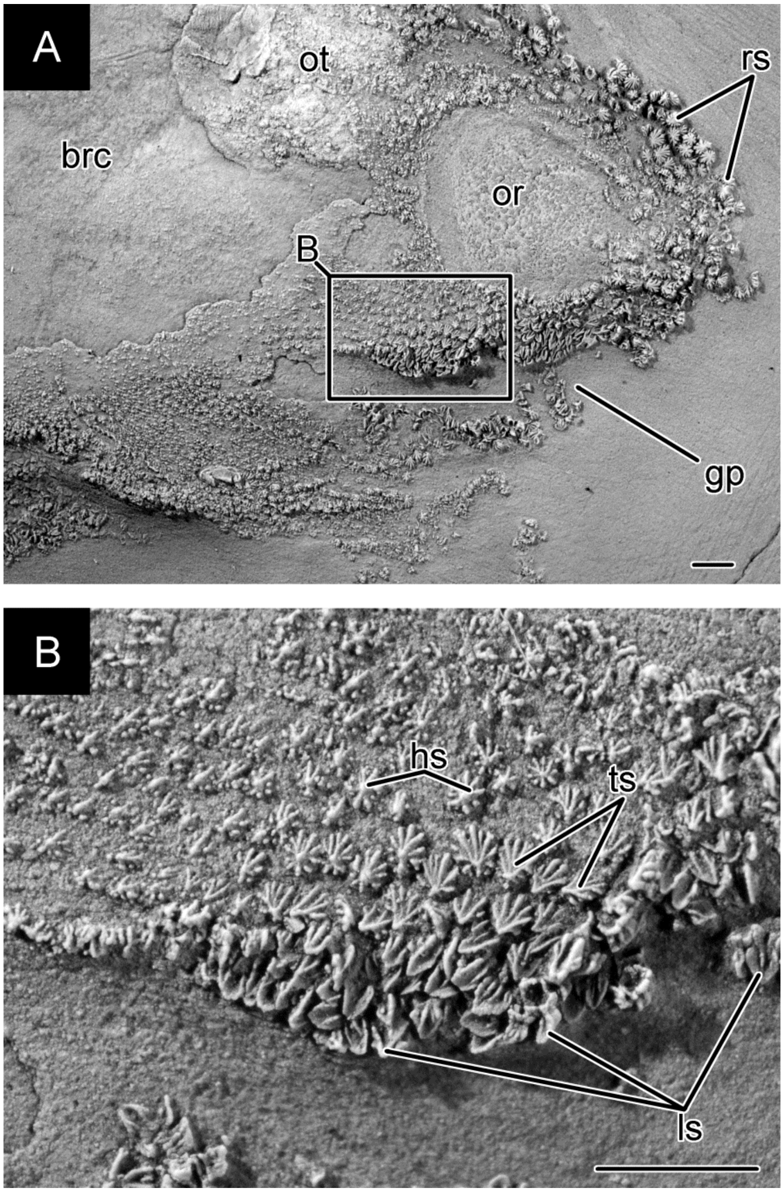

FIGURE 5.7. Modified lip scales in *Obtusacanthus corroconis*, UALVP 41488, right lateral view. **A**, cranium of *Obtusacanthus*; **B**, close-up of lip scales. **Abbreviations**: **brc**, branchial cavity; **gp**, gape; **hs**, head scale; **ls**, lip scale; **or**, orbit; **ot**, otic material; **rs**, rostral scale; **ts**, transitional scale. Scale bars equal 5 mm.

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CHAPTER 6

JAW BONE GROWTH AND TOOTH ADDITION IN ISCHNACANTHIFORMES

ABSTRACT

Despite relative uncertainty regarding their phylogenetic position, acanthodians and Ischnacanthiformes in particular can provide valuable insight into the ancestral conditions of crown-group gnathostomes. Because dermal tooth-bearing jaw bones are often the only source of information available for ischnacanthiform acanthodians, an in-depth study of the jaw bones is necessary to compare their growth and development to that of jaw bones in other early gnathostome groups. Ischnacanthiform dentigerous jaw bones from the MOTH locality were examined externally as well as internally using petrographic thin sections and micro-computed tomography. The arrangement of vascular tissue in ischnacanthiform jaw bones suggests jaw bone tissue was added in layers, and teeth were subsequently attached to the jaw bone tissue via a spongy layer of bone, interpreted here as alveolar bone. This suggests dermal jaw bone growth by addition of layers of bone tissue and attachment of teeth to the jaw bones via alveolar tissue may represent ancestral states for toothed gnathostomes. In addition, the presence or absence of tooth attachment tissues such as alveolar bone is proposed as a means for distinguishing teeth from denticles in fossil taxa, in which developmental indicators such as a dental lamina may not be preserved.

INTRODUCTION

Living jawed vertebrates are divided unambiguously into two very well-supported sister clades: the cartilaginous Chondrichthyes, and the bony Osteichthyes (comprising in turn the ray-finned Actinopterygii and lobe-finned Sarcopterygii). When fossil taxa are included, this clear picture becomes somewhat more complicated. Traditionally, fossil taxa have been assigned to two additional clades of gnathostomes: the heavily armoured Placodermi and the small, spiny Acanthodii. Recently, the validity of these two groups has been called into question as our understanding of early vertebrate evolution has undergone a major shift. New discoveries, particularly those from the Silurian and Early Devonian of China (e.g., Zhu et al., 2009, 2010, 2012, 2013a, 2013b; Zhao and Zhu, 2015) and Australia (Trinajstic et al., 2007; Long et al., 2008, 2015a, 2015b; Long and Trinajstic, 2010), have revealed new insights into the diversity and anatomy of early members of the jawed vertebrate groups.

Reinterpretation and redescription of existing and new material with more inclusive phylogenetic analyses (Brazeau, 2009; Friedman and Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Brazeau and Friedman, 2014; Dupret et al., 2014; Giles et al., 2015) has resulted in a veritable forest of hypotheses regarding the phylogenetic affinities of fossil vertebrates. The armoured placoderms have been resolved by these analyses as an assemblage of stem-gnathostomes, although this is complicated by the discovery of unique pelvic claspers (Long et al., 2015a). The second group of fossil gnathostomes, the Acanthodii, have most recently been resolved as a paraphyletic assemblage of stem-chondrichthyans (Zhu et al., 2013; Giles et al., 2015; Long et al., 2015a). However, the placement of both of these assemblages is still very much open to reinterpretation; all of the analyses mentioned here are based on the data set from one study (Brazeau, 2009), all have thousands of most-parsimonious trees, and none has very strong support for acanthodian nodes. In the most recent analysis at the time of writing (Giles et al., 2015), ‘acanthodians’ are grouped in several polytomies branching off the chondrichthyan stem between the crown-group gnathostome node and Chondrichthyes *sensu stricto*.

The assemblage of fishes traditionally known as acanthodians comprised three orders: the Climatiiformes (almost certainly a paraphyletic grade, regardless of the validity of the Acanthodii as a group), the Acanthodiformes, and the Ischnacanthiformes. Interestingly, most of the most recent phylogenetic analyses include several ‘climatiiform’-grade acanthodians, and relatively few acanthodiform and ischnacanthiform acanthodians. In the only recent analysis focusing specifically on acanthodians (Burrow and Turner, 2010), there was strong support for Ischnacanthiformes and Acanthodiformes as clades. These groups also tend to be well-supported in broader analyses, although they are usually represented by only a few taxa each. This is particularly true for the Ischnacanthiformes, which are in most cases (e.g., Giles et al., 2015; Long et al., 2015a) represented only by *Ischnacanthus* and *Poracanthodes*, representatives of the two major families within the order, the Ischnacanthidae and Poracanthodidae.

Interestingly, the Ischnacanthiformes and Acanthodiformes, once thought to be the most derived acanthodians (Burrow and Turner, 2010), in more recent phylogenetic analyses split from the chondrichthyan stem between the crown-group gnathostome node and the ‘climatiiform’ assemblage, the latter forming successive sister groups to the Chondrichthyes *sensu stricto*. This would suggest that ischnacanthiform and acanthodiform acanthodians may have shared a more basal common ancestor with chondrichthyans than did ‘climatiiforms’. Having diverged from the chondrichthyan stem at a more basal node than ‘climatiiforms’ and chondrichthyans *sensu stricto*, it is possible that ischnacanthiforms and acanthodiforms retain some of the characters of this common ancestor that were lost in more derived groups.

