How to build a bony vertebrate in evolutionary time

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ABSTRACT

Jawed vertebrates (gnathostomes) account for over 99% of living vertebrate diversity, with origins that stretch back nearly half a billion years, and comprise two groups: Osteichthyes (fishes and land-dwelling vertebrates) and Chondrichthyes (sharks, rays and chimaeras). Osteichthyans are the dominant clade, with at least 60,000 species approximately evenly divided between two clades: the Actinopterygii and the Sarcopterygii. However, our understanding of early osteichthyan evolution is skewed in favour of sarcopterygians, leaving the origin of nearly half of all vertebrate diversity critically understudied. Furthermore, recent upheavals in the early gnathostome tree have destabilised relationships amongst fossil taxa and eroded our understanding of primitive anatomical conditions of key groups. Central to understanding early gnathostome evolution is the braincase, an anatomically complex structure that provides a wealth of morphological characters. However, braincases rarely fossilise, and their position inside the skull makes them difficult to attain. X-ray tomography allows a comprehensive description of the internal and external anatomy of fossils, including the braincase. This thesis sets out to target phylogenetically pivotal taxa and incorporate new anatomical data in building up a picture of character evolution in early jawed vertebrates. In particular, I target the gnathostome stem, describing a new taxon that helps bridge the morphological gap between placoderms and crown gnathostomes, allowing a more comprehensive understanding of both dermal and endoskeletal evolution. I also focus on early actinopterygians, describing the endoskeleton of the first members of the group in order to understand primitive anatomical conditions. I then investigate actinopterygian braincase anatomy in the context of a revised phylogenetic analysis, illuminating the early evolution of the actinopterygians. Finally, I present a synthetic review of braincase anatomy across the early gnathostome tree. These results provide a more accurate picture of braincase evolution across gnathostomes and actinopterygians, clarifying our understanding of their evolution while revealing new information about when key innovations arose in the brains of the very first ray-finned fishes.

EXTENDED ABSTRACT

Vertebrates are an extraordinarily successful and diverse group of animals that today number over 61,000 species, encompassing everything from lampreys to hammerhead sharks and goldfish to orangutans and our own species. The overwhelming majority of vertebrates are jaw-bearing (Gnathostomata), with about 100 or so species of lamprey and hagfish comprising the jawless fishes (Cyclostomata). The evolutionary roots of vertebrates stretch back over half a billion years, and fossils are instrumental for understanding their history. Bony vertebrates (Osteichthyes) are by far the dominant modern group, with 60,000-odd species split into two lineages: the lobe-finned vertebrates (Sarcopterygii), like coelacanths and land-dwelling vertebrates, including ourselves; and the ray-finned fishes (Actinopterygii), which include staples of the aquarium and fishmonger like goldfish and cod. The cartilaginous fishes (Chondrichthyes) number a mere 1000 species. Actinopterygians account for over half of living vertebrate diversity, and are of great scientific, ecological and economic importance.

The fossil record provides critical clues for understanding the runaway success of living vertebrates. However, our understanding of the vertebrate family tree is uneven, with areas of uncertainty concerning the stem membership and early evolution of many groups. A series of recent publications have caused upheavals in the early vertebrate tree, changing our perception of groups such as placoderms and acanthodians. This problem is compounded by a failure to investigate and/or identify critically important taxa that sit on the gnathostome, osteichthyan and actinopterygian stem, resulting in a confused picture of primitive conditions and sequences of character acquisition.

Central to understanding early jawed vertebrate evolution and the phylogenetic placement of fossils is the braincase, a complex structure housing the brain and other sensory organs and pierced by numerous nerve and blood vessels. As such, it provides a wealth of morphological characters, forming the basis for analysing relationships between different species. An infilling of the internal cavity of the braincase, known as an endocast, can be used as a proxy for brain morphology, and provides a further rich source of phylogenetic data as well as checks of anatomical interpretations based solely on external examination of the braincase. Many of the most important novelties of the vertebrates may relate to innovations in brain and skull structure, and as such are extremely useful data sources. However, braincases rarely fossilise, and their position inside the skull makes them difficult to study when they are preserved. X-ray tomography allows a comprehensive and non-destructive account of the internal and external anatomy of fossils, including the braincase. This thesis sets out to target phylogenetically pivotal taxa and incorporate new anatomical data in building up a picture of character evolution in the earliest ray-finned fishes.

The anatomy of the last common ancestor of modern gnathostomes (osteichthyans and chondrichthyans) is contentious. A succession of recent publications variably finds support for either a bony fish-like or shark-like form. Traditional views place the acanthodians—a group of early shark-like fishes—on the osteichthyan stem. Thus it was long thought that living jawed vertebrates were primitively micromeric, with the macromeric skeletons of osteichthyans not homologous with that of placoderms. This has recently been challenged, however, by the discovery of a placoderm with osteichthyan-like jaw bones. We applied CT scanning to an enigmatic 415 million year old fish from Siberia, originally described as an actinopterygian on the basis of its dermal skeleton, in order to understand the structure of its braincase (Chapter 2). We found a unique combination of skull and braincase features, suggesting a stem gnathostome placement. As well as providing new insights into character

evolution in early gnathostomes, phylogenetic analysis of this taxon provides strong evidence for macromery being primitive for gnathostomes, and corroborates the shift of all acanthodians onto the chondrichthyan stem.

Few braincases have been described for early members of the Actinopterygii, and as a result the Late Devonian (380 Ma) *Mimipiscis*, described in great detail from both its endoskeleton and dermal skeleton, is generally used as the default proxy for the primitive actinopterygian condition. However, there is little evidence for the structure of the endoskeleton in the first members of the group. As the sister group of all other actinopterygians, the Middle Devonian (390 Ma) *Cheirolepis* occupies a critical position in vertebrate phylogeny. Despite a long history of study of this taxon, and extensive descriptions of its dermal skeleton, its braincase has never been described, leaving questions of neurocranial evolution in early actinopts unanswered. Synchrotron-based CT scanning was used to examine the braincase and other elements of the internal skeleton of *Cheirolepis* (Chapter 3), revealing new anatomical data that demonstrate that its endoskeleton is remote from existing early actinopterygian examples, sharing many plesiomorphic features with lobe-finned fishes. Collectively, these new data help clarify primitive conditions within actinopterygians, which in turn have important implications for understanding features likely present in the last common ancestor of living osteichthyans.

The scarcity of actinopterygian braincase data from the Devonian has made it difficult to test how representative the anatomy of *Mimipiscis*, the sole Devonian actinopterygian that has been exhaustively described, is for taxa crownward of *Cheirolepis*. The discovery of a remarkably well-preserved specimen representing a new taxon from the Late Devonian (375 Ma) of France provides exceptional new data on the dermal skull, braincase, hyomandibula and gill skeleton (Chapter 4). The 3D articulated nature of the fossil sets it apart from most

contemporaneous taxa, and allows direct comparison with more derived ray-finned fishes as well as outgroup representatives. The presence of large vestibular fontanelles, an aortic notch, and elongate grooves for the lateral dorsal aortae in this new taxon represent conspicuous differences from the braincase structure of *Mimipiscis.* This new taxon represents an important contribution to our understanding of early ray-finned fish diversity and provides a framework for a revised phylogenetic analysis of the first actinopterygian radiation. The phylogenetic analysis presented in this chapter incorporates a substantial proportion of braincase and endocast anatomy for the first time. It provides evidence for *Dialipina* and *Meemannia* as stem actinopterygians, and corroborates the position of *Cheirolepis* as sister taxon to all remaining members of the group. It does not find support for a clade comprising *Mimipiscis*, *Moythomasia* and *Gogosardina*, and furthermore suggests that the genera *Moythomasia* and *Kentuckia* are in need of taxonomic and anatomical revision.

Cranial endocasts, infillings of the skeletal void that once contained the brain and associated soft tissues, represent rich sources of anatomical data, but have not been fully exploited in early actinopterygians. As such, there is a poor understanding of brain evolution in the early members of the group. CT scanning of the Late Devonian (380 Ma) *Mimipiscis* and the early Carboniferous (350 Ma) *Kentuckia*, both of which serve as key representatives of early ray-finned fishes in studies of early vertebrate relationships, provides novel details of the endocast (Chapter 5). Although the anatomy of the *Kentuckia* endocast is as expected for a stratigraphically younger actinopterygian, many of the new features revealed in the *Mimipiscis* endocast are plesiomorphies shared with ray-finned fish outgroups, most notably divergent olfactory tracts, small optic lobes, and a dorsally projecting labyrinth. These findings provide new insights into how and when specialisations of the actinopterygian brain evolved, and suggest that they were absent in the group’s early history.

The braincase is of vital importance when reconstructing relationships, and allows patterns of character transformation to be easily traced across the vertebrate tree of life. However, this is hampered by a failure to draw clear comparisons across different taxonomic assemblages; indeed, many features are given assemblage-specific names. I present a synthetic review of braincase and endocast anatomy across the early gnathostome tree, drawing together accounts from the literature along with the results presented in this thesis (Chapter 6). This review encompasses placoderms, stem gnathostomes, chondrichthyans (including acanthodians), and osteichthyans, facilitating comparisons and identification of homologies across groups, as well as recognising specialisations of groups and individual taxa. I present proposed sequences of character acquisition and loss across the tree, suggesting primitive anatomical conditions at key nodes.

The work presented in this thesis provides answers to long-standing questions concerning the stem membership and primitive anatomical conditions of major vertebrate groups, namely Gnathostomata, Osteichthyes and Actinopterygii. In using CT methods to describe (and redescribe) braincase anatomy of critical taxa, this thesis greatly adds to our knowledge bank, while permitting clear schemes of character transformations to be drawn up across the tree. As well as providing a model for the last common ancestors of crown gnathostomes, osteichthyans and actinopterygians, this thesis highlights the efficacy of endocast and other braincase characters, and the phylogenetic analyses included within present new hypotheses of relationships amongst the first animals with jaws.

STATEMENT OF ORIGINALITY

The thesis I am submitting is entirely my own work except where otherwise indicated; work done in collaboration with others is outlined at the start of each chapter. No part of this thesis has been accepted or is currently being submitted for any degree, diploma or certificate or other qualification in this University or elsewhere. I have clearly indicated the presence of all material I have quoted from other sources. This work does not exceed the page limit set out by the Degree committee.

Candidate’s signature: ……..………………………….. Date: ………………………..

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Thesis Contents

4.5 Description

CHAPTER 1: THE ORIGIN AND EVOLUTION OF JAWED VERTEBRATES

1.1 OVERVIEW

Jawed vertebrates (Gnathostomata) are a hugely diverse and successful group, with over 60,000 living species (Nelson, 2006) ubiquitous throughout the sky, sea and land. Given that the group's evolutionary roots stretch back nearly half a billion years, the modern day gives a very biased snapshot: it is vital to look at the fossil record to understand how the body plan that drove this vast radiation arose. The origin and evolution of the jawed vertebrates has naturally been the focus of much research, but recent upheavals in our understanding of relationships between major vertebrate groups have challenged the status quo and forced a reassessment of the early gnathostome tree of life (Johanson, 2002; Coates, 2003; Johanson & Smith, 2005; Friedman, 2007; Brazeau, 2009; Zhu et al., 2013). This thesis aims to address the resultant gaps in our knowledge by using innovative 3D x-ray imaging techniques to target key anatomical features of pivotal taxa, answering fundamental questions about gnathostome origins and building up a detailed picture of their evolution through deep time.

1.2 EVOLUTIONARY DOMINANCE OF JAWED VERTEBRATES

The earliest articulated vertebrates with jaws appear in the fossil record some 420 million years ago (Zhu et al., 2009, 2013), although presumably evolved many millions of years earlier (hinted at by the description of purported acanthodian-like scales from the Ordovician, (Karatajute-Talimaa & Predtechenskyj, 1995; Janvier, 1996) and possible shark-like scales from the Ordovician, Sansom et al., 1996). Before the appearance of jawed vertebrates, the seas were dominated by jawless vertebrates, including heterostracans, anaspids, galeaspids, pituriaspids and osteostracans (Janvier, 1996), with gnathostomes initially representing only a small proportion of the biota. This is in contrast to the Modern, where the living Agnatha, hagfishes and lampreys, account for just 1% of living vertebrate diversity.

Placoderms represent the earliest diverging vertebrates with jaws, and have a fossil record dating back to the Silurian (Wang, 1991). Although extinct, they are more closely related to living jawed vertebrates than living jawless vertebrates, and are therefore classified as stem gnathostomes. The placoderms have a complicated taxonomic history: traditionally held as a monophyletic group, they were long regarded as having ties to chondrichthyans (Quenstedt, 1838; Stensiö, 1925, 1963a, 1969; Holmgren, 1942; Ørvig, 1960, 1962; Jarvik, 1964, 1980; Goujet, 1982; Young, 1986). This view was disputed by many, however (e.g. Westoll, 1962; Patterson, 1965; Romer, 1966; Schaeffer, 1975; Miles & Young, 1977; Young, 1986b; Janvier, 1996), and, eventually, a consensus that placoderms were stem gnathostomes (in modern parlance) emerged. Since then, further doubts have arisen over the monophyly of the group, with Johanson (2002) and Johanson & Smith (2005) suggesting that, in fact, placoderms are paraphyletic, with arthrodires more closely related to living jawed vertebrates than other placoderm groups. Although this argument continues to attract a number of dissenters (e.g. Young, 2008, 2010), the majority of recent analyses have tended to recover placoderms as a paraphyletic assemblage on the gnathostome stem (e.g. Friedman, 2007; Brazeau, 2009; Davis et al., 2012; Zhu et al. 2013; Dupret et al., 2014, Long et al., 2014).

The living jawed vertebrates (the crown group) comprise the reciprocally monophyletic chondrichthyans and osteichthyans, with a projected divergence date between the two clades of around 420-430 Ma (Zhu et al., 2009; Betancur-R et al., 2013; Broughton et al., 2013). Modern chondrichthyans are made up of the sharks, rays and chimaeras, and number approximately 1000 species. The distinction between these two clades is firmly entrenched in the literature as far back as the 18th century, with Cuvier classifying jawed vertebrates either as 'Chondropterygii' (chondrichthyans) or 'Ossei' (osteichthyans).

Over 99% of extant vertebrate diversity, some 60,000 species, falls into two more or less equally speciose groups: the actinopterygians, which include everything from trout to seahorses to mudskippers, and the sarcopterygians, which include the fish-like coelacanths and lungfishes, but also all four-legged vertebrates. Although actinopterygians and sarcopterygians are now well established as monophyletic groups, traditional schools of thought, which relied only on morphological characteristics and general similarities, favoured a more complex system of relationships. The order Ganoidei was established in Agassiz' seminal work (1833-1844), and included polypterids, holosteans, some teleosts and many 'palaeoniscids', but also lungfishes, rhipidistians, coelacanths and acanthodians. Müller (1845) attempted to refine and define Ganoidei, removing extant teleosts and lungfishes and assigning the remaining members to two divisions: Holostei*,* which included *Lepisosteus, Amia* and *Polypterus*; and Chondrostei*,* which included *Acipenser* and *Polyodon*. The Teleostei were established as a separate order. Huxley (1861) also attempted to reassess Ganoidei, naming a suborder, Crossopterygidae, into which he placed *Polypterus*, as well as various coelacanths, lungfishes and rhipidistians. Despite these efforts, numerous authors rejected the validity of Ganoidei on the basis of a lack of characters (e.g. Müller, 1845; Kner, 1866; Lütken, 1868), and eventually Cope (1872) divided the group into two, attempting to establish definitive characters for each: the Crossopterygii (following Huxley) and the Actinopteri. This did little to defuse the situation, however, and the status of Actinopteri in particular was met with criticism (e.g. Gill, 1872;

Huxley, 1876; Traquair, 1877; Bridge, 1878; Günther, 1880). By 1877, Cope was forced to retract the original definition of the term Actinopteri, establishing instead the Hyopomata, which included the Crossopterygia, Chondrostei and Actinopteri, the latter now restricted to refer to a subset of palaeoniscids. It was not until Woodward's (1889) work on sturgeon evolution that the link between palaeoniscids and chondrosteans was understood, and he soon re-established the Actinopterygii (Woodward, 1891), a move that was generally accepted. In addition to those put forward by Woodward (1891), additional characters defining the actinopterygians were proposed by Goodrich (1909). It was not until the 1920s and 30s that cladistians were recognised as belonging to Actinopterygii (Goodrich, 1928, 1930; Aldinger, 1937; White, 1939).

The final class of gnathostomes, the acanthodians, is an extinct assemblage that lived from the early Silurian to the Permian. As with the placoderms, the taxonomic background and allegiances of the acanthodians is complex. Acanthodians have been recognised in the fossil record quite as long as members of extant lineages, and were also dealt with by Agassiz (1833-1844). Although originally allied with chondrichthyans (Quenstedt, 1851; Nielsen, 1932; Woodward, 1932; Holmgren, 1942; Ørvig, 1957; Nelson, 1968, 1969), the acanthodians also have a tradition of being associated with osteichthyans (Huxley, 1861; Traquair, 1890; Nielsen, 1949; Romer, 1966; Schaeffer, 1968, 1969), placoderms (Woodward, 1935; Watson, 1937), and gnathostomes more generally (Watson, 1937), although this latter suggestion attracted extensive criticism (e.g. Holmgren, 1942; Stensiö, 1947, 1963a; Jarvik, 1963, 1980; Miles, 1964, 1965, 1968, 1973). Advocates for the idea of a close relationship between acanthodians and chondrichthyans remained vocal throughout much of the 20th century (references above; Jarvik 1977, 1980), but Miles' (1973) redescription of *Acanthodes* provided seemingly compelling evidence for some acanthodians as the extinct sister group of osteichthyans (Gardiner, 1984a; Maisey, 1986;

Janvier, 1996). The status of acanthodians as the sister group of osteichthyans seemed secure until Brazeau's (2009) reassessment of early gnathostome evolution, which recovered acanthodians as a paraphyletic assemblage of stem chondrichthyans and osteichthyans, a finding upheld by later analyses (Davis et al., 2012). The discovery of *Entelognathus*, a Silurian placoderm with osteichthyan-like jaws, has had the effect of moving all acanthodians on to the chondrichthyan stem (Zhu et al., 2013), but this result is awaiting independent corroboration.

1.3 RISE OF THE BONY FISHES

The divergence of actinopterygians and sarcopterygians occurred some 420 Ma (Zhu et al., 2009; although significantly younger dates of ~380-400 Ma have been recovered by molecular analyses: Betancur-R et al., 2013, Broughton et al., 2013, Faircloth et al., 2012, Near et al., 2012 etc.). The sarcopterygian fossil record is well sampled, with articulated and well preserved material known back into the Ludlow (Zhu et al., 2009; Zhu et al., 2013; Choo et al., 2014). Identifiable members of the extant sarcopterygian lineages - actinistians, dipnomorphs and tetrapodomorphs - are present in the Early Devonian (Chang, 1995; Zhu & Fan., 1995; Zhu & Yu, 2002; Friedman, 2007; Lu et al., 2012; Zhu et al., 2012). The actinopterygian crown is also considered to have a Devonian origin, but this is based on equivocal evidence, namely the branching pattern produced when the extant taxon *Polypterus* is included in cladistic analyses with Palaeozoic actinopterygians, where it typically assumes a position as sister taxon to all remaining actinopterygians excluding *Cheirolepis* (Patterson, 1982; Gardiner, 1984a; Long, 1988; Gardiner & Schaffer, 1989; Taverne, 1997; Coates, 1999: Xu & Gao, 2011; Xu et al., 2014). Hence, Devonian taxa such as *Mimipiscis* and *Moythomasia* are used as fossil calibration nodes for the actinopterygian crown (Hurley et al., 2007; Saitoh et al., 2011; Near et al., 2012; Betancur-R et al., 2013;

Broughton et al., 2013). Taxa which can be confidently ascribed to modern lineages on the basis of morphological similarity do not appear in the fossil record until the early Triassic or latest Permian (Nielsen, 1949; Liu & Wei, 1988; Hurley et al., 2007), and the earliest polypterid fossils are Late Cretaceous in age (Dutheil, 1999; Grandstaff et al., 2012). Quite aside from the question of the crown age, our understanding of bony fish evolution is heavily biased in favour of the sarcopterygians, for reasons ranging from better research effort to a more complete fossil record and the overwhelming diversity of the actinopterygians (Nelson, 1969; Sallan, 2014).

Despite the modern dominance of the osteichthyans, surprisingly little is known about their early evolution and the sequence of character acquisition leading to the crown. This is often referred to as the 'problem of the naked stem' (Schaeffer, 1968; Friedman & Brazeau, 2010), and reflects the scarcity of extinct taxa resolved as more closely related to the osteichthyan than the chondrichthyan radiation. Ever since Miles' (1973) reassessment of *Acanthodes*, acanthodians have been generally accepted as occupying a position on the osteichthyan stem (Gardiner, 1984a; Maisey, 1986; Janvier, 1996), with the potential to inform our understanding of how the bony fish body plan arose. *Acanthodes* aside, the other candidate taxa on the osteichthyan stem are represented only by scraps of dermal bone, and can inform little more than an understanding of scale evolution (Schultze, 1968; Friedman & Brazeau, 2010). The stem has been further depopulated by a spate of recent analyses that remove some or all acanthodians to the chondrichthyan stem (Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013). This uncertainty has resulted in problems when trying to understand character evolution and reconstruct common ancestral states.

1.4 THE BRAINCASE: AN ANATOMICAL 'ROSETTA STONE'

The braincase, which sits inside the vertebrate skull, is an anatomically complex structure and thus of great use in understanding phylogenetic relationships. The primary function of the braincase is to house the brain, which itself is surrounded by layers of meningeal tissue, fat and fluid. In addition to the brain, the braincase accommodates key sensory organs such as the eyes and inner ear. The neurocranial walls are pierced and grooved by the passage of the cranial nerves and vascular supply. As the brain is made of soft tissue and therefore does not typically fossilise (with the potential exception of the specimen described by Pradel et al. 2009), the braincase provides the only route to understanding its anatomy. An infilling of the cavity inside the neurocranium gives a cast - known as an endocast - of the space occupied by the brain and meningeal tissues and fluids, potentially providing evidence of brain anatomy in extinct taxa.

Perhaps the main advantage of the braincase, in the context of understanding evolutionary relationships, is the ease with which it can be compared across groups. While the dermal skeleton is more frequently preserved, it can be highly modified to reflect external pressures and influences, and may be reduced or lost entirely in some lineages (such as the chondrichthyans). These factors combine to make the dermal skeleton difficult to homologise across groups, an issue that has plagued the field for decades (e.g. the dermal plates of placoderms and osteichthyans: Stensiö, 1959, 1963a; Gross, 1962; Forey, 1980; Gardiner, 1984b; Zhu et al., 2013). In contrast, the braincase is fairly conserved in its function and morphology, and is present and easily comparable across the vertebrate tree of life, including Recent taxa (although, of course, distinct modifications do occur in some groups, such as the ptyctodonts, Miles & Young, 1977, and holocephalans). Indeed, the morphology of the braincase was perceived to be so conserved in early actinopterygians as to be of no use in reconstructing relationships (Gardiner & Schaeffer, 1989: p.137). However, as foreseen by Gardiner & Schaeffer, this view is based on a failure to adequately sample the relevant part of the tree: only a handful of Palaeozoic actinopterygian braincases had been described at the time. Subsequent discoveries have made clear the complexity of braincase characteristics across actinopterygians, and studies in other groups have demonstrated how instrumental neurocranial data are to understanding relationships (e.g. chondrichthyans, Coates & Sequeira, 1998, 2001, Maisey & Anderson, 2001; lungfishes, Friedman, 2007; tetrapodomorph fishes, Coates & Friedman, 2010). Problems are still faced, however, by a confused understanding of early gnathostome relationships and a tendency to treat different fossil assemblages as isolated groups, with assemblage-specific terms employed to refer to anatomical features. This is most notable in the dermal skeleton, where the large dermal plates of osteichthyans and placoderms are given different names (see above for references), but also affects the braincase and endoskeleton. This makes it difficult to build a detailed picture of character evolution as jawed vertebrates began to diversify.

The utility of the braincase is countered by a preservational bias: as part of the endoskeleton, the braincase is formed initially from cartilage, which may ossify or become calcified. In many taxa, however, this mineralisation does not occur (or is only partially completed), and the cartilage leaves no trace in the fossil record (e.g. antiarchs, derived arthrodires, Stensiö, 1969; many acanthodians, Brazeau, 2012; lungfish, Cloutier, 1996; chondrosteans, Hilton et al., 2011). Additionally, the braincase is typically not preserved in flattened specimens, which represent the majority of fossil remains.

Even where the braincase is preserved, a major obstacle to study and description is its inaccessibility. In placoderms and osteichthyans, a suite of dermal bones surrounds the neurocranium, largely shielding it from view. Furthermore, the fragile nature of the braincase means that preservation is often best when enclosed in a nodule or concretion, or undisturbed within a bedding plane, providing an additional barrier to study. While acid preparation can be employed with great success in some instances (e.g. *Mimipiscis* and *Moythomasia* from the limestone concretions of the Gogo Formation, Australia: Gardiner, 1984a), this method is of little use in lithologies such as shales and sandstone (e.g. *Kentuckia deani* from concretions of the New Providence Shale Member, USA: Rayner, 1951). Even when acid preparation can be employed, the specimens are often extremely fragile and susceptible to damage (e.g. *Gogosardina*, Choo et al., 2009), and insufficient rinsing of the specimen can lead to eventual degradation (e.g. *Griphognathus* NHMUK collections, pers. obs.).

Traditionally, destructive techniques were employed in order to access internal anatomies, most notably Sollas' grinding method (Sollas, 1903). This approach was first developed in the early 1900s, and was designed to expose the internal anatomy of a specimen while allowing a record to be kept. The fossil would be attached to Sollas' machine and ground away, with the process halted at regular intervals (of around 100 micrometers) in order for a photograph or camera lucida drawing to be made, typically at a magnification of about 10x. This was repeated until the entire fossil was ground away and a complete series of drawings had been made, a process that could take years or even decades. The drawings were then etched on to wax leaves and assembled to create a three-dimensional model of the specimen. One of the first vertebrates studied using this method was the enigmatic *Palaeospondylus gunni* (Sollas & Sollas, 1904). Sollas' method was adopted by the Stockholm school, most notably Erik Stensiö (Stensiö, 1925, 1927; 1963a, b), Erik Jarvik (Jarvik, 1942, 1954, 1972, 1975, 1980) and Philippe Janvier (Janvier, 1985). Despite its efficacy, the grinding method is not without its downsides. Chief amongst these was the complete destruction of the material, restricting its application to taxa that were well represented in the fossil record. The wax models that were constructed have degraded badly over time, and are no longer suitable for study, leaving only the author's descriptions and interpretive reconstructions as a record of the original fossil material. While these have been indispensible in informing an understanding of early vertebrate relationships, they are typically highly stylised and subjective, and rely heavily on extant anatomical models. As Stensiö considered placoderms to be closely related to sharks, many of his anatomical interpretations are interpreted after this fashion (e.g. Stensiö, 1926, 1963a). These relationships are no longer accepted, throwing into question the reliability of many of Stensiö's interpretations. A variation on the grinding method is Poplin's microtome technique (Poplin & de Ricqlès, 1970), where slices cut through the fossil are affixed to a glass slide, thus ensuring a physical record of the fossil is preserved.

Although these methods were used with great success in the past, they are no longer workable today. In addition to being too time consuming and not repeatable, the use of destructive techniques on articulated material is, by and large, no longer permitted.

Despite the obstacles outlined above, the anatomical record of braincases is fairly well sampled across the major vertebrate groups. Several gaps in our knowledge remain, however, either due to a true lack of data (e.g. acanthodians) or a failure to adequately focus research effort (e.g. actinopterygians). Closing these gaps will have very real implications for understanding the sequence of character acquisition in early gnathostome evolution and for reconstructing the anatomy of the last common ancestor in major groups.

1.5 CT SCANNING

The advent of CT (computed tomography) scanning presents a solution to the problem of how to access internal anatomy without damaging the fossil. First used in a medical setting in the 1970s, CT scanning was initially applied to fossil specimens in the 1980s and 1990s (e.g. Tate & Cann, 1982; Conroy & Vannier, 1984; Haubitz et al., 1988; Rowe et al., 1992), but the limitations and expense of the technique meant that it did not gain traction as a common method until the early 2010s. Since then it has been applied across the biological and palaeontological disciplines, providing new insights. A comprehensive review of the technique, its applications and limitations, has recently been produced by Sutton et al. (2013). The basic lab-based CT setup comprises an x-ray source, chamber and X-ray detector. The specimen to be studied is placed on a rotating stage within the chamber, and X-rays are fired as it rotates 360 (or 180) degrees. As materials with different chemical compositions attenuate (i.e. scatter or absorb) X-rays to different degrees, a map of X-ray attenuation throughout the entire specimen can be built up and processed into sinograms. In turn, the sinograms are processed into 'slices', by being laid down successively at their angle of acquisition to build up a three-dimensional picture of the specimen. Each 'slice' represents a virtual cut through the specimen, and specialised software can stack the slices to build up a complete series of slices through the entire specimen. When viewed in software such as Mimics (biomedical.materialise.com/mimics; Materialise, Leuven, Belgium), Avizo (VSG Inc., Burlington, Massachusetts, USA) or SPIERS (Sutton et al., 2012), the slices are displayed as a pattern of voxels (3D pixels), with the grey value (or contrast) of each voxel reflecting the X-ray attenuation of the material. As fossils typically have a different chemical composition to the surrounding rock matrix, they are represented by a distinct set of voxel grey values, and can thus be picked out and used to build up a three-dimensional representation of the fossil. This 3D model can be described and manipulated within the software, exported to additional software for imaging (e.g. Blender - http://blender.org; Stitching Blender Foundation), and even 3D printed.

An alternative method to lab-based CT scanning involves synchrotron radiation (SR). Although the underlying principle is the same, the setup and X-ray source is different, and

SR can be used to provide a much more detailed and higher resolution picture of anatomy, although admittedly at a much smaller scale than in lab-based CT scanning.

Although CT scanning presents an excellent opportunity for studying the internal and external anatomy of fossils, with obvious ramifications for exploring the braincase of early gnathostomes, it is not without its limitations. Chief among these relates to the composition of the host rock: as the technique essentially exploits the density difference between the fossil and surrounding matrix, rocks with a lithology close in chemical composition to fossil bone (made of calcium phosphate) will present a particular problem. As many Devonian fossils are preserved in limestone (calcium carbonate), both rock and fossil have a similar X-ray attenuation, causing problems when trying to visualise the fossil. Various approaches can be taken to maximise the difference, for example adjusting the beam energy, using filters to remove low energy X-rays, and increasing exposure times. In many cases, however, the voxel contrast will remain low, and segmentation will have to be carried out painstakingly by hand.

Other problems relate to the size, shape and density of the host rock. Lithologies that are very dense, for example that contain a high concentration of iron minerals, will make it difficult for the X-rays to penetrate through to the fossil. This is also an issue with very large specimens, or those with a high aspect ratio. The solutions outlined above can be used to reduce the magnitude of some of these problems.

1.6 THESIS AIMS

In this thesis I attempt to significantly improve our understanding of endocranial anatomy at the base of the gnathostome crown and in early actinopterygians. I will use CT scanning to investigate braincase anatomy in previously described and newly discovered taxa, with the aim of revealing new anatomical data that can inform our understanding of character evolution in these hugely successful groups, as well as answering questions pertaining to stem group membership and anatomical condition of the last common ancestor of key groups.

Chapter 2 - Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome. This chapter presents a redescription of the cranium of an Early Devonian fish using CT scanning, and considers the implications this taxon has for the structure of the last common ancestor of living jawed vertebrates.

Chapter 3 - Endoskeletal structure in *Cheirolepis* (Osteichthyes, Actinopterygii), the earliest ray-finned fish. A redescription of the sister taxon to all other actinopterygians is given, and an overview of the evolution of the actinopterygian character suite is discussed.

Chapter 4 - Exceptionally preserved actinopterygian from the Late Devonian of France. A new actinopterygian from the middle Devonian is described with the use of CT scanning, and a revised analysis of actinopterygian interrelationships is presented.

Chapter 5 - Virtual reconstruction of endocast anatomy in early ray-finned fishes (Osteichthyes, Actinopterygii). CT scanning is used to describe the endocast morphology of two key early actinopterygians, and the implications of these for the evolution of the endocast in jawed vertebrates discussed.

Chapter 6 - Endocranial evolution in early gnathostomes. The current state of knowledge of endocranial evolution in jawed vertebrates is reviewed, and key areas of uncertainty highlighted.

Chapter 7 - Conclusion. The contribution that this thesis has made to our understanding of endocranial evolution in jawed vertebrates is put into context.

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CHAPTER 2: OSTEICHTHYAN-LIKE CRANIAL CONDITIONS IN AN EARLY DEVONIAN STEM GNATHOSTOME

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MF and MDB scanned the material. SG generated the CT renderings and assisted with the production of all main text and extended data figures. All authors contributed to specimen interpretation, phylogenetic analyses and main and supplementary text preparation.

Extended Data accompanying this paper can be found at the end of the chapter; Supplementary Information can be found in Appendix 1.

2.1 Overview. The phylogeny of Silurian and Devonian (443–358 million years (Myr) ago) fishes remains the foremost problem in the study of the origin of modern gnathostomes (jawed vertebrates). A central question concerns the morphology of the last common ancestor of living jawed vertebrates, with competing hypotheses advancing either a chondrichthyan- (Miles, 1973; Brazeau, 2009; Davis et al., 2012) or osteichthyan-like (Zhu et al., 2013; Dupret et al., 2014) model. Here we present *Janusiscus schultzei* gen. et sp. nov., an Early Devonian (approximately 415 Myr ago) gnathostome from Siberia previously interpreted as a ray-finned fish (Schultze, 1992), which provides important new information about cranial anatomy near the last common ancestor of chondrichthyans and osteichthyans. The skull roof of *Janusiscus* resembles that of early osteichthyans, with large plates bearing vermiform ridges and partially enclosed sensory canals. High-resolution computed tomography (CT) reveals a braincase bearing characters typically associated with either chondrichthyans (large hypophyseal opening accommodating the internal carotid arteries) or osteichthyans (facial nerve exiting through jugular canal, endolymphatic ducts exiting posterior to the skull roof) but lacking a ventral cranial fissure, the presence of which is considered a derived feature of crown gnathostomes (Maisey, 2001; Maisey & Anderson, 2001). A conjunction of well-developed cranial processes in *Janusiscus* helps unify the comparative anatomy of early jawed vertebrate neurocrania, clarifying primary homologies in 'placoderms', osteichthyans and chondrichthyans. Phylogenetic analysis further supports the chondrichthyan affinities of 'acanthodians', and places *Janusiscus* and the enigmatic *Ramirosuarezia* (Pradel et al., 2009) in a polytomy with crown gnathostomes. The close correspondence between the skull roof of *Janusiscus* and that of osteichthyans suggests that an extensive dermal skeleton was present in the last common ancestor of jawed vertebrates (Zhu et al., 2014), but ambiguities arise from uncertainties in the anatomy of *Ramirosuarezia*. The unexpected contrast between endoskeletal structure in *Janusiscus* and its superficially osteichthyan-like dermal skeleton highlights the potential importance of other incompletely known Siluro-Devonian 'bony fishes' for reconstructing patterns of trait evolution near the origin of modern gnathostomes.

Gnathostomata Gegenbaur, 1874

Janusiscus schultzei gen. et sp. nov.

2.2 Etymology. Generic name refers to double-sided nature of the specimen, with an osteichthyan-like dorsal skull roof, but a braincase that displays an array of plesiomorphic gnathostome characters (Latin *Ianus*, the god of doorways and transitions, often depicted as having two faces; *[p]iscis*, fish). Specific name in honour of Hans-Peter Schultze (University of Kansas), who first described these specimens (Schultze, 1992).

2.3 Holotype. GIT (Institute of Geology, Talinn, Estonia) 496-6 (Pi.1384), skull roof and braincase, both missing anterior region (Fig. 1 and Extended Data Figs 1a, 3).

2.4 Referred material. We refer a second, more complete skull roof (GIT 496-7 (Pi. 1383); Extended Data Fig. 1c) from the type locality to Janusiscus. Rhombic scales lacking clear dorsal pegs are also known from this deposit (GIT 496-8–496-16; Extended Data Fig. 2a–c), but cannot be definitively associated with cranial material. All of these remains were previously attributed (Schultze, 1996) to *Dialipina markae*, the type of which is an isolated scale bearing a modest peg from the Lower Devonian of Kotelny Island, New Siberian Islands (Schultze, 1977) (approximately 1,500 km from the Sida River site).

2.5 Locality and horizon. Lower member, Kureika Formation, Sida River, Kotui Basin, Siberia. The presence of the zone fossil *Rhinopteraspis crouchi* in a lateral equivalent of the Kureika Formation (Blieck & Janvier, 1993) restricts the age of this deposit to middle Lochkovian (approximately 415 Myr ago; Gradstein et al., 2012). This is consistent with evidence drawn from other biostratigraphic markers (Appendix 1A).

2.6 Diagnosis. A jawed vertebrate characterized by a rectilinear pattern of skull roof bones bearing vermiform ridges but lacking endochondral bone, a ventral cranial fissure and vestibular fontanelles. Skull roof differs from those attributed to the type species of *Dialipina* (*Dialipina salgueiroensis*; Schultze & Cumbaa, 2001) in having postparietals longer than parietals, and parietals lacking anterolateral extensions. Principal autapomorphy of *Janusiscus* is a boundary between parietals and postparietals that slopes posteriorly towards the midline, with the postparietals forming distinct anterolateral processes (as per the original description; Schultze, 1992). Braincase with broad otic region, and narrow sphenoid pierced by large hypophyseal opening and bearing pronounced ventrolateral ridges.

2.7 Description. The skull roof comprises paired parietals and postparietals, and a median

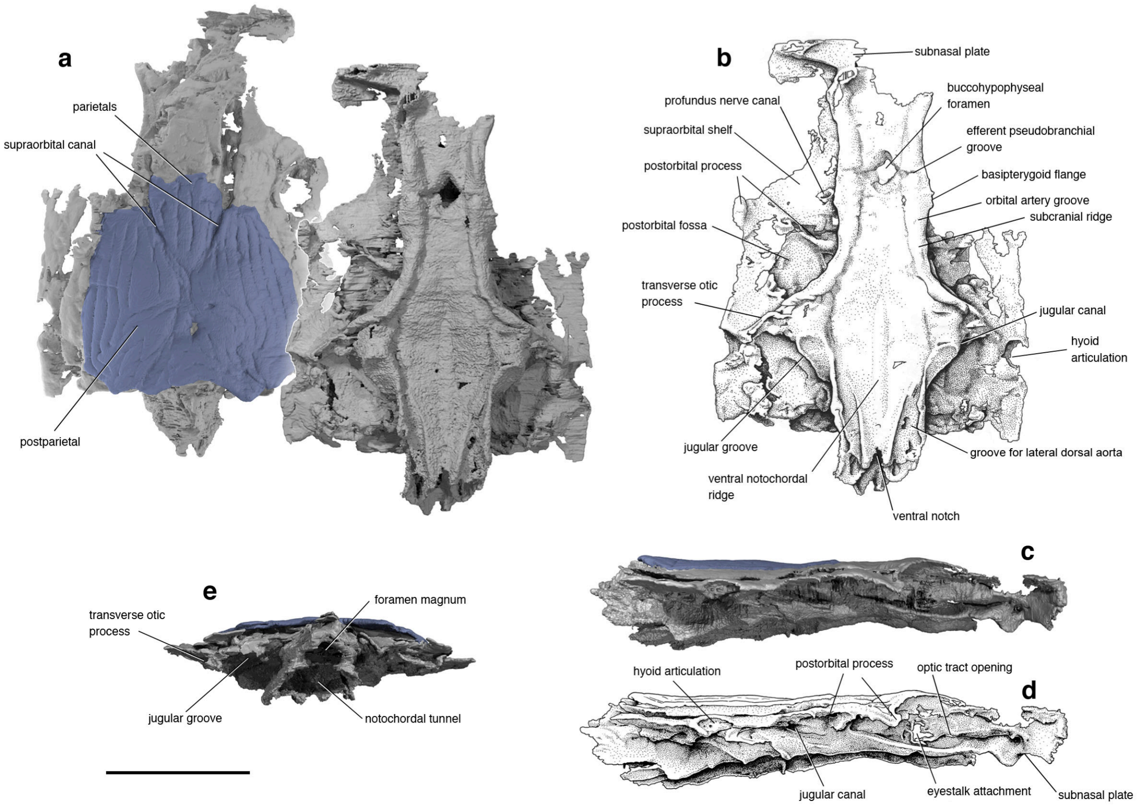

Figure 1 | The skull of *Janusiscus schultzei* gen. et sp. nov. based on high-resolution CT of GIT 496-6 (Pi.1384). **a**, Dorsal (left) and ventral views. **b**, Interpretive drawing of ventral view. **c**, Right lateral view. **d**, Interpretive drawing of right lateral view. e, Posterior view. Scale bar, 5 mm.

pineal plate (Fig. 1a and Extended Data Fig. 1). The anterior part of the skull roof, including the pineal, is not preserved in the holotype. All bones are ornamented with vermiform ridges, although the histological structure of these ridges is not preserved (Extended Data Fig. 2h–j). The supraorbital sensory canals extend across the parietals and postparietals in open grooves but are enclosed in bony tubes posteriorly (Extended Data Fig. 3). The postparietal bears a middle pit-line behind the termination of the supraorbital canal. The pattern of dermal ornament in the posterior part of the skull suggests the presence of posteriorly placed pitlines (as in '*Ligulalepis*'; Basden & Young, 2001).

High-resolution CT scanning of GIT 496-6 reveals a nearly complete perichondrally ossified neurocranium, lacking evidence of endochondral mineralization (Fig. 1 and Extended Data Figs 4, 5). The incompletely preserved ethmoid is co-mineralized with the remainder of the braincase. The basisphenoid is elongate and mediolaterally narrow, resembling conditions in *Acanthodes* (Davis et al., 2012) and osteichthyans (Jarvik, 1980; Gardiner, 1984). The basisphenoid bears a large, diamond-shaped hypophyseal opening but no evidence of a parasphenoid. Subcranial ridges like those of *Doliodus* (Maisey et al., 2009) define the lateral margins of the basisphenoid and extend posteriorly to the otic region (Extended Data Fig. 5). The modest basipterygoid processes emerge as slight flanges posterior to the level of the hypophysis. Like 'placoderms' (Stensiö, 1963; Goujet, 1984) and many chondrichthyans (Schaeffer, 1981; Maisey, 2005), *Janusiscus* lacks a ventral cranial fissure. The gently concave parachordal region tapers towards the occiput, where its edges form ventral cristae that border grooves for the lateral dorsal aortae. The occipital margin bears a notch that is aligned with a midline thickening of the parachordal surface.

Two prominent transverse processes are present (Fig. 1a, b). The postorbital process defines the rear margin of the orbit. The passage of the jugular vein through the postorbital process is unclear. It bears a ventral notch and a posterodorsal opening, either of which may have accommodated the jugular vein. The transverse otic process is separated from the postorbital

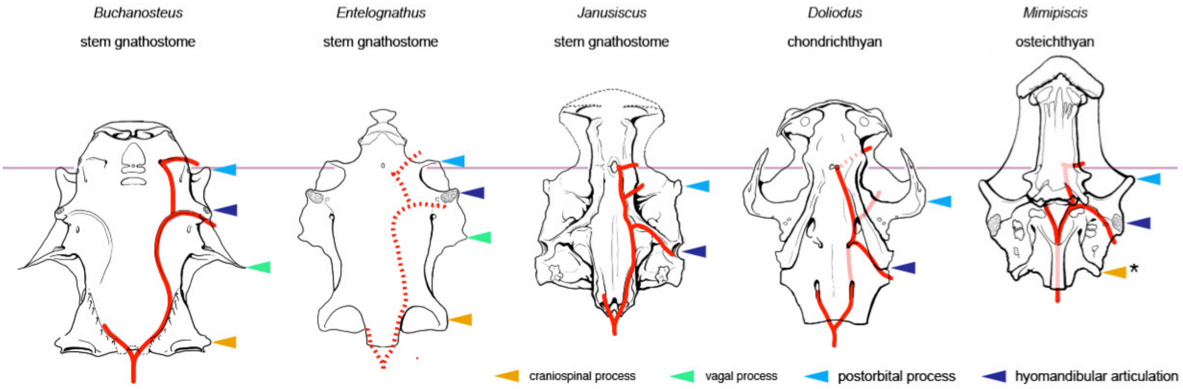

Figure 2 | Comparative braincase morphology of selected Palaeozoic gnathostomes. Braincases are aligned on the hypophyseal opening, the position of which is indicated by the horizontal pink line. The path of the major cranial blood vessels is shown in red, with inferred paths represented by dotted lines. Character distributions reject the homology of craniospinal processes in 'placoderms' and actinopterygians. Illustrations are redrawn with permission from Young, 1979; Gardiner, 1984; Maisey et al., 2009; and Zhu et al., 2013.

process by a wide postorbital fossa. This process terminates distally in a single hyomandibular facet, and is pierced by the jugular canal. An enclosed canal for the hyomandibular branch of the facial nerve intersects that of the jugular (Extended Data Fig. 3).

The suborbital and supraorbital shelves are well developed. The orbital wall is interrupted by a large eyestalk attachment with a raised posteroventral rim (Fig. 1c, d and Extended Data Fig. 6c–e). The optic nerve exited through a foramen anterior to the eyestalk area. Foramina for the oculomotor, profundus and abducens nerves, along with associated myodomes, are present along an arc in the rear of the orbit (Extended Data Fig. 6).

The otic capsules are broad, protruding well beyond the lateral margins of the basicranium (Extended Data Fig. 3). Paired endolymphatic ducts emerge from the roof of the braincase immediately posterior to the skull roof (Extended Data Figs 2j and 3). Vestibular fontanelles are absent, but the condition of the metotic fissure is unclear. The narrow occipital region extends well behind the otic capsules. A mineralized shelf separates the cavum cranii from the notochordal canal (Fig. 1e).

Janusiscus presents an unexpected suite of osteichthyan, chondrichthyan and generalized gnathostome traits. A rectilinear pattern of skull roof bones bearing vermiform ornament, partially buried sensory canals, endolymphatic ducts opening posterior to the dermal skull roof, and the exit of the hyomandibular branch of the facial nerve into the jugular canal are features typically associated with osteichthyans (Friedman & Brazeau, 2010; Brazeau & Friedman, 2014). However, the combination of a flat-based braincase, weakly developed basipterygoid processes, the absence of vestibular fontanelles, and the absence of a ventral cranial fissure are inconsistent with *Janusiscus* as a crown-group osteichthyan and therefore also with the original actinopterygian diagnosis (Schultze, 1992) and its current use as a fossil calibration in ray-finned fish molecular clocks (Broughton et al., 2013).

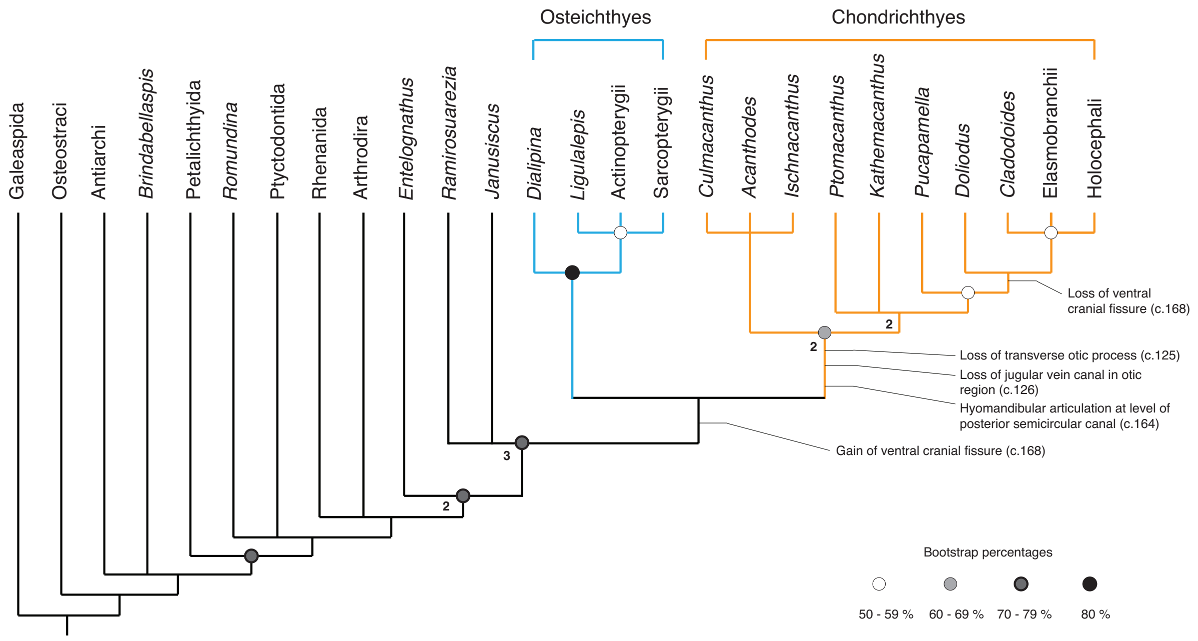

Figure 3 | Summary result of phylogenetic analyses. Some clades are collapsed or omitted for simplicity. Shaded disks represent ranges of bootstrap support, numbers at nodes are decay indices. Numbers refer to characters in character list (Supplementary Notes). Full cladograms are provided in Extended Data Figs 8, 9 and Supplementary Fig. 1.

Janusiscus possesses some chondrichthyan-like features, including the absence of paired openings for the internal carotids, a condition also shared with *Acanthodes*. Instead, the internal carotids entered the braincase through the large hypophyseal opening. The subcranial ridges flanking the ventrolateral angle of the braincase in *Janusiscus* strongly resemble those in the early chondrichthyan *Doliodus* (Maisey et al., 2009).

At least four pairs of transverse cranial processes are present on the braincases of some early gnathostomes (Appendix 1A, Fig. 2 and Extended Data Fig. 7). The prominent transverse walls in *Janusiscus* allow us to address the primary homology of the anterior two processes. Comparison with crown-group osteichthyans and placoderms reveals that the so-called 'supraorbital process' of arthrodires corresponds to the postorbital process of crown-group gnathostomes (including the postorbital pila of sarcopterygians; Yu, 1998) and the postorbital pila of *Entelognathus* (Zhu et al., 2013). The 'anterior postorbital process' of placoderms can be homologized with the transverse otic process of osteichthyans. The transverse otic process appears to be substantially reduced or lost in *Acanthodes* (Davis et al., 2012) and the earliest chondrichthyans (Maisey, 2001; Maisey & Anderson, 2001; Maisey et al., 2009), although it may correspond to the prominent lateral otic process of later chondrichthyans such as *Orthacanthus* and *Tamiobatis* (Extended Data Fig. 7). This further corroborates recent anatomical reinterpretations of *Acanthodes* (Davis et al., 2012) and its placement in the chondrichthyan total group (Zhu et al., 2013; Dupret et al., 2014).

Phylogenetic analysis recovers *Janusiscus* in a polytomy with *Ramirosuarezia* and the gnathostome crown. This corroborates our removal of the Siberian material from the genus *Dialipina*, which we recover as a stem osteichthyan (Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Dupret et al., 2014). Our result provides the first analytical placement for the enigmatic *Ramirosuarezia*, which has previously been compared with 'placoderm'-grade stem gnathostomes (Pradel et al., 2009; Anderson et al., 2011) and holocephalan chondrichthyans (Pradel et al., 2009).

Although our analysis favours the stem gnathostome hypothesis for *Janusiscus*, we consider stem chondrichthyan and stem osteichthyan placements to be reasonable alternatives: both require only one additional step. Placement of *Janusiscus* on the chondrichthyan stem may seem provocative, but the hypothesis of micromery as a derived chondrichthyan trait predicts macromeric stem chondrichthyans. While there is ambiguity in the position of *Janusiscus* relative to the three branches incident to the gnathostome crown node, we reject an actinopterygian interpretation (Schultze, 1992), which requires seven additional steps.

The new anatomical details of *Janusiscus* and our phylogenetic result corroborate the recently revived hypothesis that 'acanthodians' are, in fact, total-group chondrichthyans. The osteichthyan-like skull roof of *Janusiscus* strongly implies that the continuous dermal armour common to 'placoderms' and bony fishes is a gnathostome symplesiomorphy (Zhu et al., 2013; Dupret et al., 2014). However, uncertainty about conditions of the exoskeleton in *Ramirosuarezia* precludes more definitive statements about the nature of the dermal skeleton in the earliest crown gnathostomes. We find that chondrichthyans (including all 'acanthodians') and osteichthyans are united to the exclusion of *Janusiscus* by the presence of a ventral cranial fissure separating the otic and sphenoid regions of the braincase (Fig. 3). The revised comparative framework for gnathostome braincases provided by *Janusiscus* highlights substantial neurocranial modifications uniting total-group chondrichthyans (for example, loss of the jugular vein canal in the otic region, hyomandibular articulation at the level of the posterior semicircular canal; Fig. 3; Brazeau & Friedman, 2014), while casting doubt on the validity of some supposed osteichthyan synapomorphies (for example, exit of the hyomandibular branch of the facial nerve through the jugular canal; Extended Data Fig. 3).

This work reinforces an emerging consensus for osteichthyan-like anatomical conditions in stem gnathostomes and also in the last common ancestor of crown-group gnathostomes (Zhu et al., 2013; Dupret et al., 2014). The recognition that many features of the bony fish dermal skeleton might be general traits of modern jawed vertebrates highlights the need to revisit the roughly half-dozen supposed stem osteichthyans known only from isolated dermal fragments (Friedman & Brazeau, 2010; Botella et al., 2007; Cunningham et al., 2012). Notably, our results suggest the plausibility of alternative placements for some of these taxa as either stem gnathostomes or even stem chondrichthyans.

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2.10 METHODS

2.10.1 X-ray computed microtomography. GIT 496-6 was scanned using a SkyScan1172, combining two vertically overlapping scan series of 7,200 projections with an energy of 100 kV and 100 mA and 4.75 s exposure. Scan data were analysed using Mimics (http://biomedical.materialise.com/mimics; Materialise). After segmenting, surface meshes were exported into and imaged in Blender (http://blender.org; Stitching Blender Foundation).

2.10.2 Phylogenetic analysis. Phylogenetic analysis was performed in PAUP* v.4.0b10 (Swofford, 2003) using a data set with 236 characters (three of which were ordered: 64, 126 and 166) and 78 taxa. The data set is based on Davis et al. (2012). In addition to a number of coding changes, one highly incomplete taxon (*Rhadinacanthus*) and four characters were deleted from the matrix of Davis et al. (2012); full justification for excluded characters is given in the character list. Additional characters were taken from a variety of sources, and are referenced in the character list. In addition to *Janusiscus* and taxa carried forward from the data set of Davis et al. (2012), we added 18 taxa spanning most taxonomic assemblages of Palaeozoic gnathostomes. In the case of *Janusiscus*, we coded as unknown any characters relating to scale morphology and histology; the Siberian scales originally referred to *D. markae* were not directly associated with the braincase, and their affinity is thus uncertain (for further details, see Appendix 1A). We follow a similar convention with the braincase attributed to '*Ligulalepis*', and hence scale and histology characters are coded as uncertain. We assessed taxonomic equivalence (Wilkinson, 1995) using the software package TAXEQ3 (Wilkinson, 2001). No taxa showed non-unique combinations of character states that would permit safe taxonomic reduction, so analyses were executed with a complete taxon set. Although several taxa are highly incomplete, we followed previous recommendations (Wiens, 2003a,b) by maximizing the absolute number of characters instead of deleting incomplete or fragmentary taxa.

We conducted a heuristic search using 1,000 random addition sequence replicates, holding 5 trees at each step, and the tree bisection and reconnection (TBR) strategy. Maxtrees was set to automatically increase by 100. To prevent outgroup taxa from moving to the ingroup or collapsing of the ingroup node, we employed a rooted constraint tree, keeping only trees consistent with the following general topology: (Galeaspida(Osteostraci(Ingroup))).

Bootstrap values were calculated using 15,000 replicates of a heuristic search using random addition sequence, 10 replicates, holding 5 trees at each step, using the TBR strategy. To speed up the search, we set a limit of 20 million rearrangements per addition sequence replicate (options: rearrlimit 5 20000000 limitperrep 5 yes in the hsearch command in PAUP*).

Node decay values (that is, Bremer support) were calculated manually using 20 random addition sequence replicates of a heuristic search, rearrlimit 5 200000000, limitperrep 5 yes, and by incrementing the KEEP score by 1 over the length of the shortest tree found. Nodes retained in the strict consensus tree had their decay index incremented by one.

We conducted a set of further searches using the protocols outlined earlier with the following modifications. First, we conducted an equally weighted analysis minus *Janusiscus* to assess whether inferred patterns of relationships among early gnathostomes were robust to exclusion of the genus. To test whether the tree topology was sensitive to the removal of random taxa, we conducted an additional five searches each following the removal of a randomly selected terminal. Random selection was conducted using Microsoft Excel's RANDBETWEEN function with parameters set to 3 and 78 (we excepted the outgroup from random pruning) and used the first five results obtained to draw taxa from the list following their order in the Nexus file. To speed up these searches, we used rearrlimit 5 10000000 and limitperrep 5 yes. Finally, we reweighted all characters by their retention indices in the shortest trees recovered by our initial analysis that applied equal character weights.

2.10.3 Phylogenetic results. The phylogenetic search resulted in 522,936 trees of 639 steps. A summary strict consensus tree with some clades omitted or collapsed is shown in Fig. 3. The complete result is shown in Extended Data Fig. 8a. The Adams consensus tree is shown in Extended Data Fig. 8b. All unambiguous character state transformations are shown in Appendix 1C. A summary strict consensus tree of an analysis of the data set with characters reweighted by retention index is shown in Extended Data Fig. 9a. It preserves all major branching patterns found in the analysis of equally weighted characters, but shows greater resolution within some clades.

Inferred interrelationships are not changed when *Janusiscus* is removed from the analysis (Extended Data Fig. 9b), as its influence on how cranial processes are recognized and coded pervades large parts of the data set. The removal of an additional five taxa at random (*Cladoselache*, *Tristychius*, *Acanthodes*, *Kentuckia*, *Lupopsyrus*) each had no considerable impact on the overall tree topology, excepting differences in the degree of resolution.

The overall large number of trees results in polychotomous branchings primarily concentrated in the chondrichthyan stem compounded with a smaller number of polychotomous branchings in the gnathostome and osteichthyan stems. The Adams consensus shows two principal branching patterns that are consistent within the results. One is a clade of stem chondrichthyans comprising acanthodiforms, ischnacanthids, some diplacanthids, as well as *Latviacanthus* and *Euthacanthus*. The other branching consisted of most *Climatius*-like taxa and conventionally defined chondrichthyans (including the crown group).

Support for key nodes is summarized in Fig. 3, with full details given Extended Data Fig. 8a. Unsurprisingly, most are quite low. The highest values are found within well-studied groups (for example, sarcopterygians and actinopterygians) or associated with clades with numerous specializations (for example, holocephalans, bothriolepidid antiarchs). A decay index of 2 and a bootstrap support of 68% are recovered for the clade comprising all chondrichthyans and acanthodians. A decay index greater than 1 is consistent with the very long branch subtending this clade (Appendix 1C). The low bootstrap value might be explained by the fact that more than half of the transformations along this branch are homoplasious and have a consistency index of 0.5 or less. In spite of this, the branch is supported by five invariant, unambiguous synapomorphies (see Appendix 1C).

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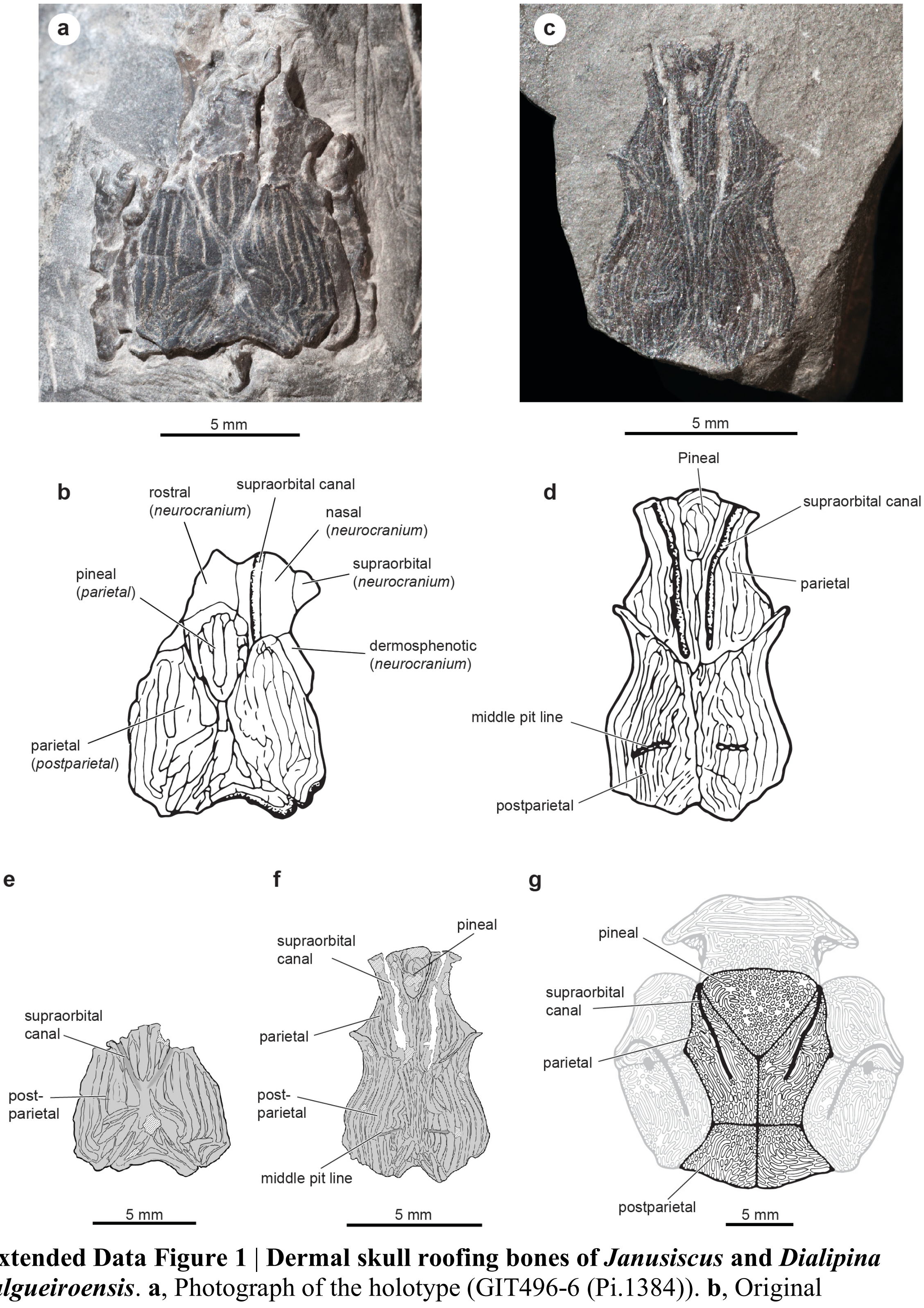
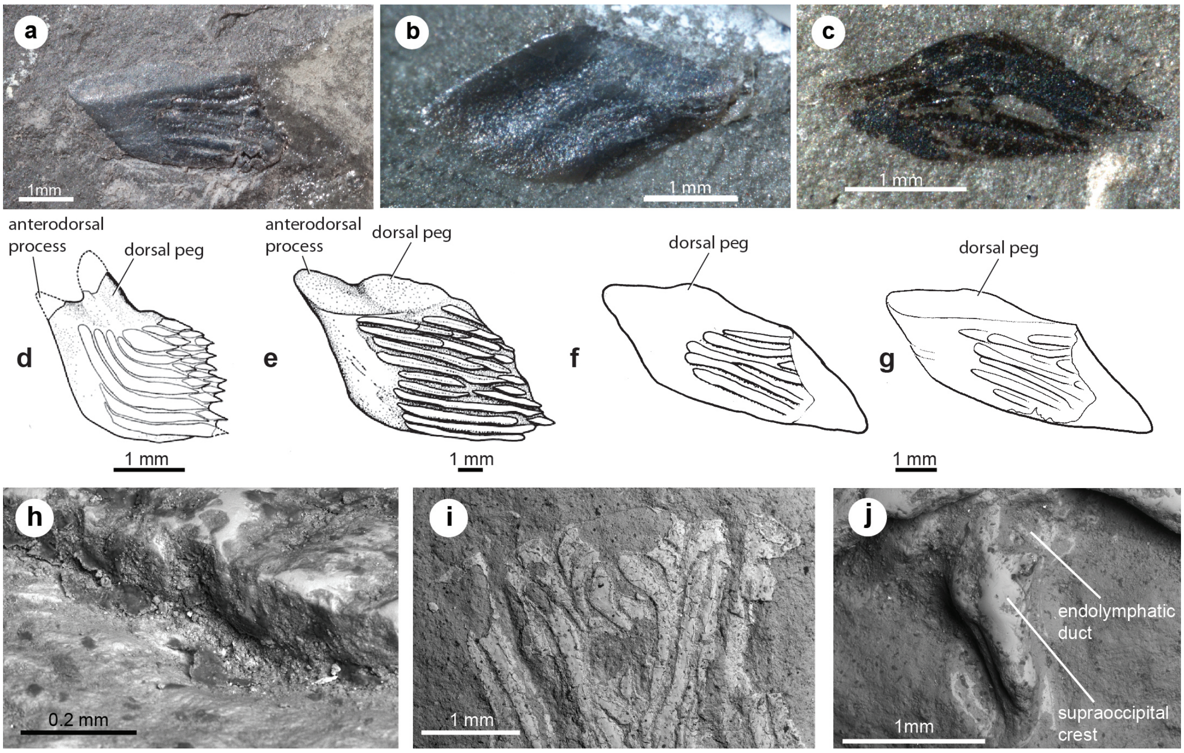
2.11 Extended Data

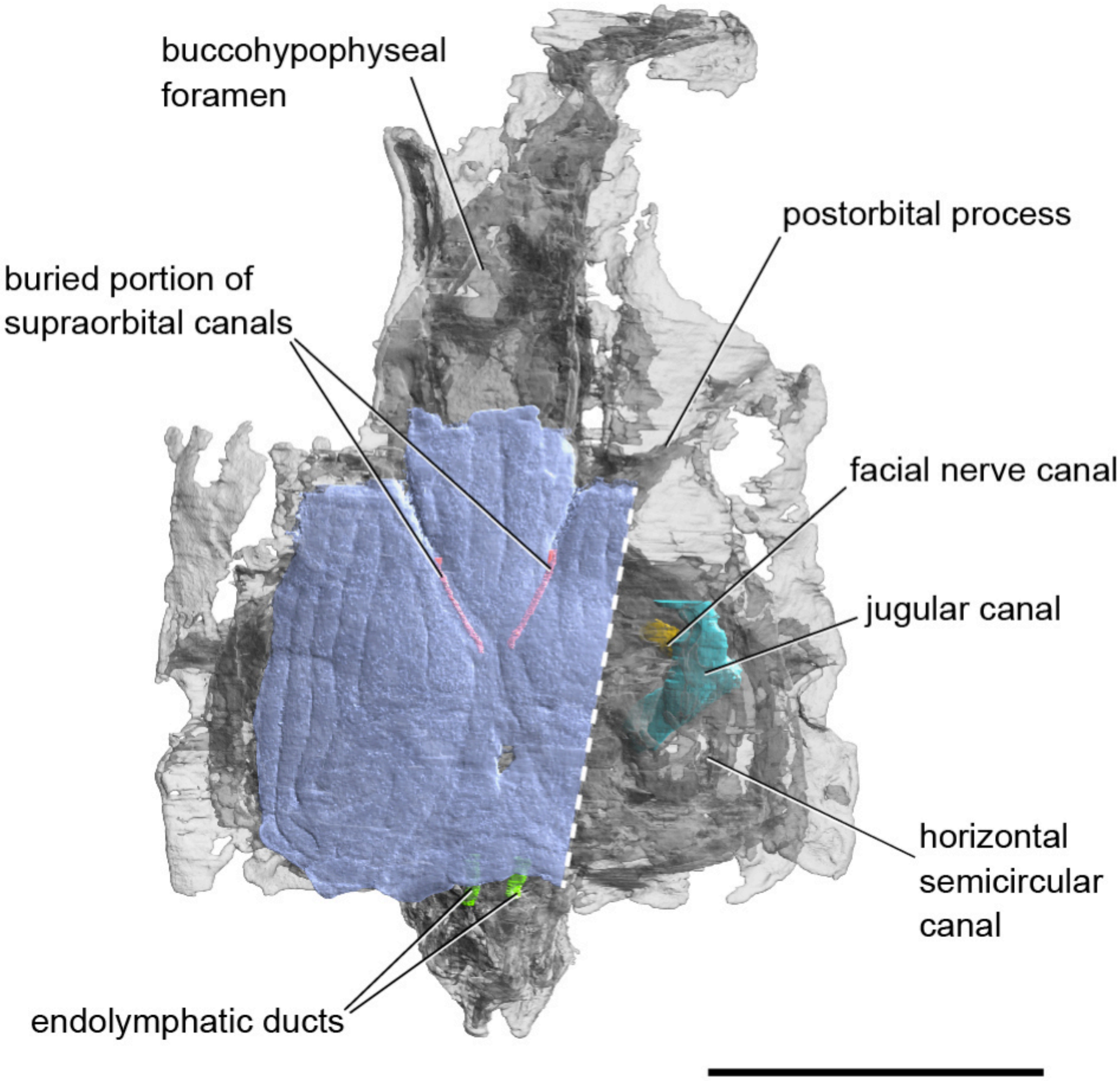
2.11.1 Anatomical figures



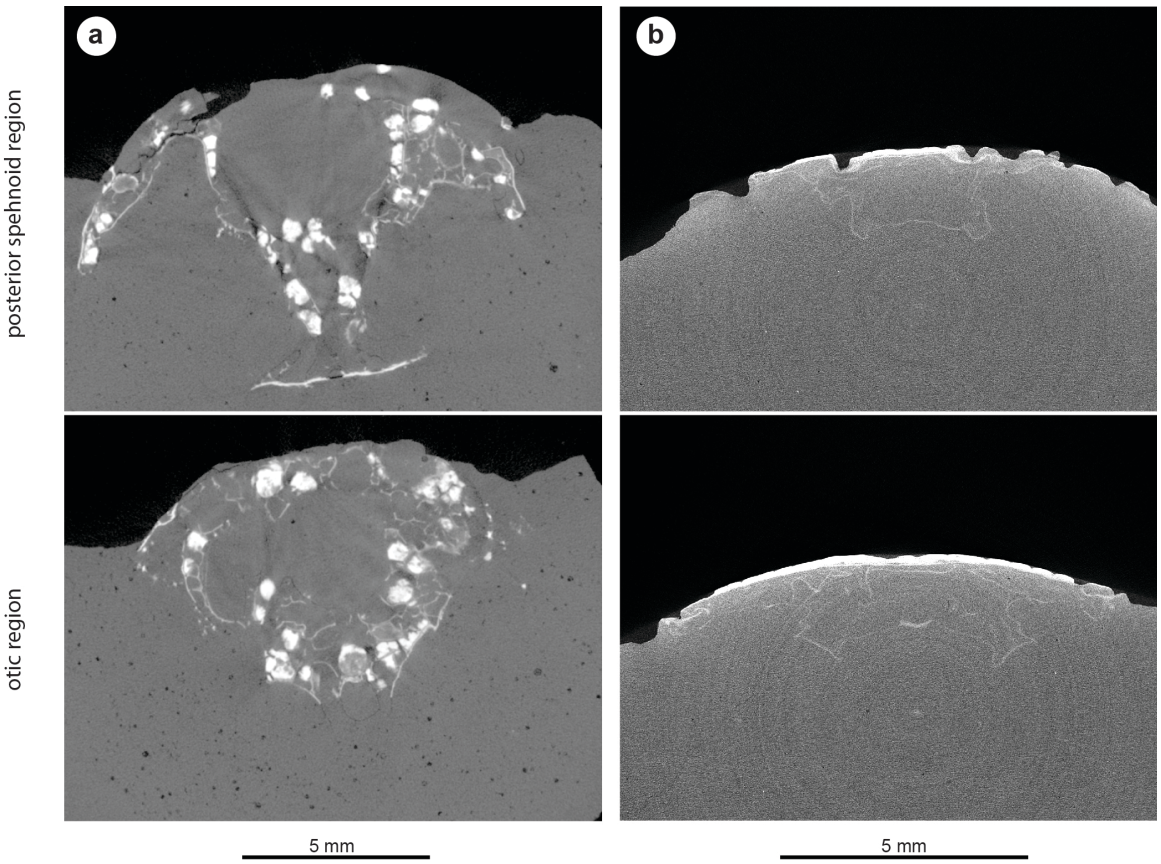
Extended Data Figure 1 | Dermal skull roofing bones of *Janusiscus* and *Dialipina salgueiroensis*. **a**, Photograph of the holotype (GIT496-6 (Pi.1384)). **b**, Original interpretation modified with permission from Schultze (1992). Reinterpretation of bones italicized in brackets (where applicable). **c**, Photograph of the referred skull roof (GIT 496-7 (Pi.1383)). **d**, Original interpretation modified with permission from Schultze (1992). **e**, New interpretive drawing of the holotype (GIT496-6(Pi.1384)). **f**, New interpretive drawing of the referred skull roof (GIT 496-7 (Pi.1383)). **g**, *Dialipina salgueiroensis*, modified with permission from Schultze & Cumbaa (2001).