Unfortunately, although the Acanthodiformes have been relatively thoroughly studied (even if they are best nown from the remains of a single taxon, *Acanthodes bronni*; see Davis et al., 2012), the Ischnacanthiformes remain enigmatic. These fishes are mostly represented by isolated scales, spines, and dermal tooth-bearing jaw bones, considered the key synapomorphy of the group (Denison, 1979; Burrow, 2004a). Because acanthodiform, 'climatiiform', and chondrichthyan taxa lack these dentigerous jaw bones and therefore they could not be used for comparison across these groups, the recent increased interest in early vertebrate paleontology has not included in-depth analyses of ischnacanthiform jaw bones. The characters of these jaw bones often represent the only information available for study of these taxa. If we are to understand the origin and evolution of crown-group gnathostomes, we must include Ischnacanthiformes in our analyses as much as possible, making it doubly important to include as much information as can be gleaned from in-depth study of their jaw bones. Their development and mode of growth may reveal shared developmental machinery conserved among early gnathostome groups.

The most recent thorough description and study of acanthodian jaw bone and tooth development was carried out by Ørvig (1973). He determined that ischnacanthiform dentigerous jaw bones grew by periodically adding new teeth, which included attached sections of bone tissue, to the front of the jaws. This mode of growth was entirely unlike that of chondrichthyans and osteichthyans, and Ørvig's (1973) conclusion was that acanthodians were related neither to osteichthyans nor to chondrichthyans, and belonged in a group of their own, a view that persisted until Brazeau's (2009) redescription of *Ptomacanthus anglicus* Miles, 1973, and associated phylogenetic analysis. Ørvig's (1973) conclusion has been called into question by Brazeau's (2009) analysis and those that followed, yet little has been done to re-examine the dentigerous jaw bones of the Ischnacanthiformes. Such a study is necessary to determine whether ischnacanthiform jaw bone material could yield any further evidence of their mode of growth, including whether it was indeed as unique as suggested by Ørvig (1973), or whether it could reveal affinities to that of any of the recently discovered fossil stem-gnathostome taxa.

Study of the external morphology of ischnacanthiform dentigerous jaw bones from the Early Devonian Man On The Hill locality known for its exquisitely preserved early vertebrate fossils (and the underlying Silurian fish layer from the same location) in the Northwest Territories of Canada has revealed some evidence of their possible mode of growth. The ischnacanthiform jaw bones from this locality exhibit fine parallel striations (Fig. 6.1, 6.2) that have been interpreted as vascular canals (Hanke et al., 2001a). In this study, I examine the arrangement of these canals histologically through the use of physical thin sections as well as micro-computed tomography (µCT) slice data and three-dimensional reconstructions. These data, as well as morphological data, were obtained in order to determine whether ischnacanthiform acanthodian jaw bones likely grew through the addition of new bone tissue at the front, and if so, how that growth was accomplished.

If the bone had grown by addition of new tissue at the front, the bone would be expected to be more heavily vascularized in the areas of most recent growth, i.e., anteriorly. If, as Ørvig (1973) hypothesized, the new sections of jaw bone were essentially extensions of the teeth being added anteriorly, the vascular canals would be expected to show some signs of truncation where the older section of bone had ended and of increased vascularization within a discrete section of the anteriormost bone; continuous vascular canals extending from below one tooth to below the next tooth would be unexpected if Ørvig's (1973) hypothesis is supported. Finally, if the new section of bone was simply an extension of the mineralization of the tooth as suggested by Ørvig (1973), there should be no clear distinction between the tooth and the jaw bone tissue to which it is attached.

If the most recent phylogenetic position of ischnacanthiform acanthodians is any indication, it is possible that, instead of being entirely unique structures, their dentigerous jaw bones may have been inherited from a recent common ancestor with other jaw-bone-bearing gnathostome taxa, such as 'placoderms' or osteichthyans. *Entelognathus* is a placoderm-like fish with osteichthyan-like dermal jaw bones; it has been resolved either as a derived 'placoderm' (Zhu et al., 2013; Giles et al., 2015) or as the sister group to the Osteichthyes (Long et al., 2015a). Its multiple jaw bones have been interpreted as homologous with those of osteichthyans and may also be homologous at some level with the jaw bones of ischnacanthiforms. Recently, the placoderms *Compagopiscis* and *Romundina* have also been suggested to have borne teeth on their jaw bones (Rücklin et al., 2012; Rücklin and Donoghue, 2015), and the jaw bones in *Compagopiscis* have been interpreted as growing by the addition of sheets of tissue associated with the tooth cusps. The tooth-bearing dermal jaw bones in ischnacanthiforms may be related to the dermal jaw bones (tooth-bearing or edentulous) of these other newly described early gnathostomes. Determination of the mode of growth and development of these jaw bones, as well as identification of tooth and tooth attachment tissue types, may provide early vertebrate workers with a means to compare ischnacanthiform acanthodians with other taxa, and reveal insights into the most likely ancestral forms of teeth and tooth-bearing structures in crown-group gnathostomes.

METHODS

All specimens described in this chapter come from the Early Devonian (Lochkovian) and Silurian (Wenlock/Ludlow) fish layers at the Man On The Hill locality, in the Mackenzie Mountains of the Northwest Territories of Canada. These fossils are preserved in finely laminated calcareous shale and shaley limestone. A dilute acetic acid solution was used to dissolve the calcareous matrix overlying the specimens, with finer-scale removal of the remaining residue accomplished through the use of soft brushes. A 5% solution of Glyptal cement in acetone was used to stabilize the specimens after the excess matrix, remaining acid, and acetate buffer were rinsed away. The specimens were whitened using ammonium chloride sublimate and photographed using a Zeiss Discovery V8 stereomicroscope and Nikon NIS-Elements F 2.20 imaging software.

Specimens selected for μCT-scanning were further prepared and embedded in Buehler EpoThin Low Viscosity Resin and Hardener in order to remove the remaining matrix from the buried side, separating the fossil entirely from the surrounding matrix to facilitate CT scanning. Specimens were then scanned using a SkyScan 1172 μCT scanner. Slice data were analysed using OsiriX, Mimics and Avizo 6.3. The stacked DICOM (Digital Imaging and Communications in Medicine format) images acquired by the μCT scanner were used to create volume renderings and isosurface meshes in Avizo.

Contiguous areas of low density, interpreted as vascular canals, were selected manually for each two-dimensional slice via Segmentation editing and a Wacom Cintiq graphics tablet, and reconstructed as new three-dimensional surfaces in Avizo.

Specimens selected for thin sectioning were embedded in Buehler EpoThin Low Viscosity Resin and Hardener and prepared petrographically using a Hilquist Thin Section Machine, and ground and polished using SiO_2 grits and CeO_2 powder. Sections were examined on a Nikon Eclipse E600POL trinocular polarizing microscope with an attached Nikon DXM 1200F digital camera. Specimens and thin sections described in this study are housed in the UALVP collections, and CT data are reposited at the University of Alberta.

RESULTS

Thin section histology

Although fossils from the MOTH locality are extraordinarily well preserved in terms of the level of anatomical detail visible externally, they are impregnated with iron and clay minerals. These opaque minerals obscure much of the detail of the internal tissues, rendering fine-scale histological study difficult. However, some of the tissues can be observed in thin section: the dentine of the tooth cusps is clearly visible, and this dentine is obviously distinguishable from the bone of the jaw itself (Fig. 6.3). Each tooth has a single large pulp cavity; although in some cases this has been infilled with calcite and appears to comprise several smaller cavities, this is likely an artefact of preservation. It may, however, indicate that the pulp cavity was convoluted internally, resulting in several smaller partially enclosed “chambers” that became infilled.

Due to the curvature of the teeth medially compared to the jaw bones, the thin sections examined here contain either the occlusal portion of the tooth cusp, or the base of the tooth cusp, but not both. In sections focused on the bases of the teeth and their attachment to the jaw bone, it is apparent that there is a layer of bone between the tooth and the jaw bone that is less dense than either (Fig. 6.3). There is a clear distinction between the teeth and the jaw bone tissue; the two are not a continuous 'block' of tissue.

Within the jaw bone itself, a series of 'tubes' running roughly parallel to the long axis of the jaw bone (and roughly perpendicular to the long axis of each tooth cusp) is visible (Fig. 6.3). These tubes correspond to the grooves visible on the external surface of the jaw bones, indicating that these most likely represent vascular canals within the jaw bone, and not surficial ornamentation. These show no signs of periodic truncation as one might expect if 'blocks' of jaw bone tissue had been added at a time.

Computed Tomographs

The two-dimensional tomograph images created for each 'slice' of the specimen were reconstructed representing differences in density of the specimen as different shades of grey. By scanning through the slices (of which there are approximately 900 for most of the specimens examined) it is possible to visually 'trace' a series of tubular areas of low density, interpreted here as vascular canals (Fig. 6.4, 6.5). Several of these connect to embayments on the outer wall of the jaw bone that represent the grooves visible on the external surface of the jaw bone, indicating that these grooves do represent vascular canals, rather than surface texture or ornament. Slices from the anterior end of the jaw bone have more numerous and generally larger vascular canals than do slices from the posterior end of the jaw bone. In addition, there appear to be more and larger vascular canals in the part of the jaw bone that is closest to the teeth, compared to the part of the jaw bone that contacts the cartilage. This corresponds to the general pattern of more numerous grooves observed on the external surface of the jaw bones from MOTH ischnacanthiforms (Fig. 6.2). The jaw bone tissue appears to have a denser cortex and a less dense core in cross sections, even posteriorly where there are fewer canals.

When sectioned digitally, it is easier to identify the pattern in which the vascular canals are arranged (Fig. 6.6). They are organized into sheets or layers and are parallel or subparallel to each other and to the curve of the jaw bone itself. The vascular canals are more numerous and more concentrated at the anterior end of the jaw bone compared to the posterior end. There are also more canals proximal to the tooth row than to the part of the jaw bone in contact with the cartilage. There is no indication of the vascular canals being truncated, and no indication of jaw bone tissue having been added in discrete sections. Instead, the vascular canals appear to be organized in continuous ‘sheets’ draping anteriorly over the older jaw bone material and away from the occlusal surface.

Although somewhat limited by the resolution available for the µCT scanner and the histological quality of the fossil material, it is also possible to identify some of the internal anatomical structures of the teeth as well as the vascularization of the jaw bone itself. Each tooth has a very well-defined, large, single pulp cavity, which is visible externally in specimens with broken tooth cusps. In cross section, the jaw bone itself is much more robust posteriorly, and anteriorly becomes flat and very thin. Instead of jaw bone tissue, much of the tissue visible externally at the anterior end of the jaw is composed of a thick layer of lower-density bone that lies between the base of each tooth and the bone of the jaw, referred to here as ‘attachment bone’ (Fig. 6.2, 6.3, 6.4). This layer is thickest anteriorly and reduced posteriorly. The tooth roots do not appear to contact the jaw bones and are at least partially surrounded by this thick layer of vascularized, spongy bone.

DISCUSSION

Jaw bone growth in Ischnacanthiformes

Based on the examination of external morphology, thin sections, and computed tomographs, there is no evidence to support Ørvig’s (1973) hypothesis that ischnacanthiform acanthodian jaw bones grew by the addition of sections of bone that were continuous with the tooth cusp to which they were attached. There is a clear distinction between the tooth and the underlying tissue of the jaw bone, and there is no evidence within the jaw bone itself of discrete sections of bony tissue being added. Therefore, I must reject the hypothesis of jaw bone growth proposed by Ørvig (1973).

The interpretation of ischnacanthiform tooth-bearing elements as unique, autapomorphous structures that are non-homologous with the dermal jaw bones in other groups was in part based on Ørvig’s (1973) interpretation of the mode of growth of ischnacanthiform tooth-bearing elements as unique among gnathostomes, and in part based on the accepted phylogenetic position of ischnacanthiform acanthodians at the time, nested within a monophyletic Acanthodii. With both of those conclusions rejected or ambiguous, there is not a compelling argument to continue to view ischnacanthiform dermal dentigerous jaw bones as unique structures that are non-homologous to jaw bones in other gnathostome groups. Based on the (albeit ambiguous) current phylogenetic position of the Ischnacanthiformes, for example that proposed by Giles et al. (2015) in which Ischnacanthiformes branch directly off the crown-group gnathostome node in a large polytomy, Ischnacanthiformes may be a member of a sister group to the rest of total-group Chondrichthyes, or may even be a possible sister group to crown-group Gnathostomata. The addition of jaw bone growth characters to a phylogenetic analysis may, if treated as directly comparable with those of other groups and not given an *a priori* distinction as unique structures, prove to be key to resolving the phylogenetic position of the Ischnacanthiformes.

Based on the evidence for attachment of teeth to the jaw (particularly the highly vascularized spongy ‘attachment bone’ discussed in more detail below), it seems evident that the youngest teeth were added following deposition of new jaw bone tissue, to which they then become ankylosed. The arrangement of the vascular canals within the jaw bone suggests the jaw bone tissue may have been added in successive sheets that draped over the existing tooth-bearing bone, with the most highly vascularized bone interpreted as the youngest ‘sheet’ (Fig. 6.7). This may have also resulted in the oldest teeth being gradually “buried” in new jaw bone tissue. This might explain why, despite not being particularly worn down according to MacKenzie (2008), the posteriormost teeth are much shorter and lower than the anteriormost teeth, and why the ‘attachment bone’ appears to disappear in posterior teeth (Fig. 6.2). Each successive ‘sheet’ of jaw bone tissue would extend out anteriorly, forming a surface to which the youngest teeth could become attached. Such an anterior extension of the jaw bone is evident in several ischnacanthiform taxa (e.g., Long, 1986; Lindley, 2000; Burrow, 2004), and this anteriormost extension of the jaw bone is generally the lingual (or mesial) ridge.

This mechanism for addition of new bone tissue has some similarity to that proposed for the 'placoderm' *Compagopiscis* (Rücklin et al., 2012), although in that case the outermost layers of tissue are continuous between the teeth and the jaw bone, and the addition of teeth and jaw bone material appear to have occurred simultaneously. In addition, teeth and jaw material in *Compagopiscis* were not added at only one end of the jaws, as in ischnacanthiforms. It is even possible that this type of jaw bone development may be plesiomorphic for toothed vertebrates: addition of new material to the tooth-bearing element coupled with addition of new teeth. This potential similarity in development would suggest that the tooth-bearing dermal jaw bones in Ischnacanthiformes may be on some level homologous with those in at least some 'placoderms' and possibly with those of Osteichthyes, although a phylogenetic analysis including this information is necessary to test this hypothesis. It may also be reflective of the statodont dentition in both Ischnacanthiformes and *Compagopiscis*; neither group shows any evidence of having replaced their teeth, and tooth replacement likely evolved independently in the Chondrichthyes and Osteichthyes.

In the case of the Chondrichthyes, this could have occurred at least in part through the loss of the tooth-bearing jaw bones, followed by loss of the bony base connecting teeth in whorls or tooth families (still present in *Doliodus* (Maisey et al., 2014)), and eventually leading to whorl-like families of independent, ligamentously supported teeth that were easily shed. This could explain the morphological similarity between extant chondrichthyan tooth families and ischnacanthiform and 'climatiiform' tooth whorls and tooth-like scales. In this scenario, the novelty of Chondrichthyes *sensu stricto* is not tooth replacement, but tooth separation: new functional teeth were already being continuously added to the whorls in acanthodians and primitive sharks such as *Doliodus*, but with the loss of the bony tooth-bearing element and the loss of the attachment tissues required to fuse the teeth to that element, the ligamentously connected teeth could be more easily shed. Tooth replacement, in which the attachment tissues of the functional tooth are at least partially resorbed and the shed tooth is literally replaced in space by the new tooth, is then a novel synapomorphy of Osteichthyes.

The mode of tooth replacement in Osteichthyes does not appear to be homologous to the mode of tooth attachment and jaw bone growth in either ischnacanthiforms or *Compagopiscis*. Even in groups with tooth whorls (e.g., *Onychodus*; see Andrews et al., 2005), the cusps are not connected to a bony base as in total-group Chondrichthyes (including acanthodians), but loosely connected to two bony elements which themselves are decoupled from the tooth attachment: teeth attach to a dental groove in the middle of the two bony elements, rotate out, and are shed. The overall whorl-like appearance may be the result of convergence or the retention of ancestral developmental patterning; the tooth whorls themselves do not appear to be homologous to those of stem chondrichthyans based on their morphology and mode of growth.

Tooth attachment in Ischnacanthiformes

There is a thick layer of spongy vascularized bone between the tooth proper and the jaw bone in Ischnacanthiformes, visible in the computed tomographs as well as obvious externally at the base of the anteriormost teeth in specimens from MOTH (Fig. 6.2, 6.4). This ‘attachment bone’ may represent the oldest described instance of alveolar bone (after Caldwell et al., 2003; Caldwell, 2007; Maxwell et al., 2012). This vascularized tissue is most distinctive at the base of the youngest teeth, suggesting the tissue may have been resorbed or otherwise obscured in older teeth, perhaps by jaw bone tissue. A similar vascularized layer of bone is visible between the tooth cusps and the jaw bone on the published volume rendering and surface cut of *Compagopiscis* (Rücklin et al., 2012), but this tissue is not discussed and the possibility of its being alveolar bone is not suggested. It is possible that this tooth attachment tissue (with presumably the accompanying cementum and periodontal ligament, although these are not visible in the thin sections and CT scans described herein) is primitive for tooth-bearing gnathostomes, and has been retained in osteichthyans, including tetrapods.