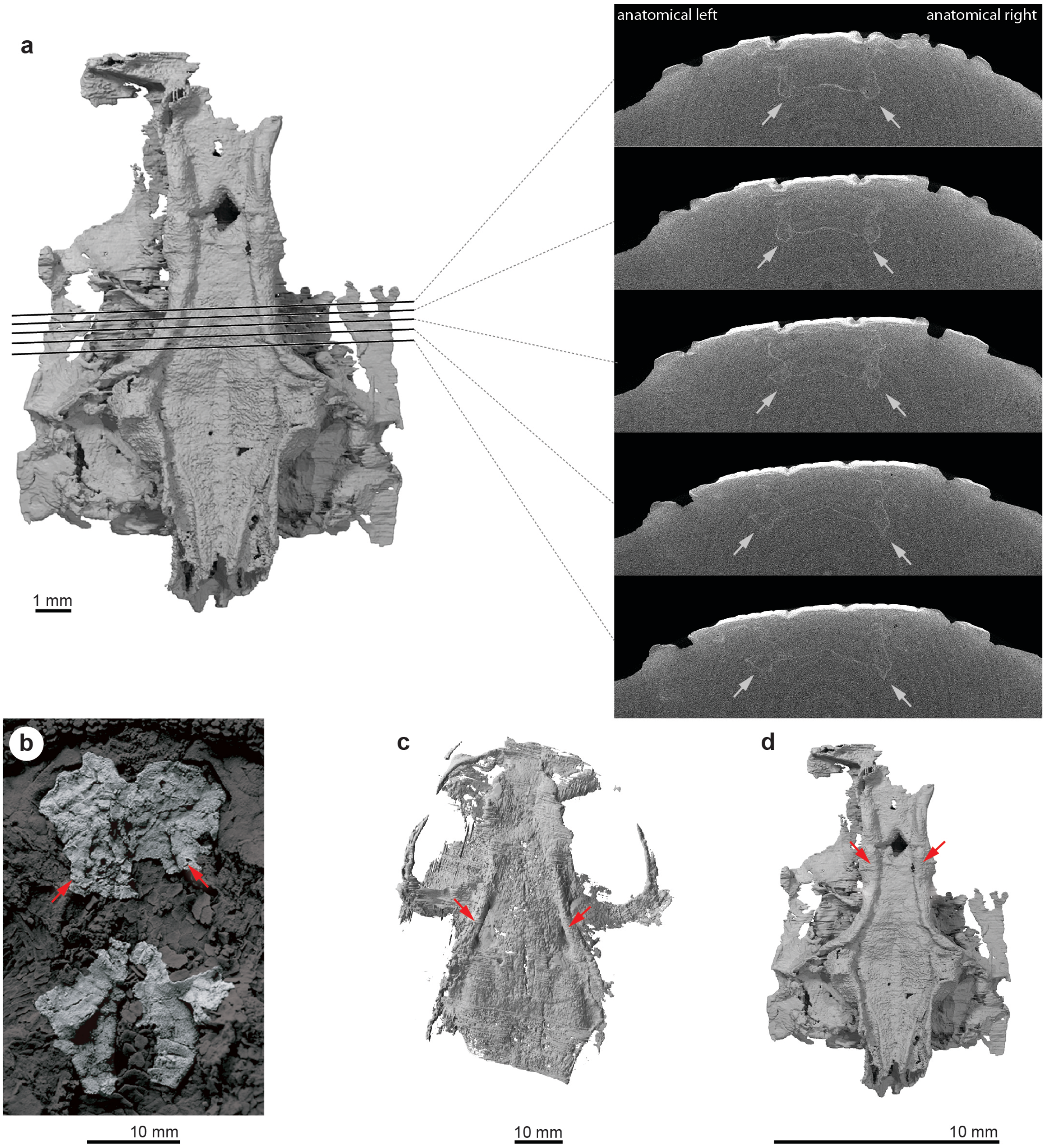
Extended Data Figure 2 | Scales attributed to *Dialipina* and SEM images of *Janusiscus schultzei* n. gen. et sp. Scales from the localities of the Kureika Formation along the Sida River, Kotui Basin, Siberia, previously referred to *D. markae*, in: **a,** external view (GIT 496-8 [Pi.1384a]), previously figured by Schultze (1992; pl.1, fig.3); **b,** internal view (GIT 496-10 [Pi.1385b]); **c,** external view (GIT 496-16 [Pi.1387]). Gross scale morphology of *D. salgueiroensis* and referred species of *Dialipina*: **d**, holotype of *D. salgueiroensis*, from the Emsian of Canada. Reproduced with permission from Schultze (1977: fig. 3h); **e**, holotype of *D. markae*, from the Lochkovian of the New Siberian Islands. Reproduced with permission from Schultze (1977: fig. 3a); **f**, scale from the Kureika Formation, Siberia, referred to *D. markae* by Schultze (1992). Photograph of specimen in **a**. Reproduced with permission from Schultze (1992: fig. 4); **g**, new interpretive drawing of scale in **c**. **h,** Broken edge of the skull roof in the holotype (GIT 496-6 [Pi.1383]). The histological structure is not preserved. **i,** The anterior part of the referred skull roof (GIT 496-7). The dermal bone is poorly preserved, with the bone in the centre of each ridge missing. The histological structure is not preserved. **j,** the holotype (GIT 496-6 [Pi.1384]) in dorsal view, showing the endoskeletal supraoccipital crest and openings of the endolymphatic ducts. Images **a**, **b**, and **c** modified slightly from that by Institute of Geology at TUT and licensed by CC 3.0. http://geokogud.info/git/specimen_image/496/496-8.jpg; http://geokogud.info/git/specimen_image/496/496-10.jpg; http://geokogud.info/git/specimen_image/496/496-16.jpg.



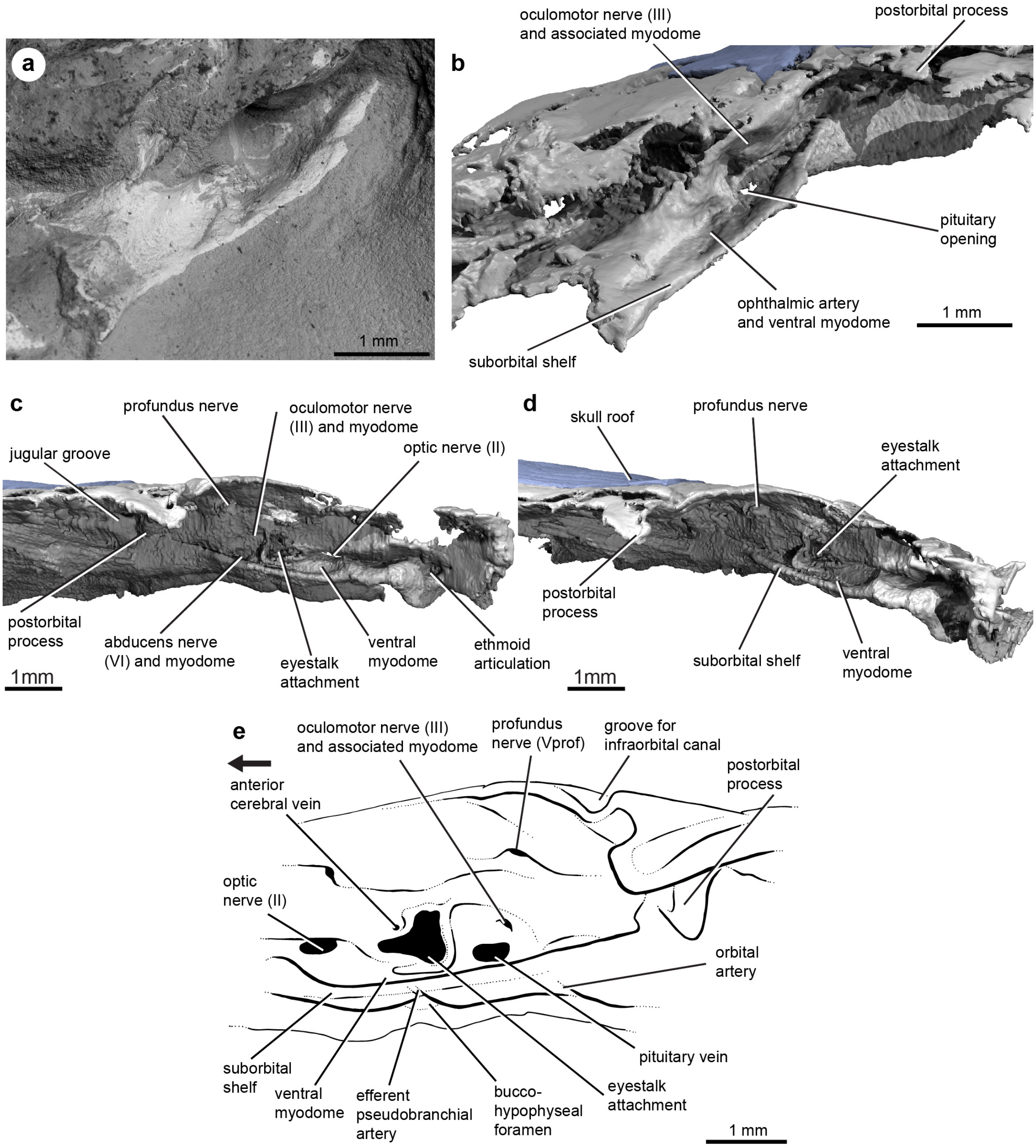
Extended Data Figure 3 | Semi-transparent rendering of the skull of *Janusiscus schultzei* gen. et sp. nov. showing osteichthyan-like traits not visible externally. Scale bar, 5 mm.



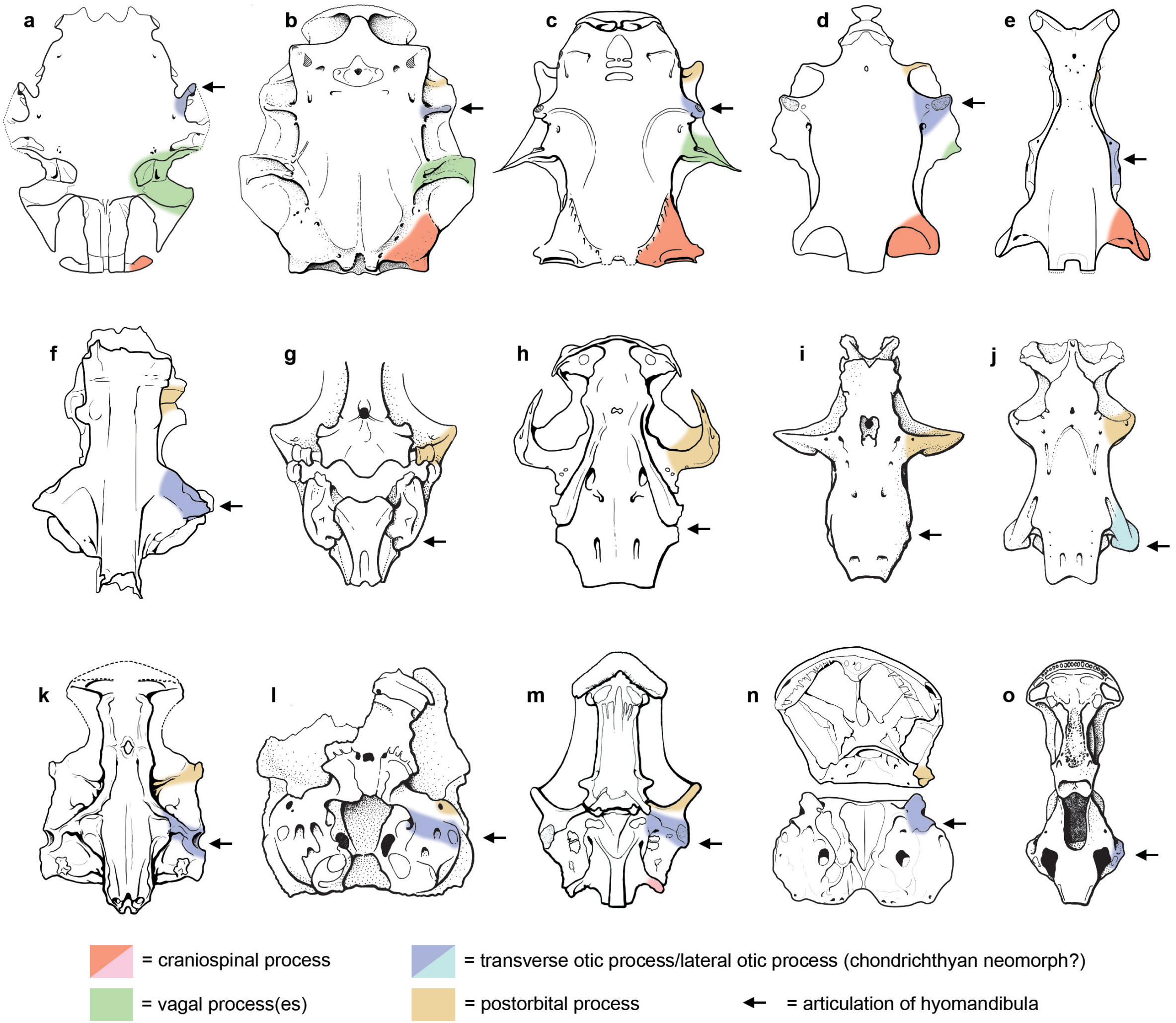
Extended Data Figure 4 | *Janusiscus* lacks endochondral ossification. a, The actinopterygian *Kentuckia deani* MCZ 5226, tomographs showing extensive and well-developed endochondral ossification in both the sphenoid (top) and otic (bottom) regions. Bright white objects in both panels are voids within spongy endochodral bone that have been diagenetically infilled with dense (likely iron) minerals. **b**, *Janusiscus schultzei* n. gen et sp. nov. GIT 496-6 [Pi.1384], tomographs showing lack of obvious endochondral ossification in either the sphenoid (top) or otic (bottom) regions. There is also no visual indication of endochondral bone in a break across the ethmoid region of this same specimen.



Extended Data Figure 5 | Subcranial ridges in *Janusiscus* and early crown gnathostomes. **a**, Reconstructed tomographs showing that the thickenings along the lateral margins of the sphenoid region of *Janusiscus* do not represent artefacts of post-mortem compression. **b**, The ‘acanthodian’ *Ptomacanthus anglicus* NHMUK PV P 24919a, silicone peel of specimen preserved in negative, dusted with ammonium chloride. Portions of the skull other than the neurocranium partially masked for clarity. **c**, The chondrichthyan *Doliodus problematicus* NBMG 10127/1a, reconstruction of neurocranium based on CT data. **d**, *Janusiscus schultzei* n. gen et sp. nov. GIT 496-6 [Pi.1384], reconstruction of neurocranium based on CT data. Red arrows in each panel indicate subcranial ridges.

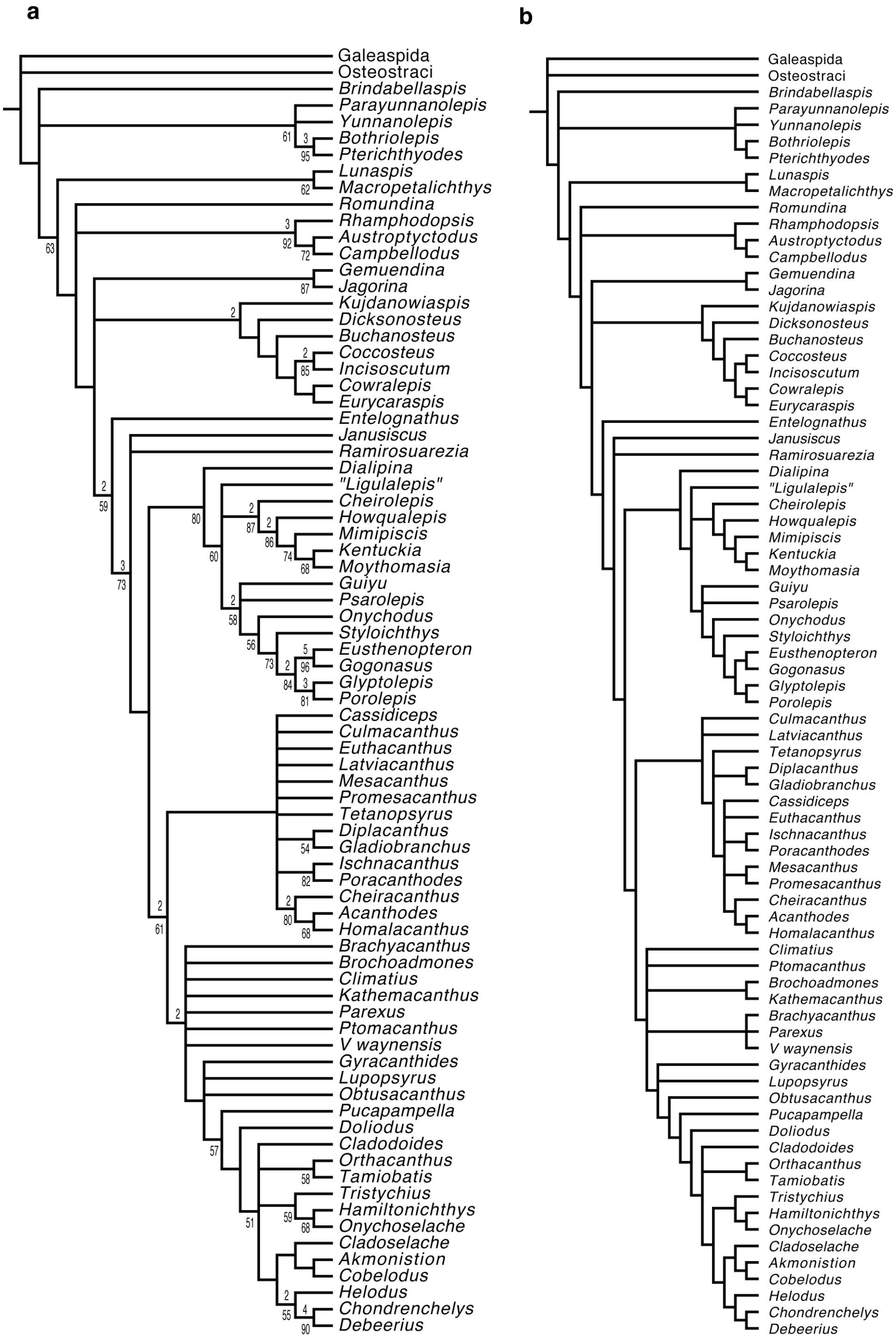


Extended Data Figure 6 | Orbit anatomy of *Janusiscus schultzei* n. gen. et sp. a, SEM image into left orbit showing endoskeletal bone and surrounding matrix. **b,** Image based on µ-XRCT scan with matrix digitally removed. **c**, Lateral view into right orbit, with matrix digitally removed. **d,** Anterolateral view into right orbit, with matrix digitally removed. **e,** interpretive drawing of the orbit, based on a composite of the left and right orbits of the holotype, (GIT 496-6 [Pi.1384]).

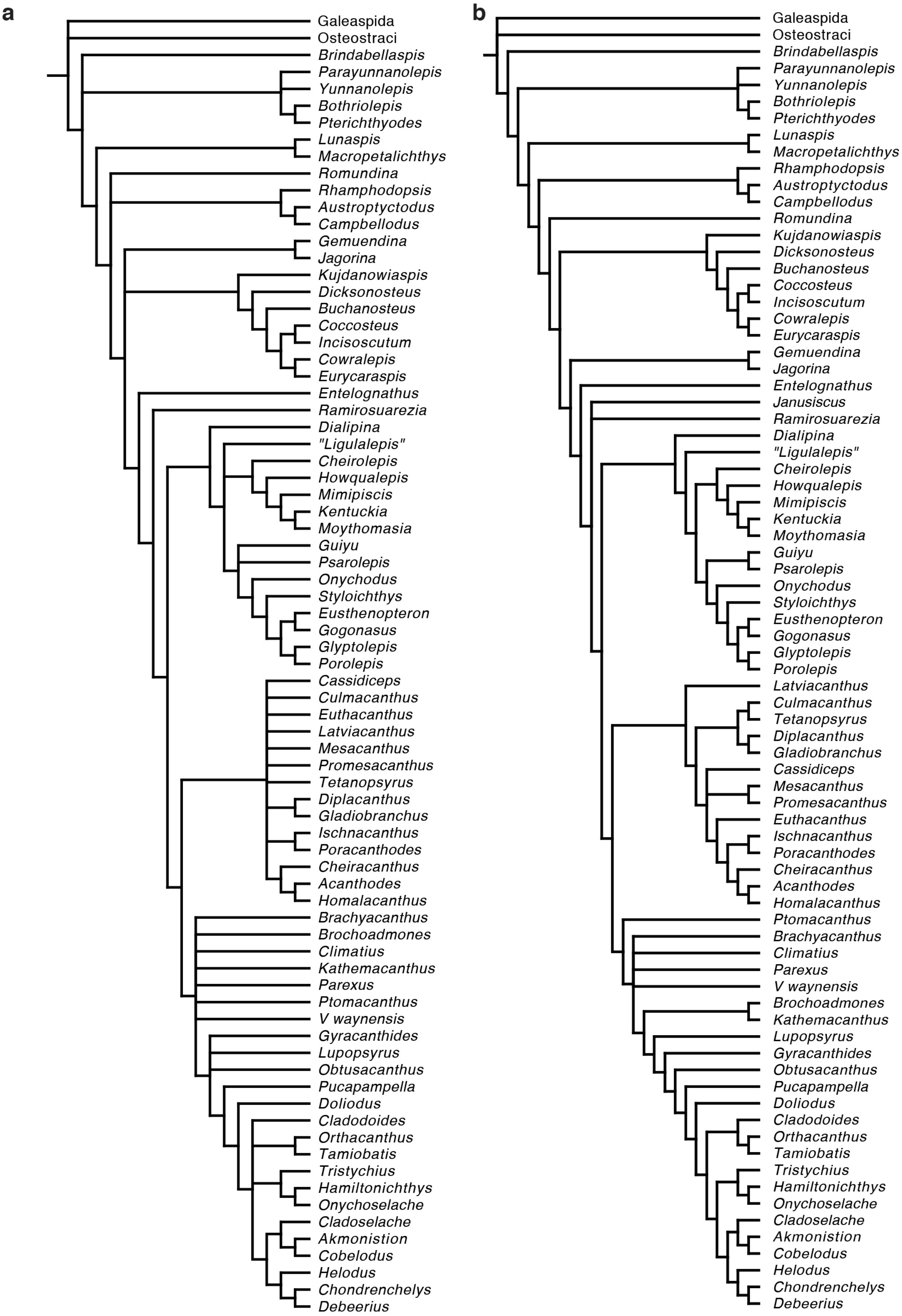


Extended Data Figure 7 | Comparison of transverse processes in the braincases of early gnathostomes. a, *Macropetalichthys* (redrawn from Stensiö, 1969). **b**, *Dicksonosteus* (redrawn from Goujet, 1984). **c**, *Buchanosteus* (redrawn from Young, 1979). **d**, *Entelognathus* (redrawn from Zhu et al., 2013). **e**, *Jagorina* (redrawn from Stensiö, 1969). **f**, *Ramirosuarezia* (redrawn from Pradel et al., 2009). **g**, *Acanthodes* (redrawn from Davis et al., 2012). **h**, *Doliodus* (redrawn from Maisey et al., 2009). **i**, *Cladodoides* (redrawn from Maisey, 2005). **j**, *Orthacanthus* (redrawn from Schaeffer, 1981). **k**, *Janusiscus*. **l**, ‘*Ligulalepis*’ (redrawn from Basden & Young, 2001). **m**, *Mimipiscis* (redrawn from Gardiner, 1984). **n**, *Psarolepis* (redrawn from Yu, 1998). **o**, *Gogonasus* (redrawn from Long et al., 1997).

2.11.2 Cladograms from phylogenetic analyses



Extended Data Figure 8 | a, Strict consensus of the 522936 shortest trees (639 steps) for 78 taxa and 236 equally weighted characters. Digits above nodes indicate Bremer decay indices above 1. Digits below nodes indicate percentage bootstrap support. **b,** Adams consensus tree of the 522936 shortest trees for 78 taxa and 236 equally weighted characters.



Extended Data Figure 9 | a, Strict consensus tree of 216 trees with a score of 452.52565 resulting from analysis of characters reweighted according to retention index. **b,** Strict consensus of the 128395 shortest trees for 77 taxa and 236 equally weighted characters, with *Janusiscus* removed from the dataset.

CHAPTER 3: ENDOSKELETAL STRUCTURE IN *CHEIROLEPIS* (OSTEICHTHYES, ACTINOPTERYGII), THE EARLIEST RAY-FINNED FISH

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SG, MF, RA, ZJ and MDB scanned the material. SG generated the CT renderings, generated the figures and prepared the supplementary information. SG wrote the text with input from MF and MIC, with comments from all authors.

Supplementary Information accompanying this paper can be found in Appendix 2.

3.1Abstract: As the sister lineage of all other actinopterygians, the Middle to Late Devonian (Eifelian-Frasnian) *Cheirolepis* occupies a pivotal position in vertebrate phylogeny. Although the dermal skeleton of this taxon has been exhaustively described, very little of its endoskeleton is known, leaving questions of neurocranial and fin evolution in early ray-finned fishes unresolved. The model for early actinopterygian anatomy has instead been based largely on the Late Devonian (Frasnian) *Mimipiscis*, preserved in stunning detail from the Gogo Formation of Australia. Here we present re-examinations of existing museum specimens through the use of high resolution lab- and synchrotron-based CT scanning, revealing new details of the neurocranium, hyomandibula and pectoral fin endoskeleton for

the Eifelian *Cheirolepis trailli*. These new data highlight traits considered uncharacteristic of early actinopterygians, including an uninvested dorsal aorta and imperforate propterygium, and corroborate the early divergence of *Cheirolepis* within actinopterygian phylogeny. Furthermore, these traits represent conspicuous differences between the endoskeletal structure of *Cheirolepis* and *Mimipiscis.* Collectively, these new data help clarify primitive conditions within ray-finned fishes, which in turn have important implications for understanding features likely present in the last common ancestor of living osteichthyans.

3.2 INTRODUCTION

Ray-finned fishes (Actinopterygii) account for nearly half of living vertebrate diversity (Nelson, 2006; Faircloth et al., 2013), but understanding of their early evolution is substantially incomplete. Despite a probable date of divergence from Sarcopterygii of around 420-430 Mya (Zhu et al., 2009, Broughton et al., 2013), no unequivocal actinopterygians are known from the Silurian. Scale taxa such as *Lophosteus* Pander, 1856, *Andreolepis* Gross, 1968 and *Naxilepis* Wang & Dong, 1989 - once considered to be primitive actinopterygians Gross, 1968; Janvier, 1978; Schultze, 1977; Wang & Dong, 1989; Märss, 2001) - are now thought to branch from the osteichthyan stem (Botella et al., 2007; Friedman & Brazeau, 2010; Zhu et al., 2013, although see Schultze (in press)). Of the handful of articulated actinopterygians known from the Devonian, the majority are described exclusively from their dermal skeletons, with only limited reports of endoskeletal remains (Gardiner & Schaeffer, 1989). Two important exceptions are the early Frasnian *Mimipiscis toombsi* (Gardiner & Bartram, 1977) and *Moythomasia durgaringa* Gardiner & Bartram, 1977, described in great detail from multiple three-dimensional, acid-prepared specimens from the Gogo Formation, Western Australia (Gardiner & Bartram, 1977; Gardiner, 1984; Choo, 2011). Given its exceptional preservation, *Mimipiscis* Choo, 2011 has understandably become the key exemplar for the primitive actinopterygian condition (Gardiner, 1984;

Gardiner & Schaeffer, 1989; Coates, 1999; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011).

Cheirolepis Agassiz 1835 is the earliest occurring taxon that can be unequivocally placed within the Actinopterygii. It is represented by articulated specimens from the late Eifelian of Scotland, the Givetian of Nevada (Reed, 1992; Arratia & Cloutier, 2004) and the Frasnian of Canada, as well as by scales from the Givetian of Germany (Gross, 1973) and Eifelian-Givetian of Belarus, Latvia and Estonia (Mark-Kurik, 2000; Blieck & Cloutier, 2000; Lukševičs et al., 2010). As part of his original description, Agassiz (1835) erected three species on the basis of Scottish material: the type species *C. trailli* from Orkney, *C. uragus* from Gamrie, and *C. cummingae* from Cromarty. A further three species were described by McCoy (1848): *C. velox*, *C. macrocephalus* (both from Orkney) and *C. curtus*, from Lethen Bar. These species were subsequently revised by Egerton (1860) and Traquair (1888), with only *C. trailli* retained. Whiteaves (1881) first reported Canadian material from the Frasnian Miguasha *Lagerstätte*, and assigned it to the new species *C. canadensis*. An additional species, *C. schultzei*, was erected by Arratia & Cloutier (2004) for specimens from the Denay Limestone of Nevada, first reported by Reed (1992) as *Cheirolepis* cf. *C. canadensis*. *C. trailli* and *C. canadensis* were comprehensively reviewed by Pearson & Westoll (1979) and Arratia & Cloutier (1996).

The affinities of *Cheirolepis* with bony fishes generally—and actinopterygians specifically—have not always been apparent. On the basis of its micromeric, non-overlapping scales, Agassiz (1835) grouped *Cheirolepis* with *Acanthodes* Agassiz, 1833 and *Cheiracanthus* Agassiz, 1835 in his Acanthodidae, a placement upheld by McCoy (1855) and Egerton (1860). Dissenters from this view included Miller (1841) and Müller (1846), who considered the combination of characters in *Cheirolepis* sufficiently unique to merit

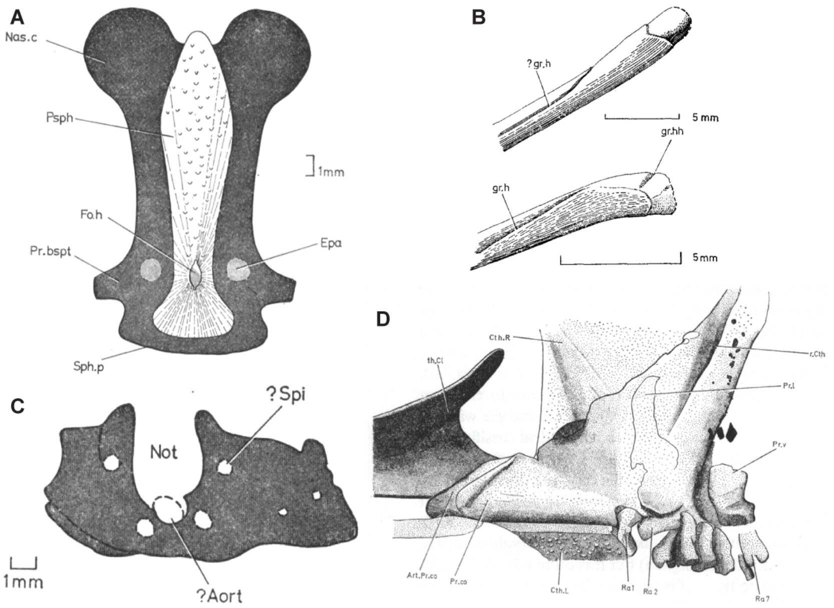

Figure 1 | Existing interpretations of the endoskeletal structure of *Cheirolepis trailli*. **A**, sphenethmoid portion of neurocranium and parasphenoid (Pearson & Westoll, 1979: fig. 1a); **B**, partial hyomandibula (Pearson & Westoll, 1979: fig. 10c, d); **C**, occipital portion of neurocranium (Pearson & Westoll, 1979: fig. 1c); **D**, shoulder girdle and fin radials (Pearson & Westoll, 1979: fig. 14a. No scale given.). Abbreviations: ?Aort, canal for dorsal aorta; Art.Pr.co, anterior articulatory surface of coracoid process; Cth.L, left cleithrum; Cth.R, right cleithrum; Epa, foramen for efferent pseudobranchial artery; Fo.h, foramen hypophyseos; :gr.h, groove on median side of hyomandibula; gr.hh, possible groove on head of hyomandibula; Nas.c, nasal capsule; Not, notochordal canal; Pr.bspt, basipterygoid process; Pr.co, coracoid process of endogirdle; Pr.l, processus lateralis of endogirdle; Pr.v, processus ventralis of endogirdle; Psph, parasphenoid; Ra, radial element; r,Cth, dorsoventrally running ridge and groove on medial surface of cleithrum; Sph.p, posterior edge of sphenethmoid (position of ventral fissure); ?spi, foramen for a spinal nerve; th.Cl, thickening on inner surface of clavicle.

placement in its own group. Similarities between *Cheirolepis* and 'palaeoniscoids' were first articulated by Pander (1860), although he too regarded *Cheirolepis* as a member of its own group. Traquair (1875) noted conspicuous differences between the structure of *Cheirolepis* and acanthodians, including several points relating to scale morphology. The most compelling similarity between these groups—scale micromery—was also rejected based on Egerton's (1864) description of micrometric squamation in the Carboniferous 'palaeoniscoid' *Myriolepis clarkei* Egerton, 1864. The structure of the fins, shoulder girdle and skull bones led Traquair (1875) to align *Cheirolepis* with taxa that are now assigned to Actinopterygii, a position universally accepted since. More recently, cladistic analyses have consistently resolved *Cheirolepis* as the sister taxon of all other ray-finned fishes (Gardiner, 1984; Coates, 1999; Gardiner et al., 2005; Friedman & Blom, 2006; Friedman, 2007; Friedman et al., 2007; Long et al., 2008; Swartz, 2009; Choo, 2011; Brazeau, 2009; Zhu et al., 2009; Davis et al., 2012; Giles et al., 2015). As only a small part of the endoskeleton of *Cheirolepis* has been described (Fig. 1; Pearson & Westoll, 1979), very limited comparisons can be drawn with other well-known early actinopterygians such as *Mimipiscis*. This makes it impossible to understand the evolution of key actinopterygian characters during the early history of the group, particularly endoskeletal structures with a major impact on osteichthyan—and gnathostome—phylogeny more generally. The paucity of endoskeletal data outside of *Mimipiscis* and *Moythomasia* has led to a situation where early actinopterygian relationships are investigated almost exclusively on the basis of dermal characters (Gardiner & Schaeffer, 1989; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011), in stark contrast to the more comprehensive character sets used when examining early gnathostome and sarcopterygian interrelationships (e.g. Zhu & Yu, 2002; Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015). Attempts to expand the actinopterygian character set (e.g. Coates, 1998, 1999; Hamel & Poplin, 2008; Giles & Friedman, 2014) have increased

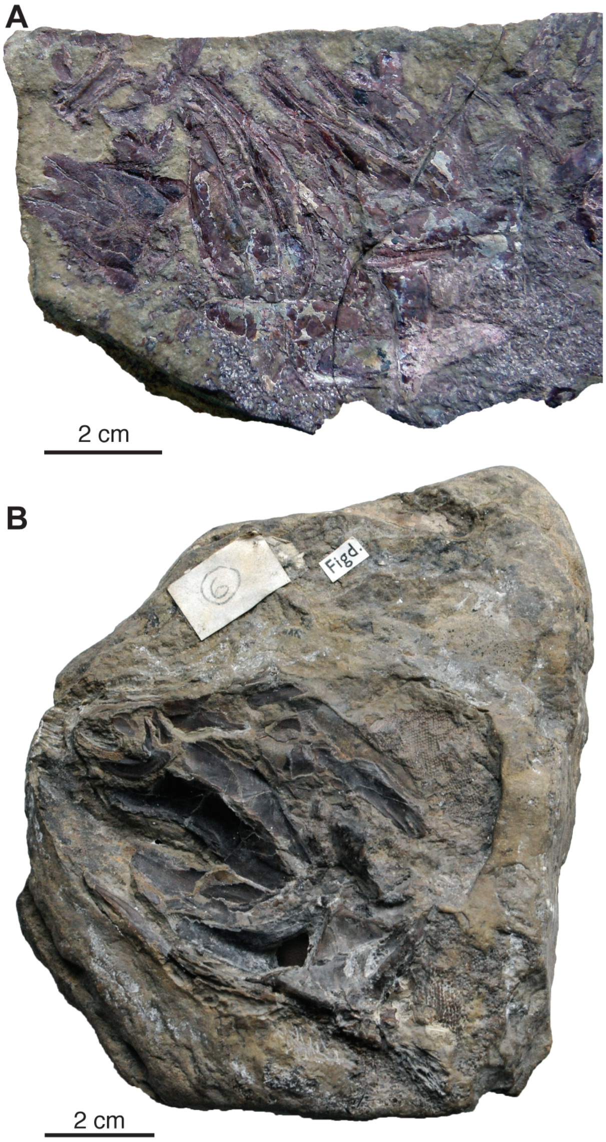

Figure 2 | Photographs of specimens described using computed tomography (CT). A, *Cheirolepis trailli* NHMUK P.62908, (Pearson & Westoll's [1979] Sp.2a), specimen in which the the base of the ethmosphenoid region and parasphenoid has become separated from the dorsal part of the ethmosphenoid region plus the otic region and occipital arch; **B**, *Cheirolepis trailli* NMS.1956.19, specimen preserving both pectoral fin endoskeletons and a hyomandibula.

the number of informative endoskeletal characters, but these are yet to be incorporated into many analyses due to the large amounts of missing data associated with taxa known principally from dermal material (see Choo, 2011).

Here we use computed tomography (CT) to examine endoskeletal anatomy in *Cheirolepis*. This study uses material previously noted as preserving endoskeletal structures, but which could only be described on the basis of surface morphology (Pearson & Westoll, 1979; Figs 1, 2, 3). Lab- and synchrotron-μCT permit the description of internal features of the specimens without recourse to destructive techniques, which could not be applied to such rare material. The specimens described herein preserve a largely complete braincase, a hyomandibula and pectoral-fin endoskeleton. In light of these data, we also revisit the neurocranium and associated bones in two other Devonian actinopterygians sometimes hypothesized to diverge outside the clade comprising *Mimipiscis*, *Moythomasia*, and more derived actinopterygians (Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011): the Givetian *Howqualepis* Long, 1988 and the Famennian *Tegeolepis* Newberry, 1988. Collectively, these new data allow us to test the suitability of *Mimipiscis* as a model of primitive ray-finned fish anatomy while also clarifying patterns of character evolution early in actinopterygian history.

3.3 MATERIALS AND METHODS

3.3.1 *Materials*

Cheirolepis. The specimens of *Cheirolepis trailli* studied herein are housed at the National Museums of Scotland, Edinburgh, UK (prefixed NMS), the Natural History Museum, London, UK (prefixed NHMUK) and the Museum of Comparative Zoology, Harvard University, Cambridge, USA (prefixed MCZ). This material originates from the Tynet Burn and Gamrie localities of the lacustrine Achnarras Limestone, Scotland, which has been dated as late Eifelian (390.4-388.1 Myr; Gradstein et al., 2012) based on the presence of spores of *Dinsosporites devonicus* (Richardson & McGregor, 1986). NMS.1877.30.5 is a near-complete specimen of *Cheirolepis*. The head is completely disarticulated, and the anterior-most region of the specimen is preserved in part (NMS.1877.30.5) and counterpart (NHMUK P.62908; Fig. 2A; Sp.2a of Pearson & Westoll, 1979). NMS.1956.19 preserves the anterior of a specimen of *Cheirolepis*, and contains a hyomandibula and pectoral endoskeleton (Fig. 2B). This specimen shows a greater degree of three-dimensional preservation than the individual represented by NMS.1877.30.5/NHMUK P.62908. Further examined specimens preserving the parasphenoid and/or ethmosphenoid are as follows: NHMUK P.4051a/b, from Gamrie; MCZ 6039, from Gamrie; NHMUK P.66863 (BMP.41410 of Pearson & Westoll, 1979), from Tynet Burn; NMS.1892.8.60, from Gamrie; Fig. 3.

Howqualepis. The specimen of *Howqualepis rostridens* examined here, AMF65495, is that of a near complete fish, missing only the snout and the anal fin. It is housed at the Australian Museum, Sydney, Australia. The material is from the lacustrine Mt. Howitt locality, southeast Australia, and has been dated by Young (2006) as Givetian (387.7-382.7 Myr; Gradstein et al., 2012) on the basis of vertebrate biostratigraphy. When first described by Long (1988), this specimen was acid prepared in dilute HCl, leaving a siliciclastic mould of the original bone.

Tegeolepis. The parasphenoid of *Tegeolepis clarkii* is seen in peels of one specimen, CMNH 5518, housed at the Cleveland Museum of Natural History, Cleveland, USA. The remains described as a parasphenoid by Dunkle & Schaeffer (1973: fig. 1) do not appear to represent that bone (see below). The specimen originates from the Cleveland Member of the Ohio Shale, which has been correlated by Over (2007) with the *marginifera-praesulcata* conodont zones (371.06-361.54 Myr; Gradstein et al., 2012).

3.3.2 *Methods*

Several specimens were selected for CT scanning. NHMUK P.62908, which preserves the braincase of *Cheirolepis*, was scanned using synchrotron radiation X-ray microtomography at the I12 beamline of the Diamond Light Source, Didcot, UK, using: an 80 keV monochromatic beam, CdW04 scintillator of 0.9mm thickness, 4008 x 2672 pco.4000 camera, and 3000 projections of 0.04 second exposure collected through 180° rotation. From the projections, slice images were reconstructed with an in-house filtered back projection reconstruction algorithm (Titarenko et al. 2010). The resulting voxel size was 12.35 μm. The part (NMS 1877.30.5), in which the parasphenoid and parts of the ethmoid region are preserved (Fig. 2A) was not scanned due to its large size and high aspect ratio. NMS.1956.19, which preserves the endoskeletal fin girdles and hyomandibula of *Cheirolepis*, was scanned at the Imaging and Analysis Centre, NHMUK, using a Metris X-Tek HMX ST 225 CT System with a 2000 x 2000 pixel detector, tungsten reflection target, and 3142 projections. Volumes were created with CTPro V2.1. AMF65495, which preserves a mould of the braincase and hyomandibula, as well as dermal material of *Howqualepis*, was scanned using the same machine at NHMUK, with the following parameters

Following scanning, the data were reconstructed and segmented manually in Mimics version 15.01 (biomedical.materialise.com/mimics; Materialise, Leuven, Belgium). As the preservation in AMF65495 is mouldic, a mask of the air was generated, producing a

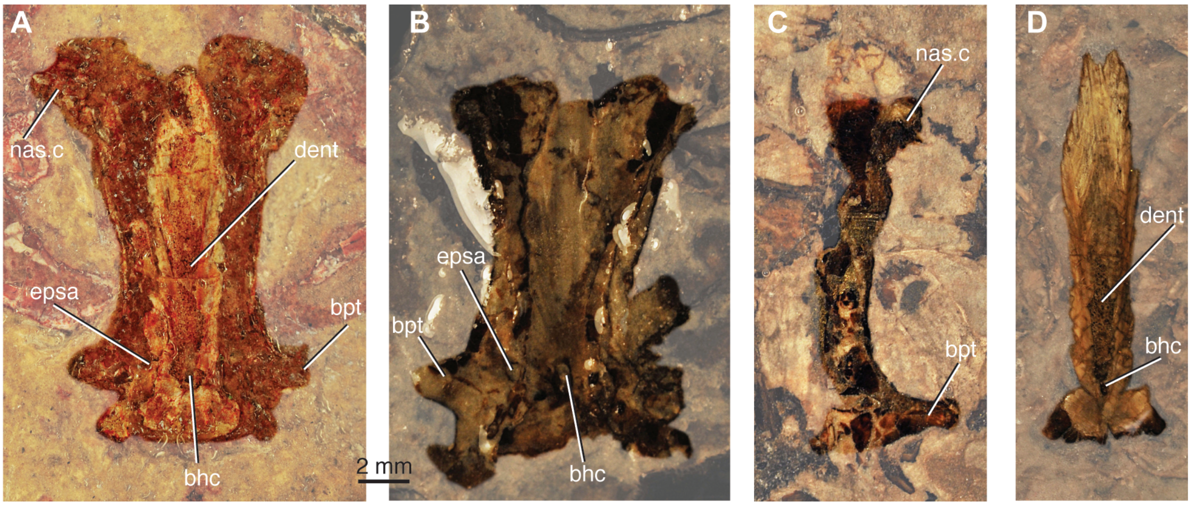

Figure 3 | Specimens of *Cheirolepis trailli* in which the parasphenoid and/or base of the ethmosphenoid region are preserved. A, NMS 1877.30.5; **B**, MCZ 6039; **C**, NHMUK P.4051b; **D**, NMS.1892.8.60. Anterior to top.

‘virtual’ cast. The use of this method, rather than producing a latex peel, minimizes any risk of damage to the specimen and results in a permanent record that will not deteriorate (original latex peels of the material, made in the 1980s, have degraded badly and been lost; J. Long, pers. comm., 2013). Meshes were exported as .ply surface files were exported to and imaged in Blender (Garwood & Dunlop, 2014). Ply files of the braincase of *Cheirolepis*, the fin and hyomandibula of *Cheirolepis*, and the cast of the *Howqualepis* specimen are made available in Appendix 2A-E. These files can be easily opened and manipulated in free programs such as Meshlab (meshlab.sourceforge.net; Cignoni et al., 2008)

Meshlab was used to downsample and prepare the two portions of the *Cheirolepis* braincase for 3D printing. The model was upscaled by a factor of five and printed using a Zprinter 350 at the Hull York Medical School, York, UK. These models aided in the interpretation of the braincase.

The parasphenoid of *Tegeolepis* is preserved as a negative impression. We studied a positive cast of this mould made using two-part flexible dental casting compound. Unlike standard latex peels, this material releases easily from matrix. For photography, this cast was coated with a sublimate of ammonium chloride.

Other specimens were studied under immersion and air, and photographed with a Nikon SLR camera with a polarizing filter. Line drawings were produced by hand.

3.3.3 *Abbreviations*

Anatomical abbreviations. alig, attachment of aortic ligament; ant.d, anterodorsal process; apal, articular facet for autopalatine; apr, anterior process of scapulocoracoid; art.cleith, articular area for cleithrum; art.fac, articular facets for secondary radials; asc.proc, ascending process; bhc, buccohypophysial canal; ?boca, branch of the occipital artery; bpt, basipterygoid process; crsp, craniospinal process; da, dorsal aorta; dent, denticle field of parasphenoid; dhy, dermohyal; epi.I, first epibranchial artery; epsa, efferent pseudobranchial artery; fm, foramen magnum; focn, foramen of the occipital nerve; f.r, fin rays; gf, glenoid fossa; hmf, articulation facet for hyomandibula; hy, hyoid artery; infc, infraorbital canal; ios, interorbital septum; jug, jugular vein; k, keel; lcom, lateral commissure; lda, lateral dorsal aorta; mpt, metapterygium; n, neck; nas.c, nasal capsule; nona, notch for the orbitonasal artery; not, notochordal canal; oims2, origin of second intermuscular septum; oof, otico-occipital fissure; p, peg; pal.a, palatine artery; p.amp, parampullary process; pdf, posterior dorsal fontanelle; por, postorbital process; proc, hyomandibula process; propt, propterygium; psp, parasphenoid; rad, radial; s, socket; scpc, scapulocoracoid; soc, supraorbital canal; spig, spiracular groove; slot, unmineralised floor of notochordal canal; sub.orb.sh, suborbital shelf; supr.orb.sh, supraorbital shelf; tp, toothplate; vof, ventral otic fissure; v.fon, vestibular fontanelle; vom, vomer; I, olfactory nerve; X, vagus nerve.

3.4 SYSTEMATIC PALAEONTOLOGY

Class OSTEICHTHYES HUXLEY, 1880
Subclass ACTINOPTERYGII COPE, 1887
Family CHEIROLEPIDIDAE PANDER, 1860
Genus *CHEIROLEPIS* AGASSIZ, 1835
Species *CHEIROLEPIS TRAILLI* AGASSIZ, 1835

Emended diagnosis (modified after Pearson & Westoll, 1979)

See Pearson & Westoll (1979: 390) with the following amendments. Cheirolepidid with lozenge-shaped parasphenoid lacking ascending processes. Spiracle housed in groove. Open groove for dorsal aorta on basicranium. Differs from other species of *Cheirolepis* in the following features: extrascapulae do not contact each other at midline, head of dermohyal projects above operculum, elongate spiracular slit.

3.5 DESCRIPTION

3.5.1 *Neurocranium*

General features. The specimen of *Cheirolepis* containing the neurocranium studied here is preserved in part and counterpart (NMS.1877.30.5/ NHMUK P.62908; Figs 2A, 3A). The bulk of the braincase is preserved in the part. The neurocranium has been dorsoventrally compressed, with the loss of internal anatomy, and is preserved as two parts: the base of the ethmosphenoid region, and the dorsal part of the ethmosphenoid region plus the otic region and occipital arch. The break between these two components occurred along the interorbital septum. Detachment of the parasphenoid and ethmosphenoid is common in specimens of *Cheirolepis*, with isolated examples found in several specimens (e.g. NMS.1877.30.5/NHMUK P.62908 [Sp.2a]; NHMUK P.4051a/b; MCZ 6039; NHMUK P.66863 [BMP.41410]; Fig. 3). The occipital region has rotated backwards during compaction such that the posterior face of the occiput is now oriented dorsally (Fig. 4) A similar style of preservation appears to characterize Pearson & Westoll's (1979: fig. 11a) 'Sp. 13' and UMZC.425 (Pearson & Westoll, 1979: fig. 4a). The basioccipital plate (lying between the vestibular fontanelles, and extending from the occiput to the ventral otic fissure) has shifted slightly to the anatomical right.

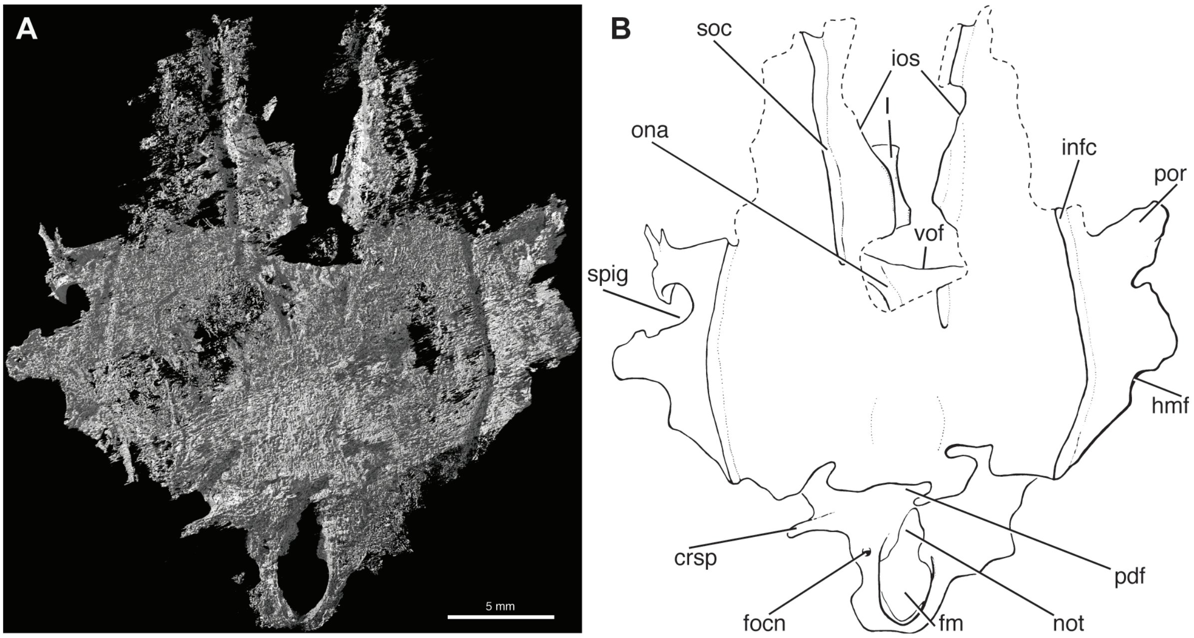

Figure 4 | The braincase of *Cheirolepis trailli* NHMUK P.62908 in dorsal view. A, three-dimensional rendering of braincase; **B**, interpretive drawing of braincase. Anterior to top.

The otico-occipital region of the braincase of *Cheirolepis* is formed as one ossification, as in *Mimipiscis* and *Moythomasia* (Gardiner, 1984). Although the crushed nature of the specimen makes it difficult to determine the location or extent of different ossification centres, the boundaries between the occipital and otic/orbital regions of the braincase can be deduced by conspicuous fissures.

Occipital region. The occiput is preserved lying face up on the surface of the rock, with the openings for the foramen magnum and notochord clearly visible (Fig. 4). The notochordal canal (not; Fig. 4B) is ovoid, and approximately twice the size of the foramen magnum (fm; Fig. 4B). As the floor of the foramen magnum is incompletely mineralized along the midline, the two openings appear confluent. Incomplete mineralization of the floor of the foramen magnum is also typical in *Mimipiscis* and *Moythomasia* (Gardiner, 1984: 189). Pearson & Westoll (1979: 345) incorrectly identified these openings as accommodating the notochord and dorsal aorta. The floor of the notochordal canal is largely complete, with the exception of a slot-shaped cavity on the midline, which likely represents incomplete fusion of paired parachordal plates, as in the Gogo actinopterygians (Gardiner, 1984; Fig. 6B). Because the braincase is flattened the notochordal canal cannot be traced anteriorly, and the relationship of this canal with the ventral otic fissure is unknown. The posterior-most parts of the occipital arch, presumably including the articular areas for the first pharyngobranchials, are preserved in the counterpart.

Lateral to the floor of the foramen magnum, the occiput is pierced by a small canal (focn; Figs 4, 6). This travels anterolaterally to open on the lateral face of the occiput (focn; Fig. 5), and comparison with other ray-finned fishes suggests that this would have transmitted the occipital nerve. This opening was cautiously identified by Pearson & Westoll (1979; fig.

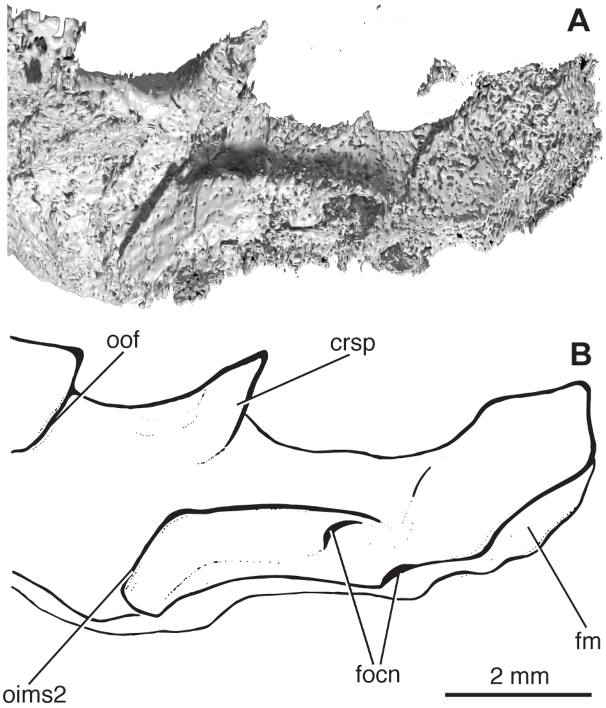

Figure 5 | Occipital portion of the braincase of *Cheirolepis trailli* NHMUK P.62908 in lateral view; this part of the braincase has rotated such that the dorsal-most part of the occiput, identified by the foramen magnum, is now at the posterior edge of the specimen. **A**, three-dimensional rendering of braincase; **B**, interpretive drawing of braincase. Anterior to left.

1c) as accommodating a spinal nerve. A distinct ridge on the lateral face of the occiput runs dorsally from the level of the occipital nerve (oims$_2$; Fig. 5). Such a ridge is also present in *Mimipiscis* and *Kansasiella* Poplin, 1975 (Poplin, 1974), and is tentatively identified in *Cheirolepis* as the ridge for the insertion of the second intermuscular septum. A modest craniospinal process is visible on the left side of the specimen, lateral to the posterior dorsal fontanelle (crsp; Figs 4-6). In life, this would have formed the dorsolateral corner of the occipital plate behind the otico-occipital fissure.

The dorsal surface of the braincase is smooth, with no evidence of a fossa bridgei (Fig. 4). Although present in later actinopterygians, a fossa bridgei is also absent in *Mimipiscis* and *Moythomasia* (Gardiner, 1984), and poorly developed in *Kentuckia deani* Eastman, 1908 (Rayner, 1951). The dorsal roof of the braincase is poorly preserved anterior to the ventral otic fissure, particularly along the midline, and the presence or absence of an anterior dorsal fontanelle cannot be determined. Mineralization of the upper surface of the braincase is complete behind the ventral otic fissure, with the exception of the posterior dorsal fontanelle (pdf; Fig. 4B); the unfinished areas anterior and lateral to the fontanelle represent areas where the bone is either too thin or too poorly mineralised to be fully resolved by the scan.

The otico-occipital fissure (oof; Figs 5-6) is completely open, as in most other early osteichthyans, and can be traced anteriorly along the ventrolateral face of the braincase before intersecting the vestibular fontanelle. A slight expansion in the line of the fissure presumably marks the exit of the vagus nerve (X; Fig. 6B). It is not possible to determine whether this is divided into a dorsal and ventral portion, as in *Mimipiscis* and *Moythomasia* (Gardiner, 1984).

The ovoid vestibular fontanelles (v.fon; Fig. 6B) are at least twice the relative length of

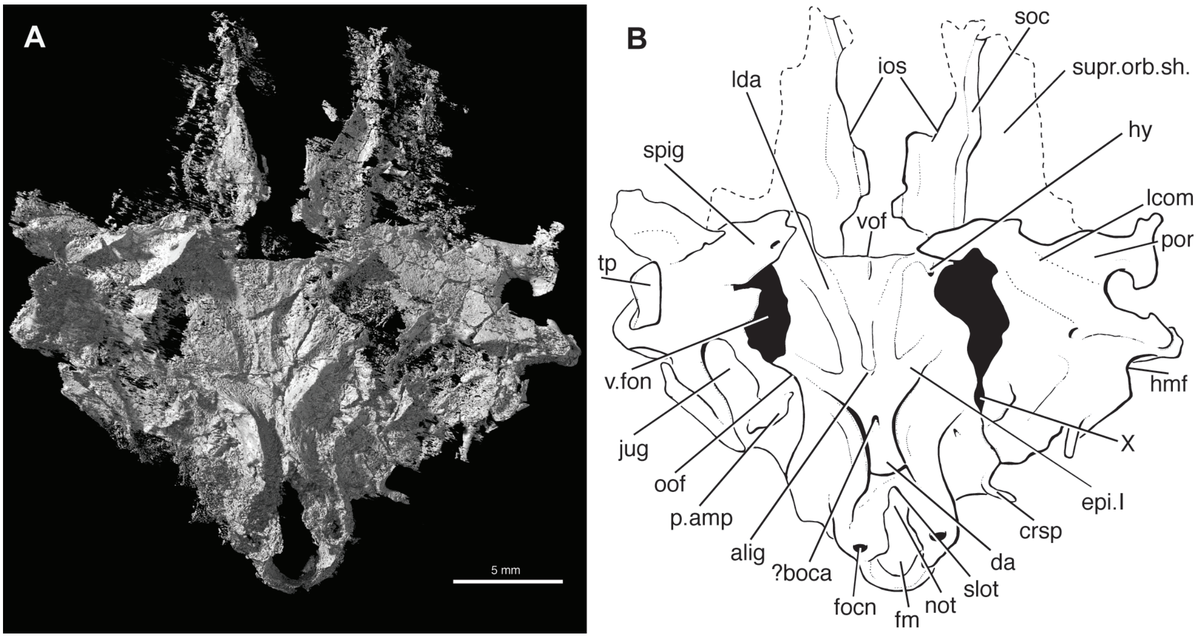

Figure 6 | The braincase of *Cheirolepis trailli* NHMUK P.62908 in ventral view. A, three-dimensional rendering of braincase; **B**, interpretive drawing of braincase. Anterior to top.

those in *Mimipiscis* and *Moythomasia*, and are more similar in size to the vestibular fontanelles of Carboniferous actinopterygians (e.g. *Kentuckia*, Rayner, 1951; *Coccocephalichthys* Whitley, 1940: Watson, 1925, Poplin & Véran, 1996; *Pteronisculus* White, 1933: Nielsen, 1942, Patterson, 1975, Coates, 1998) and sarcopterygians (e.g. *Youngolepis* Chang & Yu, 1981: Chang, 1982; *Eusthenopteron* Whiteaves, 1881: Bjerring, 1971, Jarvik, 1980; *Gogonasus* Long, 1985: Holland, 2014). The large fontanelles presumably formed a point of weakness about which the otic region collapsed, and the fontanelles may in fact appear slightly larger than their original size. As in *Mimipiscis*, *Moythomasia*, *Kansasiella*, *Coccocephalichthys*, *Lawrenciella* Poplin, 1984 (Hamel & Poplin, 2008) *Boreosomus* Stensiö, 1921 (Nielsen, 1942) and *Luederia* Schaeffer & Dalquest, 1978, the vestibular fontanelles are clearly separated from the ventral otic fissure by a substantial bridge of bone. The occipital portion of the ventral otic fissure (vof; Figs 4, 6, 7), which delimits the region anteriorly, is very straight.