If this is the case, Ischnacanthiformes inherited this alveolar bone from a tooth-bearing ancestor, and it was probably lost in more derived chondrichthyans along with the loss of the dermal tooth-bearing jaw bones. This adds to the increasing body of evidence (e.g. Zhu et al., 2013; Maisey et al., 2014) that modern sharks, once thought to represent the ancestral conditions for crown-group gnathostomes, are derived and should not be considered primitive relative to the bony fishes, nor should they be assumed to represent the ancestral character states in these groups.

Interestingly, although teeth have been proposed to be present in *Romundina* (Rücklin and Donoghue, 2015), they have no such obvious attachment tissues. Perhaps rather than a soft-tissue dental lamina that is not preserved in fossil taxa, the presence or absence of clear tooth attachment tissues should be used as an unambiguous morphological character to distinguish between teeth and denticles. With this qualification, teeth would be interpreted to be present in *Compagopiscis* and absent in *Romundina*, implying that teeth either evolved crownward of the last common ancestor of *Romundina* and its sister group, or evolved convergently in some arthrodires and in crown-group gnathostomes. The position of *Entelognathus* and several toothless stem-gnathostomes is also a complicating factor. It does seem more likely, however, that gnathostomes evolved the suite of tooth attachment tissues (and teeth) once and secondarily lost them in more derived groups than that they evolved such a complex set of tissues, in such a specific arrangement, repeatedly in several unrelated groups. Further study of tooth attachment tissues in early vertebrates and the addition of these characters to phylogenetic studies is necessary to test this hypothesis.

CONCLUSIONS

Ischnacanthiform acanthodian jaw bones from the Early Devonian Man On The Hill (MOTH) locality were closely examined using microscopy and ammonium chloride photography to study their external morphology, as well as petrographic thin sections and micro-computed tomography to examine their internal structure. A series of fine parallel grooves on the jaw bones are interpreted as vascular canals. The arrangement of these vascular canals suggests that new jaw bone tissue was added to ischnacanthiform acanthodian jaw bones in sheets, with each youngest 'sheet' providing a fresh surface to which the youngest tooth subsequently attached. The successive addition of sheets of jaw bone tissue may have resulted in the posteriormost teeth becoming covered over with jaw bone material.

This mode of jaw bone growth is comparable to that suggested for the 'placoderm' *Compagopiscis* (Rücklin et al., 2012). This, as well as a statodont dentition in which teeth were retained and not replaced, is suggested here to represent the primitive condition for toothed gnathostomes, with tooth replacement being a novelty of

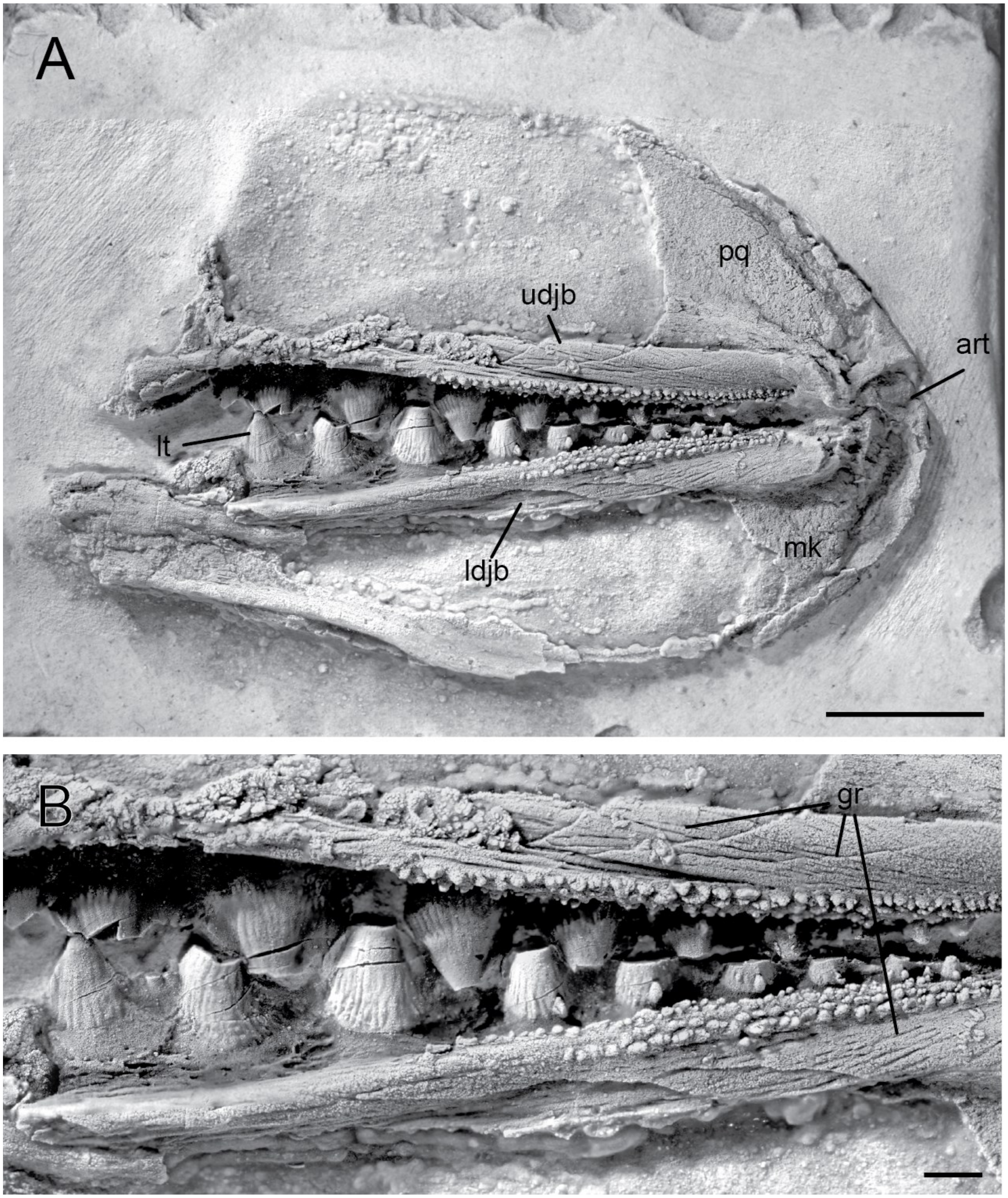
Osteichthyes, and tooth shedding (distinct from osteichthyan tooth replacement) as a novelty of Chondrichthyes. This hypothesis is supported by the basal position of the statodont Ischnacanthiformes and 'climatiiforms' relative to the Chondrichthyes *sensu stricto*, as well as the retention of teeth on bony bases identical to tooth whorls in *Doliodus problematicus*. This was likely achieved by the stepwise loss of the tooth-bearing bones in the sister group to the Ischnacanthiformes (particularly if Ischnacanthiformes resolve as the sister group to the rest of total-group Chondrichthyes), followed by the loss of the bony base supporting the tooth families, with tooth families eventually becoming composed of independent, ligamentously connected and easily shed teeth.

A thick layer of heavily vascularized tissue was observed at the base of the youngest teeth and has been tentatively interpreted here as alveolar bone, suggesting that the tooth attachment tissues generally associated with amniotes may in fact be plesiomorphic for toothed gnathostomes. The presence of this tooth attachment tissue in *Compagopiscis* (Rücklin et al., 2012) and its absence in *Romundina* (Rücklin and Donoghue, 2015) also indicates that such tooth attachment tissues can be used in fossil taxa to distinguish between teeth and denticles, instead of relying on developmental indicators such as a dental lamina which is unlikely to be preserved. If this attachment tissue is used to distinguish between teeth and denticles, teeth were absent in *Romundina* and present in *Compagopiscis*.

An in-depth study of the growth and development of ischnacanthiform tooth-bearing jaw bones from the MOTH locality has provided some insight into their possible affinities and how those affinities may affect our interpretations of the homology of tooth-bearing jaw bones and teeth in early vertebrates. A comparative histological analysis among Ischnacanthiformes and other early gnathostome groups, and the eventual inclusion of this data in a comprehensive phylogenetic analysis, is necessary to determine how these findings influence the phylogenetic position of the Ischnacanthiformes.