Unlike in all other early actinopterygians in which the condition is known (but see below for a reinterpretation of *Howqualepis*), the dorsal aorta in *Cheirolepis* is not enclosed in a midline canal. Instead, the aorta was accommodated by a groove on the basioccipital (da; Fig. 6B), as in sarcopterygians (e.g. *Youngolepis*; Chang, 1982) and *Acanthodes* (Miles 1973, Davis et al., 2012). The aortic groove is deeper than observed in members of these outgroups. This bifurcation occurs some way posterior of the vestibular fontanelles, and is positioned more posteriorly than in other early ray-finned fishes. The lateral dorsal aortae almost immediately split again; grooves for the first epibranchial artery travel anterolaterally towards the vestibular fontanelles (epi I; Figs 6, 7), and the carotids continue anteriorly towards the ventral otic fissure (lda; Figs 6, 7). Although a similar arterial branching pattern is observed in *Kentuckia* (Rayner, 1951), *Coccocephalichthys* (Poplin & Véran, 1996), *Lawrenciella* (Hamel & Poplin, 2008) and *Leuderia* (Schaeffer & Dalquest, 1978), the

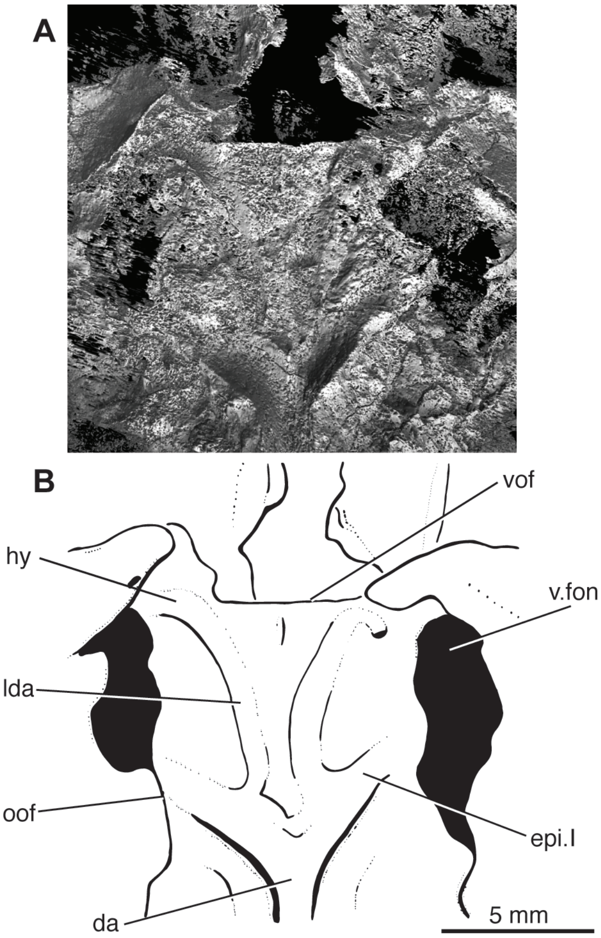

Figure 7 | Close-up of the ventral surface of the braincase of *Cheirolepis trailli* NHMUK P.62908 showing the lateral dorsal aortae and hyoid arteries. A, three-dimensional rendering of braincase; **B**, interpretive drawing of braincase. Anterior to top.

epibranchial arteries occupy a longer portion of the basioccipital in *Cheirolepis*. Similarly, the proportion of the braincase carrying the lateral dorsal aortae is longer in *Cheirolepis* than in *Mimipiscis* and other early actinopterygians. As the dorsal aorta is unfloored, the position of exit of the second epibranchial arteries is unknown in *Kentuckia*, *Coccocephalichthys*, *Lawrenciella*, *Leuderia*, *Kansasiella* (Poplin, 1974), *Boreosomus*, and *Pteronisculus* (Nielsen, 1942) these leave through a single or paired opening from the floor of the aortic canal. The branches of the lateral dorsal aortae and first epibranchial arteries are widely separated in *Cheirolepis*, and the basioccipital plate as a whole is broader than the corresponding area in *Lawrenciella*, *Kansasiella* and the Gogo actinopterygians.

Immediately posterior to the ventral otic fissure, a shallow groove branches from the lateral dorsal aorta before turning posterolaterally and entering the braincase (hy; Figs 6, 7). A similarly placed groove and foramen in other early actinopterygians (e.g. *Mimipiscis*: Gardiner, 1984: fig. 50; *Lawrenciella*: Hamel & Poplin, 2008: fig. 9) has been interpreted as housing the orbital artery. Positionally, this is implausible: it is unlikely that the orbital artery would turn posteriorly, away from the orbit. The posterolateral orientation of the groove, and comparison with other extant and extinct gnathostomes (e.g. *Chlamydoselache* Allis, 1923; *Janusiscus* Giles et al., 2015) suggests that this represents the path of the efferent hyoid artery.

A small peg is located on the midline immediately after the divergence of the dorsal aorta. Comparison with *Mimia* and *Moythomasia* (Gardiner, 1984) indicates that this likely marks the attachment point for the aortic ligament (alig; Fig. 6B). The roof of the aortic groove is pierced by an anterodorsally directed canal that opens into the notochordal canal. The canal lies on the midline, but as it is developed as a distinct groove it is unlikely to represent a gap between the basioccipitals, and the opening is too posterior to be the aortic ligament. It may represent a branch of the occipital artery (?boca; Fig. 6B).

Otic and orbital regions. The deformation of the specimen has caused the lateral face of the neurocranium to be flattened out onto a level with the rest of the ventral surface. Therefore, the otic region may appear somewhat wider than it would in life. The lateral commissure (the transverse otic processes; see revised terminology in Giles et al., 2015) is anterposteriorly broader and slightly longer than in other early actinopterygians (lcom; Fig. 6B), particularly *Mimipiscis* (Gardiner, 1984: fig. 50). Although flattened, the postorbital process (por; Figs 4B, 6B) is prominent. As in *Mimipiscis*, the long spiracular groove (spig; Figs 4B, 6B) extends along the lateral face of the otic region and onto the basisphenoid, behind the basipterygoid process. There is no trace of the open anterior pocket between the postorbital process and spiracular groove, as seen in the braincase attributed to *Ligulalepis* Schultze 1968 (Basden et al., 2000; Basden & Young, 2001). The lateralmost parts of the left postorbital and transverse otic processes and (i.e. those preserved dorsal-most after deformation) in *Cheirolepis* are preserved in the counterpart. The presence or absence of an otico-sphenoid fossa cannot be determined.

The articular area for the hyomandibula is positioned behind the spiracular groove on the posterior face of the broad postorbital process (hmf; Figs 4B, 6B). The hyomandibular facet has been distorted, and now faces posteriorly. The facet on the right of the specimen is partially obscured by a displaced, possibly spiracular, toothplate (tp; Fig. 6B).

A deep gutter marking the course of the jugular vein is visible on the lateral side of the otic region, below the shelf formed by the hyomandibular facet (jug; Fig. 6B). The groove bends dorsolaterally around the prominent parampullary process (pamp; Fig. 6B), as in *Mimipiscis* and *Moythomasia* (Gardiner, 1984), and the first suprapharyngobranchial likely articulated with this region. The posterior entrance of the jugular canal into the lateral commissure presumably also transmitted the hyomandibular trunk of the facial nerve. The exit of the glossopharyngeal nerve cannot be identified. The otic region anterior to the postorbital process has collapsed, obscuring the anterior opening of the jugular canal and the trigeminofacialis chamber.

The floor and hind walls of the orbit are not preserved. Due to the manner in which the specimen is broken, the interorbital septum (ios; Figs 4B, 6B, 7) is largely incomplete. The precise width of the interorbital septum is unclear, but appears wider than in *Mimipiscis* and *Moythomasia* (Gardiner, 1984). Details of the orbital roof are not preserved, but deep grooves are visible on the dorsal surface for the overlying supraorbital canals of the dermal skull roof (soc; Fig. 6B).

Although comparison with other early actinopterygians suggests the interorbital septum would originally have been completely mineralised, separation of the sphenoid and ethmoid from the occipital and orbitotemporal regions is fairly common in specimens of *Cheirolepis*. The neurocranium has broken through the ventral otic fissure and basiphenoid pillar and along the interorbital septum. Consequently, the parasphenoid and ventral-most parts of the ethmosphenoid are preserved in the counterpart.

The basiphenoid portion of the ventral otic fissure is incompletely resolved, but faint notches for the orbitonasal arteries are apparent posterior to the basipterygoid processes (nona; Fig. 8B,D), as in *Mimipiscis* (Gardiner, 1984) and *Coccocephalichthys* (Poplin & Véran, 1996). The basisphenoid pillar in this specimen is split open through the hypophyseal fossa, and the buccohypophyseal canal (bhc; Fig. 8B,D), which travels through the basisphenoid to open on the ventral surface of the parasphenoid, is visible. Lateral to the

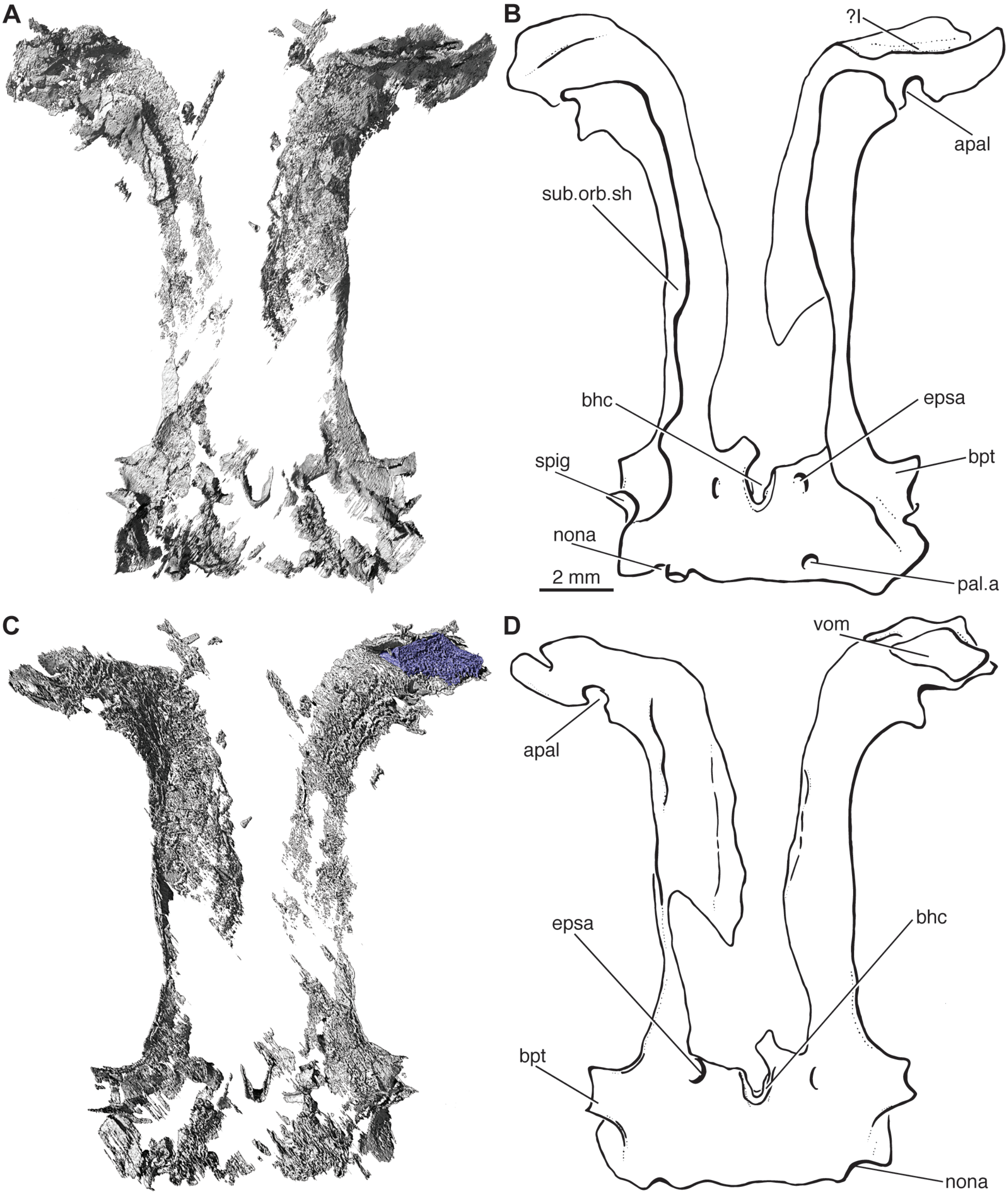

Figure 8 | Ethmosphenoid portion of the braincase of *Cheirolepis trailli* NHMUK P.62908; parasphenoid preserved in counterpart. **A**, three-dimensional rendering of braincase in dorsal view; **B**, interpretive drawing of braincase in dorsal view; **C**, three-dimensional rendering of braincase in ventral view, with vomer shown in blue; **D**, interpretive drawing of braincase in ventral view. Anterior to top.

buccohypophyseal opening are two anterolaterally directed canals, which can also be traced on to the parasphenoid. Comparison with *Mimipiscis* (Gardiner, 1984), *Moythomasia* and *Lawrenciella* (Hamel & Poplin, 2008) suggests these transmitted the efferent pseudobranchial arteries (epsa; Fig. 8B). The buccohypophyseal canal and openings of the efferent pseudobranchials were both identified by Pearson & Westoll (1979: fig 1). The entrance of the palatine artery into the basisphenoid is marked by an anteroventrally directed canal immediately in front of the ventral otic fissure (pal.a; Fig. 8B).

The sides of the basisphenoid extend laterally as small basipterygoid processes (bpt; Fig. 8B,D), as noted by Pearson & Westoll (1979). These processes are entirely endoskeletal, and are not in contact with the parasphenoid; a dermal component to the basipterygoid processes is seen in *Kentuckia* (Rayner, 1951), *Kansasiella* (Poplin, 1974), *Pteronisculus* and *Boreosomus* (Nielsen, 1942). The spiracular groove continues onto the basisphenoid (spig; Fig. 8B) behind the basipterygoid processes.

Due to the high level of dorsoventral compression, no details of the endocast can be described. As in most fish fossils preserved in carbonate matrix, the otoliths cannot be discerned, having presumably dissolved during fossilization.

Ethmoid region and parasphenoid. Very little of the ethmoid region is preserved, particularly above the level of the suborbital shelf. Additionally, much of the ventral part of the ethmoid is preserved in the counterpart. Anteriorly, the subnasal shelf flares dorsally. Two distinct notches mark the articular areas for the autopalatine (apal; Fig. 8B,D).

Parasphenoids are preserved in a number of specimens (e.g. NHMUK P.62908/NMS.1877.30.5; NHMUK P.60499; NMS.1892.8.60; NHMUK P.66863

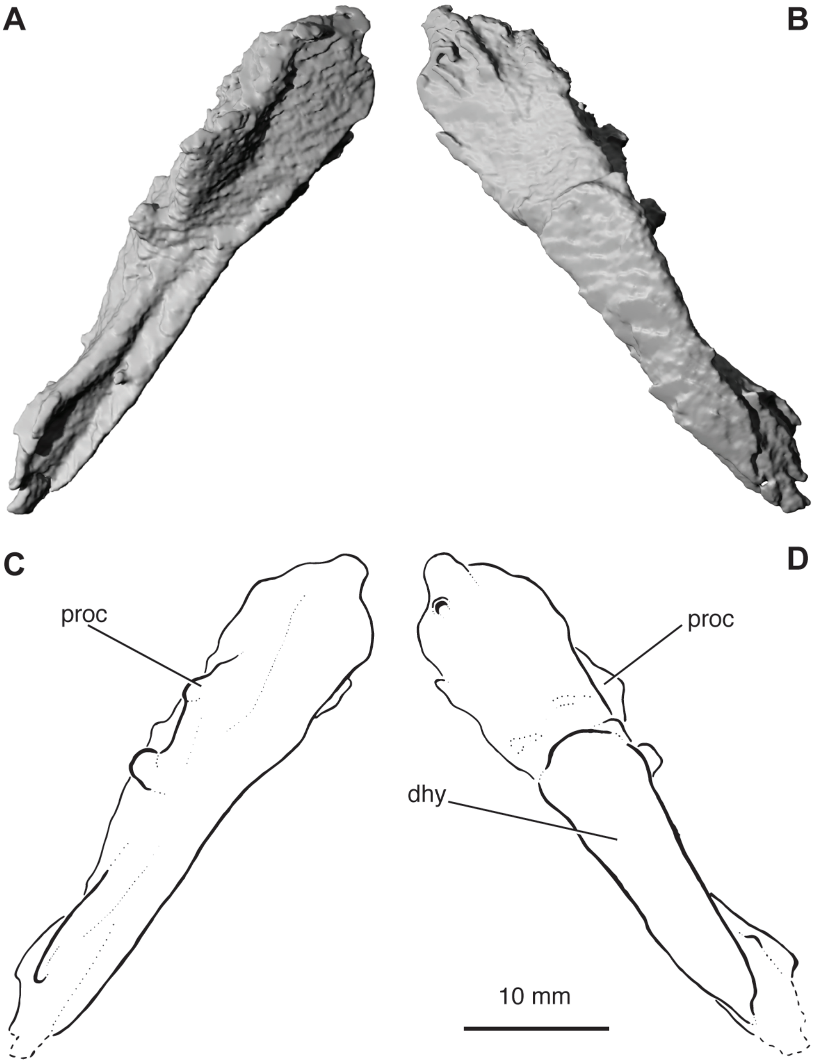

Figure 9 | Left hyomandibula of *Cheirolepis trailli* NMS.1956.19. A, three-dimensional rendering of hyomandibula in medial view; **B**, three-dimensional rendering of hyomandibula in lateral view; **C**, interpretive drawing of hyomandibula in medial view;

[BMP.41410]; NHMUK P.4051a/b; MCZ 6039; Fig. 3), and are separated from the bulk of the braincase in most instances. It is possible that these isolated parasphenoids represent individuals with poorly ossified or unossified endocrania. The parasphenoid is complete in NHMUK P.62908/NMS.1877.30.5, and is wholly preserved in the counterpart (Fig. 3A). As described by Pearson & Westoll (1979), this bone is simple, lacking a complex anterior margin and ascending processes, and quite unlike the ossifications seen in *Mimipiscis* and *Moythomasia* (Gardiner, 1984; Choo, 2011). Although the posterior part of the bone flares slightly behind the efferent pseudobranchial openings, there is no evidence of an ascending process. Ascending processes are also lacking in *Mimipiscis*. A shagreen of denticles covers much of the ventral surface of the parasphenoid in *Cheirolepis* (dent; Fig. 3A, D).

A vomerine toothplate is preserved on the left side of the ethmoid (vom; Fig. 8D). The toothplate is lozenge-shaped, and is covered in fine denticles. The vomer is small, resembling those of *Mimipiscis* (Gardiner, 1984) and *Moythomasia* (Gardiner & Bartram, 1977), rather than the enlarged vomers of sarcopterygians (e.g. *Eusthenopteron*, Jarvik, 1980; *Powichthys* Jessen, 1980, Clément & Janvier, 2004). It appears to be in life position, although it has been crushed somewhat into the ethmoid.

3.5.2 *Hyomandibula*

The left hyomandibula is preserved within NMS.1956.19, and is not visible on the surface. Although unbroken, it has been displaced to the region of the right scapulocoracoid. The hyomandibula is fairly slender and gently curved, and is firmly fused to the dermohyal (i.e., no sutures are apparent between these two ossifications in tomographs), as in *Mimipiscis* and *Moythomasia* (dhy; Fig. 9D). The dermohyal appears proportionately longer than in other early actinopts, although as the distal part of the hyomandibula appears to be unmineralised,

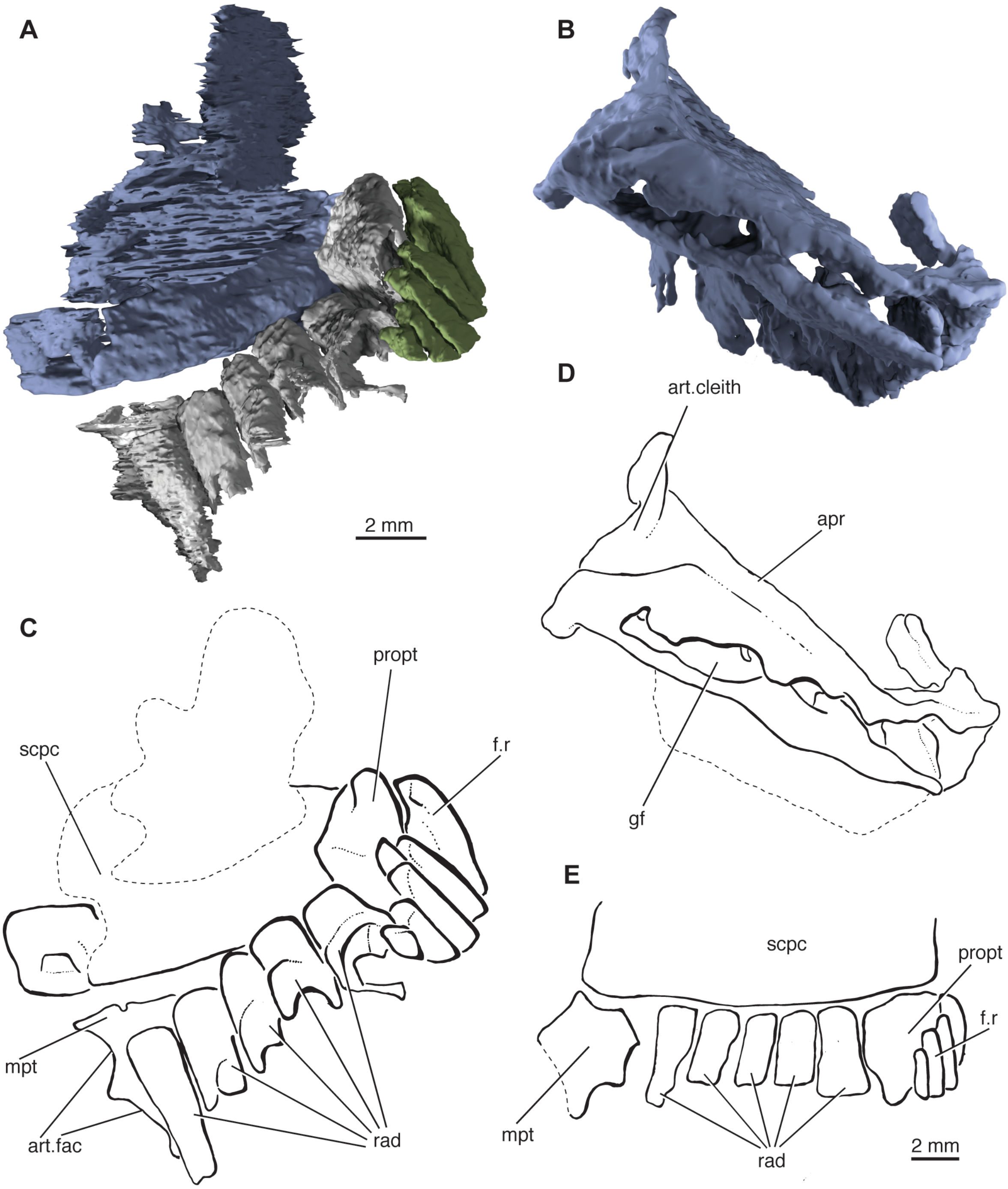

Figure 10 | Left pectoral fin endoskeleton of *Cheirolepis trailli* NMS.1956.19. A, three-dimensional rendering of fin endoskeleton in ventroposterior view; lateral edge of fin to right; **B**, three-dimensional rendering of fin endoskeleton in posterior view; lateral edge of fin to left; **C**, interpretive drawing of fin endoskeleton in ventroposterior view; lateral edge of fin to right; **D**, interpretive drawing of fin endoskeleton in posterior view; lateral edge of fin to left; **E**, reconstruction of the left pectoral fin endoskeleton in ventral view; lateral edge of fin to right.

its precise proportion cannot be determined. A distinct process on the medial face of the hyomandibular projects above the dermohyal (proc, Fig. 9C, D). Comparison with other actinopterygians suggests that this is too proximal to be the opercular process, and reference to Pearson & Westoll's (1979: fig. 20a) reconstruction suggests that this process may have contacted the internal face of the supratemporal. A deep gutter traverses the medial face of the hyomandibula. The shaft of the hyomandibula is imperforate, with the hyomandibular trunk of the facial nerve presumably passing behind and bifurcating distally, as in the extant *Acipenser* Linneaus, 1758 (Jollie, 1980), some sarcopterygians (e.g. Andrews et al., 2006), acanthodians (Miles, 1973), chondrichthyans (e.g. Maisey, 1989; Coates & Sequeira, 2001) and placoderms (e.g. Stensiö, 1961; Forey & Gardiner, 1986). No toothplates are evident on the hyomandibula of *Cheirolepis*, although these may have been present distally. The partial hyomandibulae described by Pearson & Westoll (1979: 362, fig. 10c,d) in NHMUK P.36061 and NMS.1877.30.5 appear to be fragments of other ossifications, although their correct attribution cannot be identified with any certainty.

3.5.2 *Pectoral fin endoskelton*

Both pectoral endoskeletal girdles are preserved in NMS.1956.19, although both are broken and thus cannot be exhaustively described. The left girdle is visible on the surface, and was partially described by Pearson & Westoll (1979: fig. 14a), although their reconstruction of a complete scapulocoracoid (Pearson & Westoll, 1979: fig. 12) is almost entirely hypothetical. The preserved scapulocoracoid in *Cheirolepis* is mineralised as a single ossification (scpc; Fig. 10C). The area of attachment to the cleithrum is fairly broad and elongate (art.cleith; Fig. 13D). There is no evidence of a ventral process, nor a mesocoracoid arch. Thus the scapulocoracoid appears to have had only a simple attachment to the cleithrum (art.cleith; Fig. 10D), unlike the tripartite attachment seen in *Mimipiscis*, *Moythomasia* (Gardiner,

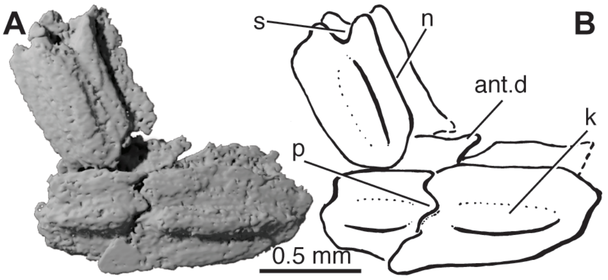

Figure 11 | Scales of *Cheirolepis trailli* NHMUK P.62908 in ventral view. A. three-dimensional rendering of scales; anterior to left. **B**. interpretive drawing of scales. Anterior to right.

1984), and other actinopterygians (e.g. Nielsen, 1942), although this may be due to poor mineralization or preservation in this specimen of *Cheirolepis*. The scapulocoracoid did not articulate with the clavicle (contra Pearson & Westoll, 1979). While tripartite scapulocoracoids are also seen in sarcopterygians (e.g. *Eusthenopteron*, Jarvik, 1980), members of the stem group, such as *Psarolepis* Yu, 1998 and *Achoania* Zhu, et al., 2001, appear to have had simple attachments to the cleithrum (Zhu & Yu, 2009). The anterior process (apr; Fig. 10D) in *Cheirolepis* appears extensive, although it is fragmented in both girdles. As a result, it is difficult to trace the course of any blood vessels. The processus lateralis identified by Pearson & Westoll (1979: fig. 14, Pr.l) appears to be an artefact on the surface of the specimen, and the processus ventralis (fig 14, Pr.v) is in fact the misplaced metapterygium.

The glenoid fossa is narrow and elongate (gf; Fig. 10D). It bears several moderately well-developed articular facets for the radials. The radials are preserved as hollow perichondral sheaths, and those of the left fin have been shifted out of the scapulocoracoid plane. The radials of the right fin are completely disarticulated. The propterygium is stout, and is clasped by four fin rays (propt, f.r; Fig. 10C). Unlike all other early actinopterygians, it is not pierced by the propterygial canal. The metapterygium is large and robust, although not noticeably elongate (mpt; Fig. 10C). It bears articular facets to support two distal radials (art.fac; Fig. 10C), although these are not preserved; these were likely cartilaginous, as in *Polypterus* and possibly *Mimipiscis* (Gardiner, 1984). The shape of the metapterygium is more similar to that of actinopterygian outgroups such as *Acanthodes* (Coates, 2003: fig. 3b) than other actinopterygians such as *Mimipiscis* (Gardiner, 1984: fig. 137). However, the presence of an elongate metapterygium in sarcopterygians makes it difficult to assess whether *Cheirolepis* has retained the primitive condition or if it is secondarily reduced. Five radials sit between the propterygium and metapterygium (rad; Fig. 13C).

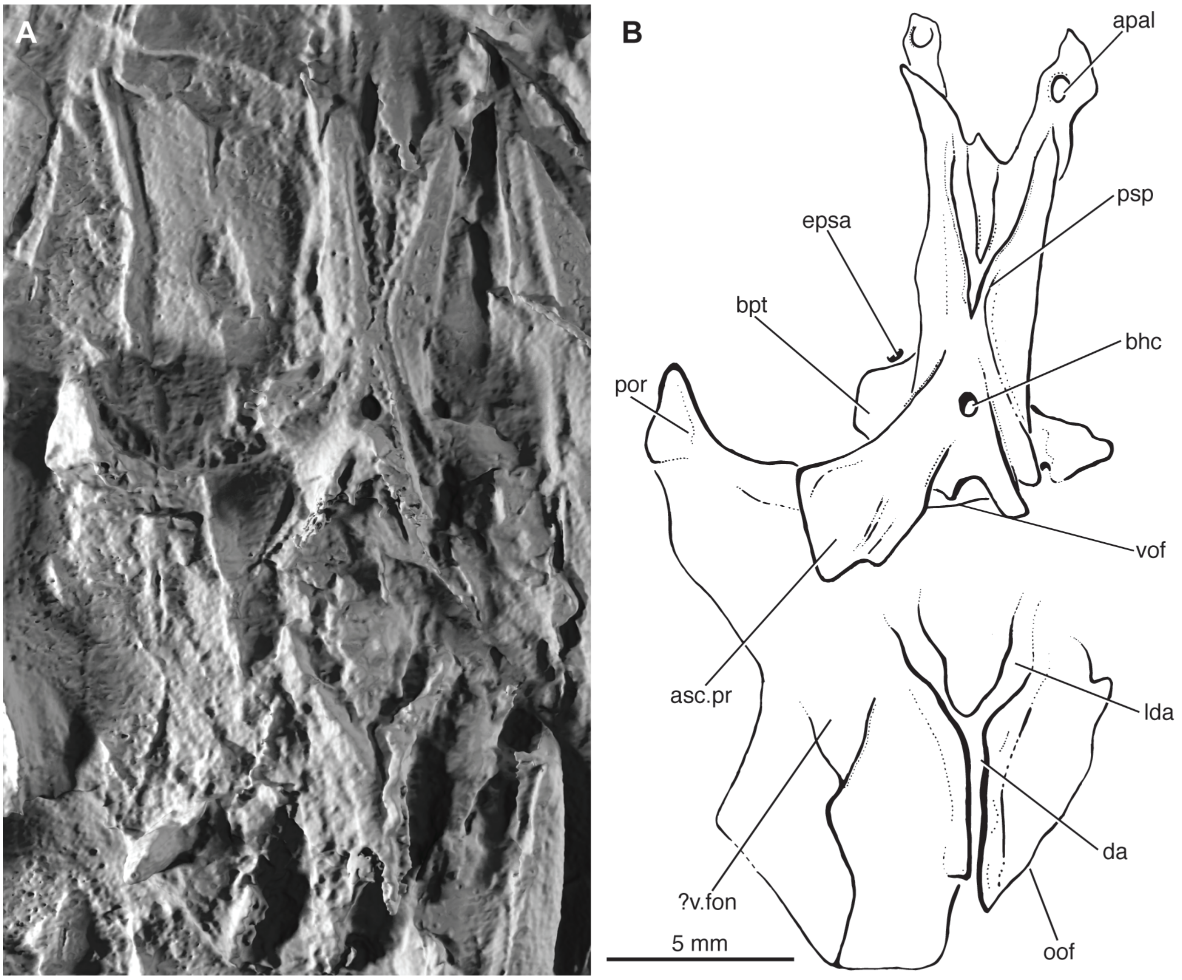

Figure 12 | ‘Virtual’ cast of the braincase of *Howqualepis* rostridens AMF65495 in ventral view. **A**, three-dimensional rendering of braincase; **B**, interpretive drawing of braincase. Anterior to top.

3.5.4 *Body scales*

Several patches of body scales are preserved in NHMUK P.62908, including a number found in articulation with each other but inside the braincase (Fig. 11). Although the external surface of the scales is poorly resolved, the internal surface is well preserved. The scales are rhomboid, with a pronounced anterodorsal process, and bear a distinct midline keel (ant.d, k; Fig. 11B). Most importantly, the scales display peg-and-socket articulation, a feature previously considered absent in *Cheirolepis trailli* (Pearson & Westoll, 1979; Gardiner, 1984; Arratia & Cloutier, 1996). As in *Psarolepis* and acanthodians, but unlike the scales of most osteichthyans (Qu et al., 2013), the rhomboid scales of *Cheirolepis* bear a distinct neck between the crown and base (n; Fig. 11B).

3.5.5 *Comparative morphology*

Howqualepis. The braincase of *Howqualepis* is known in most detail from AMF65495, where it is preserved in ventral view but is dorsoventrally compressed (Long, 1988: fig. 16). As described by Long, the ascending processes are elongate, and end in a fairly blunt edge rather than tapering (asc.pr; Fig. 12B). Although depicted as having a pointed apex in *Moythomasia* (Gardiner, 1984: fig. 7), unbroken ascending processes in this genus also tend to terminate rather bluntly (S. Giles, pers.obs.). The processes in *Howqualepis* do not appear to be denticulated. The basipterygoid processes are well developed, and are entirely endoskeletal (bpt; Fig. 12B). The shape of the parasphenoid denticle field is difficult to interpret, but the denticles are largely restricted to the anterior portion of the parasphenoid. The postorbital process in *Howqualepis* is incompletely preserved. The median dorsal aorta

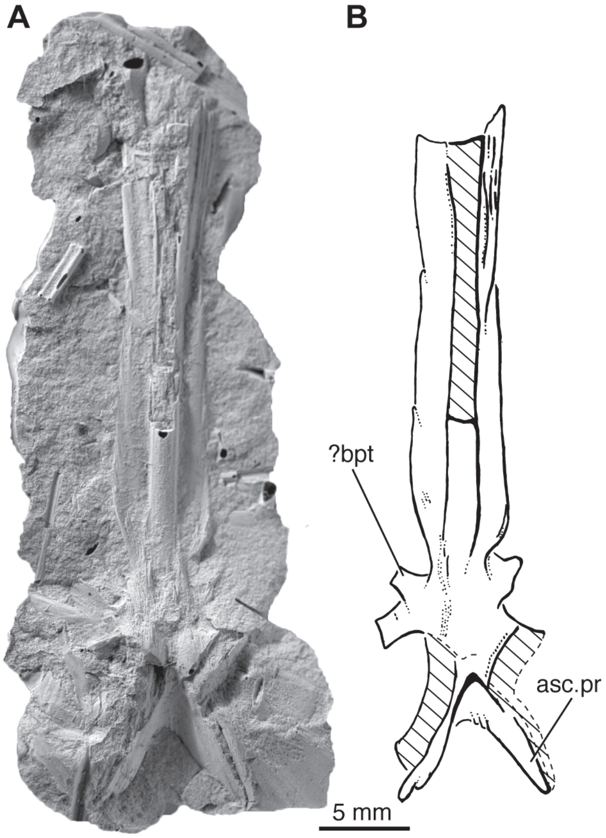

Figure 13 | Parasphenoid of *Tegeolepis clarkii* CMNH 5518 in dorsal view. A. photograph of parasphenoid; **B**, interpretive drawing of parasphenoid. Anterior to top.

is housed in an open groove, rather than an enclosed canal (da, Fig.12B).

Tegeolepis. The parasphenoid of *Tegeolepis* is preserved in dorsal view in CMNH 5518. It is slender, and is more similar in shape to the parasphenoid of *Cheirolepis* than that of any other early actinopterygian (Fig. 13). The parasphenoid is narrow anteriorly and tapers to its narrowest point just in front of the buccohypophyseal canal. It bears two small basipterygoid processes (?bpt; Fig. 13B), but it is unclear whether these have a dermal component. Posteriorly, the parasphenoid flares into two short ascending processes (asc.pr; Fig. 13B), reminiscent of those of *Howqualepis*. No details of the parasphenoid denticle field can be described.

The parasphenoid described here bears little relation to that reconstructed by Dunkle & Schaeffer (1973: fig. 1) for another specimen (CMNH 8244), in which the lateral edges of the bone are strongly fluted, the ascending processes are very narrow, and the posterior of the bone is developed as a long stalk that would have extended below the otic and occipital regions. Based on observations of this specimen, we question the interpretation of CMNH 8244 as a parasphenoid, and note that the structure in question is not intact.

3.6 DISCUSSION

3.6.1 *Cheirolepis and other early actinopterygians*

Although broadly resembling that of other actinopterygians, the braincase of *Cheirolepis* bears clear similarities with members of actinopterygian outgroups, in particular the sarcopterygians. These features, outlined below, are presumably osteichthyan symplesiomorphies (Fig. 14). The most conspicuous of these is the uninvested dorsal aorta;

an enclosed midline canal for the aorta has previously been considered an actinopterygian synapomorphy (Rayner, 1951; Miles, 1973; Patterson, 1975; Gardiner, 1984; Long, 1988; Friedman & Brazeau, 2010). Although present in all other early actinopterygians (with the exception of *Howqualepis*), the dorsal aorta is uninvested in sarcopterygians (e.g. *Eusthenopteron*, Jarvik, 1980; *Youngolepis*, Chang, 1982), and acanthodians (e.g. *Acanthodes*, Miles, 1973). The condition of the dorsal aorta in the early osteichthyans *Ligulalepis* (Basden & Young, 2001) and *Psarolepis* (Yu, 1998) is unknown, as the only described braincases for these taxa lack the ventral occipital plate. Other features that appear plesiomorphic for actinopterygians apparent in *Cheirolepis* include: large vestibular fontanelles resembling those of *Youngolepis* and *Eusthenopteron*, in contrast to the much smaller fontanelles of *Mimipiscis* (Gardiner, 1984); the elongate portion of the basioccipital on which the lateral dorsal aortae are carried, which bears a greater resemblance to sarcopterygians such as *Youngolepis*; and the imperforate propterygium (as noted by Pearson & Westoll, 1979; Friedman & Brazeau, 2010; contra Sallan, 2014), a character shared with chondrichthyans, with the presence of a propterygial canal previously considered to be an actinopterygian synapomorphy. In addition to differences in the endoskeleton, the dermal skeleton of *Cheirolepis* has also long been considered atypical of other actinopterygians, given the large number of plesiomorphic osteichthyan features it retains. These features include unconsolidated rostral bones, a tectal, elongate jaws, lobed base to pectoral fins, epichordal lobe in caudal fin, and lack of acrodin toothcaps (Gardiner, 1963; Pearson, 1982; Pearson & Westoll, 1979; Friedman & Brazeau, 2010).

Despite differing from *Mimipiscis* and other actinopterygians in certain key respects, *Cheirolepis* possesses several features that unite it with other actinopterygians: the presence of a basipterygoid fenestra in the palatoquadrate (Pearson & Westoll, 1979: fig. 7c, d), a single dorsal fin (Pearson & Westoll, 1979: fig 16; Arratia & Cloutier, 1996: fig. 4a), and the absence of a jugal canal (Pearson & Westoll, 1979: fig. 20; Arratia & Cloutier, 1996: fig. 6; Arratia & Cloutier, 2004: fig. 4; Friedman & Brazeau, 2010). The generalised conditions outlined above confirm the position of *Cheirolepis* as an early diverging member of Actinopterygii.

3.6.2 *Parasphenoid evolution in early actinopterygians*

New data on the parasphenoid in *Tegeolepis*, as well as new descriptions of the parasphenoids of *Mimipiscis toomsbi* and *M. bartrami* Choo, 2011, allow a detailed understanding of the evolution of the parasphenoid in early actinopterygians. Ascending processes of the parasphenoid, previously considered to be a derived actinopterygian character confined to actinopterygians crownward of *Mimipiscis* (Patterson, 1982; Gardiner, 1984; Coates, 1999; Gardiner et al., 2005), are present in all actinopterygianss crownwards of *Cheirolepis* (Node D of Fig. 14; Choo, 2011). The slight lateral extensions posterior to the buccohypophyseal canal in *Cheirolepis* may be homologous with the ascending process of later actinopterygians. The absence of this process in *Mimipiscis* thus appears to be a secondary loss. Several groups of sarcopterygians bear ascending processes of the parasphenoid, or expanded denticle plates that occupy a similar region as actinopterygian ascending processes (Jarvik, 1980; Jessen, 1980; Chang, 1982). However, patterns of character distribution given current hypotheses of osteichthyan interrelationships suggest that these are independently derived relative to ascending processes in actinopterygians.

3.6.3 *Implications for the actinopterygian character suite*

The recognition of features previously thought to be restricted to sarcopterygians in the braincase of an early actinopterygian, most particularly the uninvested dorsal aorta, indicates

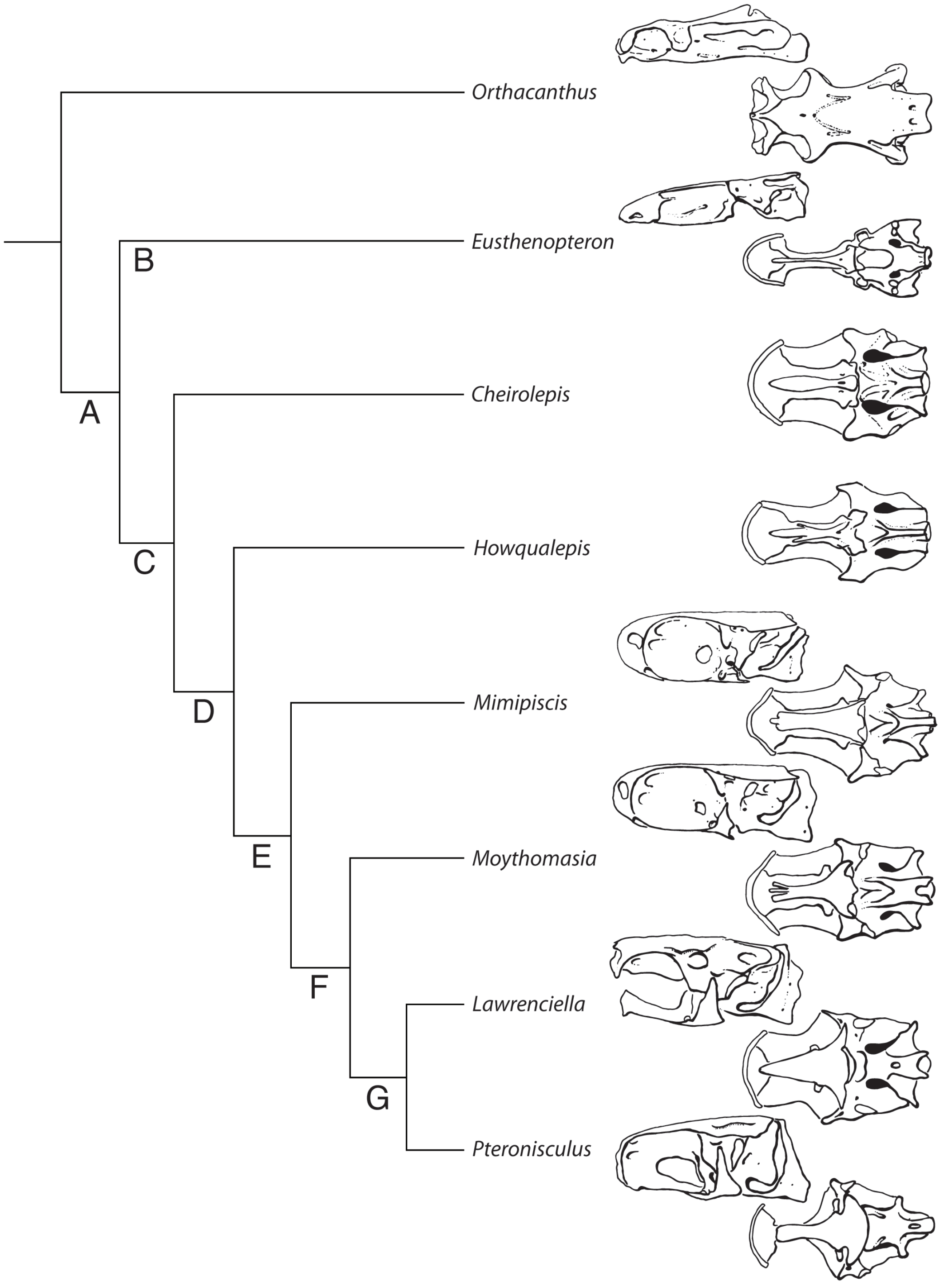

Figure 14 | Cladogram of early vertebrate relationships, with an emphasis on actinopterygians, showing potential apomorphies in the endoskeleton. Cladogram based on Choo, 2011, Zhu et al., 2013, and Xu et al., 2014. See discussion for a list of proposed synapomophies at lettered nodes. Braincase images redrawn from: *Orthacanthus*, Schaeffer, 1981; *Eusthenopteron*, Jarvik, 1980; *Mimipiscis*, Gardiner, 1984, Choo, 2011; *Moythomasia*, Long & Trinajstic, 2010; *Lawrenciella*, Hamel & Poplin, 2008; *Pteroniscuclus*, Nielsen, 1942.

that these characters represent osteichthyan plesiomorphies. *Cheirolepis* lacks several key features previously identified as actinopterygian synapomorphies, allowing a new understanding of the sequence of character evolution early in the history of the group (Fig. 14). Because these data do not change the phylogenetic position of *Cheirolepis*, only reinforce existing interpretations, this character distribution can be summarised by mapping key neurocranial and endocast characters onto a cladogram based on recent analyses of early actinopterygian and osteichthyan relationships (e.g. Choo, 2011; Zhu et al., 2013; Xu et al., 2014; Fig. 14).

The key morphological changes in the endoskeleton at successive nodes can be summarised as follows.

Node A - Osteichthyes: long olfactory tracts (Coates, 1999; Friedman & Brazeau, 2010; Brazeau & Friedman, 2014; Giles & Friedman, 2014; reversals in tetrapodomorphs and some post-Devonian actinopterygians); horizontal semicircular canal joins labyrinth level with ampulla for posterior semicircular posterior canal (Davis et al., 2012; Brazeau & Friedman, 2014; Giles & Friedman, 2014); comineralised ethmoid and sphenoid completely enclosing nasal capsules (Friedman & Brazeau, 2010; reversals in some lungfishes, limb-bearing tetrapods, and post-Devonian actinopterygians); endocranial unit dorsally restricted within sphenoid (Brazeau & Friedman, 2014).

Node B - Sarcopterygii: endoskeletal intracranial joint (Janvier, 1996; Friedman & Brazeau, 2010; reversals in some lungfishes and limb-bearing tetrapods); basicranial fenestra (Friedman & Brazeau, 2010; reversal in some lungfishes); broad or bipartite hyomandibular articulation (Miles, 1977; Lauder & Liem, 1983; Gardiner, 1984; Friedman & Brazeau, 2010); vertical component to basipterygoid process (Davis et al., 2012).

Node C - Actinopterygii: basipterygoid fenestra in palatoquadrate (Friedman, 2007; Friedman & Brazeau, 2010; reversal in some post-Carboniferous actinopterygians); single dorsal fin; dermohyal fused to hyomandibula (Patterson, 1982; Gardiner, 1984; Coates, 1999; Gardiner et al., 2005; reversals in *Tegeolepis* and some post-Devonian actinopterygians).

Node D - ascending process of the parasphenoid (Patterson, 1982; Gardiner, 1984; Coates, 1999; Gardiner et al., 2005; reversals in *Mimipiscis* and *Gogosardina*).

Node E - enclosed dorsal aorta (Miles, 1973; Coates, 1999; Friedman & Brazeau, 2010); propterygium pierced by propterygial canal (condition unknown in *Howqualepis* and *Tegeolepis*; Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Gardiner et al., 2005; Friedman & Brazeau, 2010); pectoral fin endoskeleton does not project outside of body (Coates, 1999; reversal in some post-Carboniferous actinopterygians).

Node F - enclosed spiracular canal (Patterson, 1982; Gardiner & Schaeffer, 1989; Gardiner, 1984; Coates, 1999; Gardiner et al., 2005).

Node G - anteriorly (as opposed to anterolaterally) directed olfactory tracts (Coates, 1999; Giles & Friedman, 2014); olfactory nerves carried in single midline tube (Coates, 1999; Giles & Friedman, 2014; reversal in some post-Carboniferous actinopterygians); optic lobes same width as cerebellum (Giles & Friedman, 2014); corpus cerebellum of anterior and posterior semicircular canals ventral to endocranial roof (Giles & Friedman, 2014); fossa bridgei (Miles, 1973; Gardiner & Schaeffer, 1989; Coates, 1999; Gardiner, 1984); expanded anterior dorsal fontanelle. [N.B. some or all of the latter four characters may occur at Node F, but as an endocast for *Moythomasia* has not been described this cannot be determined.]

The endoskeleton of *Cheirolepis* differs from that of *Mimipiscis* in several important respects, including: an uninvested dorsal aorta; large vestibular fontanelles; elongate basioccipital portion of the braincase; unelaborated parasphenoid lacking a multifid anterior margin and ascending processes; pectoral endoskeleton protruding from the body; and imperforate proterygium. In all of these respects, *Cheirolepis* more closely resembles early members of actinopterygian outgroups than *Mimipiscis* and other Devonian actinopterygians. The recognition of apomorphic features in the braincase of *Mimipiscis*, for example the loss of ascending processes of the parasphenoid, the presence of an elongate, fully enclosed dorsal aorta, and the very small vestibular fontanelles (Gardiner, 1984), further bring into question the suitability of *Mimipiscis* as representative of the plesiomorphic actinopterygian condition.

The description of the braincase and other endoskeletal anatomy of *Cheirolepis* adds more detail to our understanding of endoskeletal evolution in early actinopterygians. However, further data, for example from *Howqualepis* (Long, 1988) and *Gogosardina* Choo et al., 2009, are needed to fully understand the early evolution of the group. Despite distinct apomorphies in its dermal skeleton (such as micromeric squamation), the endoskeleton of *Cheirolepis* appears to largely reflect the primitive osteichthyan condition. Cladistic analyses of early actinopterygian relationships have tended to rely almost exclusively on dermal characters (Gardiner & Schaeffer, 1989; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006), reflecting Gardiner & Schaeffer's (1989) view that neurocrania were too anatomically conserved to be of use in determining early actinopterygian relationships. Consequently, placement of taxa known largely or exclusively from endoskeletal remains impossible (e.g. *Lawrenciella*, Hamel & Poplin, 2008; *Kansasiella,* Poplin, 1974*).* Further problems arise from the variable nature of the dermal skeleton. Many dermal characters reflect the overall nature of the dermal skeleton as either an armour of regularly patterned plates (as in placoderms and osteichthyans) or fields of only regionally differentiated denticles or tesserae (as in acanthodians and chondrichthyans). Neurocrania are, by contrast, present in all vertebrates, and their rich complement of characters is thus comparable across almost the entirety of vertebrate diversity. The expansion of the actinopterygian character set to include more endoskeletal characters will help place problematic taxa and facilitate their routine inclusion into phylogenetic analyses of early actinopterygian relationships, thus increasing the sample set of Devonian and Carboniferous actinopterygians. Since Gardiner & Schaeffer's (1989) denouncement of neurocranial characters, the discovery of additional taxa preserving braincases (e.g. *Lawrenciella*, Hamel & Poplin, 2008; *Gogosardina*, Choo et al., 2009), as well as work revealing new diagnostic characters within these structures (e.g. Coates 1998, 1999; Giles & Friedman, 2014), has made clear their importance for unraveling early actinopterygian relationships. The utility of neurocranial character set has also been established as a tool in resolving systematic issues in other taxonomic groups (e.g. chondrichthyans, Coates & Sequeira, 1998, 2001, Maisey & Anderson, 2001; lungfishes, Friedman, 2007; tetrapodomorph fishes, Coates & Friedman, 2010).

3.7 CONCLUSION

The endoskeleton of the Eifelian *Cheirolepis trailli*, from the Middle Old Red Sandstone of Scotland, is described here on the basis of lab and synchrotron-based computed tomography. The unique combination of primitive osteichthyan and derived actinopterygian characters revealed in the endoskeleton confirm the position of *Cheirolepis* as the sister taxon to all other actinopterygians, and mirrors the atypical actinopterygian morphology seen in the dermal skeleton (Pearson & Westoll, 1979). The presence of ascending processes of the parasphenoid in *Howqualepis* and *Tegeolepis* confirms that these appeared fairly early in actinopterygian evolution, and were secondarily lost or reduced in *Mimipiscis*, as concluded by Choo (2011).

The emerging picture of the endoskeleton in early ray-finned fishes is that it looked broadly like that of early sarcopterygians, with an uninvested dorsal aorta, large vestibular fontanelles, and an elongate basioccipital region. This is far removed from the endoskeletal anatomy of *Mimipiscis*, which shares more features with stratigraphically younger actinopterygians, as well as having secondarily lost or reduced key features. The endoskeleton of early sarcopterygians perhaps more accurately reflects aspects of the primitive osteichthyan, including those features outlined above. The discovery of further specimens of *Cheirolepis* preserving the braincase, particularly material that is three-dimensionally preserved, may provide a way of further corroborating these observations.

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CHAPTER 4: EXCEPTIONALLY PRESERVED ACTINOPTERYGIAN FROM THE LATE DEVONIAN OF FRANCE

This paper is in review as:

Giles, S., Darras, L., Clément, G., Blieck, A. & Friedman, M. An exceptionally preserved Late Devonian actinopterygian provides a new model for primitive cranial anatomy in ray-finned fishes. *Proceedings of the Royal Society B.*

All authors participated in scanning the material. SG generated the CT renderings, made the figures and prepared the supplementary information. SG wrote the text with comments from MF.

Supplementary Information accompanying this paper can be found in Appendix 3.

4.1 Abstract: Actinopterygians today are the most diverse osteichthyan (bony vertebrate) group, with a rich fossil record. However, their early evolution during the Devonian 'Age of Fishes' remains poorly resolved. This stems from an uneven understanding of anatomy in early ray-finned fishes, with a few well-known species dominating perceptions of primitive conditions in this major vertebrate radiation. Here we present an exceptionally preserved actinopterygian from the Late Devonian (Famennian: lower *triangularis* conodont zone, ca. 372 Myr) of Northern France. This new taxon is represented by a single, three-dimensionally preserved cranium. CT scanning reveals the presence of a near-complete dermal cranium and braincase along with fully articulated mandibular, hyoid and gill arches.

The braincase in particular differs from the primary contemporaneous model *Mimipiscis* in displaying a short aortic canal with a distinct posterior notch, long grooves for the lateral dorsal aortae, large vestibular fontanelles and a robust postorbital process. Identification of similar features in other Devonian actinopterygians suggests that conspicuous aspects of braincase anatomy in *Mimipiscis* are apomorphic, calling into question the ubiquity of *Mimipiscis* as representative of Devonian actinopterygian braincase anatomy. As well as presenting a new articulated model of actinopteryian anatomy, this taxon provides a framework for a revised phylogenetic analysis of the first ray-finned fish radiation.

4.2 INTRODUCTION

Actinopterygians, together with their sister group the sarcopterygians, comprise Osteichythes (bony fishes and tetrapods) and represent more than 99% of living vertebrate species richness. Over 50% of this diversity - some 32,000 species - is contained within the actinopterygians. Despite this modern dominance, details of early actinopterygian history remain obscure. Fewer than 20 species are described from the ca. 55 myr of the Devonian (in comparison to over 100 sarcopterygians), and no definitive examples are known from the Silurian despite their predicted occurrence. Detailed understanding of the structure of early actinopterygians, particularly that of the character-rich endoskeleton and braincase, has progressed little since the exhaustive description of *Mimipiscis* three decades ago (Gardiner, 1984; Choo, 2011). This is despite major new insights on the relationships and evolution of gnathostomes and sarcopterygians (e.g. Cloutier & Ahlberg, 1996; Zhu et al., 1999; Maisey, 2001; Daeschler et al., 2006; Brazeau, 2009; Zhu et al., 2009; Davis et al., 2012; Zhu et al., 2013; Pradel et al., 2014; Giles et al., 2015). *Mimipiscis* remains the only Devonian actinopterygian for which internal structure exhaustively described and illustrated, and as such is almost exclusively used as an exemplar of early actinopterygian anatomy (e.g. Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Gardiner et al., 2005; Friedman

& Blom, 2006; Long et al., 2008; Choo et al., 2009; Friedman, 2015). Although the account provided by Gardiner (1984) provides a wealth of morphological information, acid preparation of the material led to disarticulation of the specimens and a loss of important spatial information relating to complex structures like the gill skeleton.

Here we present an exceptionally preserved ray-finned fish skull from the Late Devonian (Famennian, 372 Ma; Derycke et al., 1995) Ferques Formation of Northern France. Known from a single articulated specimen, this material comprises a near-complete dermal cranium, braincase and mandibular, and hyoid and gill arches. With the exception of the heavily compressed *Cheirolepis* (Giles et al., in review), this taxon represents the first braincase of a Devonian actinopterygian outside of Australia. The use of CT scanning to investigate the specimen permits a clear idea of the three-dimensional geometry and articulation of the skull and branchial arches.

4.3 MATERIAL AND METHODS

(a) CT scanning.

HGL 1245 was scanned at the AST-RX platform of the Muséum National d'Histoire Naturelle, Paris, France using an UMS 2700. Scan parameters were as follows: 80 kV; 500 μA; 18.69 μm voxel size. Scan data were analysed and manually reconstructed in Mimics version 15.01 (biomedical.materialise.com/mimics; Materialise, Leuven, Belgium). Meshes were exported as .ply surface files to Blender (blender.org) for image and video acquisition (Garwood & Dunlop, 2014). Figures were generated by hand and in Adobe Illustrator.

4.4 SYSTEMATIC PALEONTOLOGY

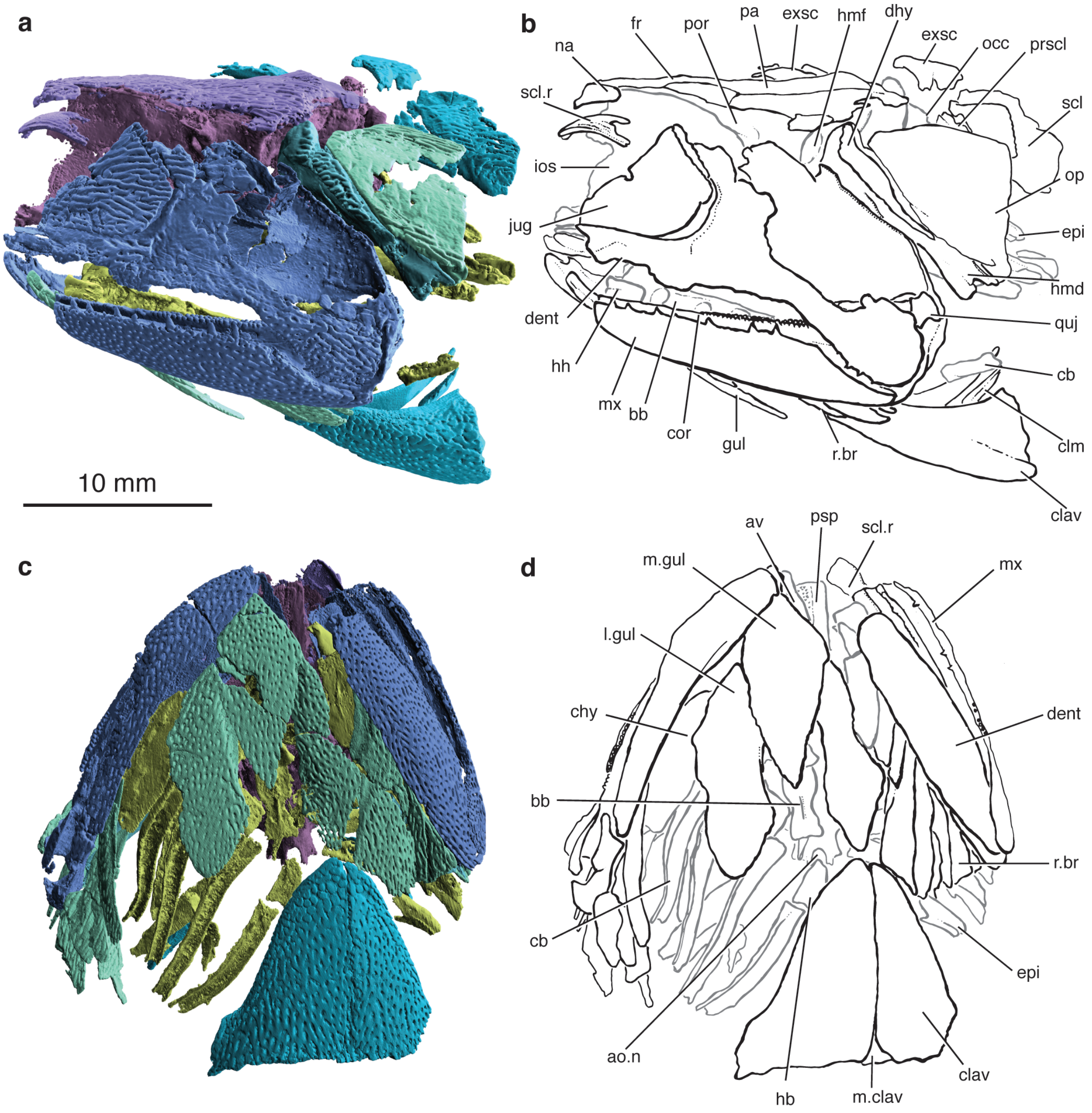
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Figure 1 | *Raynerius splendens* n. gen. et sp. from the Frasnian of France based on computed tomography renderings. Rendering (**a**) and interpretive drawing (**b**) of specimen in left lateral view. Rendering (**c**) and interpretive drawing (**d**) of specimen in ventral view; skeletal elements interior to the dermal bones (i.e. the braincase and gill skeleton) are partially masked for clarity. Abbreviations: a.on, aortic notch; av, accessory vomer; bb, basibranchial; cb, ceratobranchial; chy, ceratohyal; clav, clavicle; clm, cleithrum; cor, coronoid; dent, dentary; dhy, dermohyal; epi, epibranchial; exsc, extrascapular; fr, frontal; gul, gular; hb, hypobranchial; hh, hypohyal; hmd, hyomandibula; hmf, hyomandibular facet; ios, interorbital septum; jug, jugal; l.gul, lateral gular; m.clav, median clavicle; m.gul, median gular; mx, maxilla; na, nasal; op, operculum; pa, parietal; por, postorbital process; prscl, presupracleithrum; psp, parasphenoid; quj, quadratojugal; r.br, branchiostegal ray; scl, supracleithrum; scl.r, sclerotic ring. Colour coding of the skeleton: blue, cheek and jaw; purple, skull roof and sclerotic ossicle; pink, braincase; dark green, hyomandibula; light green, operculogular system; turquoise, shoulder girdle; yellow, gill skeleton.

Osteichthyes Huxley, 1880

Actinopterygii Cope, 1887

Raynerius splendens n. gen. et sp.

4.4.1 Etymology. Generic name after Dorothy Rayner for her contributions to palaeoichthyology. Specific name reflects the exceptional preservation and articulated nature of the specimen

4.4.2 Material. HGL 1245, representing a nearly complete cranium.

4.4.3 Locality and horizon. HGL 1245 was collected from the Ferques Formation, La Parisienne Quarry (*triangularis* conodont zone [372 Ma], Famennian, Upper Devonian) in Bas-Boulonnais, Pas-de-Calais, France.

4.4.4 Diagnosis. A small actinopterygian characterised by 'herringbone' ornamentation on skull roof; porous ornamentation on lower jaw, gulars and clavicles; dermosphenotic lacking anterior ramus; median gular equal in length to lateral gulars; distinct jugal notch.

4.5 DESCRIPTION

4.5.1 Skull

The skull roof comprises paired frontals, parietals, intertemporals and supratemporals, and resembles *Moythomasia* (Gardiner, 1984) in being ornamented with long, vermicular ridges of ganoin (Figs 1a, 2a). The pineal foramen is open. As in *Cheirolepis*, *Osorioichthys*, *Tegeolepis* and *Moythomasia*, the parietals are prevented from reaching the lateral margin of the skull by the posterior flange of the supratemporal. There are two series of extrascapulars, which rest on the posterior margin of the parietals (Figs 2a-b). The dermosphenotic of *Raynerius* possesses an elongate posterior limb, as is typical for early actinopterygians, but is unusual in lacking an anterior limb (Fig. 2d). The jugal is deep and crescent shaped, with a blunt dorsal edge (Figs 1a-b). As in primitive actinopterygians such as *Cheirolepis*, the orbital margin of the jugal is notched. The quadratojugal is present as a separate ossification.

The maxilla broadly resembles that of other early actinopterygians. The palatoquadrate, which sits on a pronounced shelf on the medial surface of the maxilla, has an almost rectangular postorbital plate and a short and relatively deep suborbital limb (Fig. 2c). The anterior part of the postorbital plate is pierced by a large basipterygoid fenestra. Over three quarters of the palatoquadrate (including the suborbital limb) is covered by a dentigerous dermal bone, in which separate ossifications cannot be identified. As in *Mimipiscis*, the dorsal margin of the dermopalatines appears to be straight. A denticulated, blade shaped bone, most likely an accessory vomer, is preserved dorsal to the suborbital limb of the parasphenoid. The dentary is long and stout, and does not taper significantly rostrally, unlike the dentary of *Mimipiscis* and *Gogosardina* (Gardiner, 1984; Choo et al., 2009; Choo, 2011). The mandibular canal traces the ventral margin of the jaw along its entire length, and reaches the anterior margin of the mandible. The ornament on the dentary is smooth and punctuated by regular large pores, similar to that of *Moythomasia* (Fig. 1a). Acrodin caps are present on the largest teeth. No surangular is present.

The clavicles are large, with a gently convex ventral plate and slender dorsal blade (Fig. 1). The ornament on the dorsal blade is unusual in being tuberculate, and in some places almost leaf shaped. Elsewhere on the clavicles the ornament is of the porous type seen on the lower

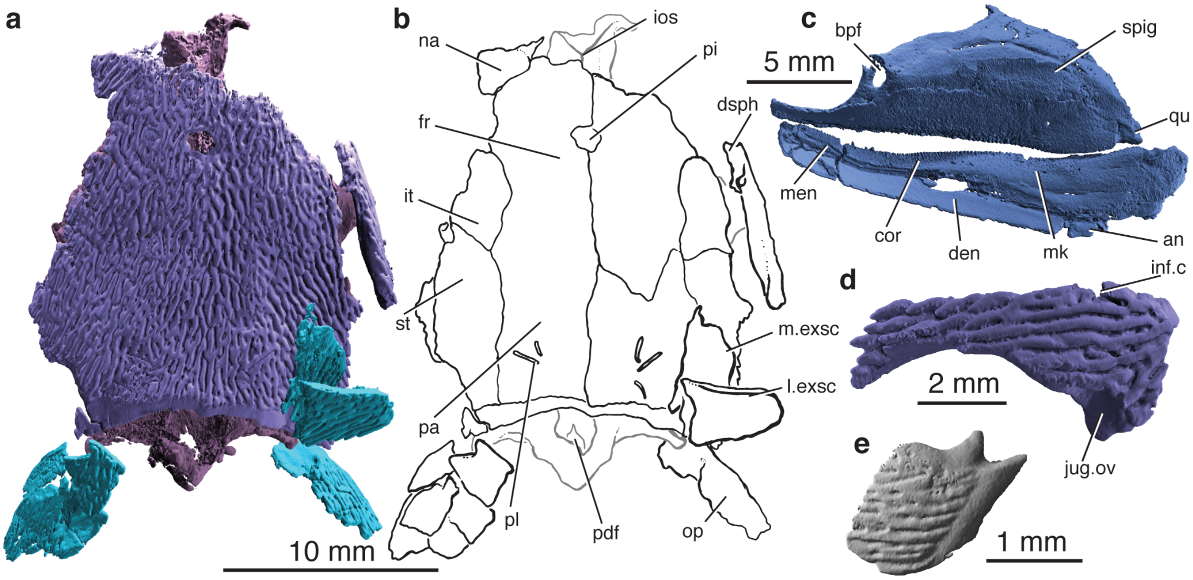

Figure 2 | *Raynerius splendens* n. gen. et sp. Rendering (**a**) and interpretive drawing (**b**) of skull roof. Right palatoquadrate and lower jaw in medial view (**c**), showing basipterygoid fenestra and ossified mentomeckelian cartilage. (**d**) Right dermosphenotic in lateral view, showing well-developed posterior limb and lack of anterior limb. (**e**) Scale in external view, showing ganoin ridges, anterodorsal process and dorsal peg. Abbreviations: an, angular; bpf, basipterygoid fenestra; cor, coronoid; den, dentary; dsph, dermosphenotic; fr, frontal; ios, interorbital septum; it, intertemporal; inf.c, infraorbital canal; jug.ov, overlape with jugal; l.exsc, lateral extrascapular; m.exsc, median extrascapular; men, mentomeckelian ossification; mk, Meckel's cartilage; na, nasal; op, operculum; pa, parietal; pdf, posterior dorsal fontanelle; ppi, pineal foramen; pl, pit line; qu, quadrate; spig, spiracular groove; st, supratemporal. For a key to colours see Fig. 1.

jaw of *Raynerius*. Only a small portion of the interclavicle is visible, and it resembles that of *Moythomasia durgaringa* (Gardiner, 1984) in shape and ornament.

4.5.2 Scales

The scales of *Raynerius* possess a well developed peg, socket and anterodorsal process (Fig. 2e). They are typically ornamented with anterodorsally oriented ganoin ridges that do not anastomose. Lateral line scales bear a distinct pore (Suppl. Fig 1).

4.5.3 Braincase and endocast

The braincase of *Raynerius* broadly resembles that of other early actinopterygians, but differs from that of *Mimipiscis* in a number of key ways. The aortic canal is very short, bifurcating at the level of the vagus nerve, and its posterior margin is notched (Fig. 3c). While this remembles the as yet undescribed braincases of *Moythomasia durgaringa* (Gardiner, 1984; Long & Trinajstic, 2010: fig. 5b) and *Gogosardina* (Choo et al., 2009: fig. 9a), it contrasts sharply with the extensive aortic canal of *Mimipiscis* (Gardiner, 1984: fig 50). The grooves for the lateral dorsal aortae in *Raynerius* are elongate, and a shallow laterally directed groove marks the path of an epibranchial artery. Consequently, the otic and occipital regions account for a larger proportion of the braincase than in *Mimipiscis*. The otico-ocipital fissure is open along its length, and terminates ventrally in a large vestibular fontanelle and dorsally in a small, ovoid posterior dorsal fontanelle (Figs 2a, 3a). The dorsolateral process of the occiput is formed by a robust craniospinal process.

The postorbital process is broad, but far less laterally produced than the corresponding process in *Mimipiscis*, a feature particularly apparent in anterior view (Fig. 3a,c,d). The

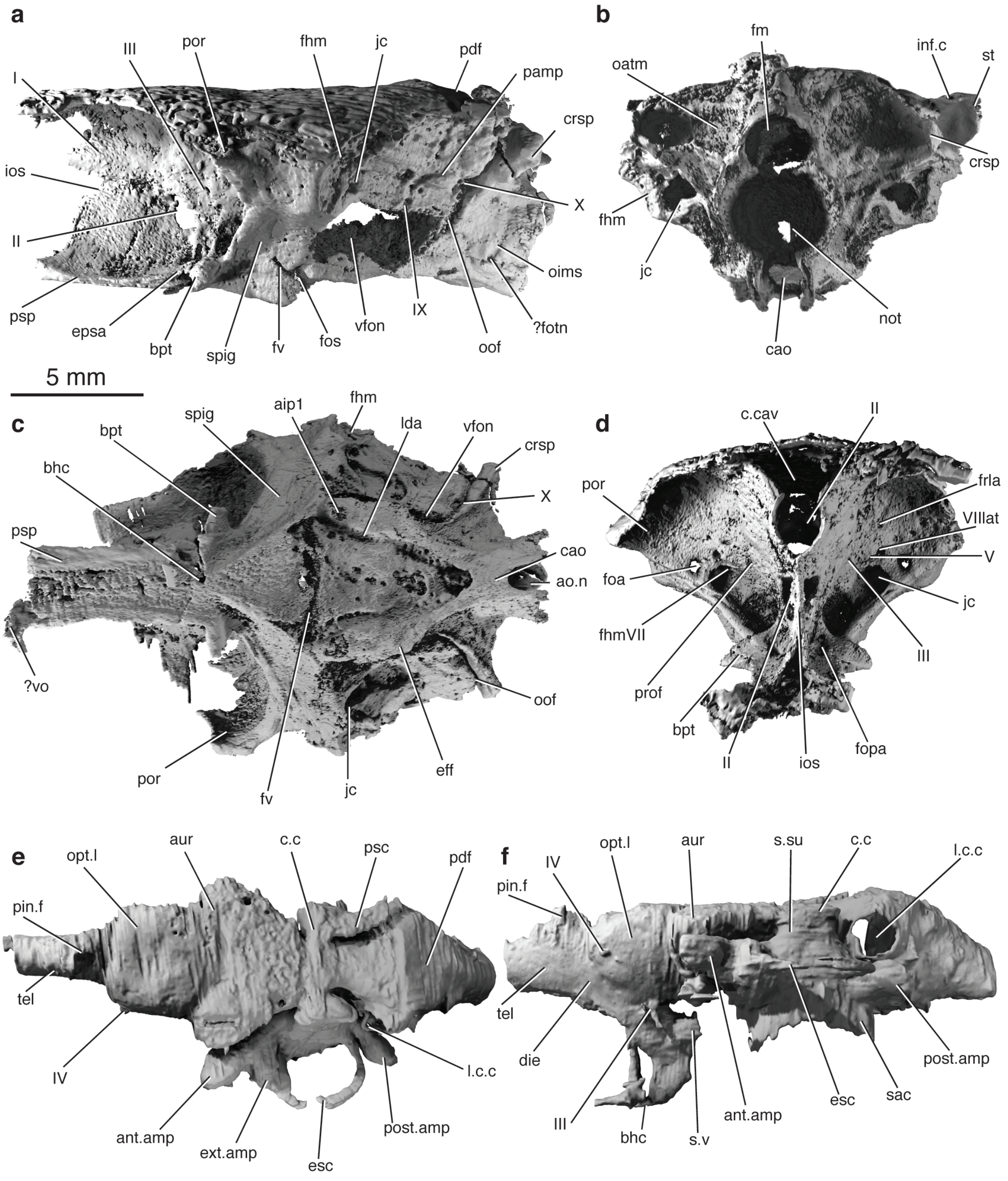
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Figure 3 | Braincase and endocast of *Raynerius splendens* n. gen. et sp. Braincase in left lateral (**a**), posterior (**b**), ventral (**c**) and anterior (**d**) view. Partial endocast in dorsal (**e**) and lateral (**f**) view; some details of labyrinth and saccular chamber unresolvable due to poor mineralization. Abbreviations: aip1, articulation of the first infrapharyngobranchial; ant.amp; ampulla of the anterior semicircular canal; ao.n, aortic notch; aur, cerebellar auricle; bhc, buccohypophysial canal; bpt, basipterygoid process; cao, canal for the dorsal aorta; c.cav, cranial cavity; c.c, crus commune; crsp, craniospinal process; die, diencephalon; eff, efferent arteries; epsa, efferent pseudobranchial; esc, external semicircular canal; ext.amp, ampulla of the external semicircular canal; fhm, hyomandibular facet; fhmVII, hyomandibular branch of the facial nerve; fm, foramen magnum; foa, foramen for orbital artery; fopa, ophthalmic artery; fos, otico-sphenoid fossa; ?fotn, foramen for otic nerve; frla, ramus lateralis accessiorus; fv; vental fissure; inf.c, infraorbital canal; ios, interorbital septum; jc, jugular canal; l.c.c, lateral cranial canal; lda, lateral dorsal aorta; not, notochordal tunnel; oatm, origin of anterior trunk muscles; oims, origin of intermuscular septum; oof, oticoccipital fissure; opt. l, optic lobe; pal, palatine nerve; pamp, parampullary process; pdf, posterior dorsal fontanelle; pin, f, pineal foramen; por, postorbital process; post.amp, ampulla of the posterior semicircular canal; prof, profundus nerve; psc, posterior semicircular canal; psp, parasphenoid; sac, sacculus; spig, spiracular groove; s.su, sinus superior; st, supratemporal; s.v, saccus vasculosus; tel, telencephalon; v.fon, vestibular fontanelle; ?vo. vomer; I, olfactory nerve; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; VIIlat, lateralis trunk of facial nerve; fhmVII; IX, glossopharyngeal nerve; X, vagus nerve.

hyomandibular facet sits lateral to and above the jugular groove on the posterior face of the postorbital process. The spiracular groove is wide, with no hint of the enclosing canal seen in *Moythomasia* (Gardiner, 1984; M. Coates pers. comm.) and stratigraphically younger actinopterygians (e.g. *Kansasiella*; Poplin, 1974). A break in the lateral commissure suggests the presence of an otico-sphenoid fossa (Fig. 3a), previously identified only in the Gogo actinopterygians. The orbits are separated by a narrow interobital septum, the two halves of which are joined at the midline (Fig. 3d). The optic nerves enter the orbit through a single confluent opening. The parasphenoid is long and fairly narrow, and is denticulated along most of its length (Fig. 3c). The anterior margin is incompletely preserved, but does not appear to be tripartite. *Raynerius* resembles *Cheirolepis* (Pearson & Westoll, 1979; Giles et al., in review) and *Mimipiscis* (Gardiner, 1984; Choo, 2011) in lacking ascending processes.

As the internal face of the braincase is poorly mineralised in places, particularly in the region of the inner ear, only a partial endocast can be described. The olfactory tracts and bulbs are not preserved. The hypophysial chamber projects posteriorly, and is continuous ventrally with the buccohypophyseal canal (Fig. 3f). Although narrower than the cerebellum, the optic lobes are somewhat wider than in *Mimipiscis* (Fig. 3e), but do not approach the proportions seen in Carboniferous and statigraphically younger actinopterygians (Giles & Friedman, 2014). The cerebellar auricles are pronounced, although it is unclear whether a corpus was developed. The semicircular canals are only partially preserved, but the crus commune of the anterior and posterior canals clearly extends dorsal to the endocranial roof (Fig. 3f), a condition seen elsewhere in *Mimipiscis* and actinopterygian outgroups (Giles & Friedman, 2014). The lateral cranial canal is large, and projects through the loop of the posterior semicircular canal. As in *Mimipiscis*, the ampulla of this canal is not confluent with the cranial cavity.

4.5.4 Hyoid and branchial skeleton

A near-complete and articulated hyoid and branchial skeleton is preserved. The hyomandibular is slender, and pierced by a single canal for the hyomandibular nerve (Figs. 1a, 4). The ceratohyal is ossified as one bone. It is flat and shallow, and bears a groove for the afferent hyoid artery on its lateral face (Fig. 4). The distal end of the hypohyal, which would have articulated with the ceratohyal, is inflated to approximately twice the size of the proximal end. As in *Mimipiscis* (Gardiner, 1984), the basibranchial is a single midline ossification, with clear articular areas for the hypobranchials (Fig. 4b-c). Unlike in *Mimipiscis*, the first hypobranchial does not appear to have shared an articular facet with the hypohyal, instead being housed in a long, slender facet on the lateral face of the basibranchial. Five ceratobranchials are present. Ceratobranchials 1–4 are long and slender, and are grooved along their ventral surface; ceratobranchial 5 is also grooved, but is much shorter and narower (Fig. 4b-c). The first four ceratobranchials articulate ventrally with hypobranchials and dorsally with epibranchials. The epibranchials are typically shorter than the ceratobranchials, and bear a dorsal groove (Fig. 4e). The first two branchial arches include an anteriorly directed infrapharyngobranchial and anterodorsally directed suprapharyngobranchial, which articulate ventrally with facets on the epibranchials (Fig. 4d-e). Narrow, elongate toothplates, each bearing a large number of minute denticles, are present on the ceratobranchials and epibranchials.

4.6 DISCUSSION

The exceptional preservation of *Raynerius splendens* gen. et. sp. nov. contributes vital new data pertaining to the early evolution of actinopterygians. Comparison with *Mimipiscis*, the only other Devonian taxon known from an exhaustively described endocranium, highlights

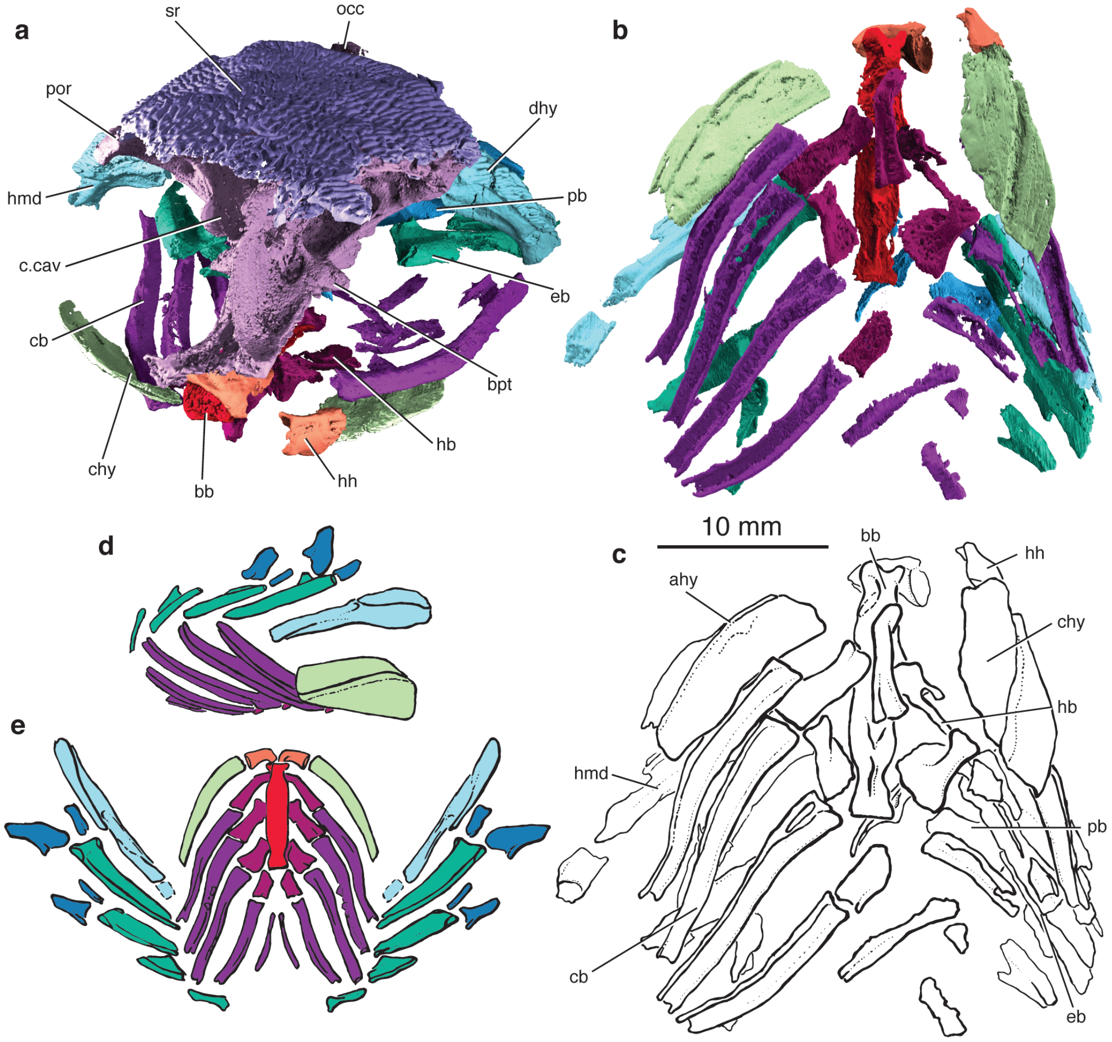

Figure 4 | Branchial and hyoid skeleton of *Raynerius splendens* n. gen. et sp. (**a**) Braincase and skull roof in anterolateral view showing articulation of gill skeleton. Rendering (**b**) and interpretive drawing (**c**) of branchial and hyoid skeleton in ventral view. Reconstruction of the branchial and hyoid skeleton in right lateral (**d**) and dorsal (**e**) view. N.B. hyomandibula moved out of life position in lateral reconstruction so as not to obscure the branchial arches. Abbreviations: bb, basibranchial; bpt, basipterygoid process; c.cav, cranial cavity; cb, ceratobranchial; chy, ceratohyal; dhy, dermohyal; eb, epibranchial; hb, hypobranchial; hh, hypohyal; hmd, hyomandibula; occ, occiput; pb, pharyngobranchial; por, postorbital process; sr, skull roof. For a key to colours see Fig. 1.

several key areas of incongruent anatomy. The elongate, narrow aortic canal of *Mimipisis* (Gardiner, 1984: fig. 50) appears apomophic, with the short, wide canal of *Raynerius*, also present (although not yet described) in *Moythomasia durgarina* (Long & Trinajstic, 2010: fig. 5b) and *Gogosardina* (Choo et al., 2009: fig. 9a) seeming to reflect the primitive aortic condition in actinopterygians. The dorsal aorta is uninvested in the most primitive actinopterygians (*Cheirolepis* and *Howqualepis*; Giles et al., in review) and sarcopterygians (e.g. *Eusthenopteron*, Jarvik, 1980; *Youngolepis*, Chang, 1982). Similarly, the short lateral dorsal aortae, small vestibular fontanelles and narrow lateral commissure of *Mimipiscis* (Gardiner, 1984) also appear to be apomorphic. The orbital region in *Mimipiscis* is very long, occupying at least half of the total neurocranial length. Furthermore, the postorbital process extends laterally and somewhat anteriorly to partially enclose the back of the orbit, a feature not seen in *Raynerius* or other early actinopterygians. These findings throw into question the ubiquity of *Mimipiscis* in analyses as the primary representative of Devonian actinopterygian anatomy (Gardiner & Schaeffer, 1989; Coates, 1999; Gardiner et al., 2005; Friedman & Blom, 2006; Long et al., 2008; Choo, 2009; Friedman, 2015). Details of the branchial skeleton seen in *Raynerius* corroborates the model of jawed vertebrate gill skeleton morphology laid out by Pradel et al. (2014). The branchial arches are arranged as a chevron, and, as in other early actinopterygians and *Ozarcus*, paired hypohyals connect to the ceratohyals, two anteriorly directed pharyngobranchials are present in at least the first two arches, and at least four of the arches articulate ventrally with the basibranchial.

A phylogenetic analysis of 50 taxa and 182 characters was used to resolve the position of *Raynerius*. The matrix is based on that of Choo (2011), but with an expanded character and taxon set. As the tree is rooted on a placoderm and chondrichthyan outgroup, the relationships within Actinopterygii can be interpreted in the context of the osteichthyan total group. *Raynerius* is resolved in a clade with *Moythomasia durgaringa* and *M. nitida*.

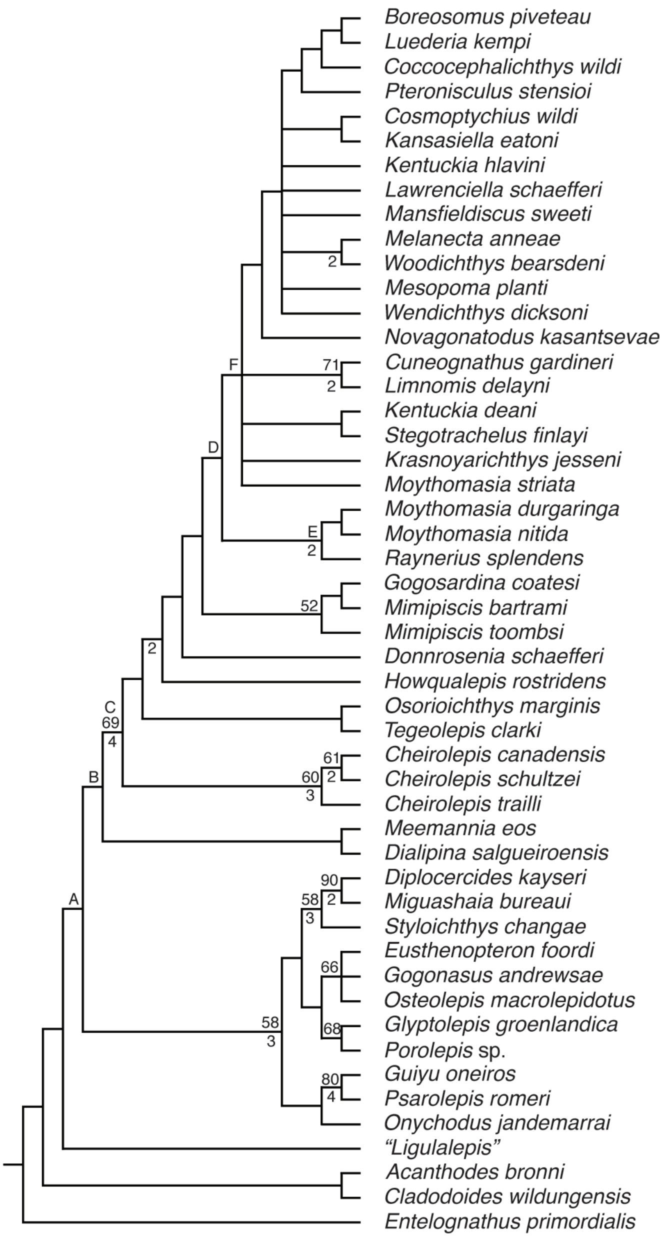
Boreosomus piveteau
Luederia kempi
Coccocephalichthys wildi
Pteronisculus stensioi
Cosmoptychius wildi
Kansasiella eatoni
Kentuckia hlavini
Lawrenciella schaefferi
Mansfieldiscus sweeti
Melanecta anneae
2
Woodichthys bearsdeni
Mesopoma planti
Wendichthys dicksoni
Novagonatodus kasantsevae
F
71
Cuneognathus gardineri
2
Limnomis delayni
Kentuckia deani
Stegotrachelus finlayi
D
Krasnoyarichthys jesseni
Moythomasia striata
Moythomasia durgaringa
E
Moythomasia nitida
2
Raynerius splendens
Gogosardina coatesi
52
Mimipiscis bartrami
Mimipiscis toombsi
2
Donnrosenia schaefferi
Howqualepis rostridens
C
Osorioichthys marginis
69
4
Tegeolepis clarki
61
Cheirolepis canadensis
B
60
2
Cheirolepis schultzei
3
Cheirolepis trailli
Meemannia eos
Dialipina salgueiroensis
90
Diplocercides kayseri
A
58
2
Miguashaia bureaui
3
Styloichthys changae
Eusthenopteron foordi
66
Gogonasus andrewsae
Osteolepis macrolepidotus
58
68
Glyptolepis groenlandica
3
Porolepis sp.
80
Guiyu oneiros
4
Psarolepis romeri
Onychodus jandemarrai
“Ligulalepis”
Acanthodes bronni
Cladodoides wildungensis
Entelognathus primordialis

Figure 5 | Phylogenetic placement of *Raynerius splendens* n. gen. et sp. Strict consensus of 336 most parsimonious trees. Numbers above nodes represent bootstrap support; numbers below indicate Bremer support values. Apomorphic features at selected nodes are as follows (numbers refer to character list; see Supplementary Materials): **A**, c.90 eyestalk absent; c.126 elongate olfactory tracts. **B**, c.31 extrascapular does not reach lateral edge of skull roof; pelvic fin has long-based insertion. **C**, c.25 dermosphenotic with posterior ramus; c.55 median gular present; c.58 expanded dorsal lamina of maxilla; c.77 two infradentaries; c.150, enamel layers applied directly to one another; c.159 fringing fulcra; c.181 one dorsal fin**.** **D**, c.52 anterodorsal process of suboperculum absent; c. 91 VII pierces roof of ventral myodome; c.92 VI dorsally positioned; c.94 pituitary vein canal enlarged; c.157 anastomosing linear ornament absent; c.171 pectoral fin ray segmentation roughly even to base. **E**, c.30 two pairs of extrascapulars; c.72 remodeled porous ganoin on lower jaw; c.155 scales with pores. **F**, c.18 frontal longer than parietal; c.88 expanded anterior dorsal fontanelle; c.93 anterodorsal myodome single; c.104 fossa bridgei; c.113 dorsal aorta pieced by canal(s) for second afferent branchial artery; c.127 olfactory nerve in single tract; c.129 optic lobes same width as cerebellum; c.134 crus commune ventral to endocranial roof; c.141 opercular process; c.182 anal fin posterior to dorsal fin.

Resolution of the tree above this node is poor, with many Carboniferous (and some Devonian) taxa being resolved in a polytomy. Both *Moythomasia* and *Kentuckia* are resolved as polyphyletic, supporting the view that these genera require revision. *Ligulalepis* is resolved as a stem osteichthyan on the basis of two unambiguous characters, namely short olfactory tracts and absence of a parasphenoid, a placement commonly resolved in other analyses (e.g. Friedman, 2007; Brazeau, 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Dupret et al., 2014; Giles et al., 2015). Surprisingly, *Dialipina* and *Meemannia* are resolved as stem actinopterygians, a placement supported by skull roof and paired fin characters; although *Dialipina* was originally recovered as a stem actinopterygian (Schultze & Cumbaa, 2001; Zhu et al., 2006; Zhu et al., 2009; Schultze, in press), more recent analyses have favoured a stem osteichthyan position (Friedman, 2007; Brazeau, 2009; Friedman & Brazeau, 2010; Davis et al., 2010; Zhu et al., 2013; Dupret et al., 2014; Giles et al., 2015) for this taxon. *Meemannia* has variably been resolved as a stem sarcopterygian (Zhu et al., 2006; Friedman, 2007, Zhu et al., 2010), or, more recently, as a stem osteichthyan (Zhu et al., 2013; Dupret et al., 2014). Bootstrap support values, outside of the sarcopterygian clade, are generally low.

Within the actinopterygian clade, almost all synapomorphies with a consistency index of 1 relate to characters of the braincase or endocast; this is particularly apparent among Carboniferous and Permian taxa. The emerging picture of complex endocranial anatomy in early actinopterygians indicates that the braincase is of great use in teasing out interrelationships, in contrast to previous views that braincases were too conservative in nature (Gardiner & Schaeffer, 1989). Future descriptions of the braincase and endocast anatomy of *Gogosardina* (Choo et al., 2009) and *Moythomasia durgaringa* (Gardiner, 1984), as well as understudied Carboniferous actinopterygians, will help to further clarify relationships amongst the Palaeozoic antecedents of the most diverse modern vertebrate group.

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CHAPTER 5: VIRTUAL RECONSTRUCTION OF ENDOCAST ANATOMY IN EARLY RAY-FINNED FISHES (OSTEICHTHYES, ACTINOPTERYGII)

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SG and MF scanned the material. SG generated the CT renderings, generated the figures and prepared the supplementary information. SG wrote the text with input from MF.

Supplementary Information accompanying this paper can be found in Appendix 4.

5.1 Abstract: Cranial endocasts, infillings of the skeletal void that once contained the brain and associated soft tissues, represent detailed anatomical structures that have long been the focus of palaeontological investigation. We applied CT in order to generate endocast models for the Palaeozoic actinopterygian fishes *Mimipiscis* and *Kentuckia*, which serve as key representatives of anatomically primitive, early ray-finned fishes in analyses of early vertebrate relationships. The resultant endocranial models generally corroborate existing accounts of endocranial anatomy in these genera, drawn from descriptions of the inner face of the brain cavity. However, the endocasts also provide new anatomical details, the most significant of which are the presence in *Mimipiscis* of widely divergent olfactory tracts, small optic lobes, and anterior

and posterior semicircular canals that extend dorsal to the roof of the endocranial chamber. By contrast, *Kentuckia* possesses a single, straight olfactory tract, wide optic lobes, and anterior and posterior semicircular canals that do not reach the dorsal surface of the endocast. In each of these features, *Kentuckia* resembles stratigraphically younger actinopterygians such as *Lawrenciella* and *Kansasiella*, whereas *Mimipiscis* more closely resembles sarcopterygians and other outgroups. This character distribution provides further support for earlier phylogenetic interpretations of these genera.

5.2 INTRODUCTION

The occurrence of so-called 'fossil brains' has fascinated vertebrate palaeontologists since the earliest reports of such structures in the 1800s (e.g. Owen, 1841; Marsh, 1874; Owen, 1875; Moodie, 1915). When found, preserved brain and other nervous tissues are rich sources of morphological information, but such remains are exceedingly rare in the fossil record and sometimes difficult to interpret (Trinajstic et al., 2007; Pradel et al., 2009; Pradel, 2010). More typically, the sediment-filled void within the neurocranium provides the only clues about gross brain architecture. Such endocasts have been described for a diversity of groups (see discussion in Jerison, 1973; Coates, 1999; and Walsh and Knoll, 2011), with Palaeozoic fishes receiving considerable attention due to the early application of tomographic techniques by Erik Stensiö and other members of the 'Stockholm school' to a range of early vertebrate fossils (Stensiö, 1927; Stensiö, 1963a, 1963b; Jarvik, 1980).

Two key limitations apply to the study of neuroanatomy through the use of endocasts. The first of these arises from the mismatch between the endocast and brain in many groups of vertebrates. The brains of modern chondrichthyans and lobe-finned fishes can occupy as little as 1% of their associated cavities (Millot and Anthony, 1965; Kruska, 1988; Pradel, 2010), suggesting this disagreement might be primitive for jawed vertebrates. Important exceptions to this generality include birds, mammals, and, apparently, early ray-finned fishes (Edinger, 1929; Jerison, 1973). The high fidelity of brain anatomy captured by fossil actinopterygian endocasts is thought to reflect the presence of only a single layer of meningeal tissue separating the brain from the surrounding bone (Bjerring, 1991; Coates, 1999). This arrangement, combined with a relative abundance of well-preserved braincases (e.g. Nielsen, 1942; Rayner, 1951; Poplin, 1974; Schaeffer and Dalquest, 1978; Gardiner, 1984; Coates, 1998; Hamel, 2005), makes temporally early fossil ray-finned fishes ideal targets for neuroanatomical study.

The second limitation associated with the study of vertebrate endocasts reflects the logistical difficulty in obtaining them. In the case of early ray-finned fishes, previous studies have often relied on the chance finding of ideally positioned or preserved specimens (e.g. Eastman, 1908; Moodie, 1915; Rayner, 1951; Coates, 1999) . Although this permits description without recourse to more invasive procedures, such circumstances often allow only a cursory description of one face of the endocast or internal wall of the endocranial cavity (e.g. Eastman, 1908). More detailed approaches available to past researchers required a fossil to be serially destroyed and studied either through Sollas' grinding method (Sollas, 1904) or Poplin's more recent microtome technique (Poplin and de Ricqlès, 1970). In addition to being time-consuming, the destructive nature of these methods means that the specimen cannot be revisited, and the author's anatomical interpretations can only be corroborated through examination of original sections or associated photographs. Furthermore, such records are fragile and are prone to damage, as are the large wax models that are based upon them.

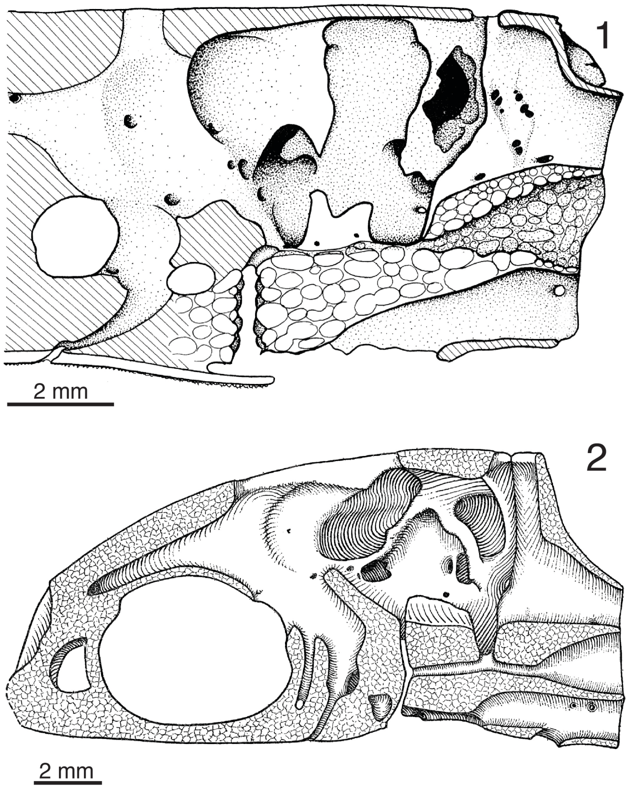

Figure 1 | Existing illustrations of the cranial cavity of *Mimipiscis toombsi* Gardiner and Bartram, 1977 and *Kentuckia deani* Eastman, 1908. 1, sagittal section through post-ethmoid region of neurocranium of *Mimipiscis toombsi*; from Gardiner (1984: fig. 26); **2**, Sagittal section through neurocranium of *Kentuckia deani*; modified from Rayner (1951: fig. 9).

Virtual palaeontology, through the use of computed tomographic (CT) techniques, provides a solution to the problems associated with mechanical tomographic techniques. Non-destructive CT methods generate datasets and resulting models that are long-lasting and portable (provided the files are stored in a way that can be accessible in the long term; Sutton et al., 2012). The results of such techniques are repeatable in the sense that the data can be revisited and the resultant hypotheses retested, and models can be digitally manipulated, sectioned and redescribed, with the ability to return to the original material as required. Furthermore, CT methods can be used to reinvestigate taxa previously studied via destructive or non-invasive methods, and to test existing interpretations in the literature (e.g. Gai et al., 2011). Importantly, specimens that were previously dismissed as too rare or fragile for destructive investigation can now be 'virtually' dissected and studied, all in a process that takes days rather than decades.

Here we apply CT techniques to *Mimipiscis toombsi* Gardiner and Bartram, 1977, and *Kentuckia deani* Eastman, 1908, two Palaeozoic ray-finned fishes that serve as key exemplars in analyses of interrelationships among early actinopterygians (Gardiner, 1984; Gardiner and Schaeffer, 1989; Coates, 1999; Arratia and Cloutier, 2004; Gardiner et al., 2005; Friedman and Blom, 2006; Long et al., 2008; Choo, 2011) and among Palaeozoic gnathostomes more generally (Zhu et al., 1999, 2006; Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Davis et al., 2012). This prominence in phylogenetic analyses stems from the Late Devonian (Frasnian) and Mississippian (Tournaisian-Visean) age of these species, along with the fact that both preserve endoskeletal and dermal components of the skull in great detail.

The endocranial cavities of *Mimipiscis* Choo, 2011 and *Kentuckia* Rayner, 1951 have previously been described in the literature, and mid-sagittal sections through the endocavity

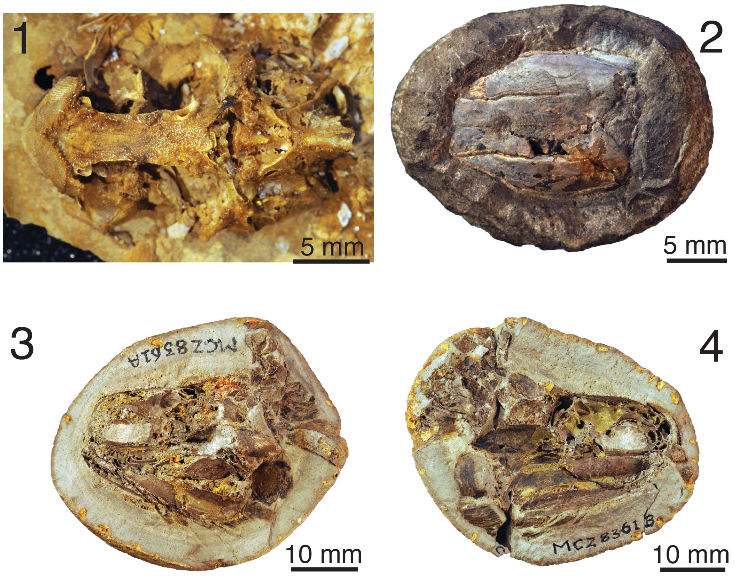

Figure 2 | Photographs of specimens used in this study. 1, *Mimipiscis toombsi* NHMUK PV P.53247; **2**, *Kentuckia deani* MCZ 5226; **3**, *Kentuckia deani* MCZ 8361, part; *3*, *Kentuckia deani* MCZ 8361 counterpart.

have been presented for both (Fig. 1). This contribution provides the first endocast reconstructions for these taxa, which serve as a check on previous structural accounts (Appendix 4A) and the phylogenetic interpretations drawn from them.

5.3 MATERIALS AND METHODS

5.3.1 *Materials and taxonomic background*.

The first specimen examined is the near-complete skull roof and braincase of a large individual of *Mimipiscis* (Natural History Museum, London, UK [NHMUK] PV P.53247). The specimen is from the Gogo Formation, Western Australia, which is dated as late Givetian-early Frasnian on the basis of conodont biostratigraphy (Long and Trinajstic, 2010). The nodule-bearing horizons of the Gogo Formation lie within the *transitans* zone and are therefore of early Frasnian age. Originally described as *Mimia toombsi* (Gardiner and Bartram, 1977), *Mimipiscis* was erected as a replacement for the preoccupied *Mimia* Evans, 1953 by Choo (2011). He also recognized two distinct species of *Mimipiscis*: the type species *M. toombsi*, and the new species *M. bartrami* Choo, 2011. In his review of Gogo actinopterygian material housed at NHMUK, Choo regarded NHMUK PV P.53247 as *M. toombsi*. The specimen measures approximately 25 mm in length from snout to back of occiput and 15 mm at its widest point (Fig. 2.1). The specimen was previously acid prepared to remove surrounding matrix, and its dorsal surface embedded in a thin resin block. Although some sediment remains in the dorsal-most parts, the brain cavity itself is largely free of infillings and is preserved as void space.

Two individuals of *Kentuckia deani* were examined, both of which are deposited at Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ). These specimens derive from the New Providence Shale Member of the Stockdale Formation of Kentucky, USA, which is referred to as the Waverley Shales in older accounts. This unit has been dated to the latest Tournaisian or early Visean on the basis of ammonoids and conodonts (Work and Mason, 2003). First named as *Rhadinichthys deani* Eastman, 1908, actinopterygians from the New Providence Shale Member were subsequently transferred to the new genus *Kentuckia* by Rayner (1951). She referred all but one of the specimens to *K. deani*, with one larger individual (MCZ 5257) identified as *Kentuckia* sp. A further species, *K. hlavini* Dunkle, 1964, was placed in the genus based on an articulated specimen from the Late Devonian (Famennian) Cleveland Shale Member of the Ohio Shale Formation. Dunkle (1964) himself noted that this attribution was far from certain, and we note that there are conspicuous differences between this older species and specimens from the Stockdale Formation. Following Friedman and Blom (2006), we do not regard *K. hlavini* as belonging to the genus *Kentuckia*, and advise against the use of composite codings for the genus that draws on evidence from both species (e.g., Arratia and Cloutier, 2004).

The first specimen of *Kentuckia* studied here (MCZ 8361) is contained within a broken nodule, splitting the fossil along an oblique mid-sagittal plane (Fig. 2.3-2.4). The fossil represents a large individual, measuring 30 mm from the snout to the back of the skull. As internal parts of the cranium are visible, this specimen was one of two used by Rayner (1951) to describe the cranial cavity of *Kentuckia*. The second specimen (MCZ 5226) is contained within an unbroken nodule, the top of which has been prepared away to reveal the dorsal surface of the skull roof (Fig. 2.2). This individual is smaller than the first. The exposed part of the skull roof (from anterior margin of frontals to posterior margin of dermopterotics) measures 15 mm. A complete braincase and parasphenoid is preserved within the nodule. The two specimens exhibit clear morphological differences (see below), but we retain them within *Kentuckia* pending a much-needed taxonomic review of the genus. Specimen numbers are used when describing to morphological differences between these individuals.

5.3.2 *Tomographic methods*.

All three specimens were scanned at the Imaging and Analysis Centre of NHMUK using a Metris X-Tek HMX ST 225 CT System with a 2000 x 2000 pixel detector panel. The two halves of the nodule comprising MCZ 8361 were secured together with a rubber band during scanning. 3142 projections were made for each specimen. Other scan parameters are as follows: NHMUK PV P.53247: 150 kV, 169 µA, 1 mm thick copper filter, voxel size 27 µm; MCZ 8361: 210 kV, 200 µA, 2 mm thick copper filter, voxel size 26.5 µm; MCZ 5226: 210 kV, 200 µA, 2 mm thick copper filter, voxel size 14.5 µm.

5.3.3 *Data segmentation and rendering*.

Following scanning, the resulting .vol files were manipulated in Avizo 7.1 (VSG Inc., Burlington, Massachusetts, USA). A workflow for the following method is provided in Appendix 4B. The segmentation editor in Avizo was used to generate a new label field. Bone material, distinguishable from the surrounding air by its different x-ray attenuation, visible as grey-values, was selected and added to a new mask. The mask was then locked, and the blow tool used to segment the void space representing the endocast, cranial nerves and canals. As this tool is semi-automated, it removes an element of worker subjectivity. This method can only be used where the tissue of interest is well mineralised and of a sufficiently different contrast than the surrounding matrix. Where this is not the case, as in some parts of MCZ 5226, segmentation must be completed by hand.

Once segmentation was complete, three-dimensional rendering was achieved by generating a surface view. The data object was saved as a .ply file and exported to Blender (blender.org) for image and video acquisition (Garwood and Dunlop, 2014). The right side of the endocast of MCZ 5226 was resolved to a higher degree of completeness, but in order to follow standard practice when imaging endocasts this image has been flipped horizontally so as to resemble the left side of the endocast. Interpretive diagrams were drafted from virtual models. An animation of the endocast of *Mimipiscis* NHMUK PV P.53247 (Appendix 4C) and of *Kentuckia* MCZ 8361 (Appendix 4D) is provided. PLY 3D files of the endocast surfaces are also available (*Mimipiscis* NHMUK PV P.53247: Appendix 4E; *Kentuckia* MCZ 8361: Appendix 4F; *Kentuckia* MCZ 8361: Appendix 4G). Such files can be easily viewed and manipulated in free programs such as Meshlab (meshlab.sourceforge.net; Cignoni et al., 2008).

5.3.4 *Comparative materials*.

The morphology of the endocasts of *Mimipiscis* and *Kentuckia* was compared with descriptive accounts of this structure in other extinct and extant jawed vertebrates (Appendix 4A). Particular emphasis was placed on Palaeozoic actinopterygians (*Kansasiella* Poplin, 1974; *Lawrenciella* Poplin, 1984: Hamel, 2005, Hamel and Poplin, 2008; *Mesopoma* Traquair, 1890: Coates, 1999) and Palaeozoic sarcopterygian fishes (*Diplocercides* Stensiö, 1922: Jarvik, 1954, Stensiö, 1963b, Jarvik, 1980; *Dipnorhynchus* Jaekel, 1927: Thomson and Campbell, 1971, Campbell and Barwick, 1982, 2000; *Ectosteorachis* Cope, 1880: Romer, 1937; *Eusthenopteron* Whiteaves, 1881: Bjerring, 1971, Jarvik, 1980; *Youngolepis* Chang and Yu, 1981: Chang, 1982). Extant actinopterygians used for comparison are *Polypterus* Lacépède, 1803 (Senn, 1976; Nieuwenhuys, 1982); *Acipenser* Linneaus, 1758 (Nieuwenhuys, 1982; Rupp and

Northcutt, 1998; Gómez et al., 2009); *Amia* Linneaus, 1766 (Nieuwenhuys, 1982); and *Lepisosteus* Linneaus, 1758 (Balfour and Parker, 1882).

5.3.5 *Anatomical Abbreviations*.

acv, canal for anterior cerebral vein; ant.amp, ampulla of anterior semicircular canal; asc, anterior semicircular canal; aur, cerebellar auricle; bhc, bucco-hypophysial canal; b.oc.a, canal for branch of occipital artery; c.c, crus commune; ccc, communication between cranial cavity and notochordal canal; c.co, cerebellar corpus; die, diencephalon; esc, external semicircular canal; ext.amp, ampulla of external semicircular canal; ica, canal for internal carotid artery; l.c.c, lateral cranial canal; ldv, canal for longitudinal dorsal vein; mcv, canal for middle cerebral vein; nc, nasal capsule; olf.b, olfactory bulb; oof, otico-occipital fissure; opt.f, optic fenestra; opt.l, optic lobe; pdf, posterior dorsal fontanelle; pin.f, pineal foramen (anterior dorsal fontanelle); pit.f, pituitary fenestra; post.amp, ampulla of posterior semicircular canal; psc, posterior semicircular canal; sac, sacculus; s.oph.a, canal for small ophthalmic artery (branch of anterior cerebral artery); spio, canal for spino-occipital nerve; s.su, sinus superior; s.v, saccus vasculosus; tel, telencephalon; v.fon, vestibular fontanelle; I, canal for olfactory nerve; III, canal for oculomotor nerve; IV, canal for trochlear nerve; V, canal for trigeminal nerve; Vprof, canal for profundus nerve; VI, canal for abducens nerve; VII, canal for facial nerve; VIIlat, canal for lateralis branch of facial nerve; IX, canal for glossopharyngeal nerve; X, canal for vagus nerve. Dotted lines in figures indicate unresolved regions.

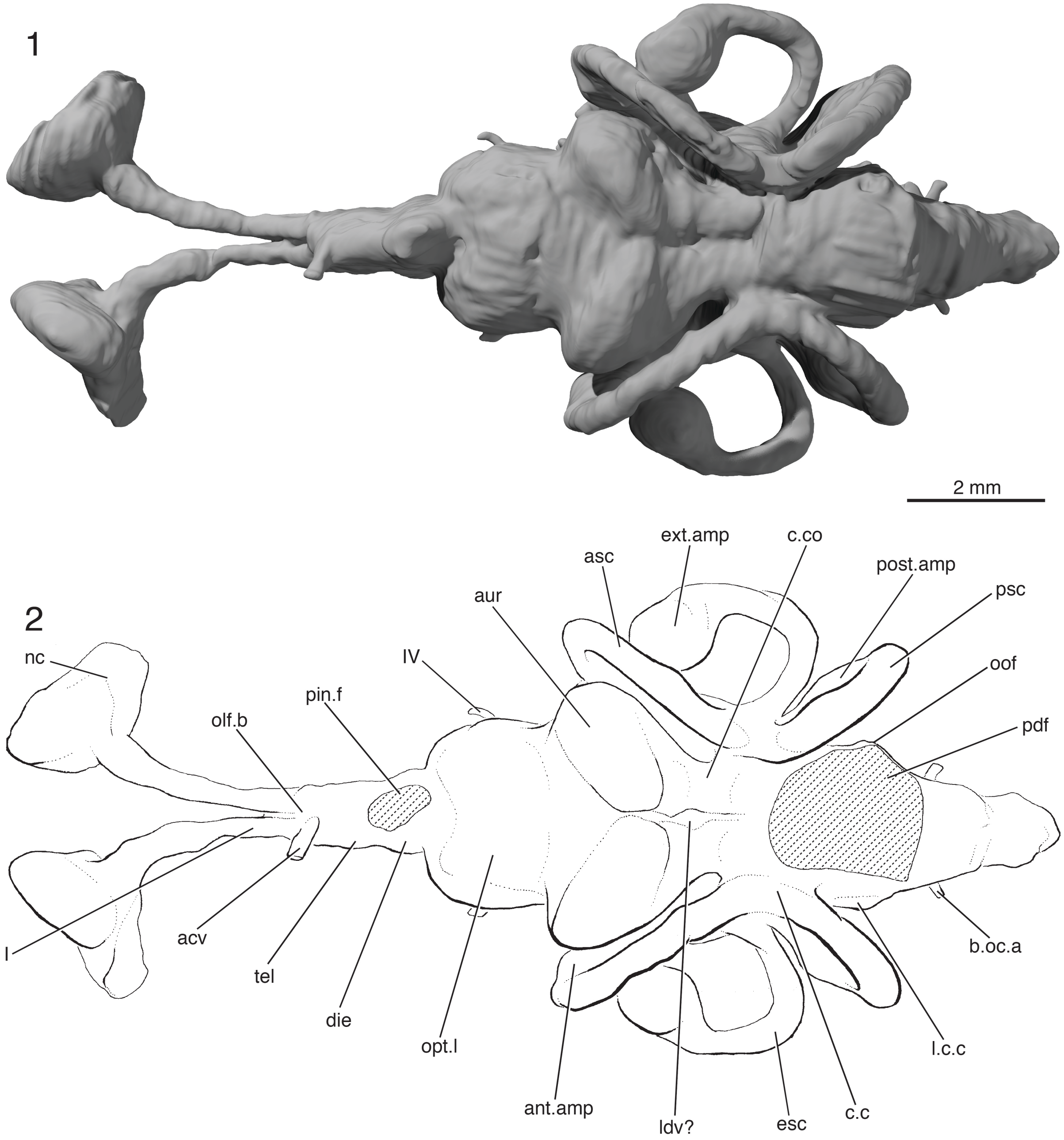

Figure 3 | Reconstruction of the endocast of *Mimipiscis toombsi*, NHMUK PV P.53247, in dorsal view. 1, three-dimensional rendering of endocast; **2**, interpretive drawing of endocast.

5.4 ANATOMICAL DESCRIPTION: *MIMIPISCIS*

General endocast morphology. The endocast is long and narrow, with elongate, anterolaterally-directed olfactory tracts (I, Figs. 3-5). The endocast of *Mimipiscis* has unusual proportions relative to that of other early extant and extinct actinopterygians listed above. The forebrain (excluding olfactory tracts) accounts for less than 20% of the total length, as opposed to the more usual 25-30%, and the hindbrain takes up over 60% of total brain length rather than around 50%.

Forebrain. This region of the endocast corresponds to the diencephalon, telencephalon and olfactory bulbs. The separation between the diencephalon (die) and the mesencephalon (mes) is marked by a constriction dorsally and laterally (Figs. 3-4), and the diencephalon and telencephalon (tel) are continuous. As in most primitive extant and extinct actinopterygians, such as *Polypterus*, *Acipenser*, and *Lawrenciella*, the olfactory bulbs (olf. b, Figs. 3-5) are confluent with the telencephalon. However, it is almost impossible to distinguish two olfactory bulbs in *Mimipiscis*. This contrasts with the situation in the fossil taxa *Lawrenciella* and *Mesopoma*, as well as many extant chondrosteans and neopterygians*,* where the olfactory bulbs are well developed and clearly divided. The region of the olfactory bulbs is confined to the posterior part of the orbit (Coates, 1999). The roof of the telencephalic region is perforated by a single foramen for the anterior cerebral vein (acv, Figs. 3-4). This anterior exit is unusual, as the more standard early actinopterygian arrangement is for it to exit from the roof of the diencephalon as in *Lawrenciella*, *Kentuckia* and *Kansasiella*.

The diencephalon in NHMUK PV P.53247 is visible dorsally only as a slight swelling. Ventrally, however, it extends downwards and slightly posteriorly under the mesencephalon

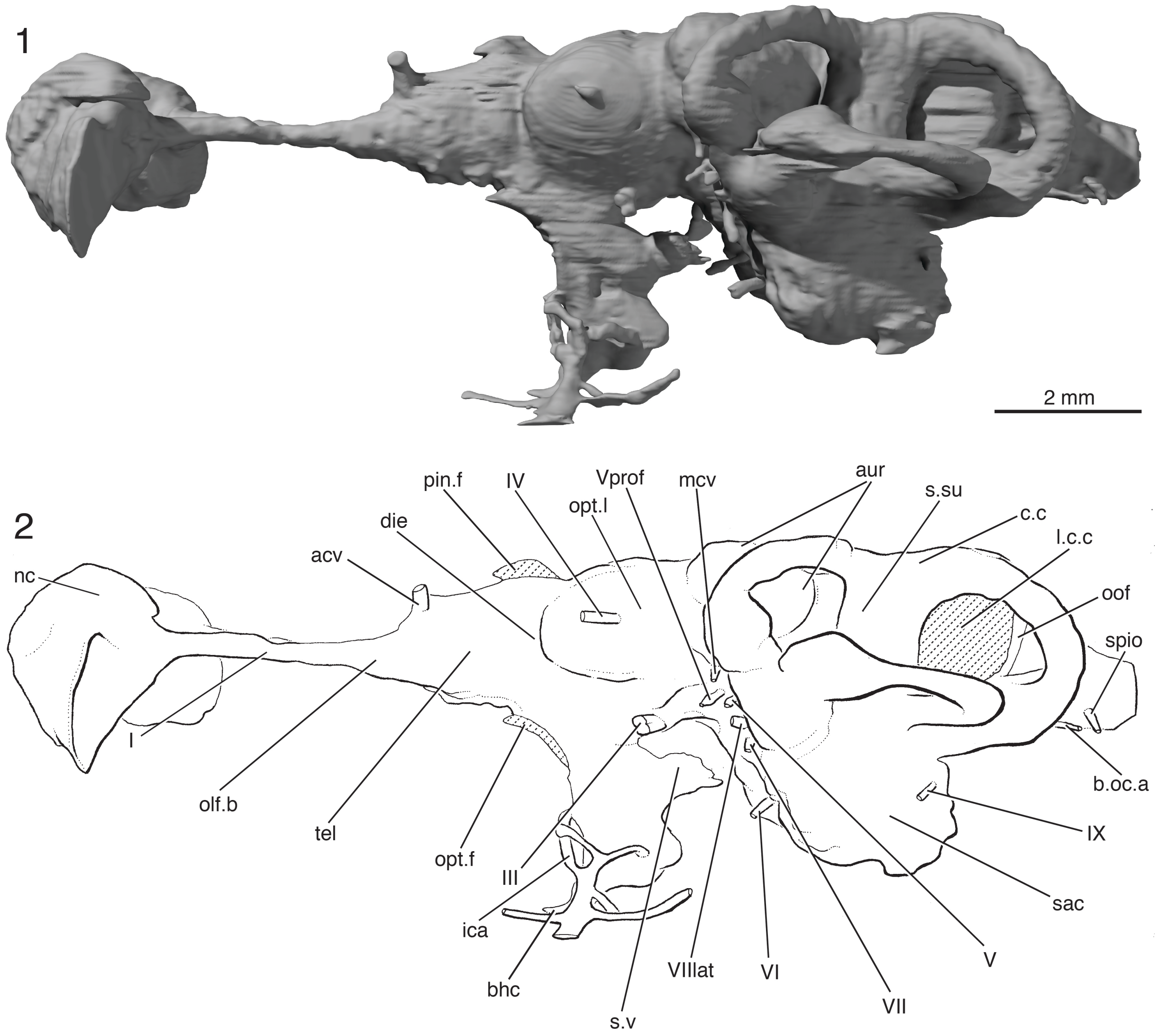

Figure 4 | Reconstruction of the endocast of *Mimipiscis toombsi*, NHMUK PV P.53247, in left lateral view. 1, three-dimensional rendering of endocast; **2**, interpretive drawing of endocast. The lateral cranial canal has been only been partially filled so as to avoid obscuring details of the labyrinth.

(die, Fig. 4), in a similar orientation to that of *Acipenser*. The diencephalon is mostly confined beneath the optic lobes, unlike in *Lawrenciella*, *Mesopoma* and *Polypterus*, where it extends posteriorly beneath the cerebellar auricles. Anteriorly, the interorbital wall is unfinished and thus does not delimit the endocast (opt.f, Figs. 4-5). The optic (II) nerves were likely transmitted through this opening, and foramina for the internal carotids are visible just beneath (ica, Fig. 5). Unlike in *Lawrenciella*, there is no groove or foramen for the small ophthalmic artery; the apparent opening in this region illustrated (but not identified) by Gardiner (1984: fig.13) does not penetrate the bone. The hypophysial canal, carrying the pituitary vein, extends ventrally into the diencephalon. The saccus vasculosus is developed as a somewhat dorsally-directed pouch on the caudal face of the diencephalon (s.v, Figs. 4-5), and is of a similar relative size to that of *Lawrenciella* and *Kansasiella*, but smaller than that of *Mesopoma*. An anterior prolongation at the bottom of the diencephalic region marks the passage of the bucco-hypophysial canal through the parasphenoid (bhc, Figs 4-5).

As a whole, the endocranial cast of the forebrain in *Mimipiscis* is very narrow, being barely wider than the olfactory tracts. These tracts, transmitting the olfactory (I) nerves, diverge almost immediately upon leaving the olfactory bulbs and extend anterolaterally towards the nasal sacs (Fig. 3, 5). This differs from the condition seen in the fossils of almost all other early actinopterygians, where the two nerves share a common canal for most of their length. The anterolateral orientation of the tracts is also unusual, but is similar to that seen in sarcopterygian fishes such as *Youngolepis* and *Ectosteorachis*, as well as extant chondrosteans.

Midbrain. The mesencephalic region in *Mimipiscis* is about twice the width of the forebrain, but does not reach the maximum width of the cerebellum (Fig. 3). As with *Acipenser*, the two optic lobes (opt.l, Figs. 3-5) lack a well-defined median groove. In comparison to other Carboniferous

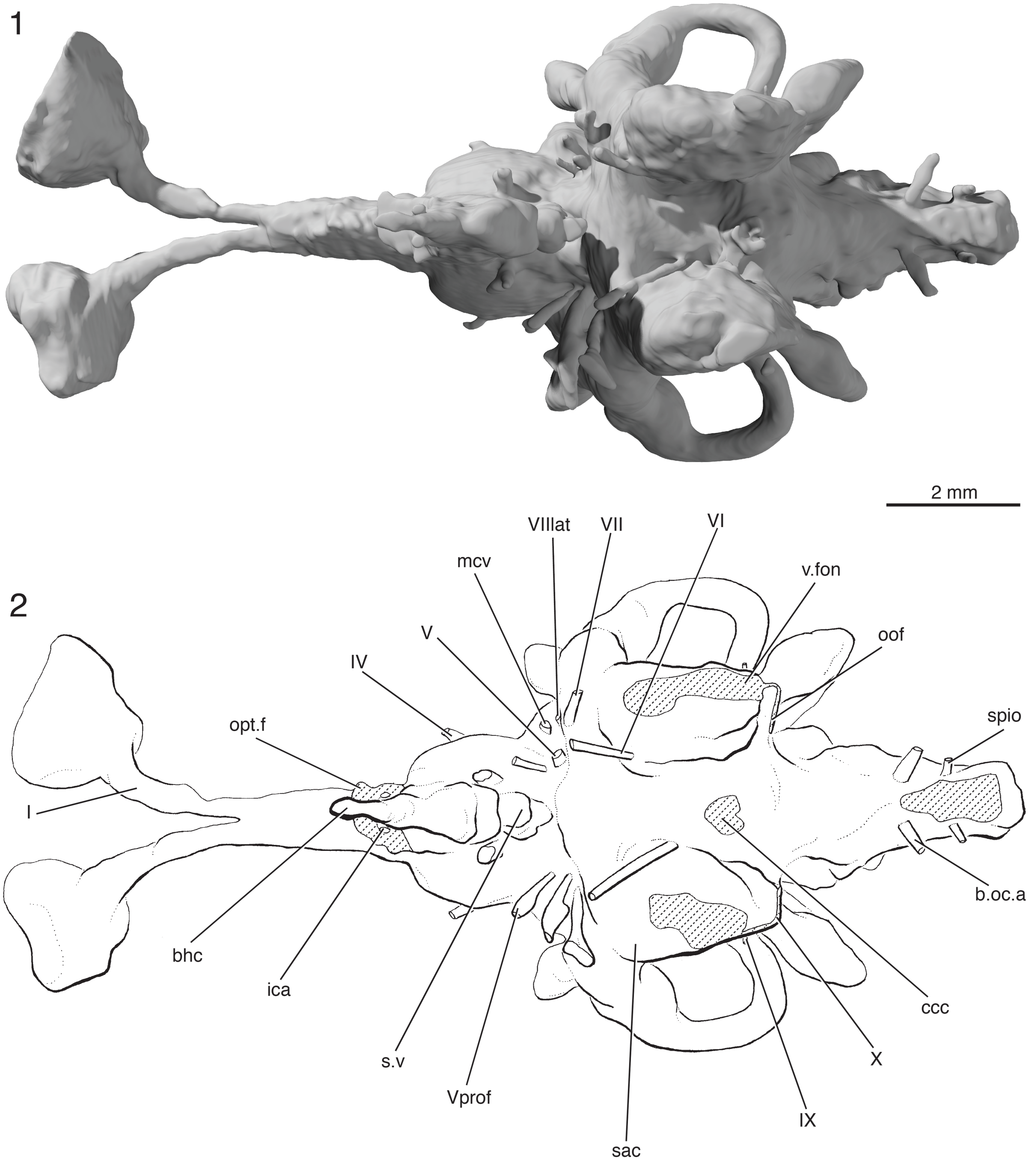

Figure 5 | Reconstruction of the endocast of Mimipiscis toombsi, NHMUK PV P.53247, in ventral view. 1, three-dimensional rendering of endocast; **2**, interpretive drawing of endocast.

ray-finned fishes, the optic lobes of *Mimpiscis* are poorly developed. The root of the trochlear (IV) nerve pierces the lateral limit of each lobe (Fig. 4), a position somewhat higher than the corresponding foramen in *Lawrenciella*, *Mesopoma* and *Kansasiella*. The oculomotor (III) nerve leaves the floor of each optic lobe and, as in *Lawrenciella*, bifurcates almost immediately to enter the orbit through two closely spaced foramina (III, Fig. 4).

Hindbrain. This region of the endocast relates to the cerebellum and rhombencephalon. In *Mimpiscis*, the cerebellar auricles resemble those of *Acipenser* in being robust but short (aur, Fig. 3-4). As in *Lawrenciella*, *Kansasiella* and extant chondrosteans, they are separated from the optic lobes by a deep sulcus. In *Lawrenciella*, dorsal ridges within the sulcus are thought to be related to the middle cerebral vein. No such ridges are present in *Mimipiscis*; instead, a canal that exits from the bottom of the auricle and extends ventrally has been suggested to carry this vessel (Gardiner, 1984). A similar canal is reported in *Pteronisculus* White, 1933 (Nielsen, 1942), where it leaves the auricle and passes directly into the orbit above the trigeminofacialis chamber. Somewhat unusually, the canal in *Mimipiscis* appears to enter the trigeminofacialis chamber (mcv, Figs. 4-5). Gardiner (1984) commented upon a similarly close relationship between the middle cerebral vein and trigeminal (V) nerve in teleosts, and it is likely that in *Mimipiscis* the vein entered the chamber and exited again almost immediately by way of an anterodorsally-directed canal.

Relative to the placement seen in other ray-finned fishes, the auricles in *Mimipiscis* are positioned far anteriorly, with the anterior limits level with the ampulla of the anterior semicircular canal and the posterior extent no further than the external ampulla (Fig. 3). Dorsally, the auricles stand proud of the rest of the endocast, a condition uncommon in early fossil ray-finned fishes, as well as extant chondrosteans and neopterygians. It is hard to compare

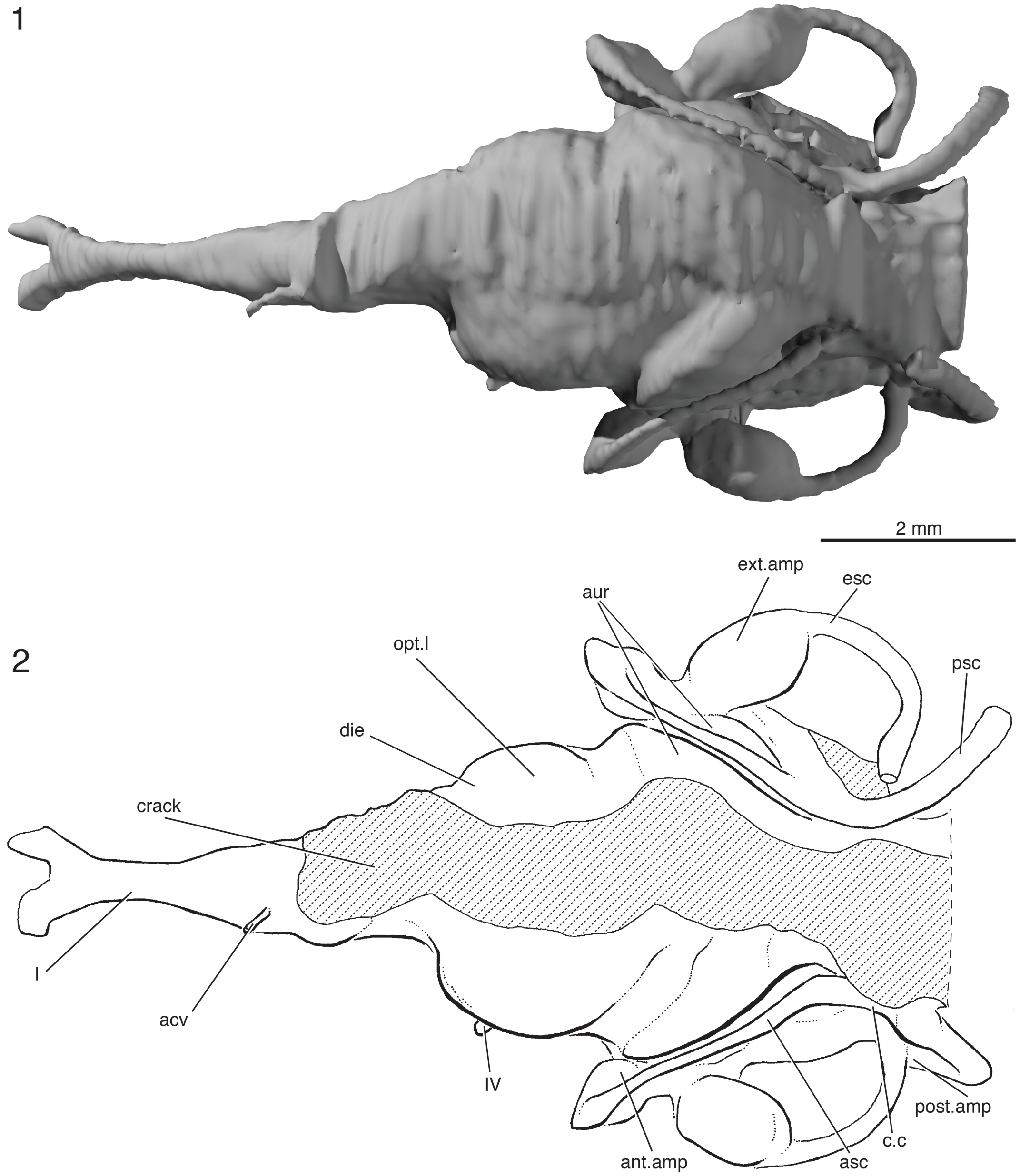

Figure 6 | Reconstruction of the endocast of *Kentuckia deani*, MCZ 8361, in dorsal view.

1, three-dimensional rendering of endocast; **2**, interpretive drawing of endocast.

this with the condition seen in actinopterygian outgroups as the endocranial cavity typically does not conform well to the shape of the brain in this region. However, in *Ectosteorachis* and *Youngolepis*, there is a suggestion of an increase in depth of the endocavity in the region of the cerebellum. Similarly, in *Latimeria* Smith 1939, the cerebellum extends above the rest of the brain, although the auricles sit somewhat lower (Northcutt et al., 1978).

Beneath the auricles, the lateral limits of the endocast slope inwards to meet a short distance above the saccus vasculosus. This lateral wall is pierced by two foramina: the more medial for the anteriorly directed profundus (Vprof) nerve canal, and the more lateral for the trigeminal (V) nerve canal (Figs. 4-5). The canal for the trigeminal nerve travels laterally to enter the trigeminofacialis chamber, intercepting and carrying the middle cerebral vein en route (see above). Lateral and slightly ventral to these two openings are two additional foramina. The more dorsal of these most likely transmitted the lateralis branch of the facial (VIIlat) nerve, which also travels into the trigeminofacialis chamber. The more ventral transmitted the facialis (VII) nerve ventrolaterally. The canal for the abducens (VI) nerve pierces the zygal plates and extends anterolaterally along the medial boundaries of the saccular recesses (Fig. 5). The glossopharyngeal (IX) nerve leaves the sacculus ventral to the ampulla for the posterior semicircular canal (Fig. 4).