FIGURES

FIGURE 6.1 (following page). Holotype of *Euryacanthus rugosus*, UALVP 45648, with the fine parallel grooves on the dentigerous jaw bones visible. **A**, entire specimen, preserved in right lingual view; **B**, close-up of the dentigerous jaw bones. Anterior is to the left. **Abbreviations**: **art**, articulation of the palatoquadrate and Meckel's cartilages; **gr**, grooves on the dentigerous jaw bones; **ldjb**, lower dentigerous jaw bone; **lt**, lateral tooth; **mk**, Meckel's cartilage; **pq**, palatoquadrate cartilage; **udjb**, upper dentigerous jaw bone.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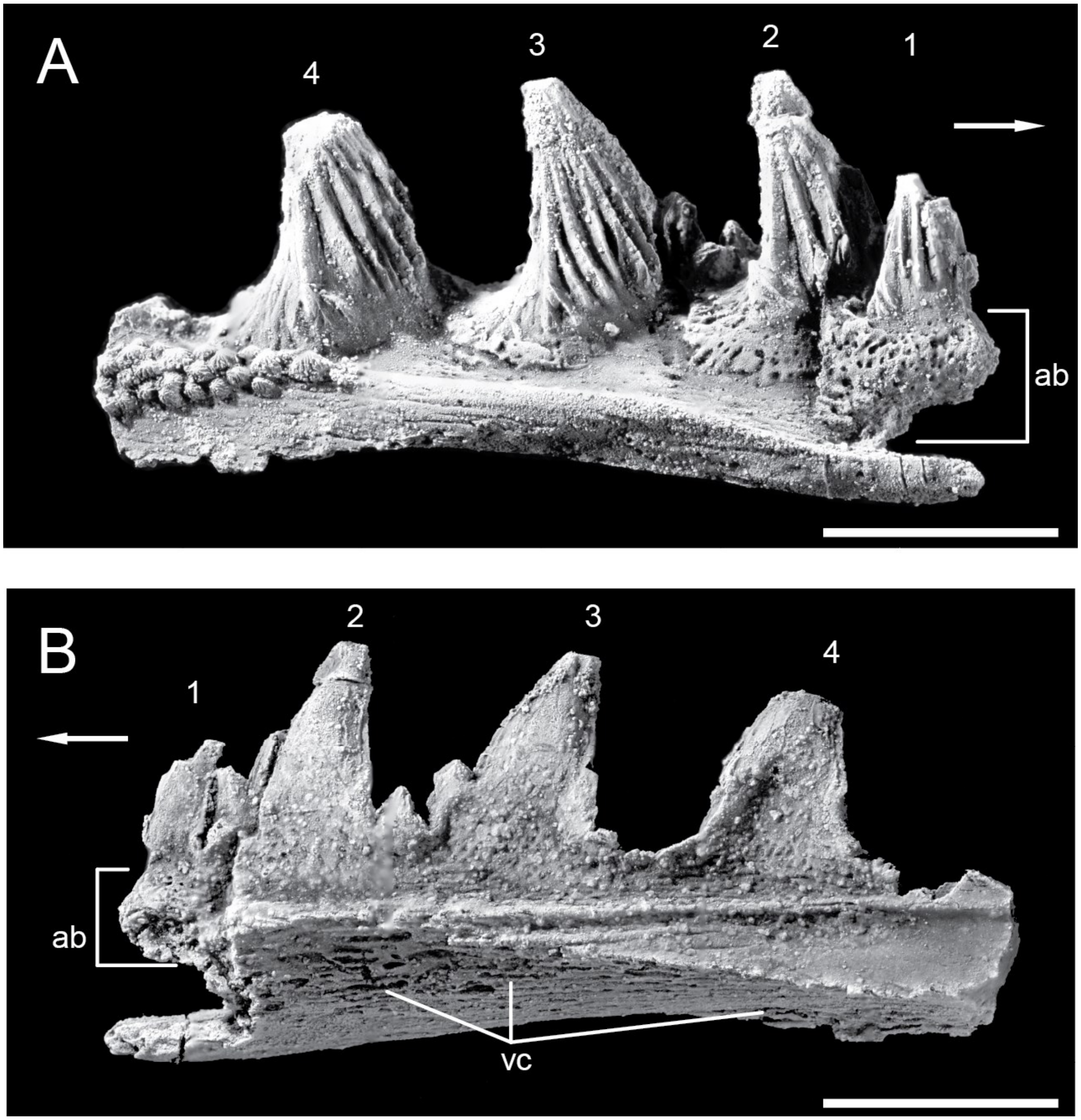


FIGURE 6.2. Proposed holotype of *Oroichthys theobromodon*, showing the vascularisation of the jaw bone and the attachment bone connecting the teeth to the jaw bone. **A**, lingual view; **B**, lateral view. **Abbreviations**: **ab**, attachment bone; **vc**, vascular canals. Scale bars equal 5 mm. Arrows indicate anterior. Numbers indicate tooth age in the row, with 1 being the youngest tooth and 4 being the oldest tooth.