A deep groove between the two auricles presumably marked the course of the longitudinal dorsal vein (ldv, Fig. 3; Coates, 1999). This groove extends posteriorly, but does not appear to continue forwards between the optic lobes, unlike the condition inferred for *Mesopoma*. The hind part of the cerebellum is elongate and bilobed, as in *Mesopoma*, *Boreosomus* Stensiö, 1921 (Nielsen, 1942) and *Polypterus*, and is continuous with the auricular lobes. These features, combined with the posterior elongation (presumably projecting into the fourth ventricle), and a

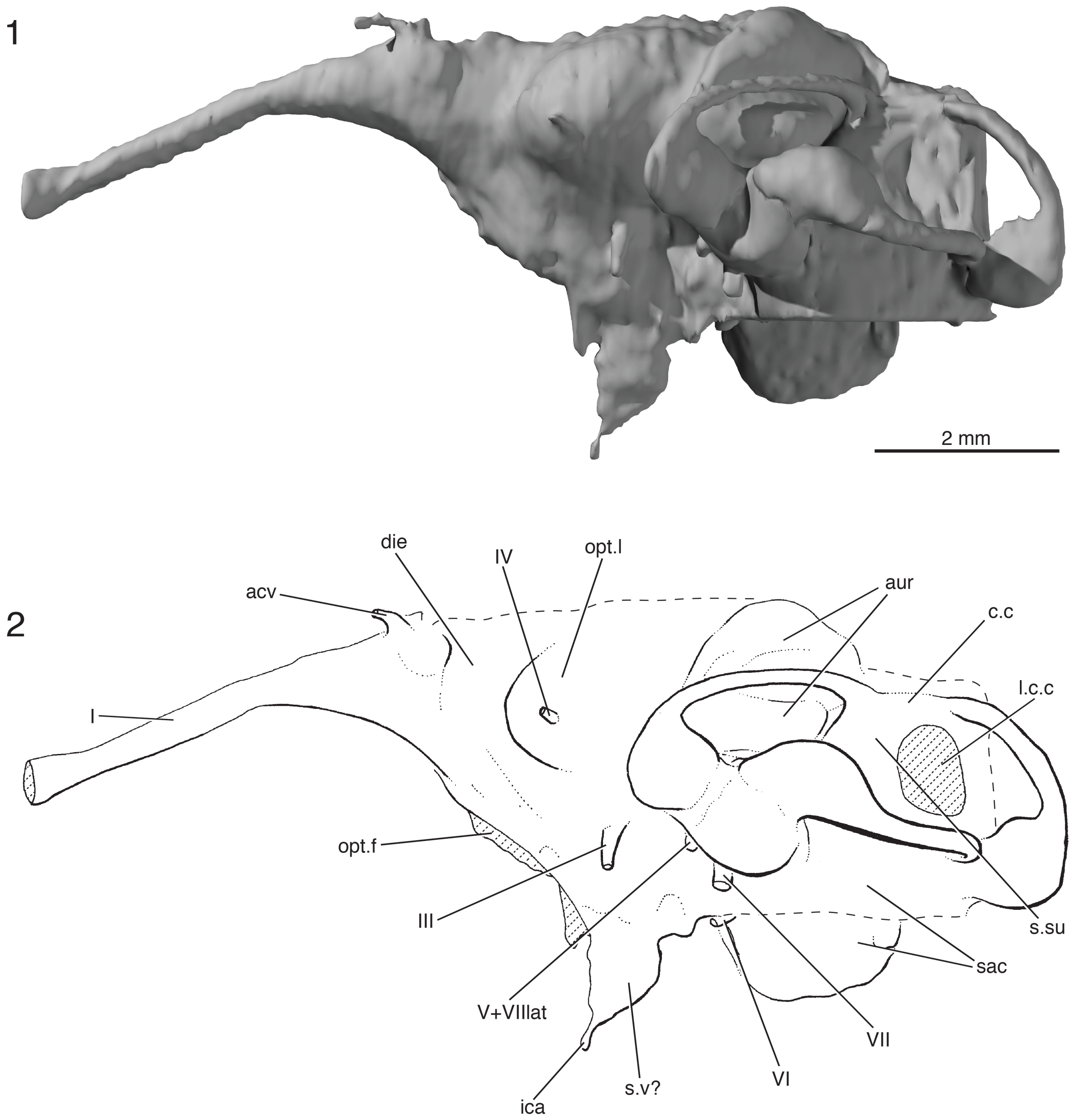

Figure 7 | Reconstruction of the endocast of Kentuckia deani, MCZ 8361, in left lateral view. 1, three-dimensional rendering of endocast; **2**, interpretive drawing of endocast. The pocket of the lateral cranial canal has been 'cut' to avoid obscuring parts of the labyrinth.

lack of tubercula acustica, suggest that this region corresponds with the corpus cerebellum (c.co, Fig. 3). The lateral wall of the endocast between the sinus superior and otico-occipital fissure is interrupted by a large foramen for the lateral cranial canal (l.c.c, Fig. 4). Although the canals are complete in the specimen, they have only been partially segmented so as to avoid obscuring any parts of the labyrinth. Behind the fissure the endocast sloped downwards to assume a cylindrical shape, from which canals issue for branches of the occipital arteries (b.oc.a, Figs. 3-5) and, further posteriorly, the spino-occipital nerves (spio, Figs. 3-5).

Labyrinth. The overall morphology of the labyrinth region in *Mimipiscis* is as expected for an early actinopterygian (Figs. 3-5). The three semicircular canals (anterior, posterior and external) are robust, with a relatively large separation between them and the lateral walls of the endocast. The sinus superior (s.su, Fig. 4) is wide and is underlain by a large saccular recess that lacks an obvious lagena (sac, Fig.4). Despite being widespread among vertebrates, a separate lagenar pouch is also unknown in all other early actinopterygians, as well as in the extant *Acipenser*, *Amia*, and *Lepisosteus* (Popper, 1978; Mathiesen and Popper, 1987; Lovell et al., 2005). Its absence in early members of other groups, for example in some sarcopterygians (Jarvik, 1980; Platt et al., 2004) and chondrichthyans (de Burlet, 1934; Gauldie et al., 1987; Maisey, 2005, 2007; Pradel, 2010), suggests that a distinct lagenar pouch may have arisen independently several times in vertebrates. No otoliths are preserved within the saccular chambers of *Mimipiscis*, and were presumably dissolved during acid preparation, as otoliths have been found in other material examined by Gardiner (1984: p.227). The curvature of the anterior and posterior canals is such that they rise above the level of the hindbrain, causing the crus commune to sit just above the level of the endocast roof (c.c, Fig.4).

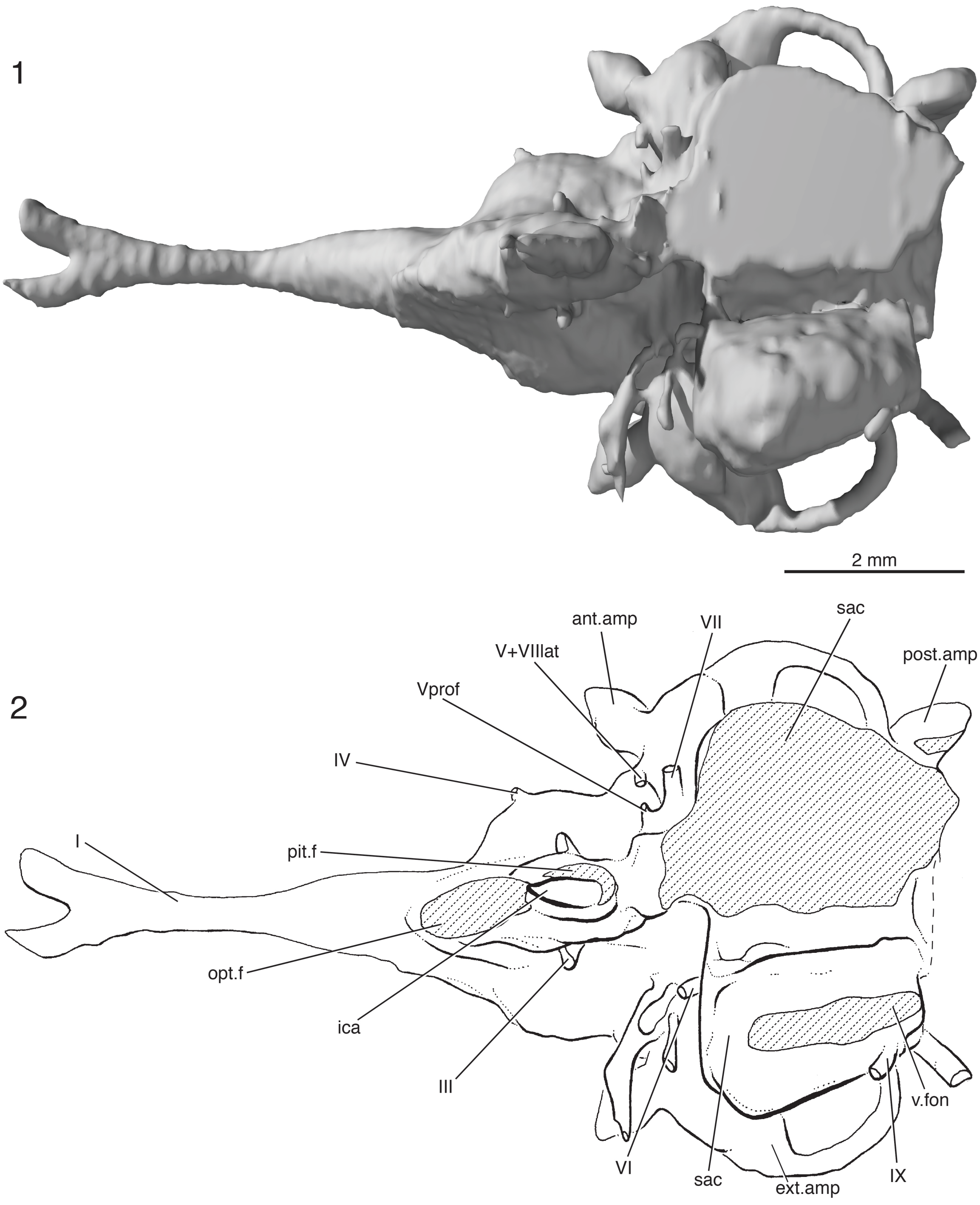

Figure 8 | Reconstruction of the endocast of *Kentuckia deani*, MCZ 8361, in ventral view.

1, three-dimensional rendering of endocast; **2**, interpretive drawing of endocast.

5.5 ANATOMICAL DESCRIPTION: *KENTUCKIA*

General endocast morphology. In both MCZ 5226 and MCZ 6381, the endocast is markedly less slender than that of *Mimipiscis* (Figs. 6-10). The relative proportions assumed are more typical of previously described endocasts of primitive extant and extinct ray-finned fishes (see references above); the forebrain constitutes around 25% of the total brain length and the hindbrain around 50%. Although the endocasts of the two specimens agree in these general proportions, they differ in a series of more specific features: the optic lobes are better developed and more spherical in MCZ 5226 than in MCZ 8361; the cerebellar auricles are proportionally longer in MCZ 5226 than in MCZ 8361; the posterior semicircular canal is more tightly curved and thus shorter in MCZ 8361 than MCZ 5226; and the canal for the third cranial nerve bifurcates in MCZ 5226 but remains undivided in MCZ 8361. These are reviewed in more detail in the relevant sections below.

Forebrain. Similar to in *Mimipiscis*, *Lawrenciella* and *Kansasiella*, the cast of the forebrain of *Kentuckia* is narrow. The separation between the diencephalon (die) and the mesencephalon (mes) is marked by a constriction dorsally and laterally (Figs. 3-4). As in *Mimipiscis*, olfactory bulbs cannot be identified in either MCZ 5226 or MCZ 8361, and it is difficult to distinguish between the diencephalon and telencephalon (Figs. 6, 9). The telencephalon can be identified with confidence only in MCZ 5226, where a slight bulge is visible laterally (tel, Fig. 10). In both *Kentuckia* specimens, the dorsal limit of the endocast is uncertain immediately in advance of the anterior dorsal fontanelle (pin.f, Fig. 9), and it seems likely that this region of the brain was not closely applied to the walls of the endocranial chamber. In MCZ 8361, a canal exits from the top of the diencephalic region. This corresponds to the single foramen for the anterior cerebral vein (acv, Figs. 6-7). The bone in MCZ 5226 is poorly mineralised in this region, and

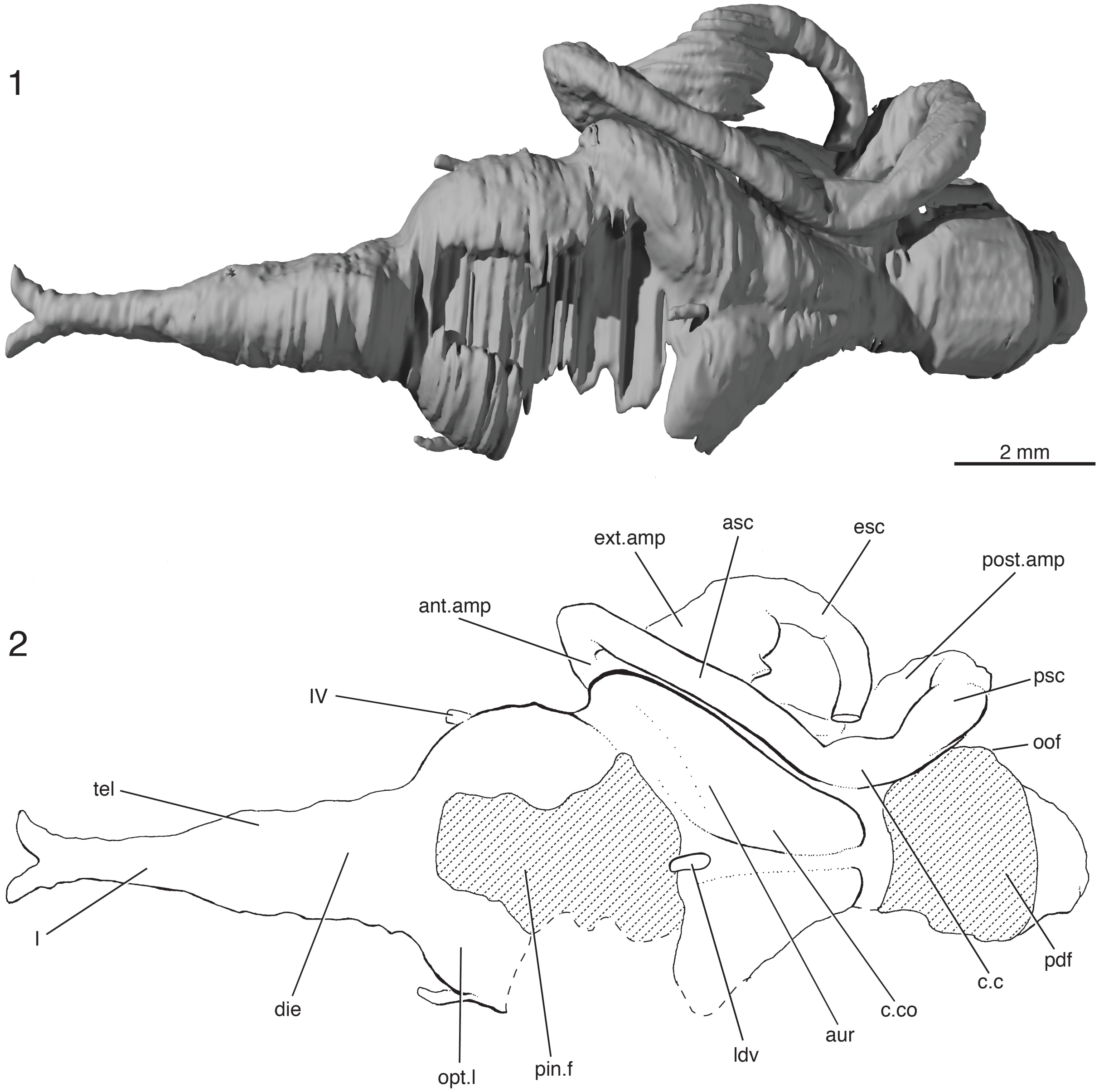

Figure 9 | Reconstruction of the endocast of *Kentuckia deani*, MCZ 5226, in dorsal view.

1, three-dimensional rendering of endocast; **2**, interpretive drawing of endocast.

no such passage is visible. In both specimens, the olfactory (I) nerves are carried through a single tract, which travels anteriorly before diverging into two anterolateral canals immediately before reaching the nasal capsules (Figs. 6, 9). Curiously, the shared tract extends ventrally as well as anteriorly (I, Fig. 7, 10). This is not reported in any other fossil actinopterygian, but is very similar to the condition in *Acipenser*.

The ventral portion of the diencephalon is poorly preserved in MCZ 8361, but can be described in more detail from MCZ 5226. A shared opening for the optic (II) nerves is visible anteriorly (opt. f), and above this lie two small anteriorly directed canals that likely transmitted the small ophthalmic arteries, as in *Lawrenciella* (s.oph.a, Fig. 10). In both specimens, the internal carotids (ica, Figs. 7, 10) extend downwards from the optic foramen. Posterior to this, the hypophysial stalk extends ventrally under the optic lobes, as in *Acipenser* and *Lepisosteus*, ending in the bucco-hypophysial canal (bhc, Fig. 10). The full extent of the saccus vasculosus is uncertain in either specimen of *Kentuckia*.

Midbrain. The mesencephalic region of the endocast is well developed, with the optic lobes over twice the width of the forebrain. Large optic lobes are known in *Mesopoma* and *Lawrenciella*, as well as extant chondrosteans and neopterygians. The lobes are relatively larger and more rounded in MCZ 5226 than in MCZ 8361, and extend dorsal to the more anterior parts of the endocast (opt.l, Figs. 6-7, 9-10). The trochlear (IV) nerve pierces the lobe in a slightly more ventral position than in *Mimipiscis*, although the oculomotor (III) nerve bifurcates before entering the orbits in the same way (III, Fig. 10). This bifurcation is not seen in MCZ 8361. The region between the optic lobes is occupied by a large anterior dorsal fontanelle (pin.f, Fig 9), obscuring any median groove. In MCZ 5226 this extends from the front of the optic lobes to the posterior limit of the cerebellar auricles. This fontanelle has been traversed by a crack in MCZ

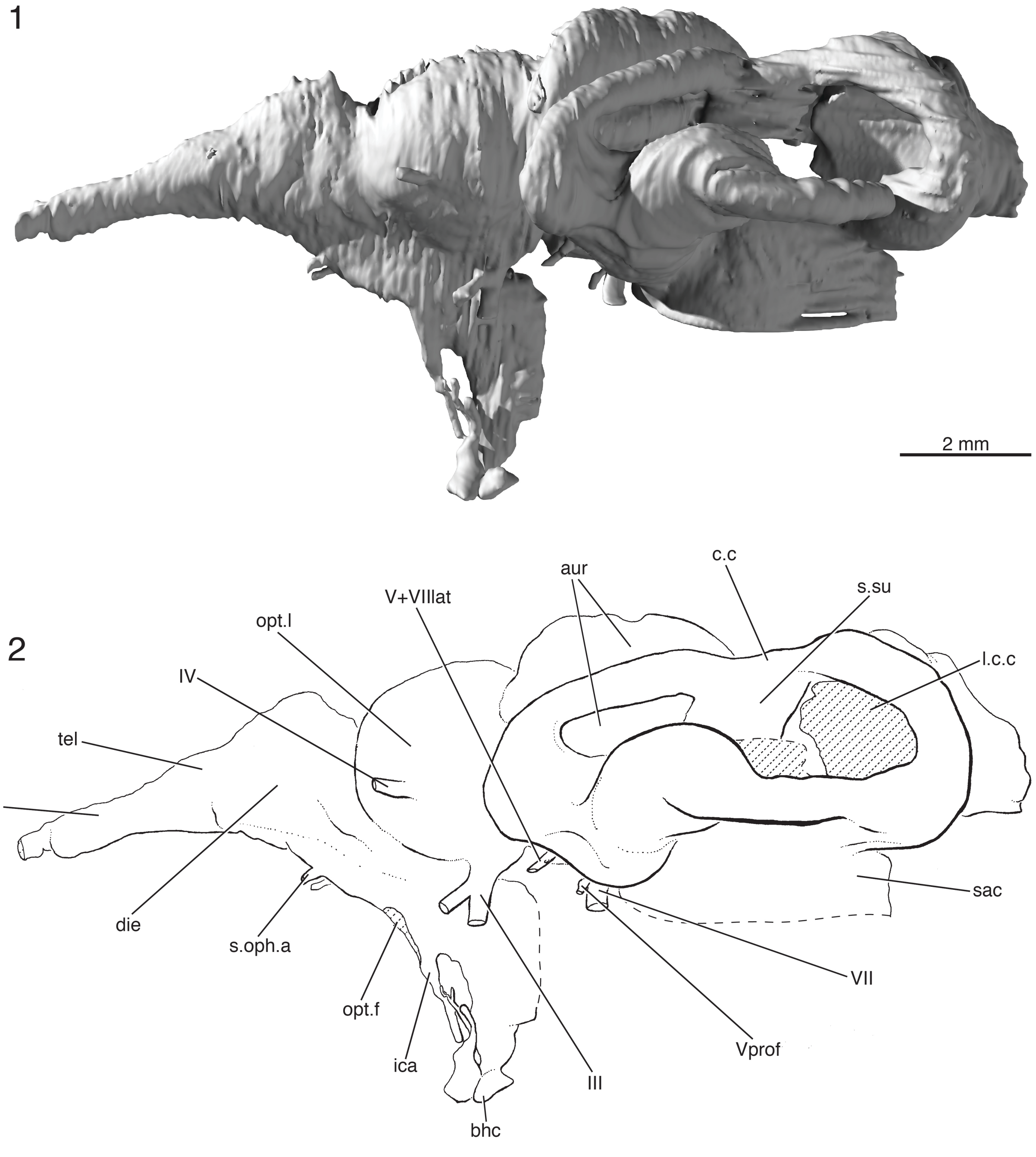

Figure 10 | Reconstruction of the endocast of *Kentuckia deani*, MCZ 5226, in left lateral view. This image has been flipped horizontally and in fact is of the right side of the endocast. **1**, three-dimensional rendering of endocast; **2**, interpretive drawing of endocast. The pocket of the lateral cranial canal has been 'cut' to avoid obscuring parts of the labyrinth.

8361, and as a result much of the dorsal surface of the portion of the endocast relating to the mid- and hindbrain is obscured. A thin canal extends along the midline behind the fonanelle in MCZ 5226. Comparison with *Mesopoma* and teleosts (Zwehl, 1961; Coates, 1999) indicates that it transmitted the longitudinal dorsal vein (ldv, Fig. 9).

Hindbrain. The cerebellar region of the endocast is separated from the mesencephalon by a groove. Although this may have housed the middle cerebral vein (Hamel and Poplin, 2008), no supporting ridges are apparent. Dorsally, the cerebellar auricles display a similar morphology in both specimens of *Kentuckia*, extending from the ampulla of the anterior semicircular canal back to the crus commune of the anterior and posterior canals (aur, Figs. 6-7, 9-10). Rather than being laterally separated from the endocast, the anterior semicircular canal is set into a deep groove extending along the auricle, producing a ventral auricular lobe that continues towards the utriculus (Figs. 5-6, 9). This unusual arrangement is seen elsewhere only in *Kansasiella*, where the auricles are so reduced that they only display this ventral lobe. The auricles are relatively larger in MCZ 5226 than in MCZ 8361, standing proud above the rest of the dorsal surface of the endocast.

The layout of the canals in the lateral region of the diencephalon is fairly similar in both specimens of *Kentuckia*. The most medial of the three canals leaves the lateral wall of the cranial cavity and extends laterally and slightly anteriorly to the trigeminofacialis chamber. This carried the profundus (Vprof) nerve. Its position is slightly more ventral in MCZ 5226. Two canals exit medial and ventral to the utriculus. The more dorsal of these is very short, and transmits the trigeminal (V) nerve and lateralis branch of the facial (VIIlat) nerve into the trigeminofacialis chamber (Fig. 8). The more ventral projects laterally to enter the orbit, and carried the facial (VII) nerve. The exit for the abducens (VI) nerve, on the anterior face of the sacculus, is visible only in MCZ 8361 (Fig. 8).

The posterior portion of the rhombencephalon is very poorly known in MCZ 8361, especially dorsally. The sinus superior (s.su) is incompletely resolved in both specimens, but appears to be similar in size to that of *Mimipiscis* and *Lawrenciella*, as is the saccular recess (sac). Only the upper portion of the saccular recess is known in detail, but it appears fairly extensive (sac, Figs. 7, 10), and a canal for the glossopharyngeal (IX) nerve exits the lateral edge of the sacculus in MCZ 8361 (Fig. 8). The opening for the lateral cranial canal is small (l.c.c, Figs. 7, 10), and appears to protrude through the posterior semicircular canal as a 'pocket', as in *Lawrenciella*. The region is better resolved in MCZ 5226. As in *Mimipiscis*, *Mesopoma* and *Pteronisculus* (Nielsen, 1942), the endocast in this specimen of *Kentuckia* displays two lobes divided along the midline, and there is a suggestion that they are further subdivided transversely (c.co, Fig. 9). These lobes are smooth and confluent with the cerebellar auricles, and represent the cerebellar corpus. The endocast narrows to a cylinder behind the posterior dorsal fontanelle.

Labyrinth. At first glance, the morphology of the semicircular canals in MCZ 8361 and MCZ 5226 appears strikingly different. The canals in MCZ 8361 are very delicate and narrow in comparison to those of MCZ 5226. This, however, appears to be a preservational artefact; CT scans through the specimen reveal that the original bone material is not preserved. Instead, what is preserved is an infilling of the space that would have been occupied in life by the membranous labyrinth, a structure thinner than the osseus labyrinth preserved in MCZ 5226. As mentioned above, the anterior canal is set very closely into the auricle, appearing to divide it into two lobes (aur, Figs. 6-7, 10). The ampullae of the anterior and external canals in MCZ 5226 are relatively larger than those of *Mimipiscis* and *Lawrenciella*, and the utriculus is much smaller than in *Mimipisicis*. All three canals in MCZ 8361 and MCZ 5226 are tightly curved and therefore short, as in *Lawrenciella* and *Kansasiella*. The sinus superior is positioned below the upper surface of the endocast, and this gives the canals a flattened appearance, quite unlike the condition observed in *Mimipiscis*.

5.6 DISCUSSION

5.6.1 *Validation of previous interpretations*.

The morphological data described in the previous section can be used to test the anatomical descriptions laid out by Gardiner (1984) for *Mimpiscis* and those of Moodie (1915) and Rayner (1951) for *Kentuckia*.

The existing description of the endocast of *Mimipiscis* can largely be corroborated, but we are able to add several important features that have not previously been recognised. As part of his description of *Mimipiscis*, Gardiner included a short section on the morphology of the brain cavity, as well as referring to aspects of it elsewhere. He figured the dorsal structure of the endocast (anterior to the pineal foramen), but much of the morphology is obscured by the extension of the anterior myodome (Gardiner, 1984: figs. 33, 34). A sagittal section through the endocranial cavity was also illustrated (Gardiner, 1984: fig. 26). The description can largely be corroborated, with one or two exceptions in the region of the trigeminofacialis complex. Gardiner referred to the trigeminal (V) nerve and profundus (Vprof) nerve as entering the orbit independently but having a shared root, with the profundus branching from the anterior part of the facial canal. In fact, they appear to leave the cranial cavity through different openings and have entirely separate courses. Consequently, the foramen referred to as ‘V’ in fig. 26 can be reinterpreted as the opening for the root of the profundus nerve. The trigeminal nerve has a separate exit from the cranial cavity, which was misidentified by Gardiner (1984: fig. 26) as the lateralis branch of the facial nerve. The opening for the lateralis branch is not visible in sagittal section, being obscured from view by the ampulla for the anterior semicircular canal.

Gardiner's (1984) interpretation of the layout of nerves within the orbit is corroborated by our analysis. The middle cerebral vein enters the orbit via its own foramen in this specimen of *Mimipiscis*, situated dorsally and slightly anteriorly of the common opening for the trigeminal nerve and lateralis branch of the facial nerve.

We are also able to correct some interpretations of the bony labyrinth. Gardiner (1984) described the posterior opening of the exterior semicircular canal as passing through the ampulla of the posterior canal, but it is clear that they enter the cranial cavity separately. This brings the structure in *Mimispicis* in line with that seen in *Kentuckia*, as well as the Triassic *Boreosomus* and *Pteronisculus* (Nielsen, 1942). A vertical separation between the external semicircular canal and posterior ampulla, with one opening sitting above the other, is evident in placoderms (Goujet, 1984) and chondrichthyans (Schaeffer, 1981; Maisey, 2007), as well as some sarcopterygians (e.g. *Chirodipterus*; Säve-Söderbergh, 1952). The alternative condition is seen in *Kansasiella* (Poplin, 1974) and a number of Triassic actinopterygians (Nielsen, 1942). On a more minor note, the recess for the saccus vasculosus is somewhat larger than that figured by Gardiner (1984: fig. 26).

This study is also able to confirm many of Rayner's tentative interpretations concerning the endocranial cavity of *Kentuckia* while revealing new morphological data concerning overall brain structure and proportions. We are also able to test the interpretations made by Moodie (1915) of the lectotype of *Kentuckia*, a natural endocranial cast. The written account of the endocranial cavity provided by Rayner is detailed, but only one figure (1951: fig. 9), a diagrammatic sagittal section through the braincase, provides illustration. While many of the interpretations are correct, the figure as a whole is misleading. The proportions of the braincase are incorrect, and the region behind the orbit needs to be stretched by approximately one third to reflect the true shape. Once the correct proportions are resolved, it becomes clear that the optic lobes are far larger than illustrated, and the arrangement of the utriculus and exits of the semicircular canals resembles that of *Mimipiscis* and other early ray-finned fishes. The root of the abducens (VI) nerve, which Rayner could not locate, emerges from the medial portion of the sacculus and travels forward to exit into the orbit.

Other minor amendments that can be made refer to openings that Rayner could not identify with certainty. The 'deep hollow' (Rayner, 1951: fig. 9, 'x') found in the loop of the posterior semicircular canal can be confirmed as the lateral cranial canal. A smaller pocket in the loop of the anterior canal is the ventral lobe of the cerebellar auricle, rather than part of the lateral cranial canal network. Segmentation of the complete course of the oculomotor (III) nerve confirms that the tract bifurcates distally to enter the orbit through two separate foramina in at least some specimens of *Kentuckia,* such as MCZ 5226.

As described and illustrated by Rayner, three canals leave the cranial cavity to enter the trigeminofacialis chamber before continuing into the orbit. The external configuration illustrated by Rayner (1951: fig. 8) largely matches that seen in MCZ 5226. The facial (VII) nerve canal (probably also carrying the trigeminal [V] nerve) is described as opening into the orbit from the floor of the trigeminofacialis chamber. This is largely accurate, although the opening is on the medial wall of the chamber rather than its roof. The profundus nerve (Vprof) enters the orbit via an opening just dorsal to the two oculomotor (III) foramina. Rayner's

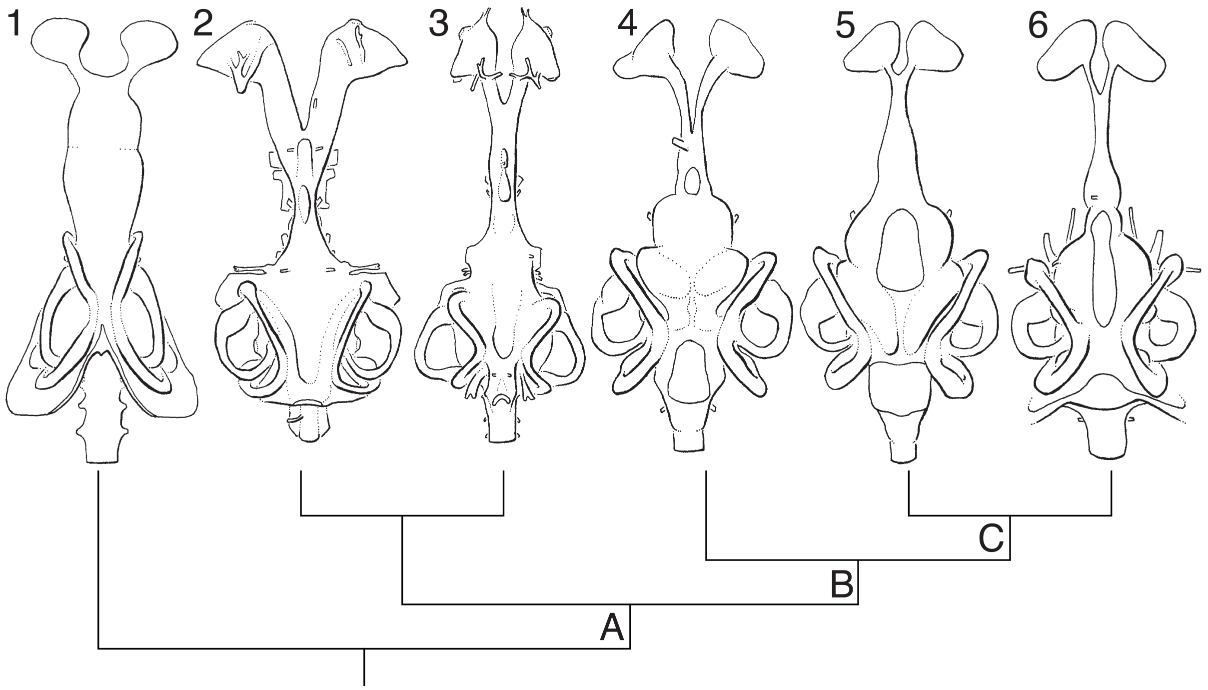

Figure 11 | Cladogram showing distribution of potential apomorphies visible in the endocast, with an emphasis on osteichthyans, particularly actinopterygians. Cladogram based on Coates, 1999; Hamel and Poplin, 2008; and Zhu et al., 2009. Proposed endocast synapomorphies are drawn from this study and others (referenced accordingly). **1**, *Orthacanthus* Agassiz, 1883, modified from Schaeffer, 1981. **2**, *Youngolepis*, modified from Chang, 1982. **3**, *Eusthenopteron*, modified from Jarvik, 1980. **4**, *Mimipiscis*. **5**, *Kentuckia*. **6**, *Lawrenciella*, modified from Hamel and Poplin, 2008. **Node A**: long olfactory tracts (Friedman and Brazeau, 2010); horizontal semicircular canal joins labyrinth level with the ampulla for the posterior semicircular canal (Davis et al., 2012). **Node B**: lateral cranial canal (Coates, 1999); cerebral hemispheres formed by evagination of telencephalon (Nieuwenhuys, 1982). **Node C**: anteriorly directed olfactory tracts (Coates, 1999); olfactory nerves carried in a singe tract; optic lobes as wide as cerebellum; crus commune of anterior and posterior semicircular canals ventral to endocranial roof.

labelling of this opening in lateral view (1951: fig. 7) is misleading; the opening identified as 'Vprof' is in fact a branch of the arterial/venous network. The true position of Vprof is somewhat more ventral, although no corresponding foramen is drawn in Rayner's figure.

The pattern of nerve exits from the cranial cavity proposed by Rayner is more difficult to ratify, particularly as the positioning of these canals differs between MCZ 5226 and MCZ 8361. This variation is even more apparent in sagittal section. Rayner's illustration (1951: fig. 9) identifies three exits: a canal for the facial nerve, leaving from the same region as the anterior ampulla; a slightly more anteriorly-placed canal for the profundus nerve; and the trigeminal nerve canal more anteriorly still. The relative position of these three nerves largely matches that of MCZ 5662, although the facial nerve exits the cranial cavity more medially than the exit from the ampulla shown by Rayner (1951: fig. 9). This is not the case in MCZ 8361, where the canal for the trigeminal nerve does in fact exit from the region of the anterior ampulla. The facial nerve in MCZ 8361 exits more medially, and the canal for the profundus nerve is situated more anteriorly. Finally, the canal for the glossopharyngeal (IX) nerve exits the cranial cavity of MCZ 8361 considerably more ventrally than indicated by Rayner (1951: fig 9). This region is not resolved in MCZ 5226, but the exit is assumed to be in a similar position.

The morphology of the lectotype (MCZ 5222) described by Moodie (1915: figs. 3-4) largely matches that of our virtual endocast models. Despite the fact that many morphological details are obscured in the lectotype, Moodie's description can generally be corroborated, although his 'tuberculum acusticum' is in fact the bilobed cerebellum.

5.6.2 *Systematic and evolutionary implications*.

As well as representing critical tests of previous morphological interpretations of *Mimipiscis* and *Kentuckia*, the virtual endocasts produced by this study permit more direct comparison with similar reconstructions available for other early gnathostomes (Fig. 11). Although the endocasts of early fossil actinopterygians are thought to faithfully record brain structure (Edinger, 1929; Jerison, 1973; Bjerring, 1971; Coates, 1999), this is not the case for other groups of vertebrates. As a consequence, palaeontological comparisons like those below are most accurately framed as being between the anatomy of endocasts rather than brains.

The endocasts of *Mimipiscis* and *Kentuckia* reveal characteristics consistent with previous phylogenetic placements of these genera. Their long olfactory tracts represent an osteichthyan synapomorphy (Friedman and Brazeau, 2010), and the presence of a lateral cranial canal unites these genera with other actinopterans (Coates, 1999), although the discovery of a putative lateral cranial canal in *Meemannia*, *Psarolepis* and *Ligulalepis* raises the possibility that this feature may be more widely distributed across osteichthyans (Zhu et al., 2010). At a finer phylogenetic scale, the endocasts of *Mimipiscis* and *Kentuckia* show some striking differences, especially in terms of overall geometry. The endocast of *Kentuckia* broadly resembles that of stratigraphically younger ray-finned fishes from the Pennsylvanian, particularly *Lawrenciella* (Hamel and Poplin, 2008) and *Kansasiella* (Poplin, 1974). All of these Carboniferous taxa are interpreted as branching from more crownward positions on the actinopteran stem than *Mimipiscis* (Coates, 1999; Gardiner et al., 2004). Our new endocast data supports this phylogenetic hypothesis by revealing generalized features shared by *Mimipiscis*, sarcopterygians and chondrichthyans, but which show apparently derived conditions in

Carboniferous and younger actinopteran ray-finned fishes (Fig. 11). These relate to the morphology of the olfactory tracts, labyrinth and mesencephalon.

As in sarcopterygians (e.g. Nieuwenhuys et al., 1977: fig. 1; Chang, 1982: figs. 17-18 ; Clément and Ahlberg, 2010: fig. 7;), the stem osteichthyan *Ligulalepis* (Basden et al., 2000: fig. 1; Basden and Young, 2001: figs. 1, 7), chondrichthyans (Schaeffer, 1981: fig. 14-15; Maisey, 2005: fig. 27; Pradel, 2010: fig. 30), and placoderms (e.g. Stensiö, 1963b: figs. 26-27, 29-33, 35), the olfactory canals of *Mimipiscis* are broadly separated along most of their length (Figs. 3, 5). This is opposed to the morphology seen in all other early actinopterygians, where the canal is present as a single midline tube (Fig. 11.5-11.6, Node C). Related to this, the tracts of *Mimipiscis* are laterally divergent, again more closely resembling the condition in actinopterygian outgroups than that found in other Palaeozoic ray-finned fishes (Fig. 11.1-11.4, Node C). A further generalised condition apparent in *Mimipiscis* relates to the geometry of the labyrinth region. In previously described ray-finned fish endocasts, the crus commune of the anterior and posterior semicircular canal is typically set into the lateral wall of the cranial cavity (Fig. 11, Node C; e.g. Hamel and Poplin, 2008: figs. 13-14; Poplin, 1974: fig, 27). This is not the case in *Mimipiscis*; instead, the crus commune sits above the cranial cavity (Figs. 3-4). This arrangement is seen elsewhere in early members of actinopterygian outgroups (e.g. Chang, 1982: fig. 19; Säve-Söderbergh, 1952:fig. 9), and is developed to such an extent in some Palaeozoic chondrichthyans that the crus commune of the left canal almost meets with that of the right canal at the midline (Fig. 11.1; Schaeffer, 1981: fig. 14). Additionally, the general arrangement of the optic lobes in *Mimipiscis* appears to be primitive relative to *Kentuckia* and other Carboniferous actinopterygians. Whereas the optic lobes are conspicuously expanded in the endocasts of these stratigraphically younger ray-finned fishes, such that the optic lobes are the same width as the cerebellum (Fig. 11.5-11.6), the endocast of *Mimipiscis* increases gradually in width from the diencephalon to the cerebellum (Fig. 3). This matches the condition in sarcopterygians and chondrichthyans (Fig.11.1-11.3); e.g. Chang, 1982: fig. 17; Maisey, 2007: fig. 26), and is presumably the primitive arrangement for crown gnathostomes.

The unusual geometry of the brain seen in *Mimipiscis* reflects the small optic lobes of the genus in comparison to other actinopterygians. Enlargement of the optic lobes in ray-finned fishes is generally interpreted as reflecting the strong reliance on vision in this group (Goatley et al., 2010). The absence of large optic lobes in *Mimipiscis* is somewhat surprising, given its proportionally large eyes and presumed reefal ecology (Long and Trinajstic, 2010). An increased dependence on vision appears to have been derived within actinopterygians, based on the relatively small eyes found in the deepest branching members of the group (e.g. *Cheirolepis* Agassiz, 1843: Pearson and Westoll, 1979; *Osorioichthys* Casier, 1954: Taverne 1997) and early sarcopterygians (e.g. *Grossius* Schultze, 1973; *Guiyu* Zhu et al., 2009 *Miguashaia*; Schultze, 1973; *Onychodus* Newberry, 1857: Andrews et al., 2006; *Osteolepis* Agassiz, 1843; *Porolepis* Woodward, 1891). Assuming that the modest optic lobes of *Mimipiscis* represent a primitive condition rather than a reversal, then enlargement of the eyes in actinopterygians preceded corresponding architectural modifications to the brain. Endocast data for other early ray-finned fishes would provide a critical test of this inference.

5.7 CONCLUSION

The study of endocast morphology in early fossil vertebrates has a long scientific history, with the majority of detailed reconstructions available in the literature representing the results of studies conducted several decades ago (Appendix 4A). We applied CT techniques in order to investigate endocranial anatomy of two phylogenetically significant genera of early ray-finned fishes, *Mimipiscis* and *Kentuckia*. Detailed accounts of the endocranial chamber had been presented for both (Rayner, 1951; Gardiner, 1984), but no endocasts had been produced that would permit more direct comparisons with similar reconstructions available for other early vertebrates. Our virtual endocasts provide a critical test of previous anatomical interpretations of structure in these Palaeozoic ray-finned fishes. Apart from some details relating to specific patterns of innervation and proportions, these older accounts are largely accurate. However, our endocasts clearly show new features not apparent in existing descriptions. Key among these are the presence of long, separate olfactory tracts and small optic lobes in *Mimipiscis*. These conditions diverge from those found in other Palaeozoic actinopterygians, but agree with those apparent in sarcopterygians, suggesting that they are general features of crown osteichthyans.

Details of the neurocranium in general and its internal structure in particular have great potential in early vertebrate systematics, especially because consistent endoskeletal comparisons can be drawn across groups with radically different dermal skeletons. Despite this promise, relatively few characters pertaining to endocast morphology are incorporated in cladistic analyses (but see Coates, 1999; Friedman, 2007; Friedman et al., 2007; Brazeau, 2009; Zhu et al., 2009; Coates and Friedman, 2010; Davis et al., 2012). In part, this reflects the historical difficulty in obtaining endocast data from fossil specimens, with the consequence that reconstructions are only available for a small number of taxa within each major group of early vertebrates (Appendix 4A). This problem is clearly illustrated by our contribution, which provides the first endocast models for pre-Pennsylvanian ray-finned fishes. However, the proliferation of tomographic techniques and virtual palaeontology, combined with a wealth of excellently preserved neurocrania, provides the means of quickly and efficiently filling these gaps in our understanding of endocranial structure in early vertebrates. As in our analysis, we anticipate that the application of CT scanning to other previously studied taxa will offer a critical test of existing endocast reconstructions (e.g., Gai et al., 2011). The revisions and new discoveries from these classic specimens can be complemented with completely novel endocasts for previously uninvestigated materials. Both will represent important sources of raw morphological data that will represent an important addition to existing character sets for early vertebrates.

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CHAPTER 6: ENDOCRANIAL EVOLUTION IN EARLY GNATHOSTOMES

6.1 OVERVIEW

As espoused elsewhere in this thesis, the braincase is instrumental in understanding relationships between early jawed vertebrates. Its primary function is to house and protect the brain and sensory organs, such as the eyes and inner ears. As soft tissues are very rarely fossilised, and the brain almost never (although see Pradel et al., 2009a), the braincase provides the only evidence for its anatomy by means of the cranial endocast, an infilling of the negative space within the braincase. In addition to aspects of brain morphology, the braincase presents a large number of anatomical characters due to its complex structure. These characters relate to its general morphology and the paths of nerves and blood vessels. As such, the braincase is of vital importance when reconstructing relationships, and patterns of character transformation can be easily traced across the vertebrate tree of life. On a smaller scale, neurocranial characters have helped answer questions about evolutionary relationships within well-defined groups, for example in chondrichthyans (Maisey & Anderson, 2001), lungfish (Friedman, 2007), tetrapodomorphs (Coates & Friedman, 2010), and, most recently, Palaeozoic actinopterygians (Chapters 3, 4, 5).

Descriptions of braincases across the early vertebrate tree of life abound in the literature, and, as outlined above, have been used to reconstruct patterns of relationships in various groups. However, a broad scale review aimed at understanding the sequence of neurocranial character transformation across the vertebrate tree is lacking, although synapomorphic schemes for the entire skeleton have recently been organised (Friedman & Brazeau, 2010; Brazeau & Friedman, 2014). A failure to identify stem members of major assemblages such as chondrichthyans and osteichthyans has led to difficulties in identifying how specific anatomical features have evolved across different groups. Additionally, key features of the braincase, for example the conspicuous lateral processes, have been given assemblage-specific identifiers, making comparisons across different groups even more complicated. In placoderms, the supraorbital process marks the posterior boundary of the orbit; the anterior postorbital process provides the articulation point for the hyomandibula; one or two posterior postorbital processes (sometimes called vagal processes), provide the articular area for the branchial arches; and the craniospinal process (sometimes known as the supravagal process), forms the posterolateral corner of the braincase and typically supports the dermal skull roof. A disparate sets of terms is used to refer to these processes in, say, actinopterygians, where the back of the orbit is delimited by the postorbital process; the hyomandibula articulates on the lateral commissure; and the craniospinal process marks the posterior boundary of the otico-occipital fissure. Although the identity and homology of these processes has been much debated the question has only been answered with limited success (most notably in placoderms, e.g. Young, 1984; Elliott & Carr, 2010). The unprecedented character suite in *Janusiscus*, combining features typically associated with placoderms, chondrichthyans and osteichthyans, presents a unique opportunity to compare these processes across the entire diversity of gnathostomes and propose new homologies for them (Giles et al., 2015; Chapter 2; Appendix 1; see discussion below). The impact of *Entelognathus* (Zhu et al., 2013) and *Janusicus* (Giles et al., 2015) on the shape of the earlyvertebrate tree, particularly the stem membership of key vertebrate groups, means that such a review is timely. This chapter aims to elucidate braincase evolution in the earliest members of key vertebrate groups (placoderms, acanthodians, chondrichthyans and osteichthyans), with a strong focus on the stem membership of these groups and their constituent clades.

6.2 STEM GNATHOSTOMES

6.2.1 ‘PLACODERMI’

Placoderms were the first vertebrates with jaws. They appeared in the Early Silurian and dominated the Devonian seas before becoming extinct at the end of the Famennian (Young, 2010). Placoderms occupied a wide range of habitats, from the benthic *Gemuendina* (Gross, 1963) to nektonic *Rolfosteus* (Dennis & Miles, 1979) and predatory *Dunkleosteus* (Newberry, 1888) to herbivorous *Holonema* (Miles, 1971). The group has a chequered taxonomic history: although traditionally regarded as a monophyletic group (e.g. Denison, 1975; Miles & Young, 1977; Goujet, 1982, 1984a, 2001; Goujet & Young, 1995, 2004; Young, 1986, 2010; Janvier, 1996), Johanson (2002) and Johanson and Smith (2005) presented a range of arguments relating to the pectoral girdle and teeth that suggested placoderm paraphyly. This conclusion was further supported by comprehensive analyses of gnathostome interrelationships by Friedman (2007) and Brazeau (2009). Young (2010) refuted this result, proposing 16 'synapomorphies' to unite the placoderms as monophyletic. However, many of these are not valid as discrete anatomical characters (e.g "distinctive pattern of dermal bones in skull roof, cheek and operculum"; "simple jaws with only two or three pairs of bony tooth plates", Young, 2010: p.539; see critical breakdown of characters in Brazeau & Friedman, 2014). As such, almost all subsequent analyses, in particular those that examine placoderms in relation to other gnathostome groups and do not use a hypothetical ancestor, have resolved placoderms as a paraphyletic assemblage on the gnathostome stem (Davis et al., 2012; Zhu et al., 2013; Dupret et al., 2014; Long et al., 2014; Giles et al., 2015).

Despite advances in our understanding of placoderms as a whole, there are still several areas of uncertainty concerning the relationships between different placoderm groups. Within the context of placoderm monophyly, antiarchs are typically regarded as primitive and arthrodires derived (Goujet, 1984a; Goujet & Young, 1995, 2004; Donoghue et al., 2000; Donoghue and Smith, 2001; although Denison, 1978 regarded arthrodires and antiarchs as sister taxa occupying a derived position within placoderms). Although a similar topology is still commonly recovered (e.g. Brazeau, 2009; Long et al., 2014; Giles et al., 2015), Davis et al. (2012) and derivative analyses (Zhu et al., 2013; Long et al., 2014) favour a derived position for ptyctodontids. *Brindabellaspis* and petalichthyids appear closely allied. The position of rhenanids is less clear cut: Goujet & Young (1995, 2004) recovered a primitive position for this group, whereas Giles et al. (2015) placed rhenanids in a polytomy with arthrodires as the sister assemblage to *Entelognathus* and crown gnathostomes. Since its description, *Entelognathus* (Zhu et al., 2013) has typically been recovered as the sister taxon to crown gnathostomes (Zhu et al., 2013; Dupret et al., 2014) or crown gnathostomes plus *Janusiscus* and *Ramirosuarezia* (Giles et al., 2015).

The braincase of placoderms is ossified as a single unit, lacking the fissures seen in other groups of jawed vertebrates. The nasal capsules present an important exception: they are housed in the rhinocapsular ossification in almost all placoderms (Stensiö, 1963a, 1969; Denison, 1978), which is discrete from the remainder of the braincase; this separate ossification was proposed by Brazeau & Friedman (2014) as a potential placoderm synapomorphy, although against the weight of evidence of placoderms as a paraphyletic group. The interorbital septum is wide, resulting in a platybasic braincase. Tropibasy and platybasy are intended to reflect the general structure of the braincase, and are contingent upon three conditions: the width of the interorbital septum, the depth of the endochondral floor, and the presence or absence of a foramen for the internal carotid. These characters, and their usefulness as synapomorphies of different groups, have recently been discussed and critiqued by Maisey (2007) and Brazeau & Friedman (2014). Generalities in braincase structure can be drawn across placoderm groups: the orbital region tends to be long in petalichthyids and short in antiarchs; the otic region is generally long, with extra lengthening having occurred in rhenanids and pachyosteomorph arthrodires; and occipital length is highly variable, ranging from short in antiarchs, rhenanids and pachyosteomorphs to long in the 'dolichothoracids' and very long in the petalichthyids and coccostemorph arthrodires (Stensiö, 1963a).

6.2.1.1 Antiarchi

Antiarch neurocrania are rarely preserved, possibly due to a lack of mineralisation, but some details can be gleaned from the visceral face of the skull roof, such as the position and shape of the large semicircular canals (e.g. the Lochkovian *Yunnanolepis*, Liu, 1963; Zhang, 1978), and the passage of the endolymphatic ducts (e.g. the Givetian *Asterolepis*; Karatajute-Talimaa, 1963). Stensiö (1969) reconstructed a shallow braincase for *Bothriolepis* (from the Eifelian-Famennian), but additional details of the palatoquadrate, as described by Young (1984), indicate that the endocranium must have been somewhat deeper than first thought. Impressions of the braincase of *Minicrania* (Lochkovian) are preserved, as well as a partial internal cast, and these reveal the presence of large semicircular canals, a posteriorly placed anterior postorbital process, and a near-confluent supravagal and craniospinal process (Zhu & Janvier, 1996; Fig. 1A). A median dorsal fontanelle may have been present level with the anterior semicircular canals, lying above the laterally expanded hindbrain (Fig. 1B). No other details of the endocast are known. The articulation point of the hyomandibula is hard to discern, but it appears to be lateral to the posterior portion of the orbit on the anterior postorbital process. Despite the small size of the braincase in *Minicrania* (some 6 mm long in adults), the orbit is large, compared to the relatively smaller orbit of *Yunnanolepis* (Liu, 1963). A comparatively large orbit is also present in *Asterolepis* (Karatajute-Talimaa, 1963). Due to the mode of preservation of most known antiarch

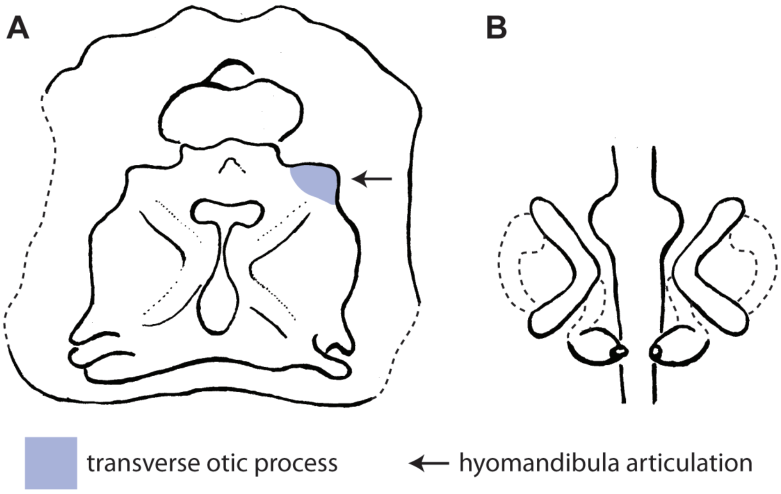

Figure 1 | Braincase and endocast anatomy of antiarch placoderms. A, Braincase of *Minicrania* in dorsal view (adapted from Zhu & Janvier, 1996). **B**, Hypothetical endocast of *Minicrania* in dorsal view (adapted from Zhu & Janvier, 1996).

braincases, it is unclear whether a parasphenoid was present. It is not clear from Denison's (1941) grinding series whether a parasphenoid was present in *Bothriolepis*. The tentative identification of a hyomandibular articulation identifies Zhu & Janvier's (1996) 'anterior postorbital process' as the transverse otic process. However, it is unclear whether the process that forms the posterolateral corner of the braincase corresponds to the vagal or craniospinal process, or indeed both.

6.2.1.2 Petalichthyida and *Brindabellaspis*

The petalichthyid braincase is known completely in *Macropetalichthys* (Stensiö, 1925, 1963b, 1969), with the occipital region also known in *Wijdeaspis* (Young, 1978), *Epipetalichthys* (Stensiö, 1925) and *Ellopetalichthys* (Stensiö, 1969). Although generalities cannot be drawn across the anterior regions of the braincase, all known petalichthyid taxa possess well developed vagal processes, a moderately sized cuccularis fossa, and a robust occiput with a long occipital stalk.

The braincase of *Macropetalichthys* (Stensiö, 1925, 1963b, 1969; Fig. 2A; Givetian) is well ossified. The general proportions of the neurocranium differ substantially from the few details known in antiarchs: the braincase is broad and shallow, with short otic and orbital regions and elongate ethmoid and occipital regions. There does not appear to be a separate rhinocapsular ossification, although Young (1980) suggests that the two units ossified separately originally and fused later in ontogeny. The orbits are small and dorsally-facing, with no distinct process at the posterior boundary, and the articular area for the hyomandibula is situated lateral to the orbit on the transverse otic process (the anterior postorbital process of Stensiö). An eyestalk attachment area is present. The two articular areas for the branchial arches (i.e. the vagal processes) straddle the subvagal fossa, and a

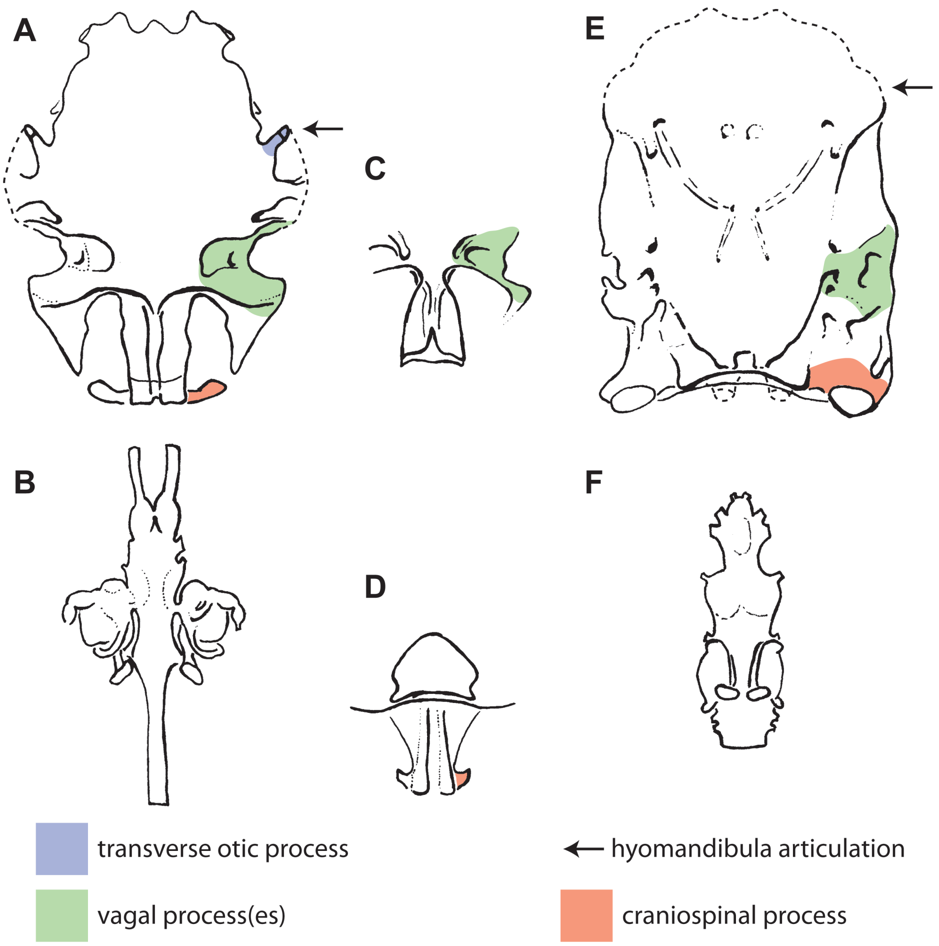

Figure 2 | Braincase and endocast anatomy of petalichthyid placoderms and *Brindabellaspis*. **A**, Braincase of *Macropetalichthys* in ventral view (adapted from Stensiö, 1969). **B**, Endocast of *Macropetalichthys* in dorsal view (adapted from Stensiö, 1963b). **C**, Occipital region of *Wijdeaspis* in ventral view (adapted from Young, 1978). **D**, Occipital region of *Ellopetalichthys* in ventral view (adapted from Stensiö, 1969). **E**, Braincase of *Brindabellaspis* in ventral view (adapted from Young, 1980). **F**, Endocast of *Brindabellaspis* in dorsal view (adapted from Young, 1980).

large cuccularis fossa, which is only partially roofed by dermal bone, sits between the vagal and craniospinal processes. The craniospinal processes are conspicuous and project from a long occipital stem. The dorsal aorta (or, as suggested by Young, 1978 for *Wijdeaspis*, the paired lateral aortae) ran along a groove (or grooves) along the midline of the occipital stem before diverging at the level of the vagal processes. Stensiö (1925: fig 1) figures grooves for the lateral dorsal aortae running anterolaterally along the basicranium before becoming buried slightly anterior to the foramen for the glossopharyngeal nerve, but these grooves are not shown in his later, more comprehensive reconstruction (Stensiö, 1969: fig 22A). The endocast is well preserved in *Macropetalichthys*, and appears to reflect the anatomy of the brain closely in parts (Fig. 2B). The area of the endocast corresponding to the forebrain is well developed, as are the olfactory bulbs, and the olfactory tracts are elongate. The widest part of the endocast corresponds to the cerebellar auricles and metencephalon. Although the semicircular canals are large, they differ from those of antiarchs in that the anterior and posterior canals do not resemble each other. The anterior canal is very short and tightly curved, and the utriculus and ampullae of each canal are bulbous. Additionally, the sacculus is extensive. The labyrinth as a whole is much more compact than in most other placoderm groups (see below).

A well-preserved occipital region has also been described in *Wijdeaspis* (Young, 1978; Fig. 2C; Eifelian). As in *Macropetalichthys*, there is a short anterior division and an elongate occipital stem. The ventral face of the occiput is clearly grooved for the lateral dorsal aortae. Although large, the posterior extent of the vagal process (supravagal process of Young) is less pronounced than in *Macropetalichthys*, and, at its lateral extent, turns posteromedially as a ridge. The cuccularis fossa is smaller than in *Macropetalichthys* and has an endocranial roof. The fossa, as well as the entire occipital region, is covered by the dermal skull, and the craniospinal processes are not preserved. As noted by Young (1978), as the massive vagal process, enlarged cuccularis fossa and occipital stem extending posterior to the skull roof are not seen in other petalichthyids, they may represent specialisations of *Macropetalichthys*, with *Wijdeaspis* displaying the primitive petalichthyid condition. The long, posteriorly oriented projections issuing from the back of the vagal process also seem to be unique to *Macropetalichthys.* The endocranial cavity in *Wijdeapis* is barely exposed and therefore has not been described.

The braincase of *Epipetalichthys* (Stensiö, 1925; Givetian) is poorly preserved, again due to being incompletely ossified, especially internally and in the otic region. The craniospinal processes and the posterior-most part of the occipital stem are not preserved. In other respects, the braincase appears to resemble *Macropetalichthys*, with the exception that the occipital region seems to be ossified in two pieces; it is unclear whether this is an artefact of incomplete mineralisation or if it reflects the presence of persistent fissures. The braincase is also partially known in *Ellopetalichthys* (Givetian), although only the occipital region is mineralised (Fig. 2C). The occipital stem is slightly shorter than in *Macropetalichthys*, but it is unclear whether the posterior margin of the stem and the craniospinal processes are preserved: Ørvig (1957: p.311) states that they are not present, but Stensiö (1969: fig. 24) reconstructs them as present on the basis of the same specimen. The orbits are rather larger than in *Macropetalichthys*, although still face dorsally. As in *Epipetalichthys*, Ørvig (1957) describes the occipital region as comprising two ossifications, although is is equivocal. There is no hypophyseal fenestra in petalichthyids, and no parasphenoid has been described.

The affinities of *Brindabellaspis* (Emsian) are unclear. Although first described as a rhenanid (Young, 1980), similarities with jawless outgroups prompted Janvier (1996) and other to suggest a branching position further towards the base of the placoderm assemblage. More recently, analyses have placed *Brindabellaspis* crownward of antiarchs and either in a clade with petalichthyids (e.g. Dupret et al. 2014) or in a polytomy with petalichthyids and more crownward taxa (e.g. Brazeau, 2009, Davis et al. 2010, Zhu et al. 2013, Long et al. 2014). Giles et al. (2015), however, recovered *Brindabellaspis* in a polytomy with antiarchs. Although the braincase of *Brindabellaspis* is ossified as a single unit, the presence of internal laminae between the nasal capsules and the rest of the braincase prompted Young (1980) to suggest that these regions originally ossified separately but fused at some point during ontogeny. The neurocranium is heavily ossified, and is broad and unusually deep (Fig 2E). The orbit is large, with a well-developed attachment area for an eyestalk; the posterior margin of the orbit almost reaches the halfway point of the braincase, and is partially enclosed by the extensive subocular shelf. The hyomandibula articulates laterally and almost anterior to the orbit. Uniquely for a placoderm, the lateral dorsal aortae are enclosed in canals on the basicranium for part of their length. The vagal processes (termed the infravagal and supravagal process and postglossopharyngeal ridge by Young) flank the posterior paravagal fenestra, and craniospinal processes are prominent. The endocast is fairly well known in *Brindabellaspis* (Fig. 2F). Olfactory lobes do not appear to be developed, but the olfactory tracts are elongate and anterolaterally directed. The area of the endocast corresponding to the mid- and forebrain is narrow, with the greatest width being attained by the metencephalon, as in *Minicrania* and *Macropetalichthys*. Along with a large sacculus, the anterior and posterior ampullae are partially preserved, but details of the semicircular canals are unknown (the anterior canal was lost during preparation). Cerebellar auricles may have been developed, but poor preservation in this region of the endocast makes this unclear. Young (1980) states that a utricular recess is not present, but this appears hard to judge on the basis of the figured material.

Macropetalichthys and 'petalichthyid-like forms' such as *Brindabellaspis* share with jawless outgroups a lateral expansion of the braincase surrounding the orbit (Brazeau & Friedman, 2014). Similarly, the hyomandibula articulates on this process - lateral and often slightly anteriorly to the orbit - in *Macropetalichthys* (Stensiö, 1925) and *Brindabellaspis* (Young, 1980). The articulation point is posterior to the orbit in *Romundina* (Ørvig, 1967), arthrodires (e.g. *Lehmanosteus*: Goujet, 1984; *Parabuchnosteus*: White & Toombs, 1972), and crown gnathostomes (e.g. *Cladodoides*: Maisey, 2005; *Eusthenopteron*, Jarvik, 1980; *Mimipiscis*: Gardiner, 1984). Brazeau & Friedman (2014) also note that the facial (VII) nerve branches anterior to the postorbital process in *Brindabellaspis* (Young, 1980) and *Macropetalichthys* (Stensiö, 1925), a condition again shared with jawless outgroups (e.g. osteostracans: Janvier, 1985); the division takes place posterior to the postorbital process in *Romundina* (Dupret et al., 2014), arthrodires (e.g. *Kujdanowiaspis*: Stensiö: 1963b) and crown gnathostomes.

6.2.1.3 Rhenanida

The braincase is fairly well known in three rhenanids, *Jagorina* (Frasnian) and *Asterosteus* (Eifelian), described by Stensiö (1950, 1969; Fig. 3A,C), and *Bolivosteus* (Goujet et al., 1985; Eifelian). In all taxa, the braincase is slender and elongate. The dorsal roof is barely wider than the ventral floor, and the lateral processes are much less pronounced than in most other placoderm groups. The postorbital process (suborbital process of Stensiö)is absent in *Bolivosteus*. It barely projects above the orbit in *Jagorina*, although it is slightly more extensive in *Asterosteus.* The hyomandibula articulates on an antero-posteriorly elongate lateral process, identified here as the transverse otic process and by Stensiö as the anterior postorbital process. In *Bolivosteus*, this process extends posteriorly to the level of the craniosponal process. Young (1980) suggests that the transverse otic process and vagal process (identified by him as the anterior and posterior postorbital processes) are confluent in rhenanids. However, there is no evidence in Stensiö’s or Janvier et al.’s original figures for a posterior projection, and it seems likely that the process simply represents an elongate transverse otic process. The posterolateral corner of the braincase extends dorsally as a slender process. This part of the braincase is rather modified in comparison to other placoderms, and it is difficult to interpret this process. It sits just posterior to the exit of the vagus (X) nerve and forms the anterior boundary of the cuccularis fossa, suggestive of it being the craniospinal process, albeit one pierced by the jugular vein. This is contrary to the interpretation of supravagal process by Stensiö (1969), Jarvik (1980) and Young (1980). The process in *Bolivosteus* is much less developed than in either *Jagorina* or *Asterosteus.* As in antiarchs and petalichthyids, parasphenoids in rhenanids are unknown. The endocast of *Jagorina* was described by Stensiö (1950; Fig. 3B). It is tubular, and appears to be a poor fit for the brain. The morphology of the telencephalon and the olfactory tracts is unknown. The entire endocast is narrow, being only slightly wider in the region of the mesencephalon. The labyrinth is not as large relative to the brain as in petalichthyids, although the sacculus and ampullae are robust and the semicircular canals wide. Although a utricular recess is labeled by Stensiö, Young (1980) points out that it is hardly developed. The endocast is also partially known in *Bolivosteus* from a radiograph, and largely resembles that of *Jagorina*. A partial braincase is preserved in *Nefundina* (Leliévre & Carr, 2009).

6.2.1.4 'Acanthothoraci'

The validity of acanthothoracids as a natural group is dubious, a problem compounded by a failure to include multiple members of the purported group in phylogenetic analyses; typically, only *Romundina* is included. Given the lack of any other evidence, they will be considered together here. The braincases of four taxa are known in some detail: *Romundina* (Ørvig, 1975; Dupret et al., 2014; Lochkovian), *Arabosteus* (Olive et al., 2011; Pragian-early Emsian), *Kosoraspis* (Gross, 1958, 1959; Stensiö, 1969; Pragian) and *Radotina* (Gross,

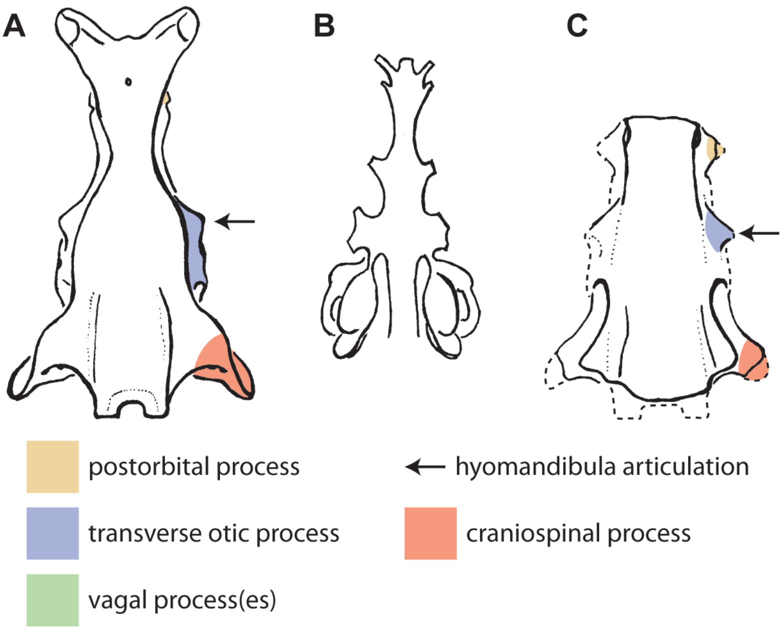

Figure 3 | Braincase and endocast anatomy of rhenanid placoderms. A, Braincase of *Jagorina* in ventral view (adapted from Stensiö, 1969). **B**, Endocast of *Jagorina* in dorsal view (adapted from Stensiö, 1969). **C**, Braincase of *Asterosteus* in ventral view (adapted from Stensiö, 1969).

1958, 1959; Stensiö, 1969; Lochkovian). The braincases of *Romundina* and *Arabosteus* are broad and deep, with a separate rhinocapsular ossification, dorsally directed orbits, a laterally developed transverse otic process and bifid vagal process. In contrast, the braincases of *Kosoraspis* and *Radotina* are slender and comprise only a single ossification, with small transverse otic processes and a single vagal process.

First described by Ørvig (1975), the braincase of *Romundina* is broad and fairly deep, especially in the orbital region (Fig. 4A). The rhinocapsular ossification is separate from the remainder of the braincase. The orbits are dorsolaterally facing, and there is no supraorbital process, but the hyomandibula articulates lateral to the orbit on the transverse otic process (named the anterior postorbital process by Ørvig). Moreover, the orbits are so large that the interorbital septum is thin, making the braincase appear tropibasic. The suborbital shelf is extensive, and an eyestalk is present. More posteriorly, the vagal process (posterior postorbital process of Ørvig) is strikingly similar to that of arthrodires such as *Kujdanowiaspis* in being bifid and laterally extensive. Although the specimen was radiographed, few details of the endocast and labyrinth are discernable. Dupret et al. (2014) CT scanned and redescribed the braincase of *Romundina*, and the endocast is partially figured. The metencephalon appears to be very wide and the labyrinth large relative to the brain, with slender semicircular canals and large ampullae and sacculus (Dupret et al. 2014: fig. 2e).

The braincase of *Arabosteus* (Olive et al., 2011), although incompletely preserved, largely resembles that of *Romundina*: it is broad and fairly deep, with a transverse otic process projecting lateral to the orbit and a bifid vagal process. The cuccularis fossa (labeled by Olive et al. as the peribranchial fossa) is deeper than that of *Romundina*, but the craniospinal process is similarly pronounced. The fact that the region anterior of the orbit is not preserved

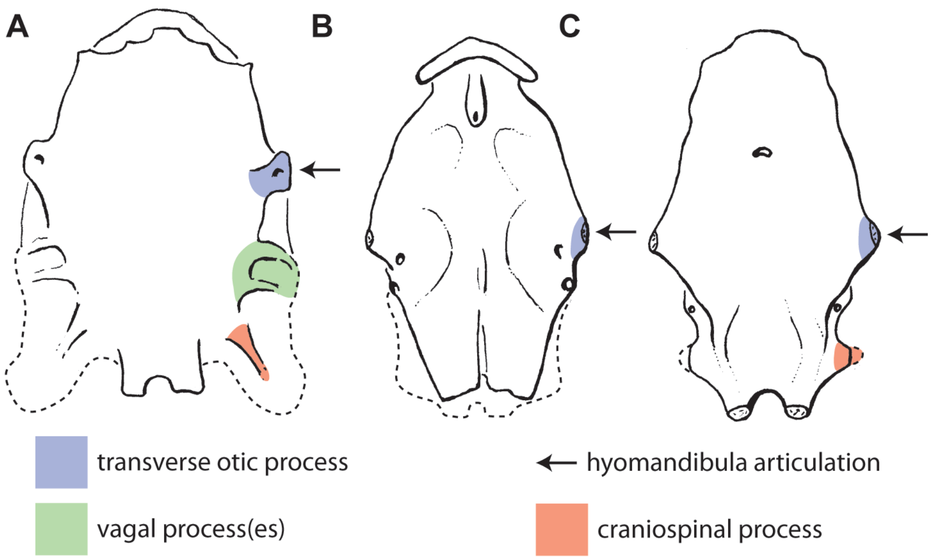

Figure 4 | Braincase and endocast anatomy of acanthothoracid placoderms. A, Braincase of *Romundina* in ventral view (adapted from Ørvig, 1975 and Dupret et al., 2014). **B**, Braincase of *Kosoraspis* in ventral view (adapted from Gross, 1959). **C**, Braincase of *Radotina* in ventral view (adapted from Gross, 1959).

suggests the presence of a separate rhinocapsular ossification that has become detached. The endocranial cavity is partially exposed, but few details can be determined.

Endocranial morphology in the other known acanthothoracids, *Kosoraspis* and *Radotina* (Gross, 1958, 1959; Stensiö, 1969; Fig. 4B-C) differs significantly from the two already described. The braincase in *Kosoraspis* and *Radotina* is ossified as a single unit, and is slender and elongate, particularly in *Radotina*. Although they lack a postorbital process, the transverse otic process (identified by Gross as the anterior postorbital process) barely projects from the main body of the braincase, and is situated well posterior of the orbit. A vagal process seems to be entirely absent. A modest craniospinal process is present in *Radotina*, but this portion of the braincase is not preserved in *Kosoraspis*. *Kosoraspis* posseses a splint shaped parasphenoid, the ventral surface of which is denticulated and pierced by the buccohypophyseal canal.

6.2.1.5 Ptyctodontida

The ptyctodontid braincase is known in varying amounts of detail in *Austroptyctodus* (Miles & Young, 1977; Long, 1997; Trinajstic et al., 2012), *Chelyophorus* (Eichwald, 1859; Long, 1997), *Masterpiscis* (Trinajstic et al., 2012), *Kimbryanodus* (Trinajstic & Long, 2009), *Rhamphodopsis* (Miles, 1967) and *Ctenurella* (Ørvig, 1962). It differs from that of other placoderms in comprising at least three pairs of ossifications, presumably joined by cartilage in life: ethmoid, orbital, and occipital. The braincase is heavily modified largely due to structural changes in the dermal skeleton, for example large, dorsally-placed orbits. The braincase is best known in *Austroptyctodus gardineri* (Frasnian), originally described by Miles and Young (1977) as *Ctenurella gardineri* and later reassigned by Long (1997). Further consideration was given to *Austroptyctodus* by Trinajstic et al. (2012). It is ossified in three pieces, with the ethmoid ossification being interpreted by Trinajstic et al. (2012) as equivalent to the rhinocapsular of other placoderms. A postorbital process appears to be entirely absent, and an attachment area for the eyestalk is present in the orbital ossification. The lateral face of the braincase is complex, with two distally expanded processes that partially fuse in larger specimens, but there is no facet for the hyomandibula, which is believed to have articulated on the dermal cheek. The otic capsule appears to have been entirely cartilaginous, and no details of the inner ear or endocast can be discerned. The occipital region is short, with a dorsal occipital process and ventral glenoid process developed on the posterior face of the occiput. The homology of these processes with those of other placoderms is difficult to reconcile.

The braincase of *Chelyophorus* (Long, 1997; Famennian) and *Masterpiscis* (Trinajstic et al., 2012; Frasnian) largely agree with that of *Austroptyctodus*. Trinajstic & Long (2009) described the braincase of *Kimbryanodus* (Frasnian) as resembling that of other ptyctodonts, but with a shorter occipital region. Partial neurocrania have also been identified in *Rhamphodopsis* (Miles, 1967; Eifelian) and *Ctenurella* (Ørvig, 1962; Givetian-Frasnian), but few details can be described.

6.2.1.6 Arthrodira

As the most diverse and speciose assemblage, more neurocrania have been described for arthrodires than any other placoderm group. A number of these braincases are known from fairly derived arthrodire taxa (Carr & Hlavin, 2010) which occur relatively late in the group's history. A further problem arises from the fact that many Middle Devonian and later placoderms reduce or stop mineralising their braincases (Stensiö, 1925, 1963a; Holmgren & Stensiö 1936; Ørvig 1951, 1957b; Long, 1995, Otto, 2005), with the result that little of the braincase is preserved in many brachythoracids, such as *Dunkleosteus* (Stensiö, 1969; Carr & Hlavin, 2010) and *Mcnamaraspis* (Long, 1995). Recent analyses (e.g. Dupret et al., 2007, 2009) have found that most arthrodires can be classified into two assemblages: the paraphyletic 'Actinolepidoidei' and Phlyctaenoidei. Phlyctaenoidei includes many of the most derived and specialised arthrodire groups, including the Pachyosteomorphi, Aspinothoraci and Selenosteidae.

6.2.1.6.1 'Actinolepidoidei'

Lehmanosteus (Goujet, 1984a; Fig. 6A; Pragian-Emsian) was resolved by Dupret et al. (2007, 2009) as one of the deepest diverging members of the 'Actinolepida', and in a similar position by Johnson et al. (2000). Its braincase is relatively long and slender, with a broad dorsal surface and somewhat narrower ventral face; the ventral part of the occipital region is particularly narrow. The supraorbital process (equivalent to the postorbital process) is modest but clearly present, and the anterior postorbital process (equivalent to the transverse otic process) is short but stout. A bifid vagal process (Goujet's posterior postorbital process), particularly the more anterior projection, is well developed. The craniospinal process (Goujet's supravagal process) is faint, and lies anterior to the posterior margin of the braincase. An eyestalk attachment area is present in the orbit. The parasphenoid is small, denticulated, and pierced by the buccohypophyseal canal.

Kujdanowiaspis (Lochkovian-Pragian) is typically regarded as a fairly primitive arthrodire, although it is nested within its group (e.g. Dupret et al., 2007, 2009), and is prevalent as a representative of arthrodires in phylogenetic analyses. The braincase of *Kujdanowiaspis* was originally described by Stensio (1963a, 1969), with further details added by Dupret (2010; although he was unable to study the ventral surface as this is not exposed in any remaining

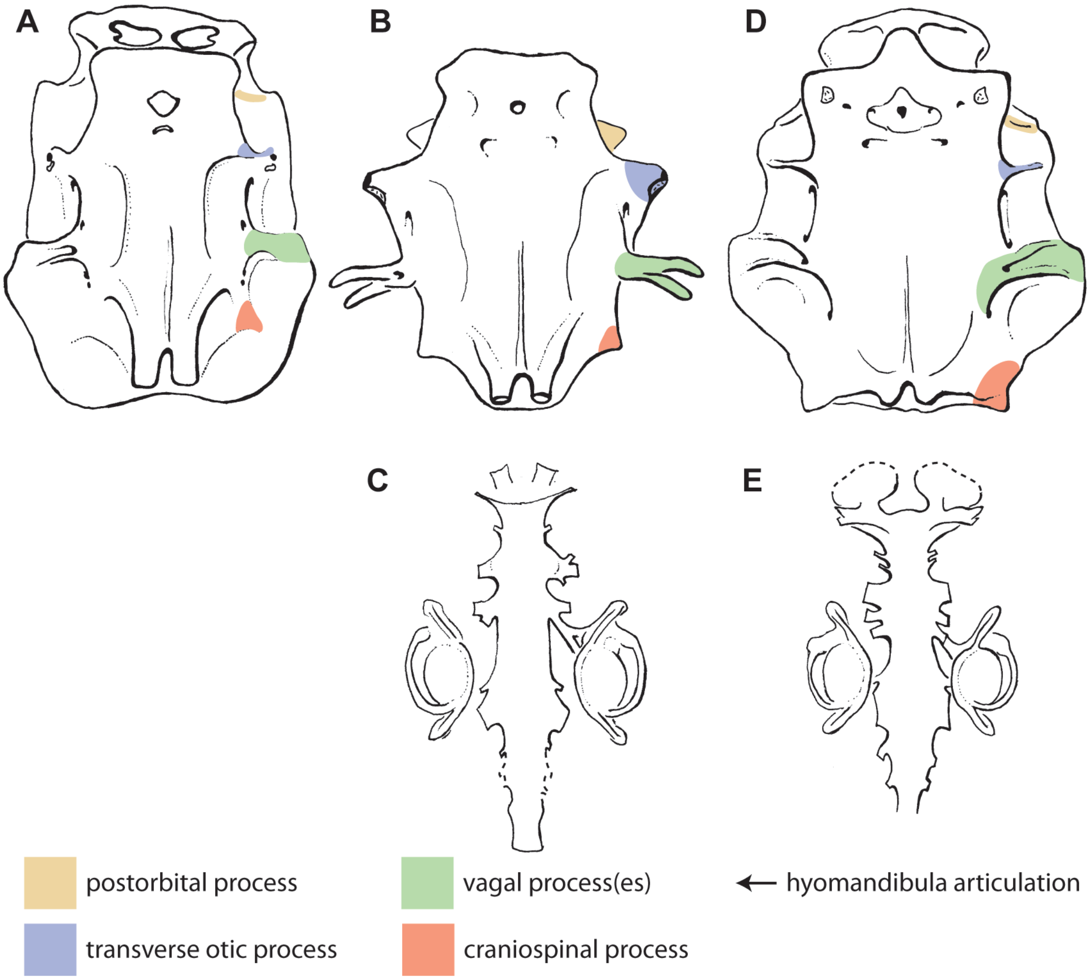

Figure 5 | Braincase and endocast anatomy of arthrodire placoderms. A, Braincase of *Lehmanosteus* in ventral view (adapted from Goujet, 1984). **B**, Braincase of *Kujdanowiaspis* in ventral view (adapted from Stensiö, 1963a). **C**, Endocast of *Kujdanowiaspis* in dorsal view (adapted from Stensiö, 1963b). **D**, Braincase of *Dicksonosteus* in ventral view (adapted from Goujet, 1984). **E**, Endocast of *Dicksonosteus* in dorsal view (adapted from Goujet, 1984).

specimens). The braincase is fairly long and low, and the dorsal surface is not much wider than the ventral floor, particularly anterior to the posterior postorbital processes (Fig. 6B). The rhinocapsular division is ossified separately, and a separate dermal rostropineal plate is also present. There is a distinct postorbital process (originally described as the supraorbital process), well developed transverse otic process (anterior postorbital process), elongate and bifid vagal processes (posterior postorbital processes), and a craniospinal process (supravagal process), the latter of which is positioned some way anterior to the posterior boundary of the braincase and thus resembles that of *Lehmanosteus*. The transverse otic process appears slight when viewed ventrally but is massive in dorsal view, and provides the articulation point for the hyomandibula. Distinct grooves, bordered by ridges, are present on the basicranial surface, and these mark the path of the lateral dorsal aortae. Stensio (1963b, 1969) extensively described the braincase of *Kujdanowiaspis* (Fig. 6C). It is essentially tubular, suggesting the fit with the brain was poor, and not much wider in the region of the metencephalon. The telencephalon is fairly wide, with moderately long olfactory tracts. There is no suggestion of cerebellar auricles. As in many other placoderms, a thick bony wall separated the large labyrinth from the rest of the endocavity. The sacculus is quite large but the semicircular canals slender, although a mechanically prepared specimen figured by Dupret (2010: fig. 11) shows at least the anterior canal to be more robust than indicated by Stensio (1963b: fig. 28; 1969: fig. 43). The parasphenoid is discussed by Stensio (1942) and Dupret (2010): although rarely preserved, there is a distinct depression upon the basicranium in which it would have sat. Fragments that have been recovered indicate that it was quadrangular in shaped, and that the buccohypophysial canal was most likely closed ventrally.

Some of the material considered by Stensio (1945) to belong to *Kujdanowiaspis* was removed to a new genus, *Erikaspis* (Lochkovian), by Dupret et al. (2007). Although the neurocranium is incomplete, it appears to be relatively longer than that of *Kujdanowiaspis*, but otherwise similar.

6.2.1.6.2 Phlyctaenioidei

The arctaspidid *Dicksonosteus* (Pragian-Emsian) has been thoroughly described by Goujet (1984a; Fig. 5D). The braincase is broad and low, and the dorsal surface of the endocranium more laterally extensive than the ventral. A postorbital process (described by Goujet as the supraorbital process) is present only as a faint ridge and the transverse otic process (anterior postorbital process) is narrow, being rather less pronounced than in *Kujdanowiaspis* and other 'actinolepidoids'. The vagal process (posterior postorbital process) is bifid, but each division resembles the slender process of more derived arthrodires such as *Buchanosteus* rather than those of *Kujdanowiaspis*. The craniospinal process (supravagal process) is posteriorly positioned, and is level with the posterior face of the braincase. Grooves on the basicranium for the lateral dorsal aortae are only faintly defined. The parasphenoid is broad and short with an anterior process, a denticulated ventral surface and a large buccohypophyseal canal. Again, the endocavity is tubular, and appears to reflect little of the underlying brain morphology (Fig. 5E). The widest region is level with the vagus (X) nerve, and corresponds to the medulla, although the telencephalon is also fairly wide, and the olfactory tracts short. The ampullae of the semicircular canals are small and the canals themselves slender. Although the full extent of the sacculus is unknown, it appears to be large.

Goujet (1984a) also presents the braincase of *Arctolepis* (Pragian-Emsian), figured by Stensiö (1963a: fig. 15; 1969: fig. 11) as an unnamed 'dolichthothoracid'. The endocranium broadly resembles that of *Dicksonosteus*, with the important exception that the rhinocapsular is a separate ossification (Fig. 5F). The craniospinal processes (identified by Stensiö and Goujet as the supravagal processes) are relatively smaller and the transverse otic process (anterior postorbital process) more robust. The parasphenoid is also narrower than in *Dicksonosteus*. The braincase of *Heintzosteus* (Goujet, 1984a) is incompletely preserved, but similar in detail to those of *Dicksonosteus* and *Arctolepis*.

6.2.1.6.3 Brachythoraci

Of the buchanosteids, the neurocranium is best known in *Buchanosteus confertituberculatus* (Fig. 6A; Pragian-Emsian), descriptions of which have been published by Hills (1936), White (1952), Young (1979) and Long et al. (2014). The braincase as a whole is broad and low, with the rhinocapsular bone ossified separately from the remainder of the braincase, and the rostropineal also a separate dermal bone. The back of the orbit is marked by a pronounced process referred to by Young (1979) as the post-ocular crest; Stensiö (1963b) identified it as the anterior postorbital process. Comparison with the placoderms described above suggests this is the postorbital process. The process considered by Young to be the 'true' anterior postorbital process is positioned more posteriorly, and distally provides the articular area of the hyomandibula, identifying it as the transverse otic process. The vagal process (posterior postorbital process) is narrow and elongate, and forms the anterior margin of the large, shallow cucullaris fossa. Long et al. (2014) note that it resembles the long, bifid postorbital process of primitive arthrodires such as *Kujdanowiaspis*. The posterolateral corner of the braincase is formed by the craniospinal process. The endocast is well preserved, although tubular in form (Fig. 6C). The telencephalon is short but wide, with very short olfactory tracts leading to the nasal capsules, and the metencephalon is wide. The labyrinth is only partially preserved, with moderately sized ampullae and sacculus and a clearly defined utriculus. The horizontal semicircular canal is fairly slender and describes a

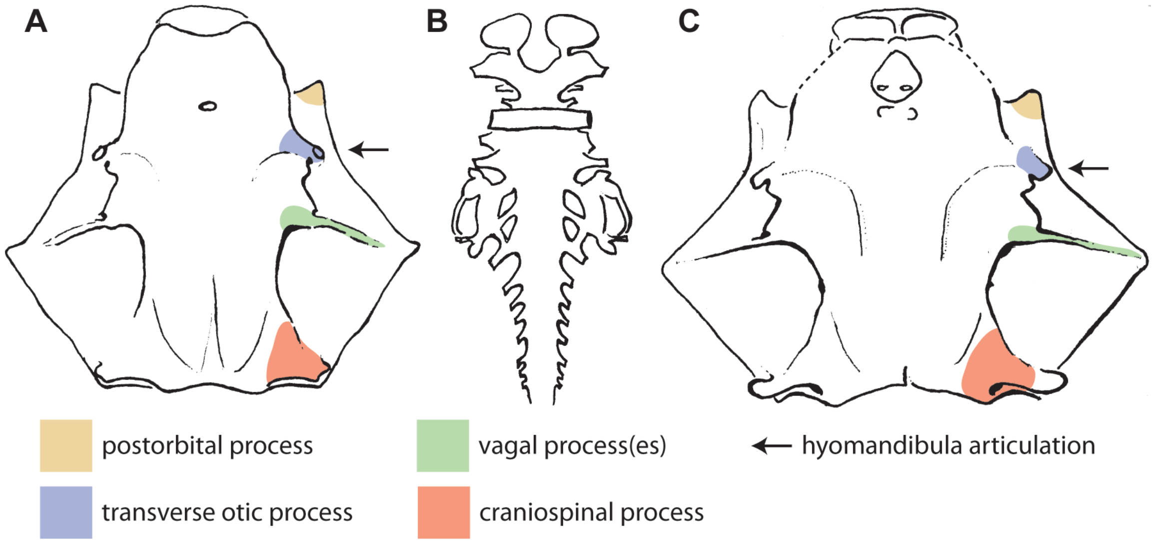

Figure 6 | Braincase and endocast anatomy of arthrodire placoderms. A, Braincase of *Buchanosteus confertituberculatus* in ventral view (adapted from Young, 1979). **B**, Endocast of *Buchanosteus confertituberculatus* in ventral view (adapted from Young, 1979). **C**, Endocast of *Parabuchanosteus* in ventral view (adapted from White & Toombs, 1972).

wide arc, but the paths of the anterior and posterior canals can only be identified from grooves on the underside of the dermal skull roof. The parasphenoid varies somewhat in shape and size, and Young (1979) notes that breadth of the parasphenoid increases with width, and growth thus appears to be allometric. The ventral surface is denticulated, and pierced by the buccohypophyseal canal. In contrast with *Kujdanowiaspis*, the parasphenoid is intimately associated with the endocranium, and Young (1979) postulates that this may be typical for 'more advanced' brachythoracids.

Another species of *Buchanosteus*, *B. guangxiensis*, generally resembles *B. confertituberculatus*, but the craniospinal process is hardly developed (Wang, 2005). Similarly, the braincase of *Parabuchanosteus* (White & Toombs, 1972; Emsian) generally agrees with that of *B. confertibuberculatus*, except for being slightly broader, and has only very faint craniospinal processes. However, the para-articular processes, which extend off the back of the craniospinal processes, are very pronounced.

Parts of the braincase are known in other buchanosteids, such as *Errolosteus* (Young, 1981; Emsian). Although the nasal capsule and orbital region are mineralised, much of the braincase is obscured by matrix and thus cannot be fully described. The endocast is more accessible: the region corresponding to the telencephalon is wide, with short olfactory tracts. In taxa where the endocranium is not preserved, for example in the buchanosteid *Arenipiscis* (Young, 1981; Emsian), details such as the position of the lateral processes and labyrinth can be determined from the visceral face of the skull roof.

Beyrichthyosteus (Otto, 2005; Givetian) is a eubrachythoracid that shares a number of features with more primitive arthrodire groups. Only the region anterior to the orbits is preserved, and rhinocapsular division appears to be ossified with the ethmoid region. The orbital wall is simple, with no visible myodomes, and an eyestalk attachement area does not appear to be present. The endocavity is unknown. The parasphenoid is rounded in shape with a central cusp, and the ventral surface is not pierced by a buccohypophysial foramen. It generally resembles the parasphenoid of *Coccosteus* (Miles & Westoll, 1968).

6.2.1.6.4 Coccosteomorphi

The braincase in coccosteomorphs displays a highly specialized morphology in addition to being poorly ossified, with part of the ethmoid region and much of the occipital region being cartilaginous. The endocranium is typically high and narrow in shape and the large size of the orbits results in a very thin interorbital septum, giving the impression of tropibasy (Stensiö, 1963a; Otto, 2005). There is no facet for the articulation of the hyomandibula on the braincase, but the hyomandibular nerve exits level with the posterior part of the orbit.

Only the front two thirds of the long and slender braincase is ossified in *Tapinosteus* (Stensiö, 1963a, 1969; Fig. 7B; Frasnian). The dorsal roof of the braincase is only slightly wider than the ventral surface. Dorsally, the pineal foramen is greatly enlarged to form the orbitotemporal fontanelle, which extends posteriorly to the level of the labyrinth, and a further occipital fontanelle extends posteriorly from the level of the endolymphatic ducts. There is no postorbital process. The process delimiting the back of the large orbit has two portions: the anterior portion is stout and anterolateral directed, and the posterior portion is elongate and posterolaterally directed. The hyomandibular nerve exits between these two processes, and the glossopharyngeal exits immediately behind the more posterior of the two. Stensiö (1963a, 1969) identified the more posterior as the anterior postorbital process, and the more anterior as the basitrabecular process. Although it is difficult to reconcile these processes with those of other placoderms, the placement of the hyomandibular nerve suggests that the more anterior corresponds to the transverse otic process. The shape of the more posterior recalls the vagal process of brachythoracids, but the position of the glossopharyngeal nerve presents difficulties: in brachythoracids, the glossopharyngeal exits anterior to the vagal process, but in *Tapinosteus*, the process in question is positioned anterior to the nerve exit. As such, the posterolaterally directed process in *Tapinosteus* may simply be a peculiar posterior extension of the transverse otic process. Stensiö identifies a slight protuberance posterior to the glossopharyngeal exit as the craniospinal process (equivalent to the vagal process of other placoderms). The posterior portion of the occiput is not preserved, but based on the relative position of the skull roof the cucullaris fossa must have been elongate. A craniospinal process forming the posterolateral corner of the braincase is not preserved, but was inferred by Stensiö to have been massive. The endocast (at least anterior to the occiput) is well known, and the fact that divisions of the brain are discernable, rather than the entire endocast being tubular, suggests that it reflect the morphology of the brain better than in more primitive arthrodires (Fig. 7C). The region of the endocast corresponding to the telencephalon is slightly wider than the rest of the forebrain, but not to the same extent as in *Kujdanowiaspis*. The forebrain gradually widens posteriorly to the metencephalon, then decreases further posteriorly. The labyrinth sits very close to the endocavity, and there was most likely not room for the thick bony wall present in taxa such as *Kujdanowiaspis*, *Dicksonosteus* and *Buchanosteus*. The labyrinth is also set into the endocranial wall in *Pholidosteus*, but the situation is unclear in *Coccosteus*. The labyrinth is fairly large relative to the endocast, and the anterior and posterior semicircular canals are wide. The full extent of the sacculus is unknown, but it was long and low. A utriculus is present.

The general shape of the neurocranium in *Pholidosteus* (Frasnian) is the same as in *Tapinosteus*, but somewhat more slender (Stensiö, 1963a, 1969; Fig. 7A); the dorsal roof is

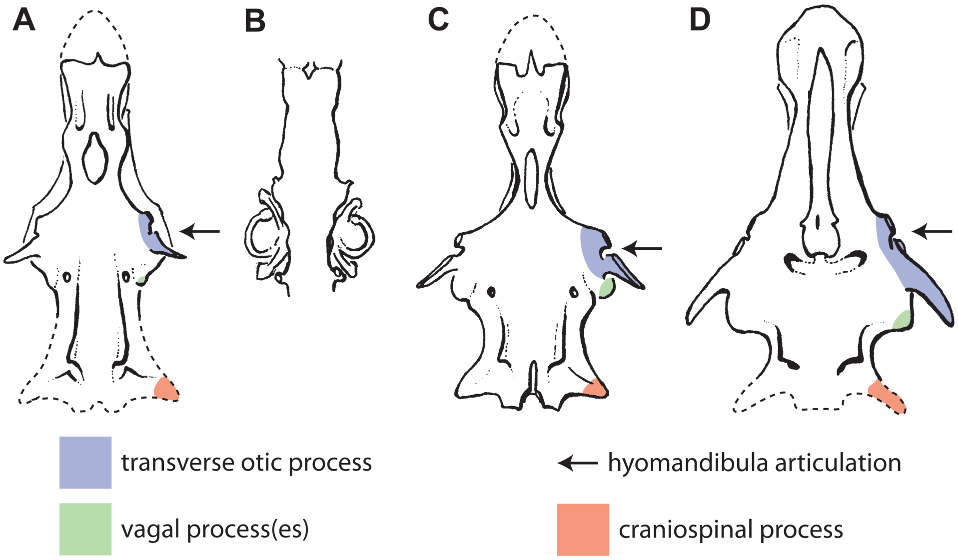

Figure 7 | Braincase and endocast anatomy of arthrodire placoderms. A, Braincase of *Tapinosteus* in ventral view (adapted from Stensiö, 1963a). **B**, Endocast of *Tapinosteus* in dorsal view (adapted from Stensiö, 1963a). **C**, Braincase of *Pholidosteus* in ventral view (adapted from Stensiö, 1963a). **D**, Braincase of *Trematosteus* in ventral view (adapted from Stensiö, 1963a).

hardly wider than the ventral floor of the braincase. The otic region is rather wide in *Pholidosteus*, and the transverse otic process (basitrabecular process and anterior postorbital process of Stensiö, 1963) is more robust. The orbital fontanelle is elongate, but the posterior limit and entirety of the occipital fontanelle is unmineralised and therefore cannot be deduced. An elongate and lozenge shaped parasphenoid with a denticulated ventral surface is present, but is not pierced by the buccohypophyseal canal.

The endocranium of *Coccosteus* (Eifelian-Givetian) is known mainly from residues and impressions on the visceral surface of the skull roof (Stensiö, 1963; Miles & Westoll, 1968; Otto, 2005). As such, it is unclear whether a separate rhinocapsular ossification was present; Miles and Westoll (1968: fig. 16) reconstructed it as such on the basis that an internasal is present, whereas Stensiö (1963a: fig. 54) interpreted it as absent. Otto (2005) points out that an internasal is also present in *Beyrichosteus*, which lacks a separate rhinocapsular, and thus this cannot be used as a line of evidence. Based on the morphology of taxa more closely related to *Coccosteus*, it seems more likely that the neurocranium was ossified in one piece.

6.2.1.6.5 Pachyosteomorphi

The pachyosteomorphs represent some of the most derived arthrodire taxa (Carr & Hlavin, 2010), and will only be briefly considered. The braincase is typically short, although depth and width is highly variable depending on the shape of the head, and the rhinocapsular may be ossified in several pieces (Stensiö, 1963a). The reduction of mineralisation is extensive, and typically only the ethmoid and anterior-most part of the orbital region is mineralised, as in *Eastmanosteus* (Dennis-Bryan, 1987), *Mcnamaraspis* (Long, 1995) *Trematosteus* (Stensiö, 1963a, 1969), *Latocamurus* (Long, 1988a), *Rolfosteus* (Dennis & Miles, 1979), and *Dunkleosteus* (Stensiö, 1963a, 1969). Some aspect of braincase morphology is known from impressions on the visceral surface of the skull roof in *Enseosteus*, *Parawalterosteus*, *Brachyosteus*, and *Homosteus* (Stensiö, 1969). Of the neurocranium and associated dermal bones, only the parasphenoid is known in *Harrytoombsia* (Miles & Dennis, 1979), *Bruntonichthys*, (Dennis & Miles, 1980) and *Tubonasus* (Long, 1988a). Although the ethmoid region is preserved in *Rolfosteus* (Dennis & Miles, 1979), there is no associated parasphenoid, and the available neurocranial material does not appear to bear an attachment surface for one.

The braincase is best ossified in *Trematosteus* (Stensiö, 1963a; Fig. 7D; Frasnian). The ethmoid region is very long, and the braincase is extremely deep anterior to the transverse otic process (basitrabecular and anterior postorbital processes of Stensiö), and roughly half this depth posterior to it. The dorsal roof of the endocranium is even narrower than the ventral floor, and the suborbital shelves are well developed. As in coccosteomorphs, the transverse otic process, identified by the position of the hyomandibular nerve, is posteriorly positioned and posterolaterally oriented, and the hyomandibula does not articulate on the braincase. A fairly robust vagal process is present. The parasphenoid is very long and narrow, and extends over half the length of the braincase. Its ventral surface is pierced by the buccohypophyseal foramen.

Unusually for a derived arthrodire, the occipital region is ossified in *Erromenosteus diensti* (=*Paraleiosteus* of Stensiö, 1959) and *E. inflatus* (=*Leiosteus*). (Stensio, 1963a; Otto, 2005). The craniospinal process (identified by Stensiö as the supravagal process) is very well developed and abuts the skull roof. Almost nothing is known of the endocast, but the region corresponding to the myelencephalon was presumable elongate.

6.2.1.7 ***Entelognathus***

As the putative sister taxon to crown gnathostomes plus *Janusiscus* and *Ramirosuaezia* (Giles et al., 2015), the braincase anatomy of *Entelognathus* (Zhu et al., 2013; Fig. 8A; Ludlow) has important implications for primitive conditions in the group. It resembles that of a typical primitive arthrodire in being broad, flat and shallow. The orbit is bounded posteriorly by the broad postorbital pila, identified here as the postorbital process, and the transverse otic process (anterior postorbital process of Zhu et al.) is narrow and laterally directed. An articular area for the hyomandibula is identifiable on its distal surface, well posterior to the orbit. The vagal process (posterior postorbital process) is very poorly developed, and quite different from the elongate, bifid process seen in primitive arthrodires such as *Kujdanowisapis* and *Lehmanosteus*. A craniospinal process is well developed, and positioned slightly anterior to the posterior face of the narrow occipital region, although specimens figured in the Supplementary Information (Zhu et al., 2013: supp. fig. 19) appear to show the craniospinal processes extending to the posterior margin. The endocranial cavity has not been described, and a parasphenoid appears to be absent.

6.2.2 *Janusiscus*

Janusiscus presents an unprecendented mix of endocranial characters typically associated with placoderms, chondrichthyans and osteichthyans. It was resolved by Giles et al. (2015) as a stem gnathostome, with a caveat that only one additional step was needed for a stem osteichthyan or stem chondrichthyan placement. In either position, *Janusiscus* has fundamental implications for the primitive anatomical structure of gnathostomes, corroborating the shift of all acanthodians onto the chondrichthyan stem.

The braincase of *Janusiscus* (Lochkovian) is elongate and shallow, with a narrow ventral

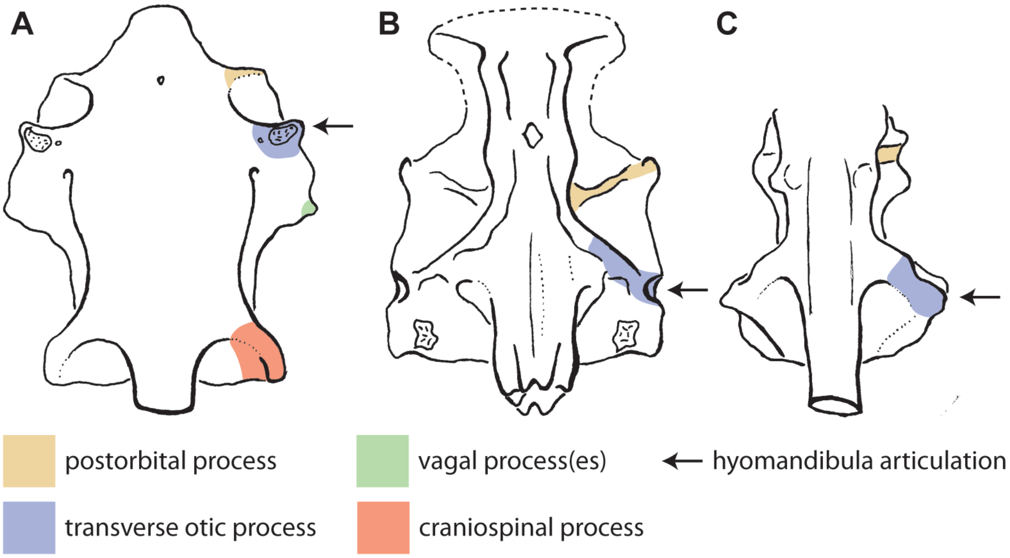

Figure 8 | Braincase anatomy of proximate stem gnathostomes. **A**, Braincase of *Entelognathus* in ventral view (adapted from Zhu et al., 2013). **B**, Braincase of *Janusiscus* in ventral view (adapted from Giles et al., 2015). **C**, Braincase of *Ramirosuarezia* in ventral view (adapted from Pradel et al., 2009).

portion and much broader dorsal roof (Fig. 8B). The nasal capsules are incompletely preserved but are comineralised with the rest of the braincase, and a ventral otic fissure is absent. It is unclear whether an otico-occipital fissure was present or not. Two conspicuous lateral processes are present: an anterolaterally directed postorbital process, which is elongate and narrow; and a robust posterolaterally directed transverse otic process, with the articular area for the hyomandibula at its distal end. Positionally, the transverse otic process and hyomandibular articulation are far more posterior than in placoderms, being level with the otic capsules rather than level with or just posterior to the orbit. An attachment area for the eyestalk is present, and the lateral margins of the basisphenoid are slightly turned out to form modest basipterygoid processes. Vagal and craniospinal processes appear to be absent. The basicranium bears paired grooves for the lateral dorsal aortae, and the lateral margins of the ventral surface of the braincase are flanked by subcranial ridges. The endocast has not been described, and there is no evidence for a parasphenoid.

6.2.3 *Ramirosuarezia*

The description of *Janusiscus* presents an opportunity for a reconsideration of the Eifelian *Ramirosuarezia*: although first described in 2009 (Pradel et al., 2009b), it was first included in a phylogenetic analysis by Giles et al. (2015). Although originally proposed as having placoderm or even holocephalan affinities, Giles et al. resolved *Ramirosuarezia* in a polytomy with *Janusiscus* on the gnathostome stem. The braincase of *Ramirosuarezia* is slender and fairly deep, particularly posteriorly, with a dorsal roof not much wider than the ventral floor (Fig. 8C). The back of the orbit is marked by a fairly indistinct postorbital process. The transverse otic process (tentatively identified by Pradel et al. as the lateral commissure) is massive, and projects posterolaterally. As in *Janusiscus*, there is no vagal or craniospinal process, and a ventral otic fissure is not present.

6.3 CROWN GNATHOSTOMES

6.3.1 ‘ACANTHODII’

Acanthodians are jawed vertebrates traditionally characterised by the presence of paired and median fin spines and micromeric scales that grow in an onion-skin pattern (Denison, 1979). As with placoderms, the acanthodians were long regarded as a monophyletic group with affinities to either chondrichthyans (Nielsen, 1932; Woodward, 1932; Holmgren, 1942; Ørvig, 1957; Nelson, 1968, 1969; Jarvik, 1977, 1980) or osteichthyans (Nielsen, 1949; Heyler, 1958, 1962; Romer, 1968; Schaeffer, 1968, 1969; Miles 1973; Gardiner, 1984; Maisey, 1986; Janvier, 1996). Miles' (1973) thorough re-examination of the braincase of *Acanthodes* and endocranial characters of early jawed vertebrates firmly cemented the view that acanthodians belonged to the osteichthyan stem. This remained largely unchallenged (although see Janvier, 1996: p. 181, fig. 9.1) until Brazeau's (2009) analysis, in which acanthodians were relegated to a paraphyletic assemblage bridging the gnathostome, chondrichthyan and osteichthyan stems. Subsequent analyses by Davis et al. (2012) upheld this result. Most recently, the discovery of *Entelognathus*, a placoderm-like form with bony jaws similar to those of osteichthyans (Zhu et al., 2013), and *Janusiscus*, a stem gnathostome (Giles et al., 2015) has resulted in all acanthodians being resolved as a paraphyletic assemblage on the chondrichthyan stem, with extensive ramifications for primitive gnathostome conditions, most notably the support for a macromeric last common ancestor. Attempts to identify acanthodian synapomorphies that uphold the monophyly of the group (e.g. Burrow et al., 2010) have failed to find any characters that withstand detailed phylogenetic scrutiny, and the status of acanthodians as paraphyletic seems secure.

The neurocranium is very rarely preserved in acanthodians, and was most likely unmineralised in many taxa. The braincase is best known in *Acanthodes* (Fig. 9A), a late occurring and undoubtedly highly specialised acanthodian from the Early Permian (Sakmarian-Asselian). Despite its unsuitability, a lack of other candidates has resulted in *Acanthodes* being used as representative of the typical acanthodian braincase (Jarvik, 1977, 1980; Denison, 1979; Janvier, 1996). Although previously examined by Jaekel (1903, 1927), Watson (1937), Holmgren (1942) and Miles (1968), a comprehensive description of the braincase of *Acanthodes* was undertaken by Miles (1973). The proportion of the braincase occupied by the orbital region is much increased relative to that of a typical placoderm, with the otic and particularly occipital region correspondingly shorter. The braincase is tropibasic, with the orbits closely spaced and a narrow interorbital septum. While the most anterior part of the orbit and the ethmoid region is not preserved, the remainder of the braincase is ossified in four parts: a dorsal ossification, the basisphenoid, the paired lateral occipital, and the ventral occipital. Conspicuous ventral otic and otico-occipital fissures are present. An anterior fontanelle is present on the dorsal surface of the dorsal ossification, and a large opening for the hypophysis is developed on the basisphenoid. Posterior to the hypophysis, the basisphenoid flares out into short, laterally directed basipterygoid processes, and narrow spiracular grooves are visible on its ventral surface. The subocular shelves are small, but the orbit is overhung by broad supraorbital crests, and delimited posteriorly by a well developed postorbital process. The posterior wall of the orbit was described by Miles as housing the trigeminofacialis chamber. As there is no obvious articular area for the hyomandibula, it seems likely that there was no transverse otic process. Supravagal and craniospinal processes are also not developed. Watson (1937) described a median groove on the ventral surface of the occipital ossification as for the dorsal aorta. Very little of the endocavity is known, but the labyrinth has been partially described by Heyler (1962) and Miles (1973). The labyrinth is relatively small, given the size of the neurocranium. Notably

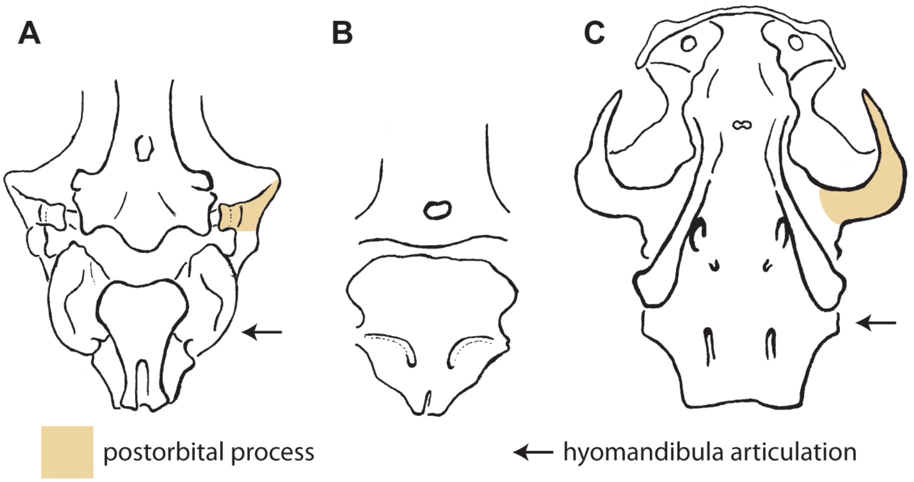

Figure 9 | Braincase anatomy of stem chondrichthyans. **A**, Braincase of *Acanthodes* in ventral view (adapted from Davis et al., 2012). **B**, Braincase of *Pucapampella* in ventral view (adapted from Gagnier et al., 1989). **C**, Braincase of *Doliodus* in ventral view (adapted from Maisey et al., 2009).

the semicircular canals are very slender and the ampullae small, but the size and extent of the sacculus is unknown. Differences from the labyrinths of placoderms are pronounced: the path of the canals describes a much wider arc than the corresponding structures in placoderms, and the anterior and semicircular canals meet in a sinus superior. Miles (1973) could not identify any trace of an endolymphatic duct. 'Otoliths' have been described in some species of *Acanthodes* (Fritsch, 1895; Rohon, 1889; Watson, 1937; Schultze, 1990). A parasphenoid does not appear to be present.

The most recent redescription of *Acanthodes* was carried out by Davis et al. (2012), who interpreted a number of characters as chondrichthyan-like, while retaining the taxon on the osteichthyan stem. They highlight the presence of a median ridge and paired fossae on the dorsal surface of the braincase, features also seen in early chondrichthyans. Davis et al. also reinterpret Miles' (1973) trigeminofacialis chamber as the exit of the jugular canal, a conclusion also reached by Maisey (2005); the true trigeminofacialis recess is situated behind the postorbital process. The hyomandibula is reconstructed as articulating on the lateral wall of the otic capsule, although not on a distinct process. The endocranial wall in the otic region indicates that a crus commune and sinus superior were present, as well as a utriculus. As in placoderms and early chondrichthyans, the horizontal semicircular canal enters the labyrinth level with the ampulla for the posterior semicircular canal.

The braincase of *Ptomacanthus* (Brazeau, 2009, 2012), from the Lochkovian, is only partially preserved. It is known from an anterior basisphenoid region and unfused parachordal plates posteriorly, but it is unclear these were originally separated by a ventral otic fissure or if the separation is taphonomic. The basisphenoid is much wider than the corresponding region in *Acanthodes*, and appears to be platybasic. The hypophyseal region is large, and a parasphenoid is not preserved. There are no spiracular grooves on the basisphenoid. As the specimen is a natural mould, the endocast and labyrinth are not preserved. Brazeau (2009) notes that many aspects of the neurocranium are more similar to those of placoderms and chondrichthyans than that of the only other well known acanthodian, *Acanthodes*.

A putative partial neurocranium has been described for '*Protodus'* (= *Nostolepis scotica*) Burrow & Turner, 2010; Lochkvoian), although the preservation is very poor. The authors tentatively identify the presence of a posterior dorsal fontanelle and precerebral fontanelle (although the presence of the latter seems unlikely; see Brazeau & Friedman, 2014). A postorbital process does not appear to be developed. However, examination of the specimen (NMS G 1891.92.696) throws doubt on the description of this material as neurocranial in origin.

Some braincase material, generally relating to the otic capsules, is preserved in the Lochkovian MOTH ischnacanthids (Blais et al., 2011, 2015), but has not been described, and few details can be discerned from the figures.

6.3.2 CHONDRICHTHYES

Modern chondrichthyans comprise the sharks, rays and chimaeras, and the origins of the group stretch back to the Devonian. Notwithstanding acanthodians, recently recovered as stem members of this group (Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015), chondrichthyan braincases are known in several taxa. Neurocranial characters that diagnose membership of the chondrichthyan total group (crownward of acanthodians) include the presence of a precerebral fontanelle.

As in acanthodians, the orbital region occupies an appreciable proportion of the braincase, although the otic region is also long. The chondrichthyan braincase is relatively slender when compared to placoderms, with the dorsal endocranial roof approximately the same width as the ventral floor. The postorbital process is prominent, and is more laterally - and anteroposteriorly - developed than in most placoderms. A more posteriorly positioned lateral otic process is variably developed, for example in *Orthacanthus* (Schaeffer, 1981), and the hyomandibula articulates in this area, far posterior to the orbit. The lateral otic process has been suggested as a homologue of the placoderm transverse otic process, but its absence (or poor development) in acanthodians and early chondrichthyans precludes this possibility (Giles et al., 2015). The lateral dorsal aortae are partially enclosed in canals on the ventral surface of the braincase. Parasphenoids are absent in chondrichthyans. A transverse otic fissure is now known to be present in at least some early chondrichthyans (*Pucapampella*: Janvier & Suarez-Riglos, 1986; Maisey, 2001; unnamed South African taxon: Maisey & Anderson, 2001), but before the discovery of these taxa it was assumed to be absent in the group; indeed, the presence of such a fissure was one of the key characters uniting *Acanthodes* with osteichthyans (e.g. Miles, 1973). The placement of all acanthodians as stem chondrichthyans (Zhu et al., 2013; Giles et al., 2015) indicates that a ventral otic fissure is a symplesiomorphy of crown gnathostomes.

Pucapampella (Fig. 9B; Eifelian) is widely regarded as a primitive stem chondrichthyan, and is typically resolved just crownward of acanthodians in recent analyses (Maisey, 2001; Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Dupret et al., 2014; Long et al., 2014; Giles et al., 2015). The posterior portion of the braincase was first described by Janvier & Suarez-Riglos (1986), with additional reconstructions provided by Gagnier et al. (1989). Additional, better preserved material studied via CT scanning was used by Maisey (2001) to augment the original description. The braincase of *Pucapampella* is elongate and slender, and fairly deep. Although incompletely preserved, a ventral otic fissure and otico-occipital fissure are clearly present. The suborbital shelf is fairly well developed, and a postorbital process delimits the back of the orbit. The trigeminofacialis chamber is situated within the orbital region, and an eyestalk attachment area is present. Posterior to the ventral otic fissure is a moderately developed lateral flange upon which the hyomandibula articulated, described by Janvier & Suarez-Riglos as the 'lateral "wing"' and Maisey (2001) as the lateral otic process. However, this feature barely protrudes from the lateral wall of the braincase, and is hardly comparable to either the transverse otic process of placoderms or the lateral otic process of later chondrichthyans such as *Orthacanthus* (Schaeffer, 1981). As in *Janusiscus* and *Ramirosuarezia*, the vagal process and craniospinal process are apparently absent. A feature in common with other chondrichthyans is the partial investment of the lateral dorsal aortae in the basicranial floor. A dorsal ridge and posterior dorsal fontanelle are developed on the dorsal surface of the braincase, and the endolymphatic ducts exit into the posterior dorsal fontanelle. The semicircular canals of *Pucapampella* were described by Maisey & Lane (2010): the canals are slender, with small ampullae, and the posterior semicircular canal is in contact with the rest of the labyrinth via a crus commune. There is no chondrified wall between the labyrinth and the rest of the endocranial cavity. A further chondrichthyan braincase from the Early Devonian of South Africa bears conspicuous similarities to that of *Pucapampella* (Maisey & Anderson, 2001), but has not formally been assigned to the genus. A greater portion of the ethmoid region is preserved in this unnamed taxon, and shows that a precerebral fossa was either absent or very much reduced. The braincase greatly resembles that of *Pucapampella* in all other respects.

Doliodus (Emsian) occupies a similarly primitive position in chondrichthyan phylogenies, typically being positioned as the sister taxa of all other chondrichthyans excluding *Pucapampella* and acanthodians (Brazeau, 2009; Davis et al., 2012 and descendent analyses;

Giles et al., 2015). The only known braincase is broad, and the ventral surface of the orbital and otic region is flanked by distinctive subcranial ridges (Maisey et al., 2009; Fig. 9C). The postorbital processes are massive, and curve anteriorly to border the orbits laterally, reminiscent of the morphology of *Brindabellaspis*, although in placoderms these lateral orbital enclosures were formed by the transverse otic process rather than the postorbital process. The hyomandibula articulates on the lateral wall of the otic capsule posterior to the subcranial ridge, and no transverse otic, vagal or craniospinal process is present. Although an otico-occipital fissure may be developed, the ventral otic fissure is absent. As in other chondrichthyans, the lateral dorsal aortae are partially enclosed on the floor of the braincase, although for a comparatively short stretch. A dorsal ridge seems to be absent, but the precerebral fontanelle and posterior dorsal fontanelle are both present. Reference to the semicircular canals is made by Maisey et al. (2009), and the labyrinth is partially described (but not figured) by Maisey & Lane (2010), who state that a crus commune is present and the capsular wall dividing the labyrinth and endocavity is not developed.

Although the exact relationships amongst more crownward stem chondrichthyans are still debated, a consensus has formed regarded the rough branching pattern. In particular, various opposing sister relationships have been proposed between *Cladodoides*, *Orthacanthus* and *Tamiobatis*, and they will be considered here together.

The braincase of *Cladodoides* (Gross, 1937; Maisey, 2005; Fig. 10A; Frasnian) is elongate, slender and deep. The only lateral process is the extensive postorbital process, which extends almost at right angles to the braincase and marks the back of the orbit. As in *Doliodus*, the hyomandibula simply articulates on the lateral wall of the braincase, although no clear facet is preserved. Unlike in placoderms and stem gnathostomes, where the two are adjacent, the articular area for the hyomandibula is positioned some way posterior to the exit

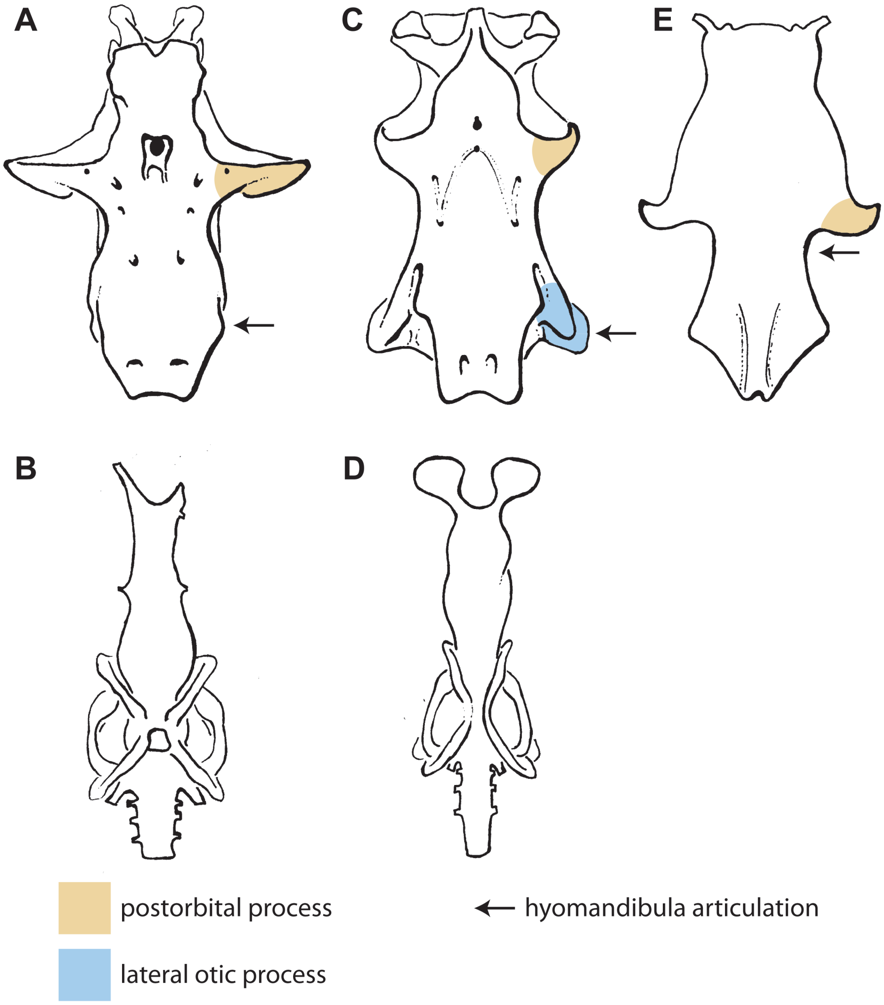

Figure 10 | Braincase anatomy of stem and crown chondrichthyans. A, Braincase of *Cladodoides* in ventral view (adapted from Maisey, 2005). **B**, Endocast of *Cladodoides* in ventral view (adapted from Maisey, 2005). **C**, Braincase of *Orthacanthus* in ventral view (adapted from Schaeffer, 1981). **D**, Endocast of *Orthacanthus* in ventral view (adapted from Schaeffer, 1981). **E**, Braincase of *Tristychius* in ventral view (adapted from Dick, 1978).

of the hyomandibular nerve. A precerebral and posterior dorsal fontanelle are present on the dorsal surface of the braincase, and CT scanning by Maisey (2005) revealed the presence of a otio-occipital fissure. There is no ventral otic fissure, and the lateral dorsal aortae were buried along a considerable part of the basicranium. The endocast of *Cladodoides* has been described in detail (Fig. 10B). As in many placoderms, it appears to have been a poor fit for the brain, and is essentially tubular. Only a small portion of the olfactory tracts is preserved, but they appear to be very thin. The region corresponding to the forebrain and midbrain is narrow, with the endocast widening slightly as it approaches the hindbrain. The labyrinth is large, with slender canals and moderately large ampullae, and the crus commune of the anterior and posterior semicircular canals sits above the dorsal roof of the endocast. A sinus superior is present, but poorly developed. There is no capsular wall separating the labyrinth from the endocavity.

The braincase of *Orthacanthus* (Schaeffer, 1981; Fig. 10C) is slightly broader than that of *Cladodoides*, with well developed supraorbital shelves, and bears two sets of prominent lateral processes: the postorbital process, which is shorter and slightly longer than that of *Cladodoides*, and a stout lateral otic process, which projects posterolaterally and provides an articular area for the hyomandibula. Phylogenetic congruence suggests that this process is not homologous with the transverse otic process of placoderms and stem gnathostomes (Giles et al., 2015). As in *Cladodoides*, the hyomandibular nerve exits far anterior to the hyomandibular articulation. The endolymphatic fossa is narrow and elongate. The proportions of the endocast (Fig. 10D) differ from that of *Cladodoides*: the regions of the forebrain and midbrain are fairly wide, and the endocast narrows towards the hindbrain. The crus commune projects above the dorsal roof of the endocranium, but the semicircular canals are less strongly curved and their ampullae smaller, and the capsular wall is partially chondrified. The braincase of *Tamiobatis* (Eastman, 1897; Romer, 1964; Schaeffer, 1981;

Williams, 1984) strongly resembles that of *Orthacanthus*. The suborbital shelves are similarly developed but the ventral surface of the braincase, particularly in the orbital region, is a little less wide. Additionally, the postorbital process is more laterally extensive and somewhat narrower, and the lateral otic process is less robust. The lateral dorsal aortae appear to have been invested along the entire length of the otic region, and only exposed externally in the occipital region. The endocast has not been fully described, but the details revealed through sectioning agree with those of *Orthacanthus*.

Hamiltonichthys and *Onychoselache* are generally regarded as crown chondrichthyans, with or without the accompaniment of *Tristychius* (Maisey, 1989; Coates & Gess, 2007; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015), and represent the first hybodonts. The braincase is fairly well preserved in *Tristychius* (Dick, 1978; Fig. 10E; Visean), although lacks several features seen in *Hamiltonichthys* and *Onychoselache*, possibly suggesting a primitive position within the group. The braincase is fairly long and shallow, and is broader anterior to the postorbital process. The ethmoid and orbital regions occupy a little under half the length of the neurocranium. Although the suborbital shelves are poorly developed, the supraorbital shelves are substantial. The postorbital processes are laterally extensive and curve anteriorly at their distal end, and the hyomandibula appears to have articulated against the braincase just posterior to this process. Lateral processes (termed the otic process by Dick 1978) extend from the braincase level with the start of the occipital region, but given the anterior position of the hyomandibula it is difficult to homologise these with the lateral otic process of *Orthacanthus.* A large precerebral fontanelle is present, but the posterior dorsal fontanelle is unusual in being small and paired about the midline, with the endolymphatic ducts opening anterior to it. The basicranial surface bears faint grooves for the lateral dorsal aortae. Few details of the labyrinth are exposed, but the anterior and posterior semicircular canals appear to meet in a sinus superior, although Dick (1978) cautions that this may simply represent part of the capsular wall.

The braincase of *Hamiltonichthys* (Gzhelian) is partially known across a number of specimens (Maisey, 1989). It is fairly short, with a narrow anterior portion and wider posterior portion. The braincase is widest in the region of the postorbital process, which are anteroposteriorly long. The otic and particularly occipital regions are short, occupying less than half of the total endocranial length, and there are no transverse otic, vagal or craniospinal processes. A ventral otic fissure and otico-occipital fissure are also absent. The pattern of basicranial circulation is unknown, as is the position of articulation of the hyomandibula. A precerebral fontanelle is present, and the posterior dorsal fontanelle, into which the endolymphatic ducts open, is small and narrow. Braincase preservation is also poor in *Onychoselache* (Dick & Maisey, 1980; Visean), but it is clear that is also had a short otic and occipital region and broad postorbital processes. Further material described by Coates & Gess (2007) confirms these observations and reveals that the posterior dorsal fontanelle is smaller and more posterior than in *Hamiltonichthys*.

6.3.3 OSTEICHTHYES

Osteichthyans are the dominant living vertebrate group, comprising over 99% of modern vertebrate species. The two constituent groups, Actinopterygii and Sarcopterygii, diverged at least 420 Ma (Zhu et al., 2009), and each number in the order of 30,000 living species. The membership of the osteichthyan stem and crown group has undergone a revolution in recent years, driven by Friedman & Brazeau's (2010) advocation for a total group rather than apomorphic definition of the clade and the uprooting of all acanthodians on to the chondrichthyan stem (Zhu et al., 2013; Giles et al., 2015). The braincase in osteichthyans is well ossified and myriad examples have been described in the literature, although the enclosure of the braincase in large dermal plates and a lack of focussed attention from practitioners of Sollas' grinding method has proved to be a barrier to description in many cases, particularly within the actinopterygians. Many of the characters that diagnose membership of Osteichthyes relate to the braincase and endocast (Friedman & Brazeau, 2010; Brazeau & Friedman, 2014), although this list has been whittled away given the loss of *Acanthodes* as a stem osteichthyan and the discovery of osteichthyan-like characters in the stem gnathostome *Janusiscus* (Giles et al., 2015). These characters are summarized by Friedman and Brazeau (2010) and Brazeau and Friedman (2014): endocranial cavity dorsally restricted within sphenoid; horizontal semicircular canal joins level with the posterior ampulla; long canals for olfactory tracts; ethmoid comineralises with sphenoid and completely encloses the nasal capsules.

As in acanthodians (*Acanthodes*: Miles, 1973; Davis et al., 2012) and early chondrichthyans (*Pucapampella*: Janvier & Suarez-Riglos, 1986; Maisey, 2001), the osteichthyan braincase bears conspicuous ventral otic and otico-occipital fissures. Braincase proportions differ between and within sarcopterygians and actinopterygians, but the orbital region is generally longer than in placoderms and chondrichthyans and the occipital region shorter. The neurocranium is typically deep, with a slender ventral floor and rather wider dorsal roof. The back of the orbit is marked by the postorbital process, typically robust in actinopterygians and reduced in sarcopterygians, and the hyomandibula articulates on the transverse otic process. In contrast to acanthodians and early chondrichthyans, where it is much further posterior, the hyomandibula articulation is primitively almost level with the ventral otic fissure.

6.3.3.1 Stem osteichthyans

The problem of the 'naked osteichthyan stem' has long been acknowledged (Schaeffer, 1968), and was most recently addressed by Friedman and Brazeau (2010). Originally populated by all acanthodians, then a subset of ischnacanthid and acanthodid acanthodians, the few remaining stem osteichthyan taxa generally comprise scales and scraps of bony of dubious affinity: *Andreolepis* (Gross, 1968), *Naxilepis* (Wang & Dong, 1989), *Orvikuina* (Gross, 1968), *Terenolepis* (Burrow, 1995). Several candidates known from more substantial material present themselves, including *Ligulalepis* (Basden et al., 2000; Basden & Young, 2001) and *Meemannia* (Zhu et al., 2006). These taxa were originally regarded as either stem sarcopterygians or stem actinopteryians, although they have also been recovered as stem osteichthyans. As their affinities are still debated, they will be considered in the context of the stem group. *Dialipina* (minus the Siberian material, which has since been moved to *Janusiscus*; Giles et al., 2015) may also occupy a position on the osteichthyan stem, but as no endoskeletal material is known from this taxa it will not be considered further in this review.

The braincase of *Ligulalepis* (Emsian) is known only from a single incomplete specimen lacking part of the nasal capsules and the occipital plate. *Ligulalepis* was diagnosed as an actinopterygian in its original description (Basden et al., 2000; Basden and Young, 2001) and by Chang (2000), albeit with many primitive characters seen elsewhere in placoderms and chondrichthyans. Subsequent analyses have favoured a stem osteichthyan position (e.g. Friedman, 2007; Brazeau, 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Dupret et al., 2014; Giles et al., 2015; Chapter 4). It is worth noting that the braincase was assigned to the scale taxon *Ligulalepis* by Basden & Young (2001) on the basis that Schultze's (1968) *Ligulalepis* is the only actinopterygian known from the Emsian of southeastern Australia, although there is no direct association between the braincase and the scales. In analyses where the braincase is coded separately from the scale material (e.g.

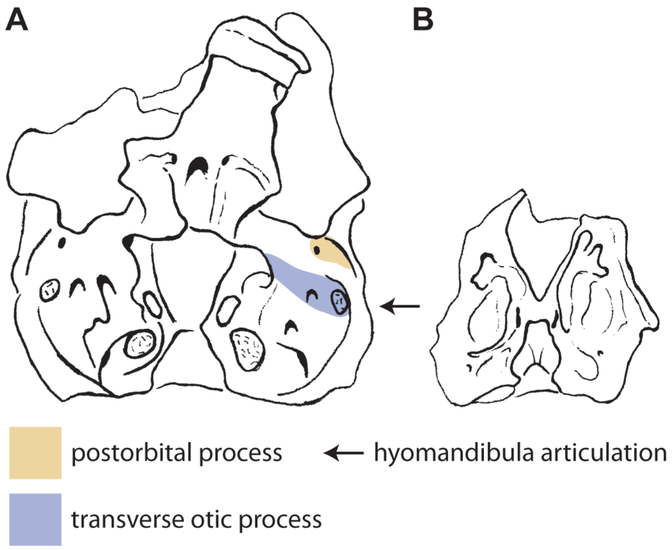

Figure 11 | Braincase anatomy of stem osteichthyans. A, Braincase of *Ligulalepis* in ventral view (adapted from Basden & Young, 2001). **B**, Braincase of *Meemannia* in ventral view (adapted from Zhu et al., 2006).