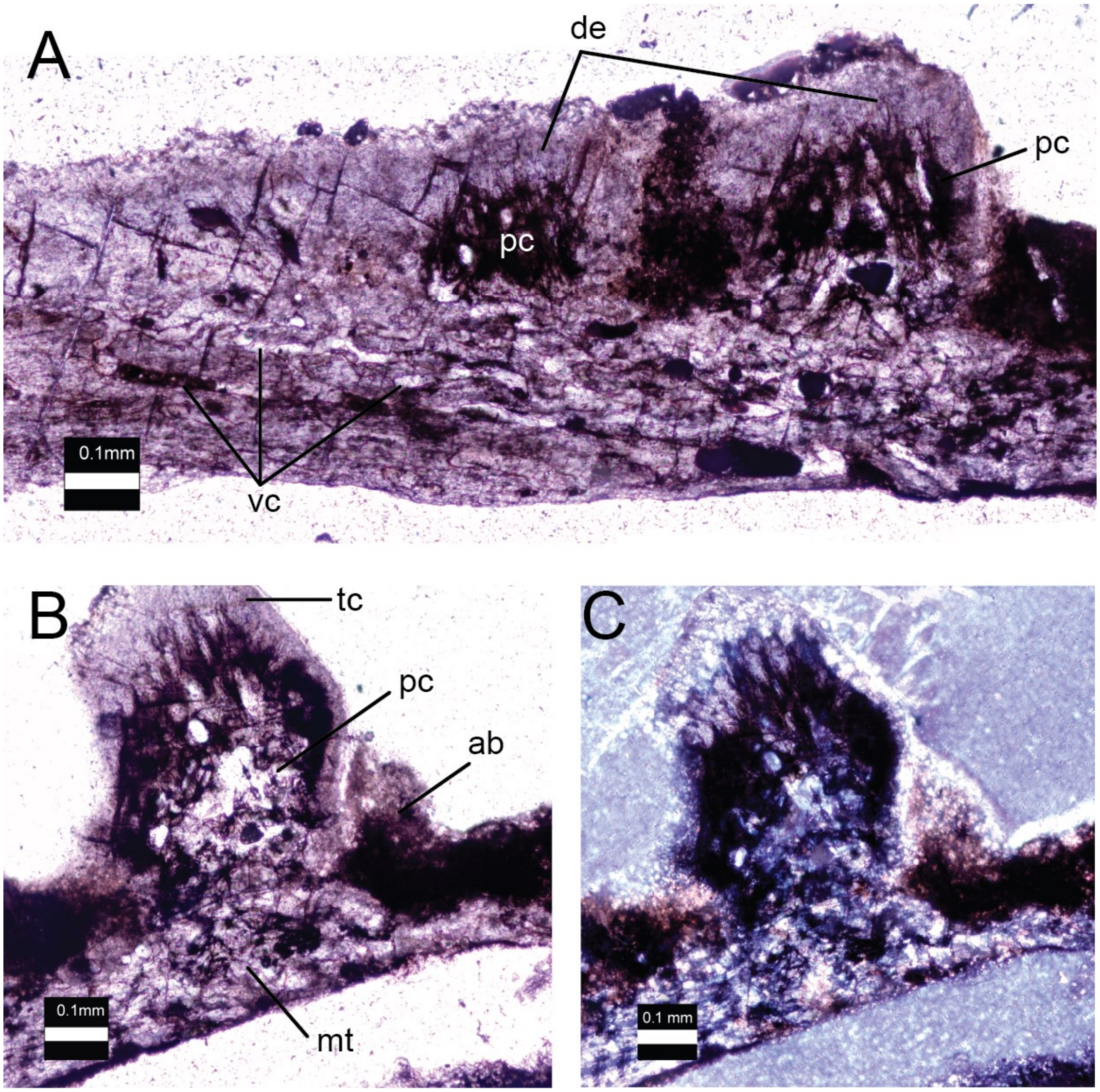
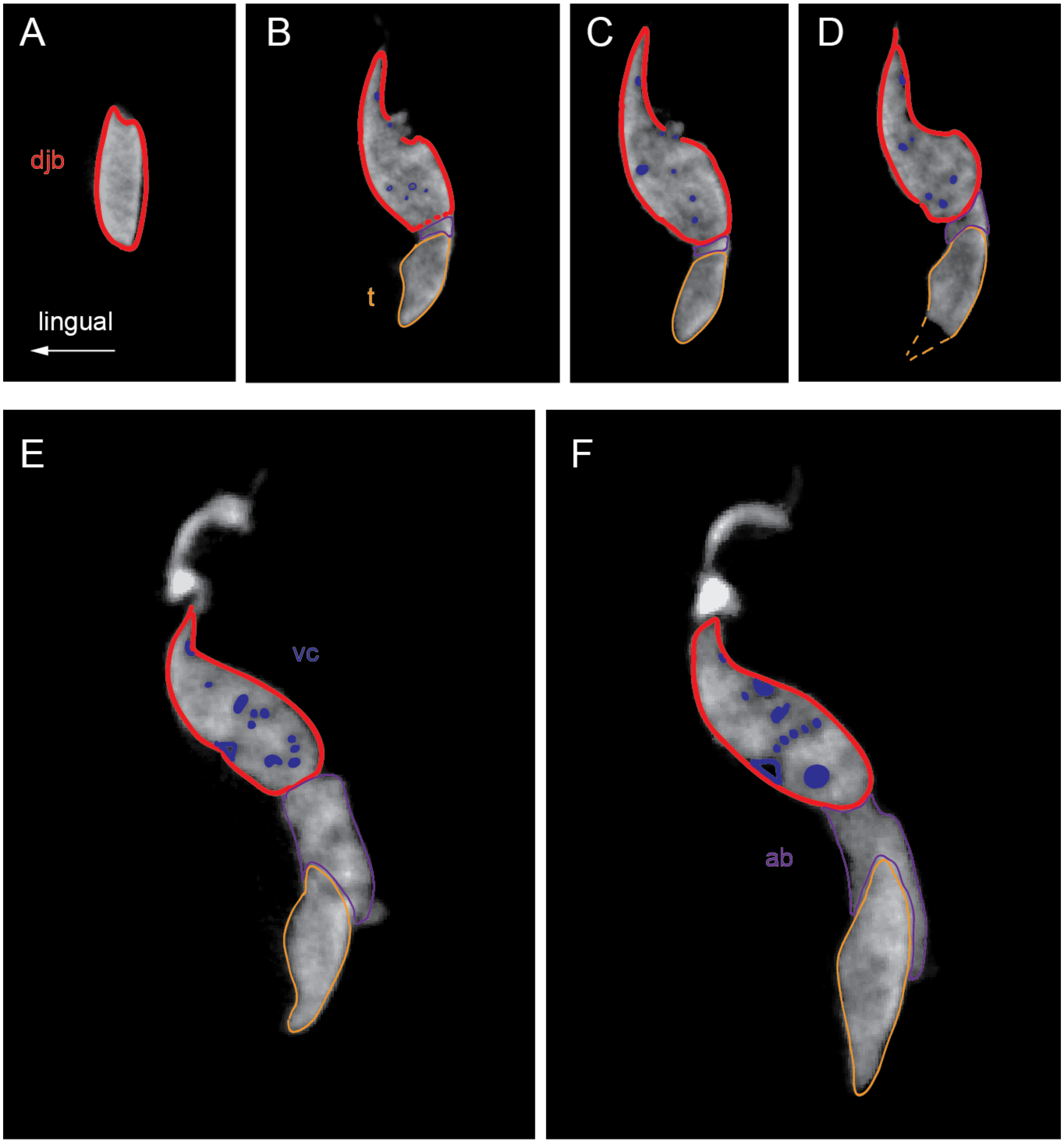


FIGURE 6.3. Longitudinal histological section of *Tricuspicanthus gannitus* jaw bone from the MOTH locality, UALVP 42015. **A**, section of the jaw bone and posterior teeth; **B**, anterior tooth in normal light; **C**, the same anterior tooth in cross-polarized light. **Abbreviations**: **ab**, attachment bone; **de**, dentine; **mt**, medial tooth; **pc**, pulp cavity; **tc**, tooth cusp; **vc**, vacular canal.

FIGURE 6.4 (following page). Computed tomographs representing a series of transverse sections progressing anteriorly through UALVP 47234, a dentigerous jaw bone of *Erymnacanthus clivus*. **A** represents the posteriormost section, and **F** represents the anteriormost section. In all cases lingual is to the left, and the occlusal surface is to the bottom. High-density areas are represented by white, lower-density areas are represented by progressively darker greys. **Abbreviations**: **ab**, attachment bone, outlined in purple; **djb**, dentigerous jaw bone, outlined in red; **t**, tooth, outlined in gold; **vc**, vascular canal, outlined in blue.


A
B
C
D
djb
t
lingual
E
F
vc
ab

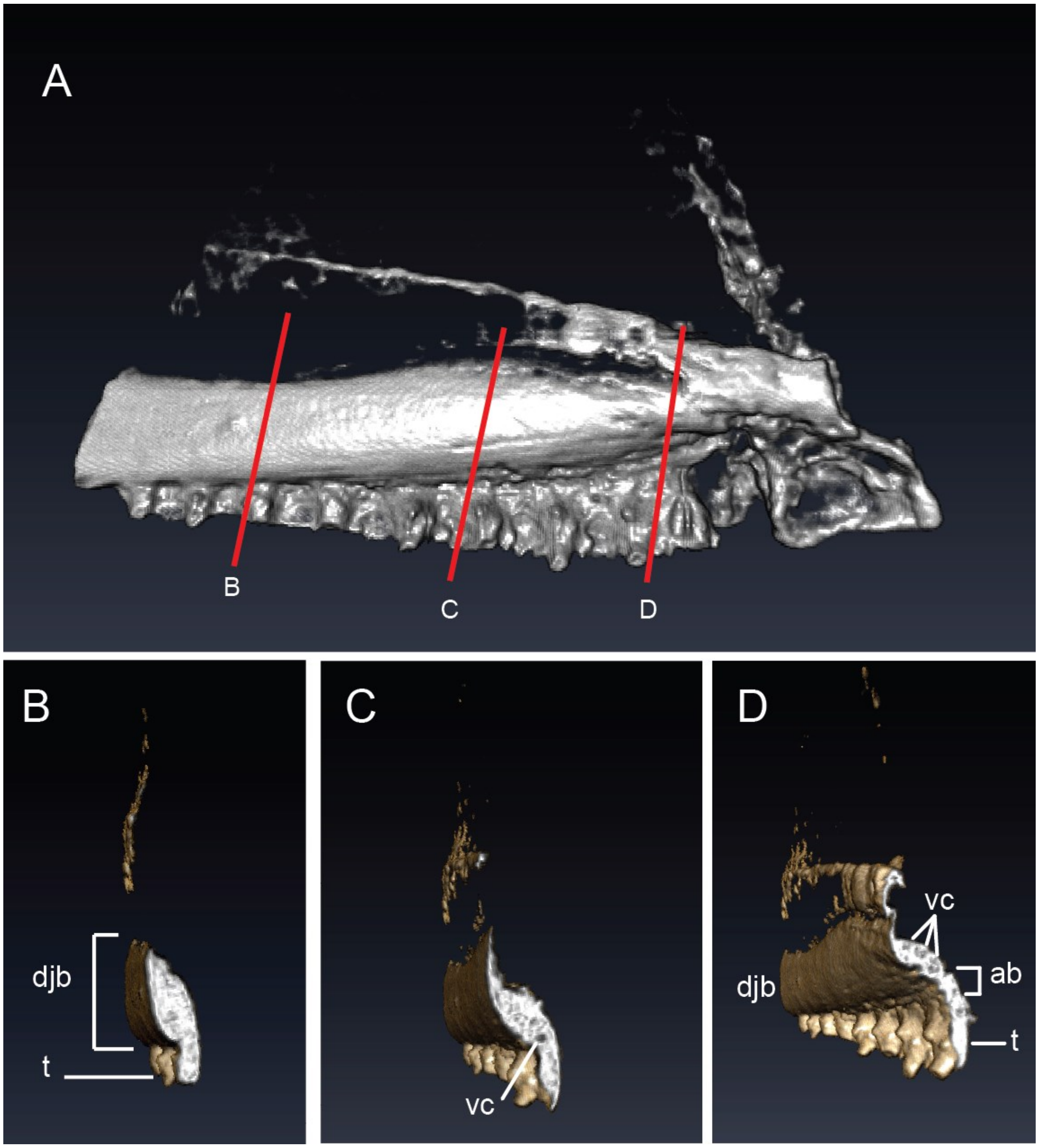


FIGURE 6.5. Volume rendering of UALVP 47234, showing posterior, middle, and anterior slices through the reconstructed volume. **A**, volume rendering of the entire specimen in lingual view, anterior is to the right; **B**, posterior section; **C**, middle section; **D**, anterior section. In all three sections anterior is to the right and out of the page. High-density areas are represented by white, lower-density areas are represented by progressively darker greys. **Abbreviations**: **ab**, attachment bone; **djb**, dentigerous jaw bone; **t**, tooth; **vc**, vascular canal.

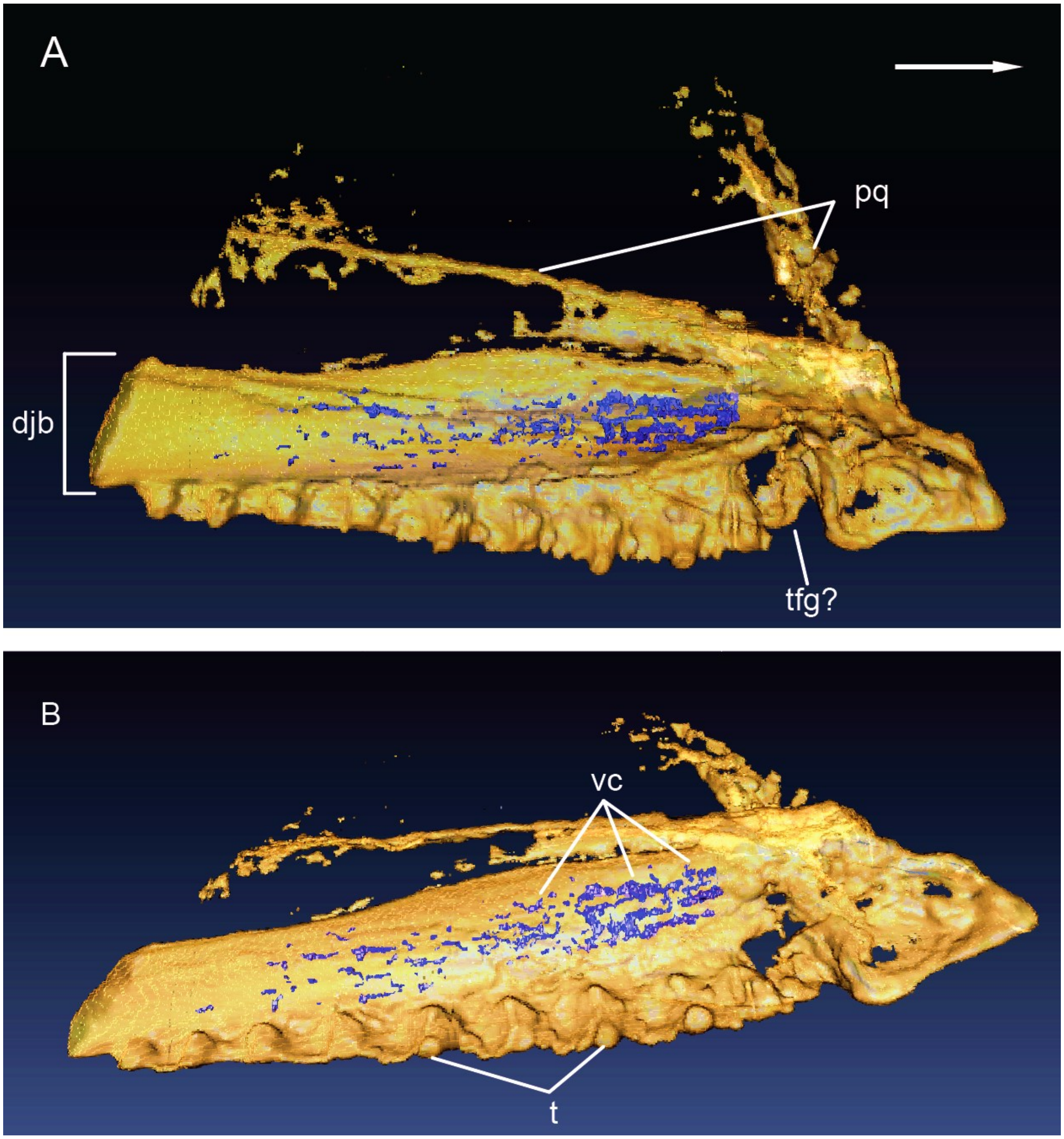


FIGURE 6.6. Isosurface rendering of UALVP 47234, with the vascular canals digitally sectioned in blue. **A**, lingual view; **B**, ventral view. Anterior is to the right. **Abbreviations**: **djb**, dentigerous jaw bone; **pq**, palatoquadrate cartilage; **t**, tooth; **tfg?**, notch in the anterior cartilage, interpreted here as possibly a ‘tooth-forming groove’; **vc**, vascular canal.

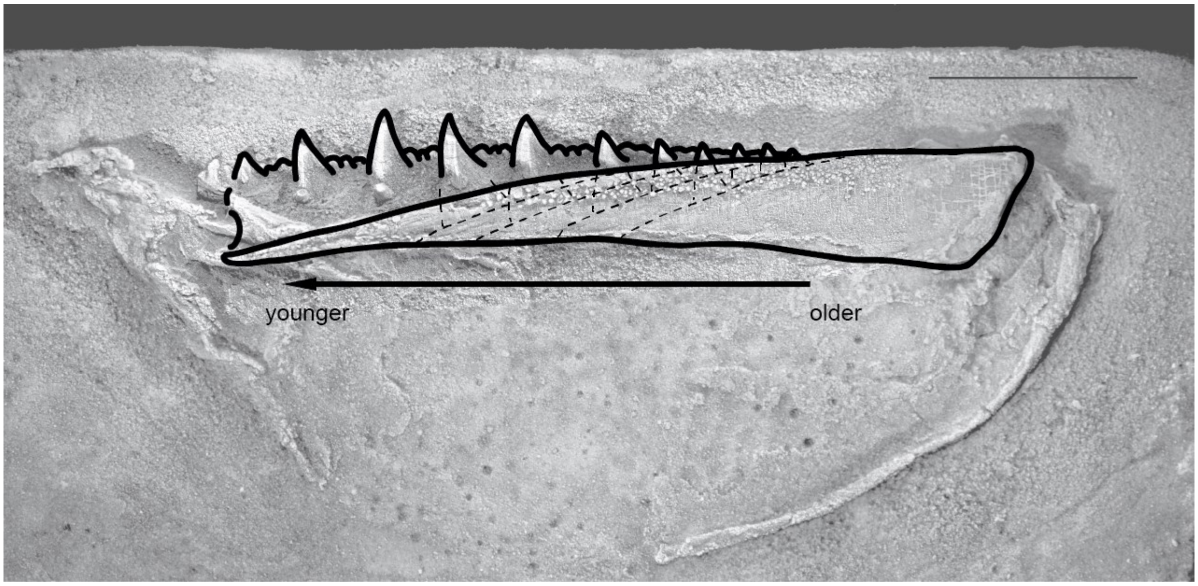


FIGURE 6.7. Hypothesized pattern of jaw bone growth and tooth attachment in ischnacanthiforms, in this case *Euryacanthus serratus* sp. nov. preserved in left lingual view. Tissue is hypothesized to have been added in sheets draping over the existing jaw bone and teeth, indicated by dashed lines. Anterior is to the left; dorsal is to the bottom.

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CHAPTER 7

CONCLUSIONS

Part 1: Diversity

Four new genera comprising six new species of ischnacanthiform acanthodian from the Silurian (Wenlock or Ludlow) B-MOTH fish layer and the Early Devonian (Lochkovian) MOTH fish layer of the Man On The Hill locality are described. Four of the new species are Early Devonian ischnacanthiforms from the MOTH fish layer that were originally assigned to *Ischnacanthus gracilis* (Egerton, 1861), so this greatly increases the number of ischnacanthiform acanthodian species known from this locality and age. All share similar overall body morphology and are distinguishable based primarily on jaw and tooth morphology, suggesting their diversity may be related to specialization in different food sources.