Giles et al., 2015; Chapter 4), *Ligulalepis* is consistently resolved as a stem osteichthyan. Despite the morphology of much of the ventral floor being unknown, the braincase is clearly short and broad, as well as very deep (Fig. 11A). An otico-occipital and ventral otic fissure are present. A postorbital process is moderately developed, but projects only laterally, and the spiracular groove extends down the lateral face of the braincase posterior to the process. The transverse otic process sits immediately posterior to the postorbital process: it is small, barely projecting from the lateral wall of the otic region, and the hyomandibula articulates at its distal end. The orbital region occupies almost half of the total neurocranial length, and is roofed by a broad supraorbital shelf, but the suborbital shelf is small. *Ligulalepis* was the first osteichthyan described with an eyestalk, and a small basipterygoid process is also preserved. A large posterior dorsal fonatanelle is present. The endocast and labyrinth have not yet been described, but are clearly preserved in the specimen and will be the subject of future study. Zhu et al. (2010) suggested that a lateral cranial canal, currently considered to be an actinopterygian synapomorphy, is present, but evidence for this is ambiguous.

As in *Ligulalepis*, the neurocranium of *Meemannia* (Lochkovian) is also incomplete, with only the parts of the braincase dorsal to the roof of the sacculus being preserved. *Meemannia* was originally described as a sarcopterygian (Zhu et al., 2006), and this position has been upheld by several other analyses (Zhu et al., 2006; Friedman, 2007, Zhu et al., 2010). A number of more recent analyses report a stem osteichthyan placement for the taxon (Zhu et al., 2013; Dupret et al., 2014), although the analysis presented in Chapter 4 suggest a stem actinopterygian position. Although little can be said about the morphology of the braincase (Fig. 11B), much of the endocavity and labyrinth is exposed. The endocast appears to be widest in the region of the hindbrain, and narrows posteriorly. A utricular recess is present, the semicircular canals are slender, and their ampullae are moderately sized. Zhu et al. (2006, 2010) identify a lateral cranial canal, but as with *Ligulalepis*, the position of the feature indicates that this attribution may be incorrect. A posterior dorsal fontanelle is present on the dorsal roof of the braincase.

6.3.3.2 Sarcopterygii

Sarcopterygians have a good fossil record back into the Silurian (Zhu et al., 2009), and a concentration of research effort has meant that understanding of the early evolution and relationships of the group is fairly robust. Modern sarcopterygians are represented almost exclusively by tetrapods: the small numbers of extant fish-like sarcopterygians, the coelacanths and lungfish, are but a remnant of the vast diversity seen in the group's early history, and the coelacanth, lungfish and tetrapod lineages can all be traced back with confidence to the Devonian. Diagnostic endocranial features for sarcopterygians, as summarized by Friedman & Brazeau (2010), are as follows: joint between ethmosphenoid and otico-occipital regions of braincase; basicranial fenestra; Y-shaped supraotic recess; broad or bipartite hyomandibular articulation. The interorbital septum is broad, lateral processes of the braincase are typically poorly developed, and the endocast is generally a poor fit for the brain

Although undoubtedly sarcopterygians, *Guiyu*, *Psarolepis*, and *Achoania* have generally been assigned to the stem, with *Onychodus* also sometimes being resolved on the stem (e.g. Janvier, 1996: fig. 9.1; Davis et al., 2012; Chapter 4), despite other analyses recovering a position within the crown (e.g. Friedman, 2007; Zhu et al., 2013; Giles et al., 2015).

The braincase of *Psarolepis* (Lochkovian) is known from both ethmosphenoid and otico-occipital divisions, although the occipital plate (and thus ventral floor of the braincase) is missing (Yu, 1998; Fig. 12A). The braincase as a whole is somewhat shallower than in actinopterygians and the stem osteichthyans described above. As in *Ligulalepis*, the braincase is broad, although the width of the ventral surface is unknown. The ethmoid region is represented ventrally by fairly large, deep internasal cavities. The orbital region has an extensive supraorbital shelf and a wide subocular ledge that is continuous with the basipterygoid process posteriorly. The postorbital process, marking the back of the orbit, is slight, and is developed dorsally as the postorbital pila. The transverse otic process (Yu's lateral commissure) forms the anterolateral corner of the otico-occipital ossification and provides the articular area for the hyomandibula. As the occipital plate is lost, part of the endocavity and labyrinth is exposed: the hindbrain is slightly narrower than that of *Meemannia*, and extends further posteriorly; however the sacculus and ampullae of the semicircular canals are exposed at a different level, so comparisons are difficult to make. The posterior dorsal fontanelle is of a similar size, but the hind margin of the skull roof in *Psarolepis* follows its outline. As in *Meemannia* and *Ligulalepis*, Zhu et al. (2010) proposed the presence of a lateral cranial canal, but evidence for this is equivocal. The lozenge-shaped parasphenoid of *Psarolepis* is very small, with a denticulated ventral face. Only the ethmoid ossification is known in *Guiyu* (Zhu et al., 2009; Qiao & Zhu, 2010; Fig. 12B) and *Achoania* (Zhu et al., 2001; Fig 12C) and but comparisons can easily be drawn with *Psarolepis*. The internasal pits are also large in *Guiyu*, but rather smaller and shallower in *Achoania*, and all three taxa have similarly extensive supraorbital and subocular shelves. An eyestalk is present in *Achoania*, and Zhu et al. (2001) also report this feature in *Psarolepis*. *Achoania* and *Guiyu* both have robust postorbital process, with dorsally extensive pilae (referred to by Zhu et al., 2001 as the postorbital pila and Zhu et al., 2009 as the postorbital pillar). The parasphenoid of *Guiyu* and *Achoania* is drop shaped, but that of *Achoania* is larger than the parasphenoid of *Psarolepis.*

The braincase of *Onychodus* (Andrews et al., 2006; Frasnian) is poorly mineralized,

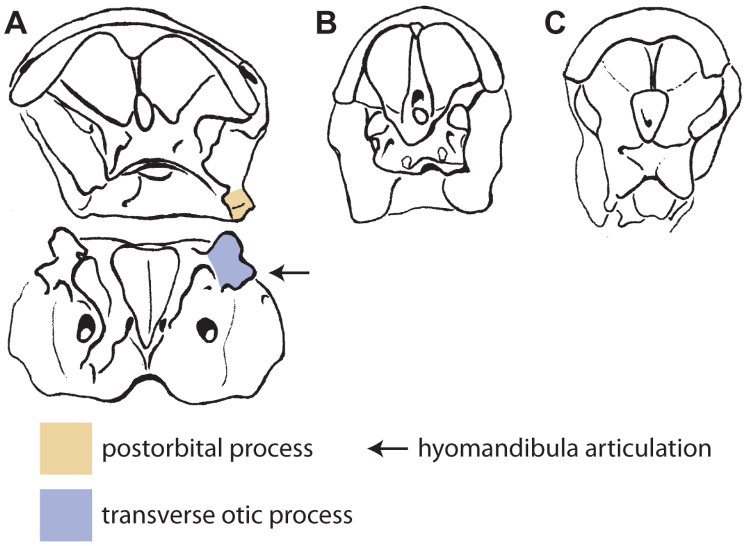

Figure 12 | Braincase anatomy of stem sarcopterygians. A, Braincase of *Psarolepis* in ventral view (adapted from Yu, 1998). **B**, Ethmosphenoid of *Guiyu* in ventral view (adapted from Zhu et al., 2006). **C**, Ethmosphenoid of *Achoania* in ventral view (adapted from Zhu et al., 2001).

particularly the otico-occipital division, but is similar in general features to *Psarolepis*. The internasal pits are massive, and the parasphenoid is small and lozenge shaped. Unusually, the ethmosphenoid division is ossified in four pieces, which appear to have fused in larger specimens. A postorbital pila is absent. As the transverse otic process and hyomandibular facet are not preserved, they were presumably unossified. Parts of the labyrinth are exposed, revealing the presence of a utriculus, and the ventral margin of the otic wall is embayed for a large vestibular fontanelle. The braincase is slightly better known in the Pragian onychodont *Qingmenodus* (Lu & Zhu, 2009; although there is some debate over whether the onychodonts are monophyletic; Janvier, 1996; Friedman, 2007). The braincase is slender anteriorly but broadens and deepens significantly in the otic region. The postorbital process has not been identified but the transverse otic process (lateral commissure of Lu & Zhu) is robust and laterally extensive, and bears a small articular area for the hyomandibula. Grooves for the lateral dorsal aortae are present on the basicranial surface, and large vestibular fontanelles and basicranial fenestrae are present.

6.3.3.2.1 Actinistia

Actinistians, the coelacanths, are generally recovered as the deepest diverging clade within the sarcopterygian crown (Zhu & Yu, 2002; Friedman, 2007; Lu et al., 2012; Chapter 4). As in other sarcopterygians, the braincase is mineralized in two ossifications, and the intracranial joint is very mobile. The joint is positioned posteriorly: it lies posterior to the exit of the profundus nerve, and the trigeminal nerve opens out in to it.

The phylogenetic position of *Styloichthys* (Lochkovian) is open to debate. In their original description, Zhu & Yu (2002) suggested it as the sister taxon to the clade comprising dipnomorphs and tetrapodomorphs, crownward of actinistians, as upheld by Zhu et al.

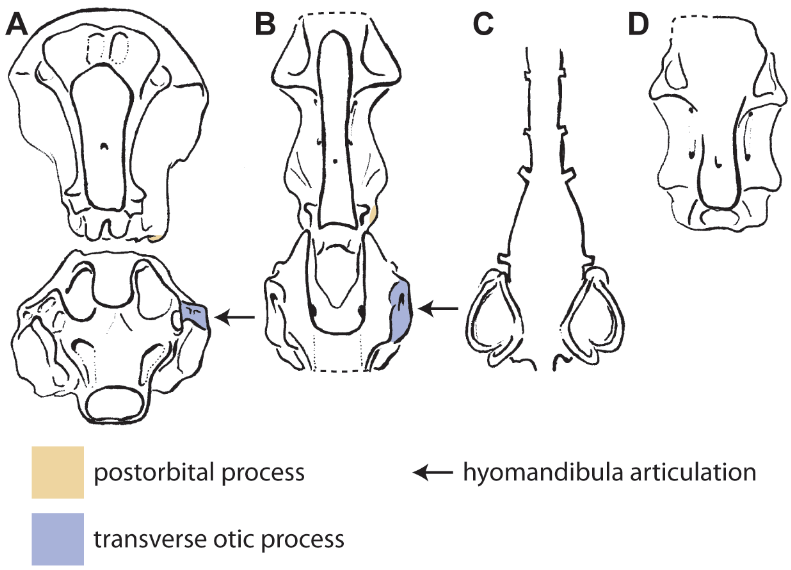

Figure 13 | Braincase and endocast anatomy of actinistian sarcopterygians. A, Braincase of *Styloichthys* in ventral view (adapted from Zhu & Yu, 2002). **B**, Braincase of *Diplocercides* in ventral view (adapted from Jarvik, 1954). **C**, Endocast of *Diplocercides* in dorsal view (adapted from Stensiö, 1963b). **D**, Ethmosphenoid of *Euporosteus* in ventral view (adapted from Stensiö, 1937).

(2006, 2009, 2013). Friedman (2007) reassessed much of the anatomy of *Styloichthys* and resolved a position at the base of the actinistians. As in most other early sarcopterygians, the otico-occipital ossification is the widest portion of the braincase (Fig. 13A). The supraorbital shelves are extensive, and the suborbital shelves fairly narrow. The internasal cavities are very small and shallow, and, unlike in *Guiyu*, *Achoania* and *Psarolepis*, a fenestra ventralis is present. Both the basipterygoid process and postorbital process (postorbital pila of Zhu & Yu) are slender, although a postorbital pila is present, and an attachment area for an eyestalk is developed in the orbit. The bipartite hyomandibular facet is situated on the lateral wall of the otic region, which is produced as a moderate transverse otic process. The basicranial fenestra is small, and a vestibular fontanelle is absent.

Of Devonian fossil coelacanths, the braincase is best known in *Diplocercides* (Givetian-Frasnian), with only the dorsal and anterior portion of the nasal capsule missing, and has been described on numerous occasions (Stensiö, 1922a,b, 1937; Jarvik, 1942, 1954, 1980; Bjerring, 1967, 1972, 1971, 1977; Forey, 1996). It is long and slender, with small subocular shelves and fairly well developed supraorbital shelves (Fig. 13B). The ethmoid and orbital region combined account for somewhat over half of the total neurocranial length. The orbital region is narrow, especially ventrally, and the ethmoid and otico-occipital regions are approximately the same width. A stout, well developed basipterygoid process is present. It is difficult to homologise lateral braincase processes with those of other gnathostomes. The short antotic process is considered to be unique to coelacanths (Stensiö, 1932; Jarvik, 1954; Forey, 1996). While the slightly more anterior suprapterygoid process may be the homologue of the postorbital process, it is not positionally equivalent to the postorbital process of other gnathostomes. Although a postorbital pila is present, the postorbital process is much reduced in both *Styloichthys* and *Psarolepis*, and may be assumed to be absent in dipnoans. Given the position of articulation of the hyomandibular, the transverse otic process is likely homologous with the anterolateral extension forming the widest portion of the otic region. There is no posterior dorsal fontanelle or vestibular fontanelle, and much of the ventral surface of the posterior braincase ossification is occupied by the large basicranial fenestra. The remainder of the basicranium is smooth, with nothing to indicate the path of the basicranial circulation. The parasphenoid is narrow and long, extending from the ethmoid region back to the ventral otic fissure. Its posterior quarter is smooth and does not bear denticles. An ascending process and spiracular groove are absent. The endocast of *Diplocercides* was described by Stensiö (1963b; Fig. 13C). The region of the forebrain is narrow, widening into the forebrain and hindbrain before narrowing again level with the labyrinth. The widest area corresponds to the medulla. Unlike in the extant *Latimeria* (Millot & Anthony, 1958), the brain appears to have extended anterior to the intracranial fissure. The labyrinth is short, with slender semicircular canals, a bulbous sacculus and small ampullae. The crus commune of the anterior and posterior canals barely extends dorsal to the endocranial roof.

A lone ethmosphenoid is known for *Euporosteus eifeliensis* (Stensiö, 1937; Fig. 13D; Eifelian). The nasal capsules are extensive and the orbit small, with internasal cavities absent. The suprapterygoid process is well developed, but the antotic process is not preserved. Although the parasphenoid is incompletely preserved it resembles a longer version of the parasphenoid of *Styloichthys* rather than the narrow parasphenoid of *Diplocercides.* The labyrinth is partially known in *Euporosteus yunnanensis* (Zhu et al., 2012; Pragian). The anterior semicircular canal is a little longer than in *Diplocercides*, and the ampullae slightly larger. The braincase in *Gavinia* (Frasnian) is incompletely preserved and damaged, but some details can be described in the otico-occipital region (Long, 1999). The hyomandibular articulation is large, and the area otherwise agrees with that of *Diplocercides*. Although the best known in terms of its dermal skeleton, the braincase in

Miguashaia (Cloutier, 1996; Givetian-Frasnian) is completely unknown, and only a fragment of parasphenoid is preserved.

6.3.3.2.2 Dipnomorpha

The dipnomorphs include the porolepiforms and the assemblage leading to the lungfishes. Unlike in actinistians, the intracranial joint lies anteriorly, with the profundus nerve opening through it and the trigeminal nerve exiting behind. The exception to this is in *Powichthys*, where the joint is posteriorly placed. The olfactory tracts of dipnomorphs typically diverge at an angle of up to 60 degrees.

Both the ethmosphenoid and otico-occipital ossifications are known in *Holoptychius* (Jarvik, 1972; Downs et al., 2013). The ethmosphenoid of *H. bergmanni* (Downs et al., 2013; Frasnian) bears narrow internasal pits and a fairly small, triangular parasphenoid, in contrast to the rounded parasphenoid of *Holoptychius* sp. (Jarvik, 1972). The supraorbital shelves are incompletely preserved, but the suborbital shelves are clearly narrow. Additionally, the basipterygoid process is quite well developed. The otico-occipital ossification shows a well developed basicranial fenestra and a robust transverse otic process (lateral commissure of Downs et al.) but lacks a dorsal fontanelle.

Ethmosphenoid and otico-occipital ossifications are also known in *Porolepis* (Bjerring, 1967; Jarvik, 1972; Pragian) and *Glyptolepis* (Jarvik, 1972; Bjerring, 1991; Frasnian). The proportions of the two braincase divisions differ in these taxa: the ethmosphenoid is longer than the otico-occipital in *Porolepis*, and vice versa in *Glyptolepis.* However, the braincases resemble each other in their general morphology. The ethmosphenoid is fairly broad, with extensive supraorbital shelves (Fig. 14A). The internasal pits are large in *Porolepis* and

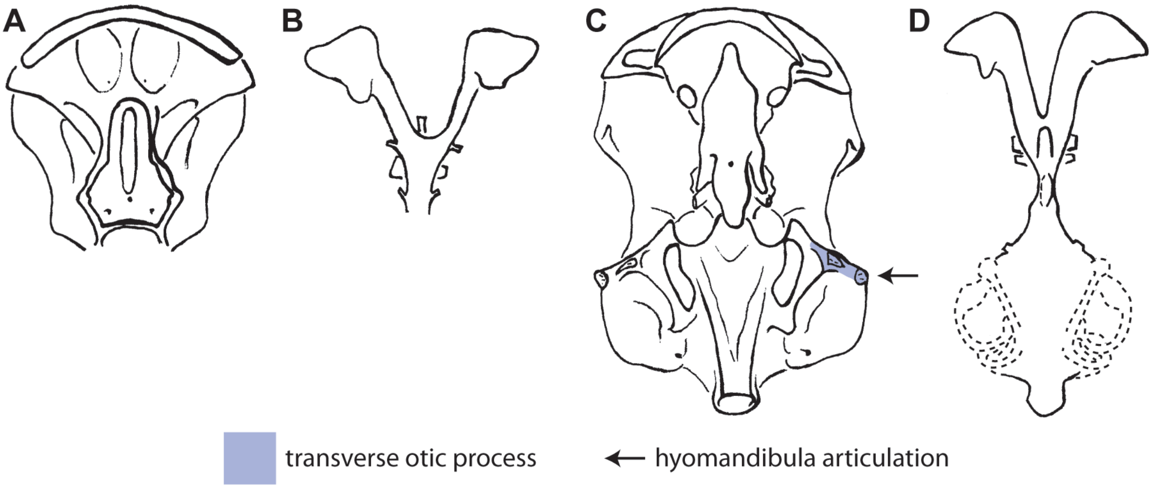

Figure 14 | Braincase and endocast anatomy of dipnomorph sarcopterygians. A, Ethmosphenoid of *Porolepis* in ventral view (adapted from Bjerring, 1967). **B**, Endocast of *Powichthys* in dorsal view (adapted from Clément & Janvier, 2010). **C**, Braincase of *Youngolepis* in ventral view (adapted from Chang, 1982). **D**, Endocast of *Youngolepis* in dorsal view (adapted from Chang, 1982).

smaller in *Glyptolepis*, and a fenestra ventralis is present in both taxa. The parasphenoid of *Porolepis* is long and fairly narrow, and bears a series of large midline denticles, but is somewhat broader and shorter in *Glyptolepis*. Unlike in *Holoptychius*, the dorsal surface of the otico-occipital ossification of *Glyptolepis* appears to have a large fontanelle posterior to the intracranial fissure, and a fossa bridgei is present. The anterior portion of the endocast is narrow, with long olfactory tracts leading to the large, triangular nasal capsules. The pineal and parapineal canals, originating in the forebrain, are separate, and the hypothesis, which extends from the ventral surface of the forebrain, is wide, and extends anteriorly.

The ethmosphenoid is known in both *Laccognathus grossi* (Vorobyeva, 2006; Givetian) and *Laccognathus embryi* (Downs et al., 2011; Frasnain), although the otico-occipital ossification is only known in the latter. The supraorbital shelves and internasal pits are narrow and the basipterygoid process robust, with a triangular parasphenoid present. A large basicranial fenestra is present on the ventral surface of the basicranium, and a fontanelle is present dorsally. Additional braincase material is known for the *Porolepis*-like *Durialepis* (Otto, 2007; Emsian).

The phylogenetic position of *Youngolepis* (Lochkovian-Pragian) has traditionally been the subject of much debate. Chang (1982) highlighted similarities with both osteolepiforms and porolepiforms, suggesting that *Youngolepis* probably fell into its own group. Subsequent work resolved a sister group relationship between *Youngolepis* and *Powichthys* and included both taxa within the porolepiforms (Chang and Smith, 2002), a placement also upheld by Zhu et al. (2002). More recently, analyses have favoured a position crownward of porolepiforms and more closely allied to dipnoans (e.g. Zhu et al., 2006; Friedman, 2007; Lu et al. 2012). The braincase and endocast are known in great detail (Chang, 1982). The braincase is very broad, with substantial supraorbital shelves and narrow suborbital shelves

(Fig. 14C). Strikingly, there is no intracranial joint, although Chang (1982) notes the presence of a variably developed but posteriorly situated intracranial fissure: the fissure passes through the trigeminal nerve canal and posterior to the exit for the profundus nerve. In the ethmoid region, the internasal pits are very small, and the fenestra ventralis large. The basipterygoid process is robust, and the postorbital process appears to be absent, although the transverse otic process (lateral commissure of Chang, 1982) is laterally extensive and bears the bipartite hyomandibula articulation. The vestibular fontanelles are large and elongate, but there is no basicranial fenestra, and the ventral otic fissure bears two deep embayments. Shallow grooves on the basicranium mark the path of the lateral dorsal aortae. As in other sarcopterygians, the endocast of *Youngolepis* appears to be a poor fit for the brain (Fig. 14D). Triangular nasal capsules are present, and the olfactory tracts are long and anterolaterally directed. The forebrain is narrow, particularly in the region of the diencephalon, and widens gradually in the midbrain; the hindbrain is the widest part of the endocast. Unlike in *Powichthys* and *Glyptolepis*, the hypophysis projects ventrally and even slightly posteriorly. The parasphenoid is broad and long, with a median posterior extension and two posterolaterally directed wings that extend somewhat dorsally. However, the absence of such processes in more primitive sarcopterygians suggests they are not homologous with the ascending processes of actinopterygians, and these ‘wings’ appear to fuse with the main body of the parasphenoid later in ontogeny (Chang, 1982: p. 27). The parasphenoid covers almost the entire ventral floor of the ethmoid and orbital division of the braincase, and is denticulated along its length.

The anterior portion of the braincase of *Powichthys spitsbergensis* (Lochkovian-Pragian) was described by Clément & Janvier (2004) and with the assistance of CT scanning by Clément & Ahlberg (2010). An intracranial joint appears to be present but is very posteriorly positioned, with the profundus nerve and trigeminal nerve both exiting through the ethmosphenoid ossification (Jessen, 1980). The general shape of the braincase is similar to that of *Porolepis*, with narrow suborbital shelves and wide supraorbital shelves. The basipterygoid process is large. The endocast (Fig. 14B) resembles that of *Glyptolepis*, with triangular nasal capsules connected to the narrow forebrain by means of long olfactory tracts, and an anteriorly directed hypothesis. Although both pineal and parapineal canals are present, the pineal canal ends blindly and does not exit through the skull roof.

6.3.3.2.1 Tetrapodomorpha

The tetrapodomorphs comprise the 'osteolepiforms', tetrapod-like fishes and fish-like tetrapods. The braincase, at least in early taxa, is ossified in two pieces, and the intracranial joint is anteriorly placed as in dipnomorphs.

Tungsenia (Pragian) has recently been recovered as the earliest stem tetrapod (Lu et al., 2012). Only the ethmosphenoid ossification is known. The subocular shelves are narrow, and the large, denticulated parasphenoid covers much of the ventral surface. Very well developed basipterygoid processes are present. As in dipnomorphs, the olfactory tracts diverge at a wide angle, but they are unusually short and wide, with the result that the forebrain and midbrain, are very long, although still narrow. Separate pineal and parapineal organs appear to be present, although they do not emit canals. A short and squat hypophysis is positioned far posteriorly, and projects anteriorly.

The osteolepiforms represent a fairly primitive tetrapodomorph grade. The endocranium of *Osteolepis* (Eifelian-Givetian) was first described by Watson (1925a,b, 1926), with later embellishments by Thomson (1965). The ethmoid region is wide, with a narrow orbital region that gradually increases in width to the otico-occipital, and the ethmosphenoid

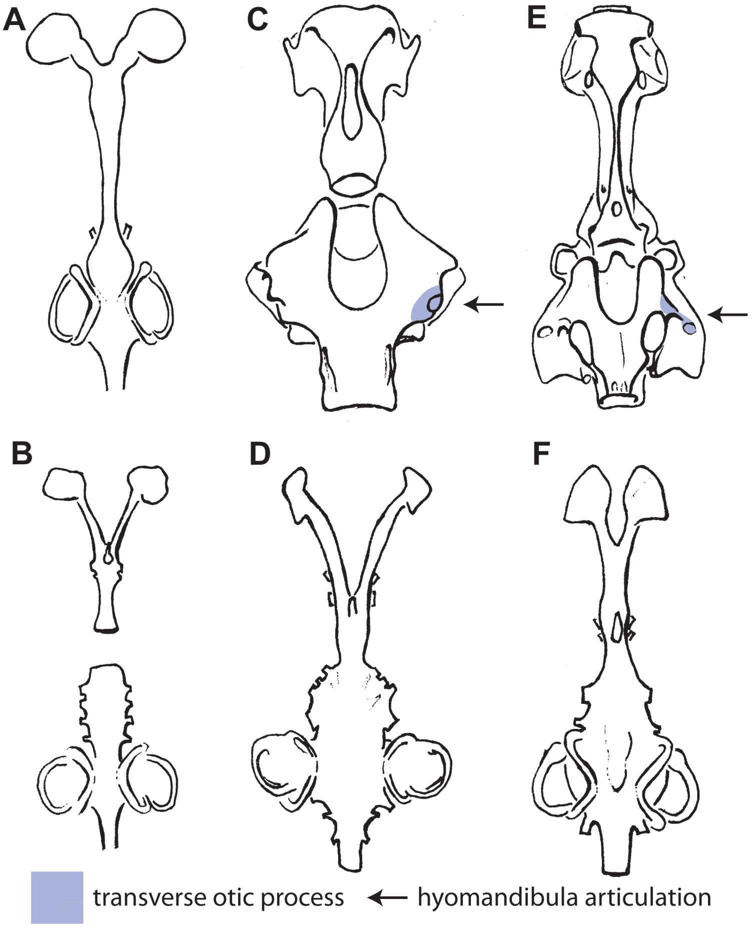

Figure 15 | Braincase and endocast anatomy of tetrapodomorph sarcopterygians. A, Endocast of *Osteolepis* in dorsal view (adapted from Thomson, 1965). **B**, Endocast of *Gogonasus* in dorsal view (adapted from Holland, 2014). **C**, Braincase of *Ectosteorachis* in ventral view (adapted from Romer, 1937). **D**, Endocast of *Ectosteorachis* in dorsal view (adapted from Romer, 1937). **E**, Braincase of *Eusthenopteron* in ventral view (adapted from Jarvik, 1980). **F**, Endocast of *Eusthenopteron* in dorsal view (adapted from Jarvik, 1980).

portion occupies roughly half of the total neurocranial length, although the occipital region is not preserved. A stout basipterygoid process is present, but the transverse otic process (lateral commissure) is poorly developed. The hyomandibula articulates far back on the lateral wall of the braincase, level with the posterior semicircular canal. Dorsally, a fossa bridgei is present. The parasphenoid is elongate and denticulated. As in *Tungsenia*, the olfactory tracts in *Osteolepis* are wide and short, with well developed olfactory bulbs attached to the rounded nasal capsules (Fig. 15A). The forebrain slightly wider than the midbrain, with the widest point reached by the hindbrain. A single pineal canal is present. The labyrinth is small, with slender semicircular canals and barely developed ampullae.

Gogonasus (Frasnian) is known from exceptionally well preserved, acid prepared (Long, 1985; Long et al., 1997) and CT scanned (Holland, 2014) material. The two ossifications are of roughly equal length, and the braincase is slender, with a moderately wide ethmoid and otic region: the suborbital shelves are poorly developed and the supraorbital shelves are only slightly wider. There is no postorbital process and only a slight basipterygoid process, although the transverse otic process is fairly well developed. This latter process, and thus the articular area for the hyomandibular, is positioned far posteriorly as in *Osteolepis*. As in *Osteolepis*, a fossa bridgei is present on the dorsal surface of the otico-occipital ossification. The basicranial fenestra is large, although does not quite reach the size of that in *Diplocercides*, and vestibular fontanelles are present. Grooves for the lateral dorsal aortae run along the lateral margin of the occiput. Holland (2014) describes a complete endocast for *Gogonasus* (Fig. 15B). It is slender along its entire length, with the telencephalon and hindbrain being slightly wider than the diencephalon and midbrain. Unlike in *Osteolepis*, the olfactory tracts are long and slender, terminating in the rounded nasal capsules, although the position of the olfactory bulb is hard to identify. The hypophysis is very wide, and barely projects anteriorly. A single pineal canal leaves the forebrain. The labyrinth is fairly typical of a sarcopterygian: the semicircular canals are slender, with the anterior canal being slightly shorter than the posterior, and the two meet in a sinus superior that projects above the dorsal endocranial roof. The ampullae and ventral portion of the labyrinth are not ossified. The parasphenoid is lozenge shaped and tapers anteriorly. It does not reach the ethmoid region or ventral otic fissure, but its entire ventral surface is denticulated.

The braincase is known in several megalichthyids, and in most detail from *Ectosteorachis* (Romer, 1937; Fig. 15C; Cisuralian). The ethmoid region is long and the orbit correspondingly shorter, and there is a sharper increase in width from the orbit to the otic region than in other osteolepiforms. The ethmosphenoid portion is very narrow but deep, with poorly developed supra-and sub-orbital shelves. The basipterygoid process is stout. Anteriorly, the otico-occipital ossification is shallow, but gradually deepens posteriorly. Although the hyomandibular articulation is fairly posterior, it is less so than in *Osteolepis*, and the transverse otic process is well developed. A large fossa bridgei is present on the dorsal surface of the braincase. Ventrally, the basicranial fenestra is large, but there are no vestibular fontanelles. Deep grooves on the lateral edges of the occiput indicate the path of the lateral dorsal aortae. The olfactory tracts as reconstructed by Romer are extraordinarily long and the forebrain correspondingly short, to the extent that the optic nerves appear to leave the cranial cavity through the ventrolateral wall of the olfactory tract (Fig. 15D). The mesencephalon is no wider than the olfactory tracts, but the hindbrain is a little over twice this width. The hypothesis projects anteroventrally. Strikingly, the labyrinth differs substantially from that of the osteolepiforms already described: it is anteroposteriorly short, with stout anterior and posterior semicircular canals, a tightly curved horizontal canal, and a globular sacculus. In general proportions, it almost recalls the broad, bulbous labyrinths of placoderms such as *Macropetalichthys* (Fig. 2B), although the canals are very slender, with small ampullae. The parasphenoid is narrow and quite short, although still rather longer than the very short bones seen in stem sarcopterygians.

The braincase is also known in *Megalichthys* (Jarvik, 1966), *Cladarosymblema* (Fox et al., 1995), *Sengoerichthys* (Janvier, 1980; Janvier et al., 2007) and *Medoevia* (Lebedev, 1995). The initial descriptions of *Sengeorichthys* (?Frasnian) concerned only the ethmosphenoid ossification, but internal moulds of the otico-occipital are reported and described by Janvier et al. (2007), who consider the taxon to approximate a gereralised megalichthyid. The braincase typically resembles that of *Ectosteorachis*, with large fossa bridgei. Although the olfactory canals are long, it is not possible to see whether the optic nerve exited through the tracts, as in *Ectosteorachis.* The braincase of *Megalichthys* is only known from the anterior region and is incompletely preserved, but strongly resembles that of *Ectosteorachis*, although the parasphenoid is slightly longer and narrower. Only fragmented portions of the braincase are known in *Cladarosymblema*, although the ethmosphenoid ossification is more completely preserved. The preserved portions show a shallow suborbital shelf, although the supraorbital shelf is somewhat wider than in *Ectosterachis*, and the basipterygoid process is robust. The otico-occipital ossification is generally poorly preserved, but it can be seen that the basicranial fenestra is large and vestibular fontanelles are absent, and the transverse otic process is barely developed. The anterior portion of the otico-occipital ossification is substantially deeper than in *Ectosteorachis*. As in *Ectosteorachis*, the optic nerves leave the cranial cavity through the wall of the olfactory tract. The parasphenoid resembles that of *Megalichthys*.

Spodichthys (Jarvik, 1985; Snitting, 2008; Frasnian) is generally resolved crownward of osteolepiforms, and often as the sister taxon to tristychopterids. Snitting (2008) more recently redescribed *Spodichthys* with the assistance of CT scanning. Both the ethmosphenoid and otico-occipital ossifications are preserved, and the otico-occipital region is rather short. The ethmospenoid region is not substantially narrower than that of *Gogonasus*, although the sub- and supraorbital shelves are less developed, and the basipterygoid processes are large. The transverse otic process (Snitting's lateral commissure), upon which the hyomandibula articulated, is moderately produced. In addition to the fossa bridgei, the basicranial fenestra is large, and well developed vestibular fontanelles are present. The parasphenoid is very narrow. Fairly long olfactory tracts are developed, although do not approach the lengths of megalichthyids, and separate pineal and parapineal canals are present. The hypophysis is long but slender, extending anteriorly, and is more anteriorly positioned than in *Tungsenia*. While the semicircular canals are mentioned by Snitting, they are not described or figured.

Thanks to the attention of Stensiö (1963b) and Jarvik (1942, 1966, 1980), *Eusthenopteron* (Givetian-Frasnian) is perhaps the most iconic tetrapodomorph, and its braincase and endocast are known in exhaustive detail (Fig. 15E-F). The ethmosphenoid ossification is longer than the otico-occipital, and is narrower than that of *Spodichthys*, with expanded nasal capsules that do not reach the width of the occipital region. Additionally, the orbits are long, with very narrow supra- and suborbital shelves, and the basipterygoid process is robust. The transverse otic process (Jarvik's lateral commissure) is well developed and projects posterolaterally. A deep fossa bridgei is present on the dorsal surface of the braincase. Ventrally there is a large basicranial fenestra and vestibular fontanelle (n.b. the small opening in Jarvik, 1980: fig. 88 represents the fenestra ovalis; the true extent of the vestibular fontanelle is shown in fig. 93). The olfactory tracts are shorter than in *Spodichthys* and diverge at an narrow angle, with the result that the nasal capsules are very close together. The forebrain is long, and narrow along its entire length, with the mid- and hindbrain being wider. The anterior and semicircular canals both describe short arcs, and meet in a crus commune some way above the endocranial roof. The ampullae of all three canals are barely developed, and the sacculus is small.

6.3.3.3 Actinopterygii

The Siluro-Devonian fossil record of actinopterygians is poor when compared to that of sarcopterygians. The earliest unequivocal actinopterygian is Eifelian in age, significantly younger than its sarcopterygian counterparts, which have a good fossil record back into the Ludlow. The scant number of taxa known from more than scales and flattened body fossils has meant that hypotheses of relationships have been built almost entirely on the dermal skeleton; indeed, Gardiner & Schaeffer (1989: p.137) considered the braincase wholly unsuitable for reconstructing relationships among actinopterygians. Understanding of the evolution of Palaeozoic actinopterygians is correspondingly coarse. The crown group is hypothesized to have originated in the Devonian, based on the branching pattern produced when *Polypterus* is included in analyses of Palaeozoic taxa (Gardiner, 1984; Long, 1988b; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates, 1999; Schultze & Cumbaa, 2001; Xu & Gao, 2011; Xu et al., 2014), but no identifiable members of the extant actinopterygian lineages are known until the latest Palaeozoic and earliest Mesozoic (e.g. Nielsen, 1949; Liu & Wei, 1988; Cox & Hutchinson, 1991; Romano et al., 2014). The description of the braincase of *Cheirolepis* (Chapter 3) has invalidated two of the three endocranial synapomorphies proposed by Friedman & Brazeau (2010). The remaining criterion, the presence of vateritic statoconia, is unknown in the earliest members of the group, and so its efficacy for diagnosing membership of the group is also in doubt.

Despite exhaustive descriptions of its dermal skeleton and its iconic status as sister taxon to all other actinopterygians, the braincase of *Cheirolepis* (Eifelian-Givetian) has only recently been described (Chapter 3; Fig. 16A). Although the taxon is known from hundreds of

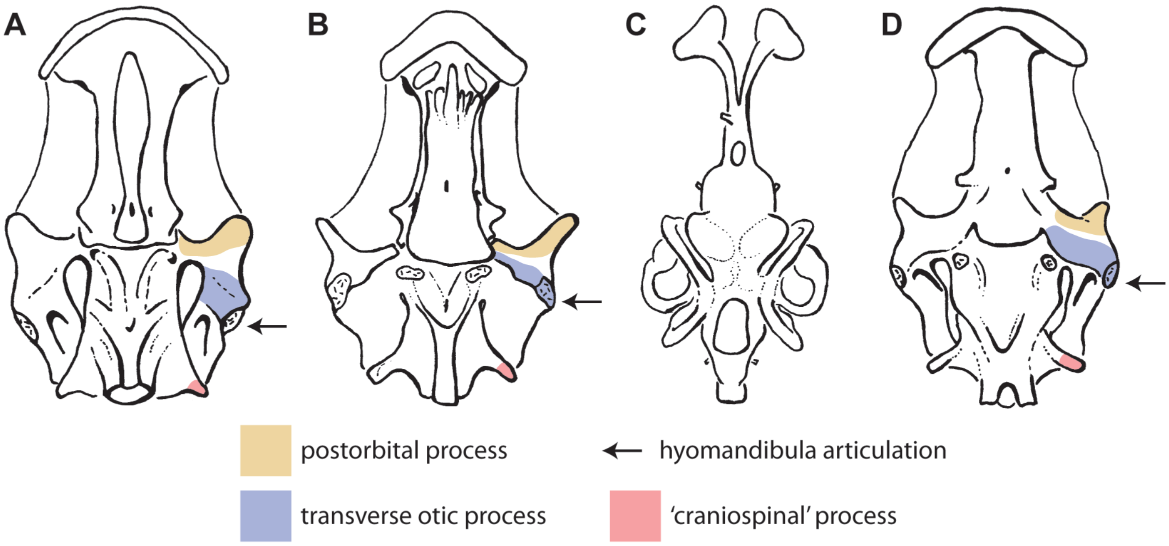

Figure 16 | Braincase and endocast anatomy of actinopterygians. A, Braincase of *Cheirolepis* in ventral view (adapted from Giles et al., in review; Chapter 3). **B**, Braincase of *Mimipiscis* in ventral view (adapted from Gardiner, 1984). **C**, Endocast of *Mimipiscis* in ventral view (adapted from Giles and Friedman, 2014). **D**, Braincase of *Raynerius* in ventral view (adapted from Chapter 4).

specimens, preservation of the neurocranium is extremely rare, and previously only passing references have been made to it (Pearson & Westoll, 1979). CT scanning allowed for the description of a nearly complete, although heavily compressed braincase. Strikingly, the neurocranium of *Cheirolepis* bears a stronger resemblance to primitive sarcopterygians rather than other actinopterygians in having large vestibular fontanelles and an uninvested dorsal aorta. The braincase lacks an intracranial joint, as in all other actinopterygians, and ventral otic and otico-occipital fissures are present. The supraorbital shelves are well developed, extending the full width of the otico-occipital region. The suborbital shelves are rather narrower, but, importantly, the interorbital septa appear fairly widely spaced. The basipterygoid processes are small, and a spiracular groove is visible on the basisphenoid. The otico-occipital region is long and accounts for slightly over half of the total neurocranial length. The postorbital processes are very well developed, forming the widest part of the braincase, and bear a wide spiracular groove. Posteriorly, the postorbital process is confluent with the transverse otic process, on the posterior of which the hyomandibula articulated. The otico-occipital fissure is continuous with the large vestibular fontanelles, but the ventral otic fissure is separate. Unusually for actinopterygians, a deep, midline groove is present on the basicranium for the dorsal aorta: the dorsal aorta is carried in a canal in all other actinopterygians, with the exception of *Howqualepis* (see below). The posterolateral corner of the braincase, just posterior to the otico-occipital fissure, is formed by a posterolaterally directed projection termed the craniospinal process in other actinopterygians. Such a process is missing from the braincases of early sarcopterygians, acanthodians and chondrichthyans, and cannot possibly be homologous with the craniospinal processes of placoderms. However, the term is entrenched in the literature and will be retained, with the caveat that no homology with the process of placoderms is implied. The dorsal surface of the braincase is smooth, with no evidence of a fossa bridgei. Dorso-ventral compression of the specimen means that the endocast is not preserved, although it can be seen that the olfactory nerves are elongate and anterolaterally directed. The blade-shaped parasphenoid is long and narrow, and extends from the ethmoid region to the ventral otic fissure. Its ventral surface is denticulated.

The pattern of relationships between *Osorioichthys*, *Tegeolepis*, *Howqualepis* and *Donnrosenia* is open to debate, with analyses reporting varying positions. Of these taxa, the braincase is completely unknown in *Donnrosenia* (Long et al., 2008), and is unexposed and therefore undescribed in *Osorioichthys* (Taverne et al., 1997; Famennian). Unpublished CT data of the only specimen of *Osorioichthys* has revealed the presence of long, anterolaterally divergent olfactory tracts, as in *Cheirolepis*, but the rest of the braincase has not yet been studied. Only the parasphenoid is known from *Tegeolepis* (Famennian), and it is possible that the braincase was unossified. The original parasphenoid description, by Dunkle & Schaeffer (1973), bears little relation to the bone known in other specimens, and a new description is presented in Chapter 3. Although only preserved in dorsal view, the parasphenoid is narrow and elongate, with moderately developed basipterygoid processes and long, wing-like ascending processes. The origin of the basipterygoid processes is unclear: as the braincase is unmineralised, they are clearly attached to the parasphenoid and may therefore be part of the dermal skeleton, a feature typically only seen in more derived actinopterygians. As the parasphenoid is only known from natural moulds, this question cannot be easily answered. The braincase is partially known in *Howqualepis* (Givetian), and was originally described by Long (1988) with additional details presented in Chapter 3. Little is known of the ethmosphenoid region, except for the presence of large basipterygoid processes, but the otic-occipital region is somewhat narrower then in *Cheirolepis*. The postorbital processes appear robust, but they are incomplete posteriorly, and a large vestibular fontanelle is present. As in *Cheirolepis*, the dorsal aorta is carried along the basicranium in a deep groove, before branching into the lateral dorsal aortae just anterior of the vestibular fontanelle. The parasphenoid is more complex of that of *Cheirolepis*: it is wider, with long ascending processes. Anteriorly, the parasphenoid is tripartite, with a long median projection and short lateral wings.

The braincase of *Mimipiscis* (Frasnian) is perhaps the best known and most exhaustively described of the Palaeozoic actinopterygians, thanks to the monographic description provided by Gardiner (1984). The orbital region is very long, with the result that the otic and occipital regions take up a mere third of the total endocranial length. In addition to the ventral otic and otico-occipital fissures, an otico-sphenoid fissure is present towards the ventral limit of the lateral commissure. As in other actinopterygians excluding *Cheirolepis*, the interobital walls meet at the midline, and the trigeminofacialis chamber is housed in the back wall of the orbit; this region is not preserved in *Cheirolepis*. Extensive supraorbital shelves roof the orbit, and the subocular shelves are fairly well developed. The basipterygoid process is stout and peg-like. The postorbital process is laterally extensive, and curves anteriorly towards the orbit. Posteriorly, however, it is very short, and the spiracular groove is narrow. The transverse otic process is poorly developed, and does not extend laterally as far as the postorbital process. The vestibular fontanelles are very small and anteriorly positioned. The dorsal aorta is enclosed in a long, midline canal that bifurcates and becomes grooves for the lateral dorsal aorta. These grooves extend a short distance before meeting the ventral otic fissure. Craniospinal processes are present behind the otico-occipital fissure, but they are poorly developed. The parasphenoid is broad, with a multifid anterior margin, and lacks any trace of ascending processes. It is denticulated along its entire width and breadth and is grooved for the passage of the spiracle. Although partially described by Gardiner (1984), a complete description of the endocast was put forward by Giles & Friedman (2014; Fig. 16C). The general shape of the endocast, with its anterolaterally directed olfactory tracts, small optic lobes and dorsally positioned laybyrinth, recalls that of sarcopterygians, although it is a much better fit for the brain. The olfactory tracts are elongate, with barely discernible olfactory bulbs, and the forebrain is very narrow, with a posteroventrally projecting hypophysis. A well developed sacculus vasculosus is present. The midbrain is approximately twice the width of the forebrain, and the hindbrain wider still, with clearly defined and anteriorly positioned cerebellar auricles. There is no corpus cerebellum. The labyrinth is proportionately longer than in sarcopterygians. Although the semicircular canals are similarly slender and project in a crus above the dorsal endocranial roof, the ampullae are much larger. The sacculus barely extends laterally beyond the sinus superior, but is ventrally extensive. A lateral cranial canal projects through the posterior semicircular canal, a feature common to all Palaeozoic actinopterygians (although its presence is as yet undertermined in *Cheirolepis*).

Gogosardina (Frasnian) was described by Choo et al. (2009) as the sister taxon to *Mimipiscis bartrami* + *M. toombsi*, a placement also resolved by Choo (2011). However, the analysis presented in Chapter 4 recovers *Gogosardina* in a clade with *M. bartrami*, with *M. toombsi* as the immediate sister taxon. The braincase of *Gogosardina* is not described by Choo et al. (2009), but a ventrolateral image reveals several aspects of anatomy that do not resemble *Mimipiscis*, despite their close relationship (Choo et al., 2009, fig 9). Instead of the long canal seen on the basicranium of *Mimipiscis*, the canal for the dorsal aorta is notched posteriorly, and the grooves for the lateral dorsal aortae are rather longer than in *Mimipiscis*. Similarities remain, however: the parasphenoid is broad and denticulated, and lacks ascending processes; the postorbital process and spiracular groove are narrow, and an otico-sphenoid fissure is present.

The clade comprising *Moythomasia nitida* and *Moy. durgaringa* is variably recovered as either in a clade with the other Gogo actinopterygians, *Mimipiscis* and *Gogosardina* (e.g.

Cloutier & Arratia, 2004; Choo, 2011) or as the next clade crownward on the actinopteran stem (e.g. Swartz, 2009; Xu & Gao, 2011; Chapter 4). *Moy. durgaringa* (Fransnian) was described by Gardiner (1984), although largely in the context of *Mimipiscis*. Additional details, particularly pertaining to the general morphology can be gleaned from an image of the braincase in ventral view figured by Long & Trinajstic (2010: fig. 5). The braincase of *M. durgaringa* is said by Gardiner to generally agree with that of *Mimipiscis*. However, although the ethmoid region is not mineralized, the orbital region is rather shorter, and robust basipterygoid processes are present. The braincase also differs from that of *Mimipiscis* in having a laterally shorter but anteroposteriorly more extensive postorbital process, with a wide groove for the spiracle, and a well developed transverse otic process. The spiracle may be enclosed in a canal near the dorsal margin of the groove. Robust craniospinal processes are present, and face posterolaterally. The dorsal aorta is enclosed in a canal with a posterior notch, and, as in *Cheirolepis, Howqualepis* and *Gogosardina*, the otic region and the grooves for the lateral dorsal aortae are long. The vestibular fontanelles are fairly large, although not quite as extensive as in *Cheirolepis*, and there is no evidence of a fossa bridgei on the dorsal surface of the braincase, only a posterior dorsal fontanelle. The parasphenoid is narrower than that of *Mimipiscis*, at least anterior to the buccohypophyseal foramen, and has a multifid anterior margin. Spiracular grooves continue onto its ventral surface, and ascending processes extend up above the otico-sphenoid fissure. An endocast has not yet been described for *Moythomasia*.

The newly described *Raynerius* (Chapter 4; Fig. 16D; Famennian) is resolved as the sister taxon to the *Moythomasia durgaringa* + *Moy. nitida* clade. The braincase resembles that of *Moy. durgaringa* in many respects: the postorbital process is large, with a wide spiracular groove, the transverse otic process is well developed, and an otico-sphenoid fissure is present. Similarly, the ventral portion of the otic region is long. There is no trace of a spiracular canal, however, and the dorsal aortic canal, while still notched posteriorly, is very short. The vestibular fontanelles are large, and the robust craniospinal process extends laterally. Unlike in *Moythomasia*, the parasphenoid is broad, and lacks ascending processes. The endocast is only partially preserved: the optic lobes are slightly larger than in *Mimipiscis*, and the hypophysis projects posteroventrally. The cerebellar auricles are robust. The labyrinth is also only partially preserved, but the ampullae are large, and the crus commune of the anterior and posterior semicircular canals sits level with the endocranial roof. The lateral cranial canal is large.

The pattern of relationships concerning stratigraphically younger taxa than *Moythomasia* + *Raynerius* is poorly understood, in part because of a tendency to include only a small number of these taxa in analyses. Furthermore, several taxa are known either exclusively from dermal bones or exclusively from the braincase, and it is difficult to reconcile these two datasets into a coherent hypothesis of relationships. The most comprehensive analysis presented thus far, seen in Chapter 4, resolves a polytomy at this node. Of these taxa, the braincase is only known in *Kentuckia deani* (Rayner, 1951; Fig. 17A; Tournasian-Visean). The orbital and ethmoid regions account for slightly less than half of the total neurocranial length. The basipterygoid processes are large, projecting ventrally, and the postorbital and transverse otic processes are confluent and fairly well developed. An otico-sphenoid fissure is absent. The spiracle is enclosed in a canal dorsally. The vestibular fontanelles are large, but it is unclear whether they were continuous with the ventral otic fissure. The dorsal aorta is enclosed in a long midline canal that branches to give off short grooves for the lateral dorsal aorta. An efferent branchial artery leaves from the floor of the canal. Although not drawn by Rayner (1951), unpublished scan data shows that the posterior margin of the canal was notched as in *Moythomasia*, *Raynerius* and *Gogosardina*. The pineal foramen is expanded to form an elongate anterior fontanelle, although the posterior dorsal fontanelle is still small. The lateral edges of the dorsal surface of the otic region are uneven and pitted, which Rayner suggests may be the beginnings of a fossa bridgei. The absence of a fossa bridgei in more primitive actinopterygians and sarcopterygians, as well as the different topographic position, indicates that this structure is not homologous with the similarly named structure present in tetrapodomorphs. The parasphenoid is incompletely known, but is described as being short, with elongate ascending processes that approach, but do not reach, the spiracular canal. A mid-sagittal section through the braincase was figured by Rayner (1951: fig.9), and additional descriptions of the endocast were published by Giles & Friedman (2014). Rather than each olfactory nerve being carried in its own tract, both are carried in a single midline tube, only diverging just behind the nasal caspules. The forebrain is slightly longer than in *Mimipiscis*, and the hypophysis projects posteroventrally. The midbrain is well developed, and only slightly narrower than the hindbrain, which displays very large auricles and a cerebellar corpus. In contrast to *Mimipiscis*, the crus commune sits below the roof of the endocavity, and the anterior and posterior semicircular canals are squat, with very large ampullae.

Relationships are also poorly known between *Mesopoma, Woodichthys, Lawrenciella, Kansasiella,* and *Cosmoptychius*, all of which have endocranial material preserved, plus several more taxa known only from their dermal skeleton.

Comprehensive descriptions of the braincase anatomy of *Kansasiella* (Kasimovian) have been provided by Poplin (1974). The ethmoid region is unknown, but the orbital region is overhung by moderately well developed supraorbital shelves and floored by narrow suborbital shelves. The basipterygoid process is quite robust and laterally extensive. As the transverse otic process is poorly developed, the postorbital processes mark the widest point of the braincase. A spiracular canal is present. The craniospinal processes are very well

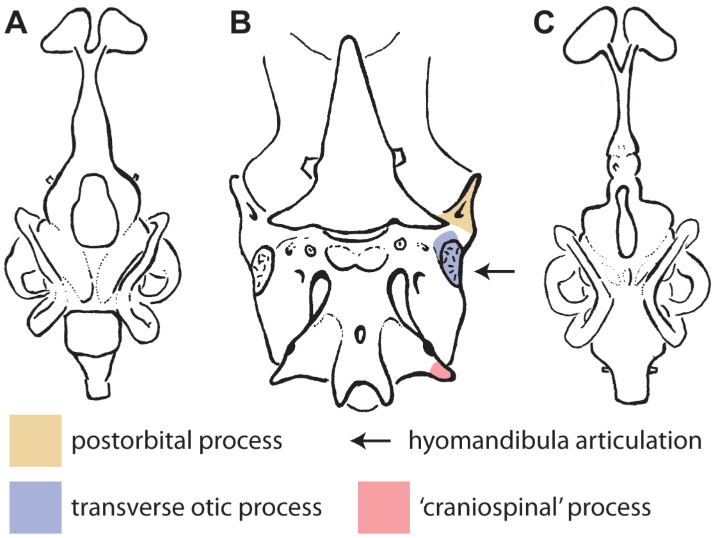

Figure 17 | Braincase and endocast anatomy of actinopterygians. A, Endocast of *Kentuckia* in dorsal view (adapted from Giles and Friedman, 2014). **B**, Braincase of *Lawrenciella* in ventral view (adapted from Hamel & Poplin, 2008). **C**, Endocast of *Lawrenciella* in dorsal view (adapted from Hamel & Poplin, 2008).

developed, and project laterally until they almost reach the same width as the postorbital process. The dorsal aorta is enclosed in a midline canal with a posterior notch along the entire length of the basicranium, with paired exits for the epibranchial arteries. The anterior dorsal fontanelle is elongate but narrow, and the posterior dorsal fontanelle is partially roofed over posteriorly by a median projection. Distinct anterior and posterior fossa bridgei are developed, and the anterior fossa sits between the posterior and transverse otic process. The parasphenoid is broad anteriorly but tapers to a point anteriorly, and contributes to the basipterygoid processes. The ascending processes are long, and reach the spiracular canal. As in *Kentuckia*, the olfactory tracts are enclosed in a midline canal. However, they are longer than in *Kentuckia*, and as a result the forebrain and midbrain are more posteriorly placed; the midbrain starts jut anterior of the anterior ampulla, whereas in *Kentuckia* (and *Mimipiscis*) the hindbrain starts at this level. The midbrain is fully the same width as the hindbrain, and the cerebellar auricles are rather small. In other respects, the endocast resembles that of *Kentuckia*.

Comparable levels of detail are known for the braincase and endocast of *Lawrenciella* (Hamel & Poplin, 2008; Fig. 17B-C; Kasimovian). The orbital region is fairly short, with wide supraorbital shelves and stout basipterygoid processes, which have a dermal component. The postorbital process is anteroposteriorly long, with a wide spiracular canal on its lateral face, and the poorly developed transverse otic process is separated from it by the anterior fossa bridgei. The dorsal aorta is enclosed in a canal for almost the entire basicranial length, with a midline opening for the epibranchial arteries, although the lateral dorsal aortae emerge in grooves just posterior to the ventral otic fissure. The aortic canal is notched posteriorly, and the craniospinal processes are shorter than in *Kansasiella*. The anterior dorsal fontanelle is slot shaped and fairly short, and the posterior dorsal fontanelle is partially roofed anterior and posteriorly. Large anterior and posterior fossa bridgei are present. The parasphenoid and endocast is generally similar to that of *Kansasiella*.

The braincase of *Woodichthys* (Serpukhovian) is known only from one dorsoventrally compressed specimen, and is described by Coates (1998). The neurocranium is difficult to describe in detail due to the state of preservation, but it appears to closely resemble that of *Lawrenciella*: the supraorbital shelves are broad; the postorbital processes well developed; and the dorsal aorta almost completely enclosed, with the lateral dorsal aortae branching just posterior to the ventral otic fissure. The parasphenoid is also similar, although ascending processes appear to be absent.

Only fragments of the incompletely ossified braincase of a juvenile are known from *Cosmoptychius* (Schaeffer, 1971; Visean). The ethmoid region is not mineralized, but the partial parasphenoid reveals the presence of elongate basipterygoid and ascending processes. Little of the posterior region of the braincase is ossified, but the aortic canal is enclosed along almost the entire length of the basicranium. The braincase is only partially known in *Mesopoma*, but aspects of the endocast were described by Coates (1999). The midbrain is the same width as the hindbrain, and the hypophysis is posteroventrally projecting, with a large saccus vasculosus. Where preserved, the remainder of the endocast resembles that of other Carboniferous actinopterygians.

Pteronisculus and *Boreosomus* were described in a monograph by Nielsen (1942), with additional details on the braincase and labyrinth of *Pteronisculus* described by Coates (1998). *Boreosomus* (Fig. 18A; Induan) more closely resembles stratigraphically younger taxa, despite often being resolved as more crownward than *Pteronisculus* (Gardiner, 1984; Long, 1988b, Xu & Gao, 2011; Xu et al., 2014; Chapter 4). The supraorbital shelves and basipterygoid process are moderately developed, although the orbits are very large, and account for over half the length of the braincase. In addition to a narrow postorbital process, the transverse otic process is poorly developed. A small vestibular fontanelle is present, and the dorsal aorta is enclosed from the occiput to the ventral otic fissure, with midline foramina for the exits of the epibranchial arteries. There is no posterior notch in the aortic canal, and the craniospinal processes are small. Unlike in the Carboniferous actinopterygians, the anterior dorsal fontanelle is very small and the posterior dorsal fontanelle is entirely closed. The lateral edges of the dorsal surface are occupied by deeply excavated anterior and posterior fossa bridgei. A long, broad parasphenoid terminates at the ventral otic fissure, although its anterior extent is unknown. Although the olfactory tracts are carried in a single midline tube, the two nerves seem to be slightly separated laterally (Fig. 18B). The midbrain and hindbrain are the same width, and the labyrinth is anteroposteriorly long.

The braincase morphology of *Pteronisculus* (Induan) is rather different from that of *Boreosomus* and stratigraphically older actinopterygians (Fig 18C). The orbital region is slightly shorter, with very narrow supraorbital and suborbital shelves and particularly extensive basipterygoid processes. The postorbital process is wider than in *Boreosomus* and anterolaterally facing, and the transverse otic process much more developed. Unlike in all of the actinopterygian braincases described above, the vestibular fontanelles are confluent with the ventral otic fissure. The aortic canal is not notched posteriorly, and the lateral dorsal aortae diverge level with the vestibular fontanelle before emerging in grooves; the divergence point is contained within the canal. The occiput extends posteriorly behind the otic region, and the craniospinal processes are stout. A broad and elongate parasphenoid extends posteriorly to cover the ventral otic fissure. Although large fossa bridgei are present, the anterior dorsal fontanelle is still fairly elongate and the posterior dorsal fontanelle open.

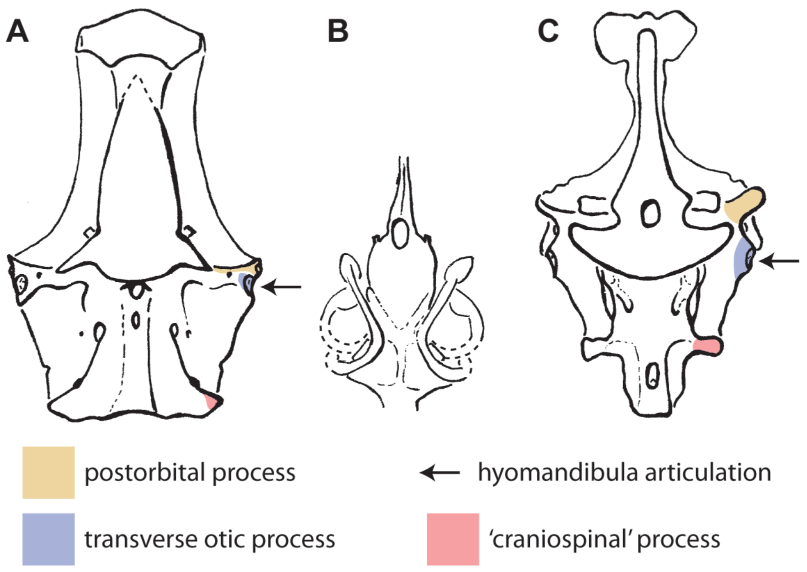

Figure 18 | Braincase and endocast anatomy of actinopterygians. A, Braincase of *Boreosomus* in ventral view (adapted from Nielsen, 1942). **B**, Endocast of *Boreosomus* in dorsal view (adapted from Nielsen, 1942). **C**, Braincase of *Pteronisculus* in ventral view (adapted from Nielsen, 1942).

6.4 A SYNTHETIC UNDERSTANDING OF CHARACTER TRANSFORMATION ACROSS THE EARLY GNATHOSTOME TREE

The review presented here, along with new observations, provides the basis for a step-wise reconstruction of character evolution across and within the major jawed vertebrate branches (Figs 19-23 and below). This hypothesis draws on recent published phylogenies and assumes placoderm paraphyly, acanthodians as stem chondrichthyans, and osteichthyan monophyly (see figure captions for references).

Rather than a proposed synapomorphy scheme, the lists below represent the stepwise sequence of character acquisition and loss across the early vertebrate tree of life. The key morphological changes in the braincase at successive nodes can be summarised as follows.

6.4.1 Character transformations in placoderms (Fig. 19)

A: Separate rhinocapsular ossification.

B: Rhinocapsular ossification secondarily fused to rest of braincase; loss of postorbital process; elongate occipital stalk.

C: Lateral expansion of braincase no longer surrounds orbit; hyomandibula articulates posterior to orbit; facial nerve branches posterior to postorbital process.

D: Loss of vagal process.

E: Bifid vagal process.

F: Jugular vein uninvested in otic capsule.

6.4.2 Character transformations in arthrodires (Fig. 20)

G: Craniospinal process level with posterior margin of braincase.

H: Rhinocapsular ossification secondarily fused to rest of braincase.

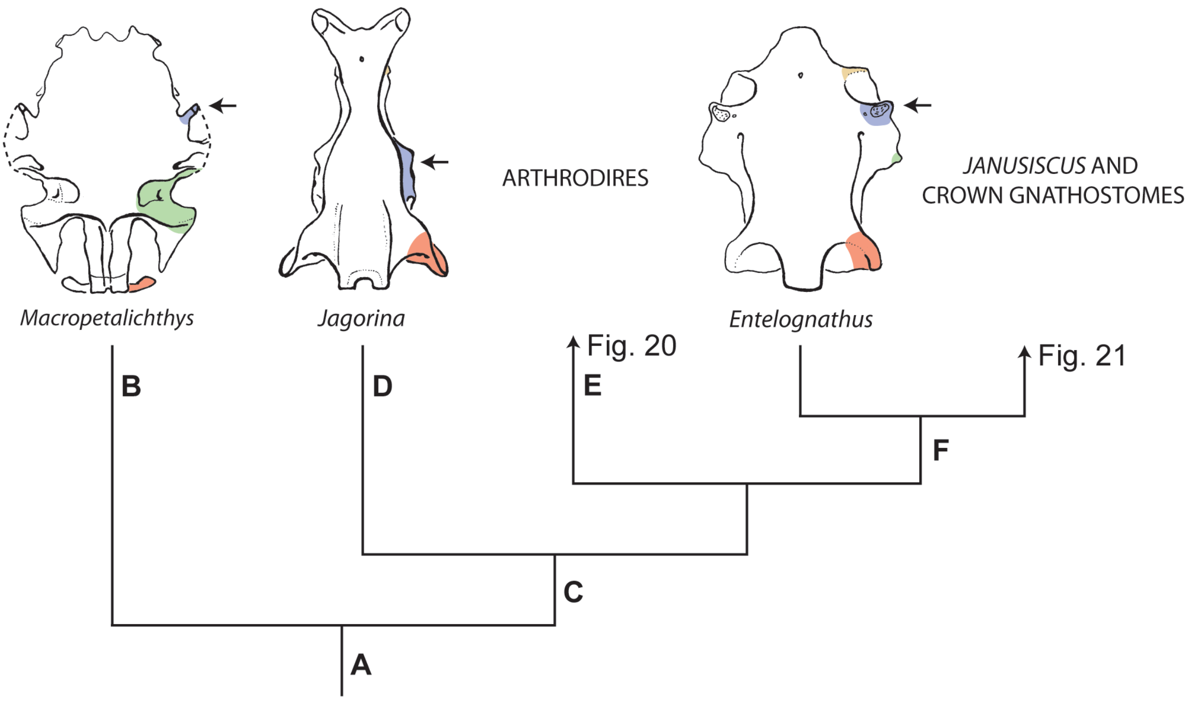

Figure 19 | Character transformations in placoderms. Cladogram based on Giles et al., 2015. See Figs 1–18 for key.

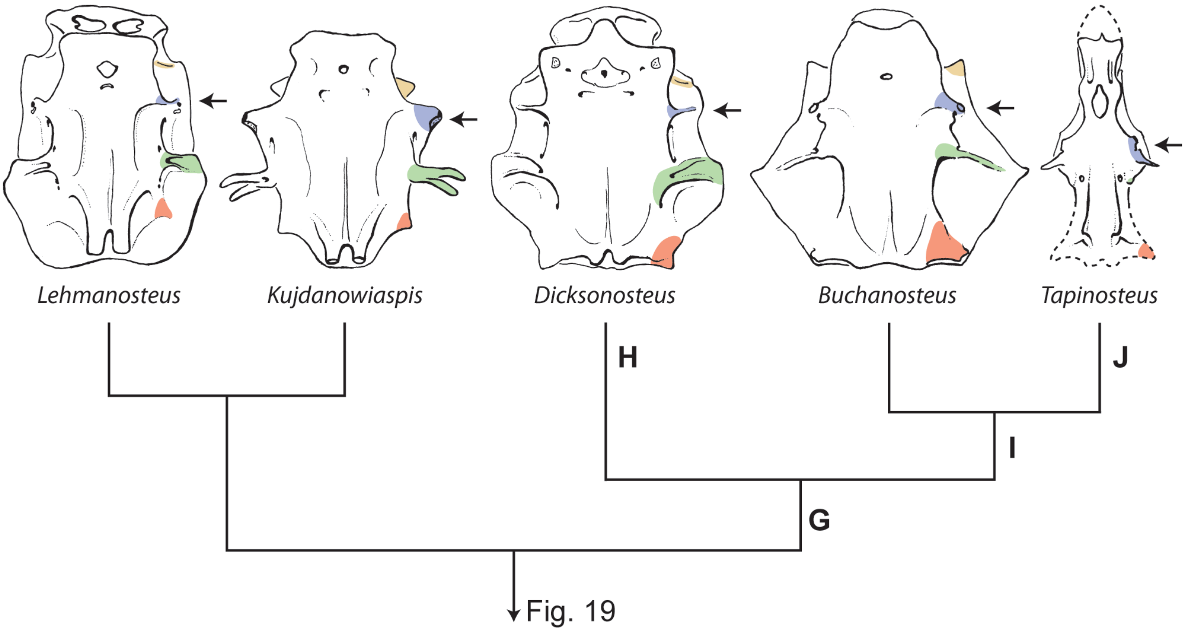

Figure 20 | Character transformations in arthrodires. Cladogram based on Dupret et al., 2007; Dupret et al., 2009; Carr & Hlavin, 2010; Davis et al., 2012; Zhu et al., 2013; Dupret et al., 2014; Long et al., 2014; Giles et al., 2015. See Figs 1–18 for key.

I: Single vagal process.

J: Narrow interorbital septum; loss of postorbital process

6.4.3 Character transformations in stem and crown gnathostomes (Fig. 21)

K: Thin endocranial wall; nasal capsule co-ossified with rest of braincase; subcranial ridges; posteriorly positioned hyomandibular articulation; vagal and craniospinal processes lost; cuccularis fossa lost.

L: Spiracular grooves present on basicranial surface*; hyomandibula articulates on lateral wall of otic capsule; ventral otic fissure; otico-occipital fissure; posterior dorsal fontanelle; sinus superior and crus commune; crus commune projects above endocranial roof; labyrinth cavity confluent with remainder of endocranial chamber (capsular wall absent); extended telencephalic region; vestibular fontanelles*.