The remaining two new species of ischnacanthiform acanthodians described here are from the Silurian (Wenlock or Ludlow) B-MOTH fish layer, located below the main Lochkovian fish layer at the same locality. Specimens of gnathostomes from this age are very rare, and the two species here increase the known diversity of Silurian ischnacanthiform acanthodians from MOTH from one to three species. One of these species, *Euryacanthus serratus* sp. nov., extends the temporal range of *Euryacanthus* from the Lochkovian to the Wenlock or Ludlow. The two Silurian species are described from specimens that exhibit some signs of tooth-on-tooth wear; the pattern of tooth wear appears to be different for each species, suggesting they may have coexisted by exploitation of different food sources. The two new species are similar to other Silurian ischnacanthiform acanthodians in having a single row of large, lateral teeth and a denticulated lingual ridge on the jaw bone; these may indicate that a single tooth row is the primitive state for the group, while the multiple tooth rows more common in Devonian ischnacanthiforms may be derived.

Part 2: Ecology

Two species of ischnacanthiform acanthodian from the Early Devonian fish layer of the MOTH locality are known from specimens with articulated upper and lower jaw bones and their associated cartilage. This provided a unique opportunity to model their occlusion. Previously, the jaws of Silurian and Early Devonian ischnacanthiforms were hypothesized to occlude differently from those of Middle-Late Devonian ischnacanthiforms (Burrow, 2004a). The modes of occlusion indicated by the three dimensional digital models created from μCT scans of prepared specimens do not support this hypothesis. Instead, these coeval species exhibit different modes of occlusion, though both display an interlocking bite. This suggests these different species may have specialized in different food sources, providing indirect evidence to support the hypothesized trophic niche differentiation proposed for ischnacanthiforms from the MOTH locality. The differences in occlusion suggested by the three-dimensional models are corroborated by the patterns of tooth wear in Silurian ischnacanthiforms.

Part 3: Homology

The exceptional quality of the acanthodian fossils from the MOTH locality has resulted in the description of morphological characters that are unknown in contemporaneous fossils from other localities. The tooth-like scales described in this thesis are one example of such a feature. These are structures external to the oral cavity in ischnacanthiform acanthodians, and they transition from a scale-like morphology to a tooth-like morphology with proximity to the margin of the mouth. These structures are interpreted here as evidence to support a hypothesis of homology between scales and teeth, called the ‘Outside-In Hypothesis’. Although ischnacanthiforms with tooth-like scales also possessed a robust dentition, the presence of these transitional structures outside the mouth itself indicates the probable presence of a ‘field’ of gene expression near the mouth margin that results in odontode with tooth-like forms. This provided the first (and so far, only) example of unambiguous morphological evidence from the Paleozoic fossil record of the capability of scales to form tooth-like structures at the margins of the mouth in early gnathostomes.

Study of the ischnacanthiform acanthodian jaw bones from MOTH has also provided some insight into their development. Based on a comparative study of jaw bone morphology, corroborated with histological evidence from thin sections and computed tomographs, a new hypothesis for the mechanism of jaw bone growth in ischnacanthiformes is proposed. This evidence suggests ischnacanthiform dentigerous jaw bones grew by the addition of material in sheets that draped around the existing jaw bone material. A layer of vascularized tissue connecting the lateral teeth to the jaw bone was also identified; this “bone of attachment” is interpreted here as alveolar bone, suggesting this tissue (and presumably its accompanying suite of tooth attachment tissues, including cementum) evolved along with teeth and have been inherited by all “higher” tooth-bearing vertebrates. The presence of tooth attachment tissues (regardless of their homology with alveolar bone) is proposed as a useful characteristic to distinguish teeth from denticles in fossil taxa, instead of relying on soft tissues such as a dental lamina. Such attachment tissues are present in ischnacanthiformes and the placoderm *Compagopiscis*, but absent in another placoderm with proposed teeth, *Romundina*.

The mode of jaw bone growth and tooth attachment proposed for ischnacanthiforms is suggested to be homologous with the mode of bone growth and tooth attachment in *Compagopiscis*, and may represent the primitive condition for all toothed vertebrates, although a phylogenetic analysis is necessary to test this hypothesis. In both cases, teeth are statodont and the addition of teeth is related to the addition of jaw bone tissue. Chondrichthyans and osteichthyans most likely independently evolved 'decoupled' jaw bone growth and tooth attachment; Chondrichthyes through the loss of the tooth-bearing bone altogether. The mode of tooth replacement in Osteichthyes does not appear to be homologous to the mode of tooth attachment and jaw bone growth in either ischnacanthiforms or *Compagopiscis*, and may represent a true evolutionary novelty.

In contrast to the mode of tooth replacement that is a synapomorphy of Osteichthyes, tooth replacement (or more accurately, tooth loss) in Chondrichthyes is suggested here to have been achieved through loss of tooth-bearing bones. The statodont condition in the stem chondrichthyans, including Ischnacanthiformes and 'climatiiform' acanthodians, is indistinguishable from that in the early chondrichthyan *Doliodus problematicus* (Maisey et al., 2014), which retained its teeth in whorl-like families connected by a bony base to which the teeth were fused. Within total-group Chondrichthyes, the organization of the teeth changed from this primitive arrangement of anterior tooth whorls as in acanthodians, to whorl-like tooth families in which the teeth were attached and retained on a bony base as in *Doliodus*, to whorl-like tooth families or tooth files lacking a bony base, as in modern sharks. With the loss of the bony base connecting the teeth and the loss of the accompanying tissues to attach the teeth to the base, the teeth could be easily shed. Teeth were already being continually added and rotated into functional positions in the tooth whorls, particularly in 'climatiiform' acanthodians like *Ptomacanthus* (Brazeau, 2009) and *Brochoadmones* (Hanke and Wilson, 2006); the novelty of Chondrichthyes *sensu stricto* was to shed the teeth once they rotate out of the functional position.

GENERAL CONCLUSIONS

In-depth study of the ischnacanthiform acanthodians from the Man On The Hill locality, Northwest Territories, Canada has revealed important insights into their diversity, ecology, and the homology of their jaws and teeth. Because of the position of the Ischnacanthiformes in several recent phylogenetic hypotheses (Zhu et al., 2013; Giles et al., 2015) as branching off the chondrichthyan stem near the crown-group Gnathostomata node, such insight is valuable for comparison with other groups. Ischnacanthiformes in particular are poorly understood among acanthodians, being known primarily from isolated dermal tooth-bearing jaw bones. By closely examining these jaw bones, I have provided new information that can be added to existing datasets, allowing these enigmatic fishes to participate, as it were, in future phylogenetic analyses.

Aside from their phylogenetic position and the ambiguity in which it remains cloaked, ischnacanthiform acanthodians are interesting in part because they are so enigmatic, and because they represent one of the first groups of jawed and toothed vertebrates in the fossil record. In providing information into their diversity and ecology, I have provided a better picture of the ancient world in which these animals lived, and how they may have interacted with their environment and with each other.

In addition, this study has provided some insight into the growth and development of the jaw bones in these animals, as well as into the mode of attachment of their teeth. It seems likely that the dentigerous jaw bones of ischnacanthiform acanthodians and the tooth whorls in ‘climatiiform’ acanthodians and stem chondrichthyans are related, as they appear to have developed in a similar way. In both cases, jaw bone tissue is added to the existing tooth-bearing element, after which point the teeth become attached to it. It is difficult to determine whether the jaw bone signals the tooth to attach, or the developing tooth signals the jaw bone tissue, but it seems plausible that the bony tooth-bearing element signals the tooth to produce attachment tissues. When the bony tooth-bearing element is absent as in later chondrichthyans, these attachment tissues are also lost.

Instead of representing a novel structure, it is possible that the bony tooth-bearing element in ischnacanthiforms was inherited from a shared ancestor with other gnathostomes. The mode of growth proposed is not dissimilar to that proposed for *Compagopiscis* (Rücklin et al., 2012), although it is more organized in the sense that tissue and teeth are added to one end of the jaw, instead of concentrically. This may represent a refinement of the primitive jaw bone growth pattern for gnathostomes that was continued in the tooth whorls of ‘climatiiformes’ and the tooth families of Chondrichthyes.

It is also plausible that the attachment tissue that is present in ischnacanthiform acanthodians is homologous to the attachment tissues present in later vertebrates. Further histological study of various groups of early vertebrates is necessary to determine whether they are in fact related, and how ubiquitous these tissues are in the vertebrate tree. Regardless of their potential homology with other gnathostome tooth attachment tissues, the presence of any attachment tissue is an unambiguous morphological character that can be used to distinguish teeth from denticles in fossil gnathostomes.

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