M: Transverse otic process lost; median ridge on dorsal surface of braincase.

N: Narrow interorbital septum; multiple ossifications in braincase.

O: Precerebral fontanelle; ventral otic fissure lost; lateral dorsal aortae partially enclosed in basicranium; hyomandibula articulates some way posterior of hyomandibular nerve; capsular wall of labyrinth chondrified.

P: Comineralised ethmoid and sphenoid completely eclosing nasal capsules; endocranial cavity dorsally restricted within sphenoid; horizontal cranial canal joins labyrinth level with posterior ampulla.

Q: Elongate olfactory tracts; vestibular fontanelles (although see note below regarding *Acanthodes*); spiracular grooves present on basicranial surface (although see note below regarding *Acanthodes*).

*These may be gained here and lost in chondrichthyans crownward of *Acanthodes*; alternatively they may be gained separately in *Acanthodes* and osteichthyans.

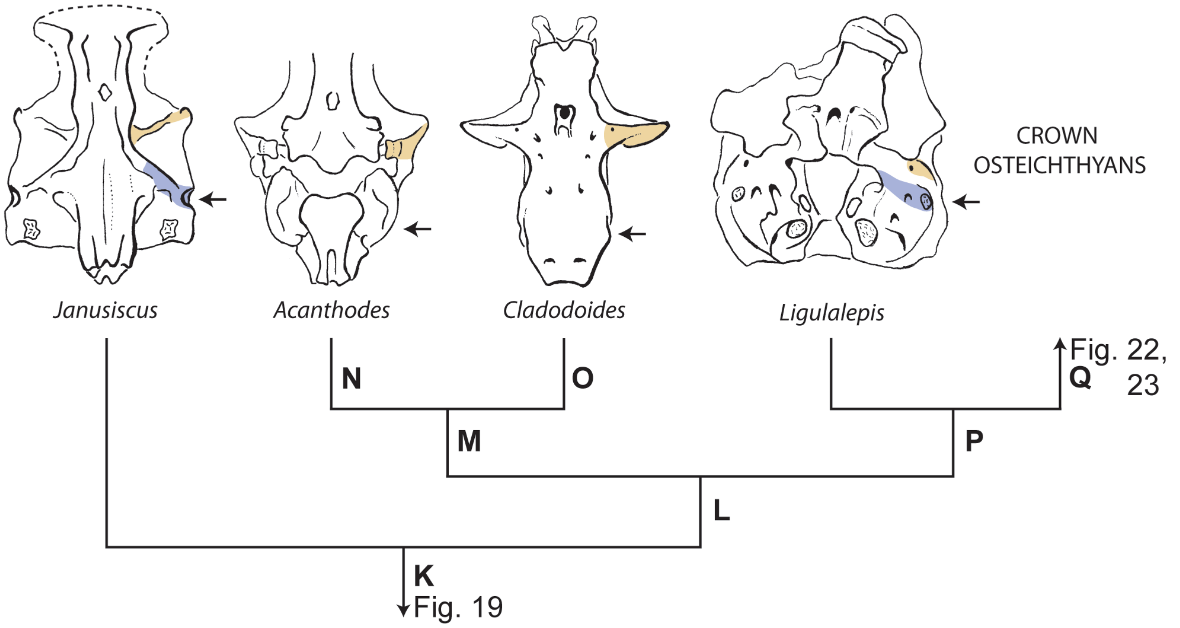

Figure 21 | Character transformations in stem and crown gnathostomes. Cladogram based on Zhu et al., 2013; Dupret et al., 2014; Giles et al., 2015; Chapter 4. See Figs 1–18 for key.

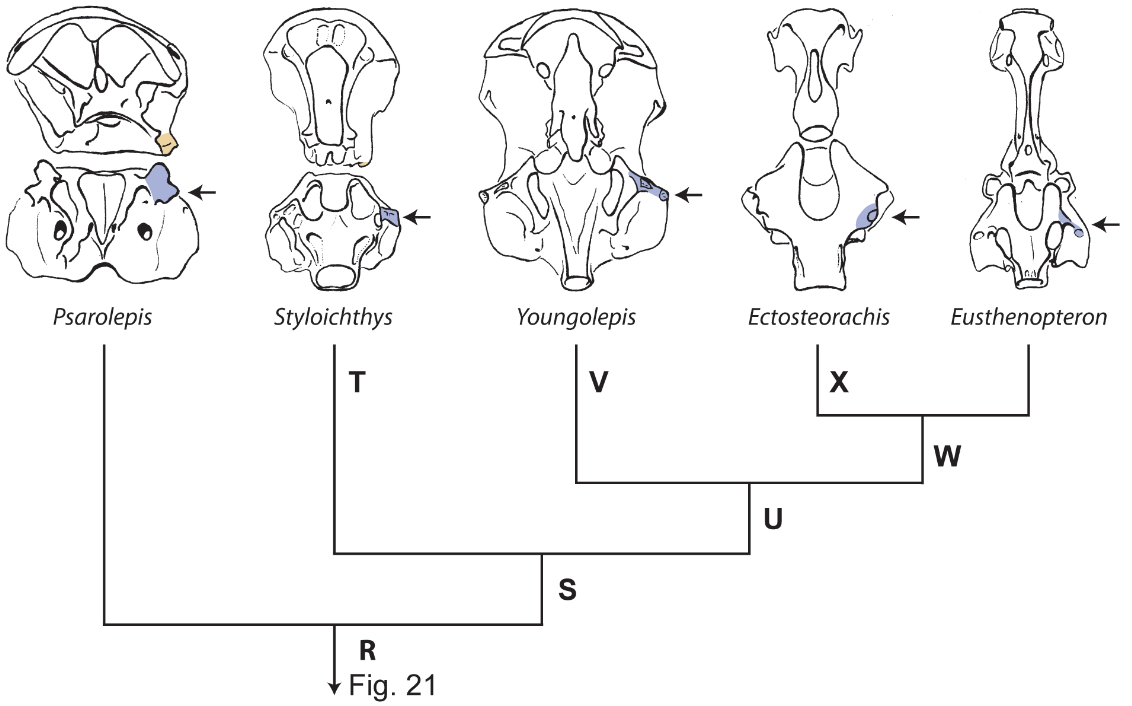

Figure 22 | Character transformations in sarcopterygians. Cladogram based on Friedman, 2007; Lu et al., 2012; Zhu et al., 2013; Giles et al., 2015; Chapter 4. See Figs 1–18 for key.

6.4.4 Character transformations in sarcopterygians (Fig. 22)

R: Joint between ethmosphenoid and otico-occipital portions of braincase; internasal cavities; vertical component to basipterygoid process; trigeminal nerve exits anterior to jugular canal; broad hyomandibular articulation; basicranial fenestra; Y-shaped supraotic recess;

S: Bipartite hyomandibular articulation

T: Vestibular fontanelle lost.

U: Anteriorly placed intracranial joint; postorbital process lost; fossa bridgei.

V: Intracranial joint lost; basicranial fenestra lost; triangular nasal capsules.

W: Rounded nasal capsules; short, wide olfactory tracts.

X: Vestibular fontanelles lost; very long olfactory tracts also housing optic nerve.

6.4.5 Character transformations in actinopterygians (Fig. 23)

Y: Intracranial joint absent; eyestalk absent; spiracular groove on postorbital process; postorbital process and transverse otic process confluent; ‘craniospinal’ process; dorsal aorta bifurcates anterior to occiput; lateral cranial canal.

Z: Narrow interorbital septum; acending processes of parasphenoid; otico-sphenoid fossa; dorsal aorta in midline canal with notched posterior margin.

AA: Ascending processes of the parasphenoid lost; reduced vestibular fontanelle; aortic notch lost.

BB: Ascending processes of the parasphenoid lost.

CC: Otico-sphenoid fossa absent; spiracular canal on postorbital process; dermal component to basipterygoid process; expanded anterior dorsal fontanelle; fossa bridgei; olfactory tracts anteriorly (rather than anterolaterally) directed; olfactory nerves carried in a single midline tube; midbrain same width as hindbrain; corpus cerebellum; crus commune ventral to endocranial roof.

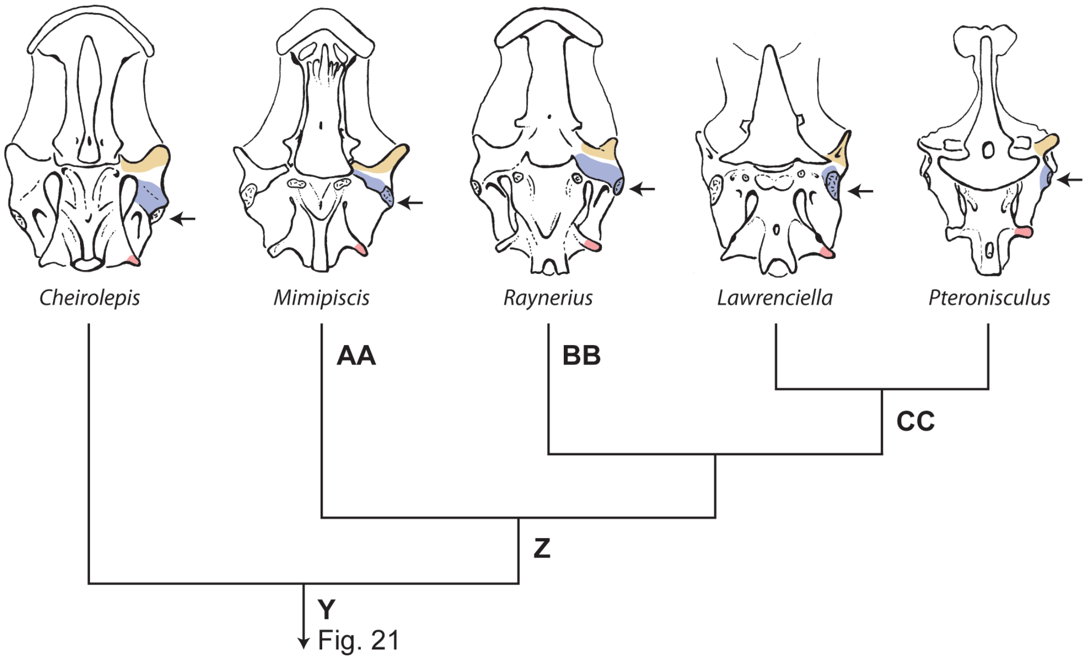

Figure 23 | Character transformations in actinopterygians. Cladogram based on Xu & Gao, 2011; Choo, 2011; Xu et al., 2014; Chapter 4. See Figs 1–18 for key.

Patterns of convergence relating to a number of traits are obvious. The most conspicuous of these is the repeated appearance of deep braincases with narrowly separated interorbital septa, most likely reflecting the evolution of large eyes (e.g. *Romundina*, coccosteomorphs and pachyosteomorphs, *Acanthodes*, actinopterygians crownward of *Cheirolepis*). The postorbital process is also lost repeatedly: in the petalichthyid *Macropetalichthys*; the rhenanid *Bolivosteus*; the acanthothoracids *Kosoraspis* and *Radotina*; ptyctodontids; the coccosteomorphs and pachyosteomorphs; and in sarcopterygians crownward of *Styloichthys*. A reduction in the level of mineralisation of the braincase is seen convergently in antiarchs, derived arthrodires and acanthodians.

In addition to highlighting the importance of the braincase to reconstructing relationships, this review highlights critical areas of uncertainty in our understanding of how this pivotal structure evolved across the vertebrate tree. In the placoderms, traditional destructive methods have resulted in the loss of important and often unique specimens, leaving behind only fragile wax models and stylised anatomical interpretations. Many reconstructions were based on a preconceived hypothesis of relationships that we now know to be inaccurate: for example, many of Stensiö's (1963a, 1969) reconstructions borrowed heavily from modern shark anatomy, as sharks and placoderms were thought to be closely related. A number of other taxa, described before the advent of CT scanning, have only been partially investigated due to a reluctance to use serial sectioning, and as such elements of buried anatomy and n particular the endocranial cavities remain undescribed. A re-examination of placoderm braincases represents a rich avenue of future study.

The state of knowledge of braincase evolution in acanthodians is also woefully poor, although this is largely due to the very limited material at hand. The firm resolution of acanthodians as stem chondrichthyans has helped illuminate some areas of uncertainty, but further questions remain unanswerable pending the discovery of additional acanthodian braincases, a prospect which seems unlikely.

The final area of uncertainty concerns braincase evolution in early actinopterygians. The problem here is not a lack of data or reliance on destructive techniques, but a failure to adequately sample the base of the actinopterygian tree, leading to over-reliance on a single taxon, *Mimipiscis*. Steps have been taken in this thesis to rectify this problem (Chapters 2-5), and future descriptions of braincase anatomy in *Gogosardina* and *Moythomasia durgaringa* will provide additional data.

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CHAPTER 7: CONCLUSION

This thesis has sought to understand how the highly successful bony vertebrate body plan arose, with a focus on the braincase of the first jawed vertebrates and the first actinopterygians. Despite the vast membership of the gnathostomes - over 60,000 species, some 32,000 of which are actinopterygians - and an extensive history of research effort, a failure to integrate morphological data from different parts of the tree, a lack of focus on the actinopterygians, and recent upheavals in our understanding of early vertebrate relationships has resulted in a failure to fully comprehend the group's early evolution. This is further compounded by the fact that only a handful of braincases have been described for some groups, and these sparse data points make it impossible to understand the step-wise evolution of characters or accurately reconstruct the anatomy of a clade's last common ancestor.

In this thesis I have used innovative x-ray CT methods to study the braincases of pivotal early vertebrate taxa, namely the stem gnathostome *Janusiscus* (Chapter 2), the first actinopterygian *Cheirolepis* (Chapter 3), and the early actinopterygians *Raynerius* (Chapter 4), *Mimipiscis* and *Kentuckia* (Chapter 5), as well as drawing together the disparate accounts of braincase anatomy across the gnathostome tree (Chapter 6). The descriptions put forward, both of newly discovered and well-established taxa, concern early members of key clades and help paint a picture of anatomy at the dawn of these groups. This has allowed me to form a synthetic understanding of how the gnathostome, osteichthyan and actinopterygian body plans were assembled on an evolutionary timescale, building on the work of Friedman & Brazeau (2010) and Brazeau and Friedman (2014). It is worth noting that the characters discussed below do not constitute a formal proposed synapomorphy scheme like that of the previous two references; rather, they indicate the stepwise sequence of character acquisition and loss across the early vertebrate tree of life.

7.1 ASSEMBLY OF THE CROWN GNATHOSTOME BODY PLAN

The terminal branches on the gnathostome stem are occupied by placoderms such as *Entelognathus* (Zhu et al. 2013) and more enigmatic taxa such as *Ramirosuarezia* (Pradel et al., 2009) and the newly described *Janusiscus* (Chapter 2; Giles et al., 2015). Before the discovery of *Janusiscus*, difficulty was faced in accounting for the morphological jump between the anatomy of stem and crown gnathostomes. Furthermore, the placement of the micromeric acanthodians on the osteichthyans stem forced the assumption that the macromeric dermal plates of placoderms and osteichthyans were not homologous. *Janusiscus* neatly bridges this morphological gap, and has the additional effect of substantiating the finding of Zhu et al. (2013) that all acanthodians are in fact stem chondrichthyans, indicating that micromery is a character of the chondrichthyan total group (Friedman & Brazeau, 2013). In combining features typically associated with placoderms, chondrichthyans and osteichthyans within its braincase, *Janusiscus* allows us to understand the sequence of character acquisition along the stem and the likely braincase structure of the last common ancestor of crown gnathostomes.

Janusiscus is united with crown gnathostomes, crownward of all placoderms, on the basis of the following neurocranial characters:

- thin endocranial wall
- nasal capsule co-ossified with rest of the braincase
- subcranial ridges
- posteriorly positioned hyomandibular articulation

- vagal and craniospinal processes lost
- cuccularis fossa lost

Neurocranial characters that unite chondrichthyans and osteichthyans, and thus were presumably present in the last common ancestor of crown gnathostomes, are:

- spiracular grooves present on basicranial surface (nb these may be gained here and secondarily lost in chondrichthyans crownward of *Acanthodes*, or alternatively gained independently in *Acanthodes* and osteichthyans)
- hyomandibula articulates on lateral wall of otic capsule
- ventral otic fissure
- otico-occipital fissure (unknown in *Janusiscus*)
- posterior dorsal fontanelle
- sinus superior and crus commune (unknown in *Janusiscus*)
- crus commune projects above endocranial roof (unknown in *Janusiscus*)
- labyrinth cavity confluent with remainder of endocranial chamber (capsular wall absent) (unknown in *Janusiscus*)
- extended telencephalic region
- vestibular fontanelles (nb these may be gained here and secondarily lost in chondrichthyans crownward of *Acanthodes*, or alternatively gained independently in *Acanthodes* and osteichthyans)

7.2 ASSEMBLY OF THE OSTEICHTHYAN BODY PLAN

Previous attempts to understand the primitive condition of the osteichthyan body plan have been predicated on the placement on *Acanthodes* and other acanthodians on the osteichthyan stem (Miles, 1973; Friedman & Brazeau, 2010; Brazeau & Friedman, 2014). As noted by the latter two papers, once *Acanthodes* is removed from this position the osteichthyan stem becomes rather bare, populated largely by scale taxa (*Andreolepis*: Gross, 1968; *Naxilepis*: Wang & Dong, 1989; *Orvikuina*: Schultze, 1968; *Terenolepis*: Burrow, 1995). Furthermore, the placement of *Acanthodes* on the chondrichthyan stem (Zhu et al., 2013; Giles et al., 2015; Chapter 2), has the effect of invalidating a number of the osteichthyan synapomorphies proposed by Friedman & Brazeau (2010) and Brazeau & Friedman (2014), namely:

- two or fewer spino-occipital nerves
- ventral surface of otic capsules mediolaterally sloping
- spiracular grooves on basisphenoid
- vestibular fontanelles
- anterior dorsal fontanelle
- hyomandibula articulates with lateral commissure/postorbital process
- enamel
- anteriorly directed infrapharyngobranchials
- hyomandibula bears deep groove or canal
- macromeric dermal skull
- pectoral girdle with substantial dermal component

Additionally, the discovery of certain osteichthyan-like characters in the stem gnathostome *Janusiscus* (Giles et al., 2015; Chapter 3) has had the effect of invalidating the following proposed characters:

- hyomandibular branch of the facial nerve exits into jugular canal
- ethmoid comineralised with sphenoid
- absence of endolymphatic duct openings in dermal skull

Topologies derived from recent phylogenetic analyses (Friedman, 2007; Brazeau, 2009; Friedman & Brazeau 2010; Davis et al. 2012; Zhu et al. 2013; Dupret et al. 2014; Giles et al 2015) suggest that, minimally, *Ligulalepis* (Basden et al., 2000; Basden & Young, 2001) and possibly *Dialipina* (Schultze & Cumbaa, 2001)) can be assigned to the osteichthyan stem. *Ligulalepis* is united with the gnathostome crown by the following, which characterise the neurocranial anatomy of the osteichthyan total group and were likely present in its last common ancestor:

- comineralised ethmoid and sphenoid completely eclosing nasal capsules;
- endocranial cavity dorsally restricted within sphenoid
- horizontal cranial canal joins labyrinth level with posterior ampulla

The crown itself is united by the following neurocranial characters:

- elongate olfactory tracts
- vestibular fontanelles (although see note above regarding *Acanthodes*)
- spiracular grooves present on basicranial surface (although see note above regarding *Acanthodes*)

7.3 ASSEMBLY OF THE ACTINOPTERYGIAN BODY PLAN

As with osteichthyans, there is a longstanding failure to identify members of the actinopterygian stem, with previous scale-based candidates (*Andreolepis*: Gross, 1968; *Naxilepis*: Wang & Dong, 1989; *Orvikuina*: Schulte, 1968; *Terenolepis*: Burow, 1995) now assigned to the osteichthyan stem (Friedman & Brazeau, 2010). Schultze's (in press) recent reinterpretation of *Naxilepis*, *Orvikuina* and *Terenolepis* as stem actinopterygians is predicated on their scales possessing multi-layered enamel, peg-and-socket articulation and an anterodorsal process. Given the presence of each of these features in at least one stem sarcopterygian, they cannot be used to diagnose membership of Actinopterygii; at best, they are crown osteichthyan apomorphies. As such, the interpretation of *Naxilepis*, *Orvikuina* and *Terenolepis* as stem osteichthyans holds. Currently, no unequivocal stem actinopterygians are known, although the analysis presented in Chapter 4 suggests that *Dialipina* (Schultze & Cumbaa), 2001 and *Meemannia* (Zhu et al., 2010) otherwise regarded as stem actinopterygians, stem sarcopterygians or stem osteichthyans, may lie in this position, having previously been misdiagnosed. Chapters 3 - 6 have built a comprehensive picture of endocranial anatomy in actinopterygians, from the earliest members, which resemble sarcopterygians in certain features, to those that have begun to develop specialisations associated with more crownward members (such as the fossa bridgei). These findings outline a general trend in braincase morphology, with the orbital region becoming longer, the parasphenoid more elaborate, and the dorsal aorta being becoming enclosed in a canal. I have also identified conspicuous morphological changes in the endocast of early actinopterygians (Chapters 4 and 5), reflecting changes in the structure of the brain as the group began to diversify. From a primitive state that resembles that of chondrichthyans (e.g. *Xenacanthus*: Schaeffer, 1981) and primitive sarcopterygians (e.g. *Youngolepis*, Chang, 1982; *Eusthenopteron*, Jarvik, 1980), the labyrinth becomes proportionately larger and more ventrally positioned, the optic lobes wider, and the cerebellar auricles more distinct. As mentioned, certain anatomical features of *Cheirolepis* are shared with sarcopterygians, and as a result must be removed from the actinopterygian synapomorphy list of Friedman & Brazeau (2010):

- midline canal in basicranium for dorsal aorta
- narrow interorbital septum
- propterygial canal

Neurocranial characters that unite actinopterygians, and were presumably present in the group's last common ancestor, are:

- intracranial joint absent
- eyestalk absent
- spiracular groove on postorbital process
- postorbital process and transverse otic process confluent
- 'craniospinal' process behind otico-occipital fissure (not homologous with that of placoderms)
- dorsal aorta bifurcates anterior to occiput;
- lateral cranial canal.

The node subtending *Mimipiscis* and more crownward taxa from primitive actinopterygians such as *Cheirolepis, Tegeolepis* and *Howqualepis* (Chapter 3) marks the appearance of more recognisably actinopterygian braincases, and is characterised by the following features:

- narrow interorbital septum
- ascending processes of parasphenoid
- otico-sphenoid fossa
- dorsal aorta in midline canal with notched posterior margin

A more sophisticated braincase anatomy is found in *Kentuckia deani* (Rayner, 1951; Chapter 5) and more crownward taxa, and marks a substantial shift away from the anatomy of Devonian actinopterygians. This is reflected in the following characters:

- otico-sphenoid fossa absent
- spiracular canal on postorbital process
- dermal component to basipterygoid process
- expanded anterior dorsal fontanelle

- fossa bridgei
- olfactory tracts anteriorly (rather than anterolaterally) directed
- olfactory nerves carried in a single midline tube
- midbrain same width as hindbrain
- corpus cerebellum
- crus commune ventral to endocranial roof

The sequences of character acquisition outlined above highlight the complex nature of the braincase, and its efficacy in understanding anatomical evolution and relationships within and between groups. This has long been realised and exploited by practitioners of Sollas' grinding method (e.g. Stensiö 1925, 1937, 1969; Jarvik, 1972, 1980; Schaeffer, 1981), Poplin's microtome technique (e.g. Poplin, 1974, 1984), traditional preparators (e.g. Nielsen, 1949; Gardiner, 1984), and those who described naturally exposed braincases and endocasts (e.g. Watson, 1925; Stensiö, 1950; Rayner, 1951). It is to be hoped that, with the ease and availability of CT scanning, braincases can be further explored and understood, increasing the neurocranial dataset and further refining our understanding of evolution and relationships.

7.4 FUTURE DIRECTIONS

While the descriptions and review of braincase anatomy presented in this thesis represent a major step forward in understanding how the gnathostome body plan was assembled, it is clear that several critical areas of uncertainty remain. The placoderms represent the largest problem: many of the braincase descriptions present in the literature are outdated and in desperate need of revision, and due to the destructive methods used the original specimens often cannot be revisited (e.g. Stensiö 1925, 1969). Although several workers have begun this task (e.g Elliott & Carr, 2010; Dupret, 2010; Olive et al., 2011), CT scanning has been used on scant taxa (Dupret et al., 2014), and represents a rich future avenue of study. The endocast in particular needs to be revisited in order to understand whether it was truly a poor fit in some taxa (e.g. *Macropetalichthys*: Stensiö, 1925; *Brindabellaspis*: Young, 1980) and a better fit in others (e.g. *Kujdanowiaspis*, Stensiö, 1969; *Dicksonosteus*: Goujet, 1984).

Although the description of *Janusiscus* (Giles et al. 2015; Chapter 2) has gone some way to answering questions concerning questions of anatomical conditions in proximate stem gnathostomes, questions remain concerning the position of *Ramirosuarezia* (Pradel et al., 2009), and until these are answered ambiguities will remain.

Further descriptions of putative stem osteichthyans such as *Ligulalepis* and *Dialipina*, particularly the neurocranium and endocast of *Ligulalepis*, will help fill in gaps concerning our understanding of stem osteichthyan relationships. New descriptions pertaining to *Dialipina*, as well as *Meemannia*, may also go some way to answering the question of why no stem actinopterygians have yet been identified.

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8.1 APPENDIX 1

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8.1.1 Supplementary Notes

8.1.1.1 Geological provenance and stratigraphy

The specimens described in this paper (GIT 496-6 [Pi.1384]; GIT 496-7 [Pi.1383]; Extended Data Figure 1) are from the lower member of the Kureika Formation on the Sida River, Kotui Basin, Siberia (Schultze, 1992). The Kureika Formation, part of the North-Western Siberian Platform, is clearly Early Devonian in age. Early stratigraphic assessments correlated the Kurieka Formation with the Siegenian (Pragian-Emsian; Krylova et al., 1967) or Gidennian-Siegenian (Early Devonian; Obruchev, 1973). More recent efforts have indicated a Lochkovian age (e.g., Cherkesova, 1988). This assessment is supported by the presence of *Rhinopteraspis* from the Norilsk outcrop of the upper part of the Kureika Formation, first described by Obruchev (1964, pl. 2: fig. 4). This specimen was identified as most likely belonging to *Rhinopteraspis crouchi*, although the possibility of it being a juvenile *R. dunensis* has been raised (Blieck, 1984, Blieck and Janvier, 1993). If the specimen belongs to *R. crouchi*, this would date the upper part of the Kureika Formation to the middle Lochkovian (ca. 415Ma; Gradstein et al., 2012); if *R. dunensis*, it would indicate a Pragian age (Blieck, 1984). Other palaeontological evidence from lateral equivalents of the Kurieka Formaton is consistent with a Lochkovian age. The Bely Kamen (or Belokamensk) beds from the central Taymir are interpreted as the lateral equivalent of the lower unit of the Kurieka Formation that yields material of *Janusiscus* (Novitskaya, 1977). A diverse fauna of amphiaspids, including *Tareyaspis*, *Gunaspsis*, *Agyriaspis* and *Prosarctaspsis*, along with acanthothoracid placoderms, the acanthodians *Gomphonchus*, *Nostolepis*, *Cheiracanthoides* and *Taimyrolepis*, and the sarcopterygian *Porolepis* have been reported from the Bely Kamen beds (Karatajute-Talimaa, 1994; Valiukevicius, 1994). The overlying Uryum beds are correlated with the middle member of the Kurieka Formation (Novitskaya, 1977), and yield the heterostracans *Rhinopteraspsis*, *Tareyaspsis*, *Gabreyaspsis*, *Agyriaspsis*, *Empedaspsis*, *Pelaspsis*, *Siberiaspsis* and *Norilaspis*, placoderms including *Romundina*, *Palaeacanthaspsis*, and indeterminate acanthothoracids and palaeacanthaspids, the acanthodians *Gomphonchus*, *Nostolepis*, *Poracanthodes*, *Cheiracanthoides*, *Taimyrolepis* material doubtfully attributed to ?*Acanthodes*, and the sarcopterygian *Porolepis* (Karatajute-Talimaa, 1994; Mark-Kurik, 1994; Valiukevicius, 1994). In light of these faunal data, we are confident that the deposits yielding *Janusiscus* are Lochkovian in age, and probably date to the early part of that stage.

The Siberian Platform is a lagoonal marine shelf deposit, with the north-western section of the platform, in which the Kureika Formation is located, deposited in a shallow water environment (Cherkesova, 1988). Although limited stratigraphical information is associated with the site where the fossil was found, the lower part of the Kureika formation at other locations is deposited as a succession of grey argillites with interbedded limestones and clay-rich dolomites (Novitskaya, 1977).

8.1.1.2 Taxonomic notes and history

The type species of *Dialipina.* The type species of *Dialipina*, *D. salguieroensis*, was erected for scales and a dermal bone fragment found in the Early Devonian (Emsian) Bear Rock Formation (?Delorme Formation) of northwest Canada (Schultze, 1968). The holotype of *D. salgueiroensis* is a scale bearing a prominent, but broken, dorsal peg and ornamented with ridges of enamel (Schultze, 1968: fig. 7; Extended Data Figure 2d). Schultze (1968) diagnosed *Dialipina* on the basis of features of scale ornament: principal enamel ridges that extend parallel to the anterior margin of the scale anteriorly, but extending parallel to the ventral margin of the scale posteriorly; fine transverse striations on the vertically oriented anterior portions of the principal enamel ridges; posterior serration of the scale produced by short enamel ridges intercalated between the principal enamel ridges. Articulated specimens assigned to this species have since been described from this locality (Schultze and Cumbaa 2001).

Referred species of *Dialipina*. Mark-Kurik (1974) described scales from the 'Gedinnian' (Early Devonian: Lochkovian) of the New Siberian Islands, Russia, and noted their morphological similarity to *Dialipina salgueiroensis* (Extended Data Figure 2e). Schultze (1977: figs 3a-g, 4a-b; pl. 14) provided a more detailed account of these scales. A more detailed description by Schultze (1977: figs 3a-g, 4a-b; pl. 14) found conspicuous differences between these scales and those of the Emsian *D. salgueiroensis*: (i) enamel ridges straight (rather than bent anteriorly as in *D. salgueiroensis*); (ii) enamel ridges smooth (*versus* ornamented with fine transverse striations as in *D. salgueiroensis*); (iii) irregular patterning of short enamel ridges intercalated between principal enamel ridges (*versus* highly regular packing pattern of these short intercalating ridges in *D. salgueiroensis*); (iv) low rounded dorsal peg and small anterodorsal process (*versus* high, pointed dorsal peg and well-developed anterodorsal process in *D. salgueiroensis*); (v) presence of cell-spaces basal bone of scales (*versus* no cell-spaces in *D. salgueiroensis*); (vi) scale bases with two layers of highly vascularized, cancellous bone bearing cell spaces (*versus* lamellar bone without lacking cell spaces and bearing non-vascular canals of Williamson). Despite these prominent differences, Schultze (1977) considered these Lochkovian scales congeneric with *D. salgueiroensis*, and erected the new species *D. markae* to accommodate them.

We regard evidence for placement of these morphologically and histologically different scales in the same genus as suspect. *D. salgueiroensis* bears scales with peg-and-socket articulations, a synapomorphy of osteichthyans crownward of *Andreolepis*, *Naxilepis*, *Orvikuina*, and *Terenolepis* (Friedman and Brazeau, 2010). With their rudimentary dorsal pegs that are little more than elaborated overlap areas, the scales of *D. markae* broadly resemble those assigned to the stem osteichthyans *Andreolepis* and *Orvikuina*. We suggest that *D. markae* likely falls outside the clade *D. salgueiroensis* + crown Osteichthyes.

Identification of fossil fish remains from the Kureika Formation. The cranial remains described here are from two localities of the lower member of the Early Devonian (Lochkovian) Kureika Formation along the Sida River in Siberia. These fossils were first reported by Schultze (1992), who attributed them to *Dialipina markae*. This assignment is based on the presence of scales in the same deposit that Schultze (1992) identified as belonging to *D. markae* (Table 1; Extended Data Figures 2a-c,f,g). The attribution of the skull roofs to *D. markae* is therefore predicated on two assertions: that the scales from the lower member of the Kureika Formation clearly belong to *D. markae*, and that the skull roofs can then be positively linked with these scales. We find both claims questionable.

Schultze (1992) attributed scales from the Kurieka Formation to *D. markae* based on the presence of parallel ridges of ornament separated by grooves and absence of a large dorsal articular peg. Both features are widely distributed among gnathostomes, and are therefore of doubtful value in specific assignments. Furthermore, Schultze (1992: p. 236) noted features in which the scales from the Kureika Formation differed from those of *D. markae*, found in a different formation some 1500 km away. Most significantly, the attributed scales from the Kureika Formation rarely show short ridges of ornament that intercalate between principal ridges at the posterior of the scale. The presence of such intercalating ridges, resulting in a serrated posterior margin of the scale, is the principal feature hypothesized to unite both species of *Dialipina* (Schultze 1977: fig. 1, ‘a.g’; Extended Data Figure 2d-e). Such pronounced serration is not apparent in scales from the lower member of the Kureika

Formation that show clear outlines or impression of the posterior margin (GIT 496-5, 496-8, 496-10; Extended Data Figure 2a,b), contradicting attribution to *D. markae*. A single scale from the lower member of the Kureika Formation does bear clear serration (GIT 496-16; Extended Data Figure 2c), but this specimen was highlighted by Schultze (1992) as bearing ridges that curve anteriorly so as to parallel the anterior margin of the scale. This feature is inconsistent with attribution to *D. markae*. Such ornament is present in *D. salgueiroensis*, however, and was considered an important feature distinguishing this species from *D. markae* (Schultze, 1977).

Specimen number in Schultze (1992)	**New specimen number**	**Outcrop**	**Description**	**Schultze (1992) attribution**
Pi 1381	GIT 496-4	C-2	?cleithrum (inner surface exposed)	?*Dialipina*
Pi 1382	GIT 496-5	C-2	rhombic scale (worn, showing ornament ridges and impression of external surface)	*Dialipina markae*
Pi 1383	GIT 496-6	C-27	skull roof and braincase	*Dialipina markae*
Pi 1384	GIT 496-7	C-15	skull roof	*Dialipina markae*
Pi 1384a	GIT 496-8	C-15	rhombic scale (external surface exposed)	*Dialipina markae*
Pi 1384b	GIT 496-9	C-15	rhombic scale (external surface exposed with broken posterior half, revealing ornament on external face)	*Dialipina markae*
Pi 1385a	GIT 496-10	C-24	rhombic scale (internal surface exposed)	*Dialipina markae*
Pi 1385b	GIT 496-11	C-24	rhombic scale (internal surface exposed)	*Dialipina markae*
Pi 1385c	GIT 496-12	C-24	indeterminate	*Dialipina markae*
Pi 1386a	GIT 496-13	C-24	rhombic scale (exeternal surface exposed)	*Dialipina markae*
Pi 1386b	GIT 496-14	C-24	rhombic scale (external surface exposed)	*Dialipina markae*
Pi 1386c	GIT 496-15	C-24	rhombic scale (external surface exposed)	*Dialipina markae*
Pi 1387	GIT 496-16	C-15	rhombic scale (external surface exposed)	*Dialipina* sp.

Table 1| Fish remains from the lower member of the Early Devonian Kureika Formation, Sida River localities, Siberia previously attributed to *Dialipina*.

In addition to contrasting ornamentation indicated by Schultze (1992) between scales from the Kureika Formation and those of *D. markae*, we note additional differences in overall scale geometry. Scales of *D. markae* figured by Schultze (1977: fig. 1a-g, pl. 14) bear well-defined dorsal pegs that range in shape from humped (fig. 1b) to triangular (fig. 1g). By contrast, the rudimentary dorsal pegs in specimens from the Kureika Formation are developed as low, broad flanges, and are less prominent than those of *D. markae* (Extended Data Figures 2a-c,f,g). In light of these clear differences, we argue that neither scale morphotype (scales with linear ridges and lacking posterior serration; scales with curved ridges and bearing posterior serration) can be reliably attributed to *D. markae* on the basis of morphology. This would seem consistent with the fact that the sites bearing these scales are remote from the type locality of *D. markae*, which yields an Early Devonian fauna considered biogeographically distinct from that of the northwestern Siberian Platform (Blieck and Janvier, 1993: 99).

Although we regard the specific attribution of scales to *Dialipina markae* dubious in any case, it is important to review the evidence suggested to link these fossils with co-occuring cranial remains. We do not accept arguments that derivation from the same geological unit is sufficient evidence to unite disarticulated remains within a single taxon. Concerning morphological evidence for attribution of the skull roofs to the scales, Schultze (1992: 236) only notes that the cranial remains "are covered by longitudinal smooth ridges similar to the ornamentation on scales of *D. markae*." Longitudinal ornament ridges are widely distributed feature of early gnathostomes, and as such their presence on both scales and skull bones from the Kureika Formation represents weak evidence for their attribution to a single species.

In light of the tenuous chain of attributions linking skull roofs GIT 496-6 (Pi1383) and 496-7 (Pi1384) to type material of *Dialipina markae*, we conclude that the most responsible taxonomic act is to erect a new species to accommodate these specimens. Even if subsequent collection provides unambiguous evidence for association of the rhombic scales from the Kureika Formation with these skull roofs (i.e., articulated or associated fossil specimens), we regard the differences apparent between these scales and descriptions provided for *D. markae* sufficient to merit species-level distinction. Should articulated or associated remains show that these different scale morphotypes are present within single individuals, and that some scales more precisely match those of *D. markae*, then we note that *Janusiscus schultzei* could be reassessed as junior synonym of that species. However, that species could not be assigned to *Dialipina*, given the profound differences in cranial and scale anatomy noted here (Extended Data Figures 1, 2), and *Janusiscus* would be available to accommodate it.

Comparison of skull roofs from the Kureika Formation with *Dialipina*. Our reexamination of these fossils has resulted in a new interpretation of dermal bone patterns in GIT 496-6 (Pi1383) relative to that given by Schultze (1992: fig. 5). He considered this specimen the anterior half of a skull roof, but its position relative to the underlying braincase clearly indicates it is the posterior half of a skull roof. The large paired bones represent postparietals, rather than parietals, and the bone previously interpreted as the pineal can now be identified as the parietals (Extended Data Figure 1). Regions described as impressions of different dermal bones are now identified as portions of the underlying braincase. This reinterpretation brings the anatomy of GIT 496-6 (Pi1383) in line with that of GIT 496-7 (Pi1384).

The ornamentation and proportions of the skull roofs from the Kureika Formation differ significantly from *Dialipina salgueiroensis* (Extended Data Fig. 1). Most notably, the Siberian specimens lack the anterolateral extensions seen on the parietals of *D. salgueiroensis*. Other major differences apparent in the Siberian skulls include: strongly concave posterior margins of the parietals (*versus* slightly convex in *D. salgueiroensis*); postparietals larger that parietals (*versus* parietals larger than postparietals in *D. salgueiroensis*); pineal plate narrow (*versus* a broad pineal plate in *D. salgueiroensis*); skull roofing bones ornamented with broad ridges that can extend the length of individual ossifications (*versus* narrow, short ornament ridges in *D. salgueiroensis*).

8.1.1.3 Lateral Processes of Early Gnathostome Neurocrania

Taxon	Studies	Postorbital process	Transverse otic process	Vagal process(es)	Craniospinal process
Sarcopterygii	Jarvik (1980)	Suprapterygoid process	Lateral commissure	n/a	n/a
	Yu (1998) Zhu and Yu (2002) Zhu et al. (2013)	Postorbital pila (in part)	Lateral commissure	n/a	n/a
Actinopterygii	Rayner (1951) Jarvik (1980) Gardiner (1984)	Postorbital process	Lateral commissure (in part)	n/a	Craniospinal process
	Zhu et al. (2013)	Lateral commissure (in part)	Lateral commissure (in part)	n/a	n/a
Ligulalepis	Basden et al. (2000) Basden and Young (2001)	Postorbital process	Unnamed	n/a	n/a
	Zhu et al. (2013)	Lateral commissure (in part)	Lateral commissure (in part)	n/a	n/a
Chondrichthyes	Jarvik (1980) Maisey (2005)	Postorbital process	n/a	n/a	n/a
	Schaeffer (1981) Coates and Sequeira (1998)	Postorbital process	Lateral otic process	n/a	n/a
Acanthodes	Miles (1973) Jarvik (1980)	Postorbital process	Unnamed	n/a	n/a
	Davis et al. (2012)	Postorbital process	Unnamed	n/a	n/a
Ramirosuarezia	Pradel et al. (2009)	Pr1	Lateral commisure + Pr3	n/a	n/a
Entelognathus	Zhu et al. (2013)	Postorbital pila	Anterior postorbital process	Posterior postorbital process	Craniospinal process
Dicksonosteus	Young (1980)	Supraorbital process	Anterior postorbital process	Posterior postorbital process + supravagal process	Craniospinal process
	Goujet (1984)	Unnamed	Anterior postorbital process	Posterior postorbital process	Craniospinal process
Kujdanowiaspis	Stensiö (1969) Jarvik (1980)	Supraorbital process	Anterior postorbital process	Posterior postorbital process	Supravagal process
	Goujet (1984)	Supraorbital process	Anterior postorbital process	Posterior postorbital process	Craniospinal process
Buchanosteus	Young (1979) Young (1980)	Supraorbital process	Anterior postorbital process	Posterior postorbital process	Craniospinal process
Jagorina	Stensiö (1969)	Supraorbital process	Anterior postorbital process	Unnamed	Supravagal process
	Jarvik (1980)	Unnamed	Unnamed	Unnamed	Supravagal process
	Young (1980)	Supraorbital process	Unnamed	Posterior postorbital process	Supravagal process
Romundina	Ørvig (1975)	n/a	Anterior postorbital process	Posterior postorbital process	Supravagal process
	Young (1980)	n/a	Anterior postorbital process	Posterior postorbital process + craniospinal process	Supravagal process
Macropetalichthys	Stensiö (1969)	n/a	Anterior postorbital process + posterior postorbital process	Supravagal process	Craniospinal process
	Jarvik (1980)	n/a	Unnamed	Supravagal process	Craniospinal process
	Young (1980)	n/a	Anterior postorbital process	Posterior postorbital process + supravagal process	Craniospinal process
Brindabellaspis	Young (1980)	n/a	n/a	Infravagal process + supravagal process + postglossopharyngeal ridge	Craniospinal process
Osteostraci	Janvier (1985)	n/a	n/a	Prebranchial ridge	n/a

Table 2| Terminology applied to lateral neurocranial processes in early vertebrates in this and previous studies.

The braincases of early gnathostomes bear a diversity of lateral processes showing variable relationships with other neurocranial landmarks like foramina for cranial nerves and circulatory vessels. These processes have attracted a range of descriptive terms, with many names being applied specifically to certain taxonomic assemblages (e.g., 'placoderms'). Unfortunately, these parallel schemes of nomenclature have hindered more direct comparisons between the character-rich braincases of early gnathostomes. The most extensive effort to rationalize naming systems in early gnathostomes was provided by Young (1980:54-61), who sought to standardize terminology across 'placoderms'. We have drawn heavily on his arguments concerning processes present posterior to the articulation of the hyoid arch (features variously termed posterior postorbital, vagal, supravagal, and craniospinal processes), with minor exceptions mentioned specifically below. The significance of *Janusiscus* to this nomenclatural problem is the conjunction of braincase structures that allow us to propose homologies between processes found in both crown gnathostomes and 'placoderms', but which have traditionally been referred to using assemblage-specific terminology.

Postorbital process: a dorsally placed process that forms the rear margin of the orbital region. It may be pierced or notched by the jugular canal or imperforate. This structure has generally been referred to as the supraorbital process in 'placoderms' (e.g., Young 1980: fig. 24). The 'placoderm' postorbital process defines the posterodorsal boundary of the orbit, and as such corresponds positionally to the primary postorbital process (*sensu* Holmgren, 1940: fig. 67) of modern elasmobranchs. 'Placoderms' lack a ventral bridge extending from the postorbital process that encloses the jugular vein against the neurocranial wall, but such a commissure is some chondrichthyans and sarcopterygians. Here we refer to the entire postorbital extension, which may or may not include a lateral commissure, as the postorbital process.

Presence or absence of a postorbital process is recorded by character 132. The presence of a jugular canal in the postorbital process (i.e., enclosure formed by a commissure) is recorded by character 133. Taxa lacking a postorbital process are coded as inapplicable ('-') for 133.

Transverse otic process: a transverse wall or process of the otic region that is associated with or supports the hyomandibular articulation. It may be pierced or notched by the jugular canal or imperforate. This structure has generally been referred to as the anterior postorbital process in 'placoderms' (e.g. Young, 1980: fig. 24). The lateral otic process of some chondrichthyans satisfies these criteria (Extended Data Figure 7), and is coded as a transverse otic process in our analysis. The absence of a promiment otic process in early chondrichthyans like *Pucapampella* and *Doliodus* suggests that the large processes in later taxa like *Tamiobatis* and *Xenacanthus* might be neomorphic (Extended Data Figure 7j; cf. optimizations shown in Extended Data Figure 9).

The presence or absence of a transverse otic process is recorded by character 125. Characters 126 and 164 accommodate further variation in the structure of such processes: the presence of absence of a canal for the jugular vein, and position relative to the skeletal labyrinth.

Vagal process(es): lateral extension (or extensions) of the posterior otic region adjacent to foramina for the vagus (X) nerve and associated with facets for the gill skeleton. Brazeau and Friedman (2014) have argued that vagal processes are modified from the interbranchial ridges of jawless vertebrates. The vagal processes define the anterior margin of an embayment interpreted by Young (1980) as the cuccularis fossa. Our definition is admittedly broad, and we do not presently propose more specific terminology for subcategories of vagal processes (e.g., supravagal and posterior postorbital processes as applied by Young, 1980 and others), some of which appear in conjunction. The geometry and size of vagal processes vary considerably among ‘placoderms’, suggesting that more refined classifications of these structures might yield important systematic information. For example, there are two separate vagal processes (according to our criteria for identification) in *Macropetalichthys* and *Kujdanowiaspis* (Extended Data Fig. 7a, c), but only a single process in *Buchanosteus* and *Entelognathus* (Extended Data Fig. 7b, d). Based on our own examination of silicone peels of the rhenanid *Jagorina*, we regard the posterolateral extensions of the braincase in this genus as craniospinal, rather than vagal (Young, 1980), processes.

The condition of vagal processes is recorded by character 166.

Craniospinal process: large process extending from the posterolateral corner of the braincase, bearing a distinct craniospinal ridge, and defining the posterior margin of the embayment identified by Young, (1980) as the cuccularis fossa. In many ‘placoderms’, this endoskeletal process is intimately associated with the dermal craniothoracic joint (e.g. *Buchanosteus*; Young, 1979: fig. 2). A more modest posterolateral extension of the occipital arch, immediately posterior to the metotic fissure, is present in some early actinopterygians (e.g. *Mimipiscis*; Gardiner, 1984: fig. 2, ‘crsp’) and has also been termed a craniospinal process (first by Nielsen, 1942). A low prominence is present in a comparable location in *Acanthodes* (Miles, 1973: pl. 5A, ‘pao.p’; Davis et al., 2012: supp. fig. 9, ‘Pao.p’), but is not nearly as well-developed as the actinopterygian or ‘placoderm’ craniospinal processes, being hardly noticeable in revised reconstructions (Davis et al., 2012 supp. fig. 15). Miles (1977: 55) drew parallels between transverse occipital processes in lungfishes in actinopterygian craniospinal processes, but remained circumspect concerning their possible homology. Gardiner (1984: 190) regarded the dipnoan and actinopterygian processes as non-homologous.

Despite similarities in orientation and position, the relationship between the craniospinal processes of ‘placoderms’ and actinopterygians is obscure. What is clear is that the craniospinal processes of actinopterygians are proportionally smaller than, and in some ways structurally distinct from, the processes of the same name in ‘placoderms’. However, we are not confident that their homology can be rejected *a priori*. We therefore consider these processes primary homologues, with this hypothesis subject to testing through congruence. This mirrors the strategy applied above for lateral otic/transverse otic processes. Based on mapped character distributions, our analysis rejects homology between the craniospinal processes of actinopterygians and ‘placoderms’ (Extended Data Figure 7m; cf. optimizations shown in Extended Data Figure 9).

The presence or absence of craniospinal processes is recorded by character 167.

8.1.2 Phylogenetic analysis

8.1.2.1 Character List

This character list is derived principally from that presented by Davis et al., (2012), itself a modified descendant of Brazeau (2009). The source of additional characters not appearing Davis et al., (2012) are listed in character descriptions. Multistate characters that could be ordered along a morphocline are indicated with an asterisk (‘*’).

Histology

1. **[DFC12: 1] Tessellate prismatic calcified cartilage:**

   Based on our examination of material of *Howqualepis*, we are convinced that the hard tissue surrounding the braincase and other endoskeletal structures in this genus is not prismatic calcified cartilage. We therefore revise the code for this genus to '0'.

   0. absent
   1. present

2. **Prismatic calcified cartilage:**

   Maisey (2001: character 17), Pradel et al. (2011: character 0).

   0. single layered
   1. multi-layered

3. **[DFC12: 2] Perichondral bone:**

   Presence of perichondral bone in *Yunnanolepis* is reported by Zhu (1996).

   0. present

1. absent

4. [DFC12: 3] Extensive endochondral ossification:

Dicksonosteus and *Macropetalichthys* are scored '0'. Even while some internal ossification has been reported in these taxa (Stensiö, 1925; Goujet, 1984), it hardly qualifies as being extensive, and the interpretation as endochondral bone is dubious.

0. absent
1. present

5. Enamel(oid) present on dermal bones and scales:

This character, along with the following three, represents an atomization of compound characters relating to suite of features characterizing ganoine and cosmine (e.g. Davis et al., 2012: character 6; Zhu et al., 2013: character 6). A similar approach to atomizing these traits was adopted by Friedman (2007: characters 131, 138 and 195) and Friedman & Brazeau (characters 36 and 37). An enameloid-like capping tissue is reported in thyestidians by Janvier (1996), so we have coded Osteostraci as polymorphic for this tissue.

0. absent
1. present

6. Enamel:

See notes above for character 5.

0. single-layered
1. multi-layered

7. Enamel layers:

See notes above for character 5.

0. applied directly to one another (ganoine)

1. separated by layers of dentine

8. Extensive pore canal network:

See notes above for character 5. Extensive pore canal networks represent a key component of the complex tissue type known as cosmine, but networks of vascular canals that open to the surface of bones and scales by pores are widely distributed among early vertebrates. Best known in sarcopterygians, pore-canal networks are also found in a range of taxa including probable stem osteichthyans (e.g. *Ligulalepis sensu stricto*; Schultze, 1968: figs 1-4), acanthodians (e.g. *Poracanthodes*; Valiukevicius, 1992: figs 4, 9), and osteostracans (e.g. *Tremataspis*, Denison, 1947: fig. 1). Sarcopterygian pore-canal networks are distinguished from these other examples in the density of pore canals, and the flask-like shape of these structures.

0. absent

1. present

9. [DFC10: 4] Dentinous tissue:

Modified based on Giles et al. (2013). *Onychoselache* and *Tamiobatis* are re-scored '?' based on the absence of figured material documenting this condition. Gross (1947) describes dentine tubules seen in sections through the scales of *Mesacanthus* and *Ischnacanthus*.

0. absent

1. present

10. [DFC10: 5] Dentine kind:

Lupopsyrus scored '0' based on Hanke & Davis (2012). *Incisoscutum* scored '1' based on Johanson & Smith (2005). Semidentine is reported in *Romundina* (Giles et al., 2013). The precise type of dentine in *Yunnanolepis* is difficult to determine (Giles et al., 2013). Because their dentine is described by Gross (1947) as tubular canals reminiscent of those in similar acanthodians, the dentine type in *Ischnacanthus* and *Mesacanthus* is here scored as orthodentine.

0. mesodentine
1. semidentine
2. orthodentine

11. Bone cell lacunae in body scale bases:

Burrow & Turner (2010: character 61). Hanke & Davis (2008) express uncertainty about bone cell lacunae in the scale bases of *Gladiobranchus*. However, Newman et al. (2012), working on the basis of better-preserved material of *Uraniacanthus* (to which *Gladiobranchus* is synonymous) show convincingly that these lacunae are lacking. *Climatius* is scored '?' in spite of Ørvig's (1967) report of acellular bases. Ørvig figured flat-based scales from the head. This character strictly concerns body scales, which may have been different. *Cheirolepis* is scored '1' based on Ørvig (1967). However, this is remarkably poorly documented in any accessioned specimens. *Acanthodes* is scored '1' based on Gross (1947) and Valiukevicius (1995). *Dialipina* is scored from Schultze (1968). *Psarolepis* is coded '0' based on Qu et al. (2013). The presence or absence of bone cells in the scale bases of *Brindabellaspisis* uncertain based on Burrow & Turner (1999).

0. present
1. absent

12. Main dentinous tissue forming fin spine:

Burrow & Turner (2010: character 60).

0. osteodentine
1. orthodentine

Squamation

13. [DFC12: 7] Longitudinal scale alignment in fin webs:

The character formulation of Davis et al. (2012) did not distinguish between ordered arrangements of fin scales and lepidotrichia. Acanthodians and *Dialipina* (uncatalogued specimen, Musem für Naturkunde, Berlin) exhibit fin web scales that are not markedly distinguished from the body scales. Fin web scales of *Dialipina* even include a distinct peg-and-socket articulation. This character thus refers to the alignment only, but not to the specialized rectangle-shaped scales in osteichthyans. *Poracanthodes* is changed to '?' because fin webs do not appear to be preserved in articulated specimens (Valiukevicius, 1992). *Brachyacanthus* and *Parexus* scored '1' (pers. obs. SG, NHMUK P.130, P.38593 for *Parexus*, and NHMUK P.6959 and P.9595 *Brachyacanthus*). *Brochoadmones* is scored '0' based on observations on UALVP 41495. *Campbellodus* scored '?'.

0. present
1. absent

14. Differentiated lepidotrichia:

Refers to the distinct rectangular shape of the aligned lepidotrichia-like scales. This character is scored contingently on the state of the previous character. *Dialipina* is coded '0' (uncatalogued specimen, Musem für Naturkunde, Berlin).

0. absent
1. present

15. [DFC12: 8] Body scale growth pattern:

Climatius is scored '1' based on Ørvig (1967) showing multiple apposed cusps on the body scales of this taxon. *Onychodus* is re-scored '1'. The scales of *Gemuendina* appear to have only a single external tubercle, implying that they may have been monodontode. However, this is not corroborated by any histological data and so *Gemuendina* is conservatively scored '?'.

0. comprising single odontode unit/generation ("monodontode")
1. comprising a complex of multipe odontode generations/units ("polyodontode")

16. [DFC12: 9] Body scale growth concentric:

0. absent
1. present

17. Generations of odontodes:

This character is scored contingently on the presence of polyodontote scales. Taxa displaying monodontode scales are coded as inapplicable.

0. buried
1. areally growing
2. resorbed

18. [DFC12: 10] Body scales with peg-and-socket articulation:

Lupopsyrus is scored '0', consistent with the description by Hanke & Davis (2012).

0. absent
1. present

19. Scale peg:

Patterson (1982: character 5), Cloutier & Ahlberg (1996: character 4), Dietze (2000: character 57), Schultze & Cumbaa (2001: character 88), Zhu & Schultze (2001: character 199), Zhu et al. (2001: character 145), Zhu & Yu (2002, character 145), Cloutier & Arratia (2004: character 178), Zhu et al. (2006: character 112), Friedman (2007, character 128), Brazeau (2009: character 139), Zhu et al. (2009: character 139), Zhu et al. (2013: character 143).

0. broad
1. narrow

20. Anterodorsal process on scale:

Patterson (1982: character 4), Lauder & Liem (1983: fig. 6, character 4), Gardiner (1984: character 1), Gardiner & Schaeffer (1989: character A20), Schultze (1992: character 2, in part), Schultze & Cumbaa (2001: character 89), Zhu & Schultze (2001: character 201), Zhu et al. (2001: character 146), Zhu & Yu (2002: character 146), Cloutier & Arratia (2004: character 179), Friedman & Blom (2006: character 33), Zhu et al. (2006: character 113), Friedman (2007: character 129), Zhu et al. (2009: character 140), Zhu et al. 2013 (character 144).

0. absent
1. present

21. [DFC12: 11] Body scale profile:

Parexus, *Brochoadmones*, *Kathemacanthus*, and *Promesacanthus* are scored '0'.

Buchanosteus is scored '?'. *Tamiobatis* is scored '0' based on the description by Williams (1998). *Dicksonosteus* and *Pterichthyodes* are scored '1' consistent with Goujet (1984, plate 14, fig. 1) and Hemmings (1978: fig. 22). *Gemuendina* is scored '0'. *Psarolepis* is scored '0' based on Qu et al. (2013).

0. distinct crown and base demarcated by a constriction ("neck")
1. flattened

22. Profile of scales with constriction between crown and base:

This character is scored contingently on the previous character, and thus refers to necked scales with a pronounced anvil-shaped profile as seen in acanthodids, diplacanthids, ischnacanthids, and similar taxa, and thus is typified by the profile of the *Gomphonchus*-type morphology.

0. neck similar in width to crown
1. neck greatly constricted, resulting in anvil-like shape

23. [DFC12: 12] Body scales with bulging base:

0. absent
1. present

24. [DFC12: 13] Body scales with flattened base:

0. present
1. absent

25. Basal pore in scales:

Growing basal tissue is absent from some scales belonging to chondrichthyans. Although shown only in the cranial cap scales (Coates & Sequeira 2001b: fig. 12E), a basal pore is seen in *Akmonistion*.

0. absent

1. present

26. [DFC12: 14] Flank scale alignment:

0. vertical rows oblique rows or hexagonal

1. rhombic packing

2. disorganised

27. Scute-like ridge scales (basal fulcra):

Patterson (1982: character 19), Gardiner (1984: character 12), Maisey (1986: N9), Gardiner & Schaeffer (1989: A19), Friedman & Brazeau (2010: character 25).

0. absent

1. present

28. [DFC12: 15] Sensory line canal:

0. perforates scales

1. passes between scales

2. C-shaped scales

Dermal bones of the skull

29. Dermal ornamentation:

0. smooth

1. parallel, vermiform ridges

2. concentric ridges

3. tuberculate

30. [DFC12: 16] Sensory line network:

Galeaspids are recoded as polymorphic based on Donoghue et al. (2000).

0. preserved as open grooves (sulci) in dermal bones
1. sensory lines pass through canals in dermal bones (open as pores)

31. Sensory canals/grooves:

Goujet (1984b: unnumbered character), Brazeau (2009: 17). A character similar to this appeared in Brazeau (2009). Davis et al. (2012) did not include this character, but did not elaborate on the rationale behind this deletion. In its present formulation, this character considers the degree to which grooves or canals for sensory lines are expressed as prominent ridges on the visceral surface of dermal bones. This modification reflects the paucity of section data indicating whether the floor of the groove or canal lies deep to the visceral surface of the body of the containing bone.

0. contained within the thickness of dermal bones
1. contained in prominent ridges on visceral surface of bone

32. [DFC 17] Jugal portion of infraorbital canal joins supramaxillary canal:

0. present
1. absent

33. [DFC 18] Dermal skull roof:

0. includes large dermal plates
1. consists of undifferentiated plates or tesserae

34. **Anterior pit line of dermal skull roof:**

0. absent
1. present

35. **[DFC 19] Tessera morphology:**

0. large interlocking polygonal plates
1. microsquamose, not larger than body squamation

36. **Cranial spines:**

This character is composed as a compound because there are no further dependent characters. Mathematically, this should be equivalent to atomizing and using inapplicability.

0. absent
1. present, multicuspid
2. present, monocuspid

37. **[DFC 20] Extent of dermatocranial cover:**

0. complete
1. incomplete (limited to skull roof)

38. **[DFC 21] Openings for endolymphatic ducts in dermal skull roof:**

Brazeau (2009) and Davis et al. (2012) have scored ptyctodont taxa as lacking endolymphatic duct openings. However, it is unclear if this is the case. Although a small circular foramen is not present in the skull roofs of ptyctodonts, many ptyctodont taxa are described as possessing a "spiracular opening" in their skull roofs (Long, 1997; Trinajstic et al., 2012). Because the spiracle of gnathostomes is situated between the hyoid and mandibular arches, we consider this interpretation extremely doubtful. The purpose of this opening remains unknown, but its interpretation as an endolymphatic opening cannot be ruled out. However, we adopt a conservative approach and code these taxa as '?'. Stensiö (1969) figures *Jagorina* with a posterior dorsal fontanelle and, presumably, interprets this as an endolymphatic opening behind the skull roof. No openings for the endolymphatic ducts are indicated in the skull roof. Examination of the specimen shows that the endolymphatic ducts are parasaggital to the cranial cavity and follow a course up to the skull roof. Because actual openings are not observed, this character is scored '?' for *Jagorina*.

0. present
1. absent

39. [DFC 22] Endolymphatic ducts with oblique course through dermal skull bones:

0. absent
1. present

40. Endolymphatic duct relationship to median skull roof bone (i.e. nuchal plate):

0. within median bone
1. on bones flanking the median bone (e.g. paranuchals)

41. [DFC 25] Pineal opening perforation in dermal skull roof:

This feature is indicated in a reconstruction of *Romundina* (see Goujet & Young, 2004: fig. 2), but this is not shown in any specimen photograph or illustration. It is thus unclear whether this is actually observed, or was merely symbolic, indicating the structure's sub-dermal location.

0. present

1. absent

42. Dermal plate associated with pineal eminence or foramen:

Among taxa sampled in this analysis, osteostracans, antiarchs, *Brindabellaspis*, and *Romundina* bear pineal plates that contribute to the margin of the orbit, corresponding to state '0'. We consider taxa where the pineal foramen is bounded by rectilinear skull roofing bones but which lack separate pineal ossifications (e.g. *Mimipiscis*) as showing state '1'. Taxa lacking macromeric cranial skeletons are coded as inapplicable for this character.

0. contributes to orbital margin

plate(s) excluded from orbital margin by skull roofing bones.

1. plate bordered laterally by skull roofing bones

43. [DFC 23] Series of paired median skull roofing bones that meet at the dorsal midline of the skull (rectilinear skull roof pattern):

0. absent

1. present

44. Broad supraorbital vaults:

Dennis & Miles (1981: character 16).This character is contingent on the presence of a dermal skull roof composed of large plates. In coccosteomorph arthrodires, the dorsal surfaces of the orbits, comprising the preorbital and postorbital plates, are formed of broad, concave laminae. Similar vaults on the visceral surface of the dermal skull are absent in other placoderms and osteichthyans.

0. absent

1. present

45. Median commisure between supraorbital sensory lines:

0. absent
1. present

46. Dermal cranial joint at level of sphenoid-otic junction:

Cloutier & Ahlberg (1996: character 81), Ahlberg & Johanson (1998: character 71), Zhu et al. (2001: character 20), Zhu & Schultze (2001: character 31), Zhu & Yu (2002: character 20), Zhu & Ahlberg (2004: character 71), Daeschler et al. (2006: character 50), Long et al. (2006: character 3), Zhu et al. (2006: character 24), Friedman (2007: character 19), Zhu et al. (2009: character 21), Zhu et al. (2013: character 147).

0. absent
1. present

47. Otic canal extends through postparietals:

Cloutier & Ahlberg (1996: character 101), Zhu & Schultze (2001: character 47), Zhu & Yu (2001: character 37), Zhu & Yu (2002: character 37), Friedman (2007: character 40).

0. absent
1. present

48. Number of bones of skull roof lateral to postparietals:

Lund et al. (1995: character 21), Cloutier & Ahlberg (1996: character 37), Ahlberg & Johanson (1998: character 49), Zhu & Ahlberg (2004: character 49), Schultze &

Cumbaa (2001: character 74), Zhu & Schultze (2001: character 27), Zhu et al. (2001: character 19), Zhu & Yu (2002: character 19), Cloutier & Arratia (2004: character 75), Daeschler et al. (2006: character 39), Zhu et al. (2006: character 22), Friedman (2007: character 18), Zhu et al. (2009: character 27).

0. two
1. one

49. Suture between paired skull roofing bones (centrals of placoderms; postparietals of osteichthyans):

Modified from Miles & Dennis (1979: character 6)

0. straight
1. sinusoidal

50. Medial processes of paranuchal wrapping posterolateral corners of nuchal plate:

0. absent
1. present
2. paranuchals precluded from nuchal by centrals
3. no median posterior skull roof bone

51. Paired pits on ventral surface of nuchal plate:

Miles & Dennis (1979: character 10), Dennis & Miles (1981: character 10).

0. absent
1. present

52. Sclerotic ring:

Coded according to Burrow et al. (2011).

0. absent

1. present

53. [DFC 24] Consolidated cheek plates:

This character is contingent on dermatocranial cover of the cheek. Taxa lacking any dermal contribution to the cheek are coded as inapplicable.

0. absent

1. present

54. Cheek plate:

This character is contingent on the presence of a consolidated dermal cheek. This character reflects whether the canal-bearing dermal cheek (preorpercular or suborbital equivalent) is composed of one or multiple bones. State '0' is apparent in actinopterygians, *Guiyu*, *Psarolepis* (preopercular), *Entelognathus* and other placoderms.

0. undivided

1. divided (i.e., squamosal and preopercular)

55. Subsquamosals in taxa with divided cheek:

Zhu & Schultze (2001: character 64), Zhu & Yu (2001: character 48), Zhu & Yu (2002: character 48), Friedman (2007: character 43).

0. absent

1. present

56. Preopercular shape:

Zhu et al. (2001: character 54), Zhu & Yu (2001: character 54), Friedman (2007: character 48). This character applies only to the subset of sarcopterygians with subdivided cheek plates. In onychodonts (Andrews et al. 2006), porolepiforms (Jarvik 1972), and coelacanths (Forey 1998), the preopercular assumes a plate-like morphology. By contrast, tetrapodomorphs bear a bar-shaped preopercular bone (Jarvik 1980; Long et al. 1997).

0. rhombic
1. bar-shaped

57. Vertical canal associated with preopercular/suborbital canal:

Friedman (2007: character 152, in part).

0. absent
1. present

58. [DFC 26] Enlarged postorbital tessera separate from orbital series:

0. absent
1. present

59. Extent of maxilla along cheek:

Friedman (2007: character 151), Zhu et al. (2009: character 81), Zhu et al. (2013: character 182).This character is contingent upon the presence of maxillae and a dermal cheek. The jaw bones of ischnacanthids are not part of the external dermal skeleton of the face and jaw (e.g. Blais et al., 2011), and so we do not equate these bones with maxillae/dentaries.

0. to posterior margin of cheek
1. cheek bones exclude maxilla from posterior margin of cheek

60. Dermal neck joint:

Zhu et al. (2013: character 169). The presence of a dermal neck joint is not a probable placoderm synapomorphy per se. Rather, the articulation of the shoulder and skull in mandibulate stem gnathostomes is distinguished from the condition in osteichthyans by being a ginglymoid articulation. The articulation in *Brindabellaspis* is peculiar in that it does not appear to be a dermal linkage but was instead an endochondral one (Young 1980).

0. overlap
1. ginglymoid

61. [DFC 15] Sensory line scales/plates on head:

See also Burrow & Turner (2010: character 66).

0. unspecialized
1. apposed growth
2. paralleling canal
3. semicylindrical C-shaped ring scales

62. [DFC 27] Bony hyoidean gill-cover series (branchiostegals):

We have re-coded *Acanthodes* and *Homalacanthus* as '1', reflecting the classic interpretation of the presence of branchiostegal rays in these taxa. Davis et al. (2012) coded the filamentous rays articulating with the hyoid arches of these acanthodids as '0', hypothesizing that they might represent endoskeletal hyoid rays like those present in modern and fossil chondrichthyans. This conclusion was based on overall morphological similarity; the structures in *Acanthodes* and *Homalacanthus* are thin and filamentous, like chondrichthyan hyoid rays and unlike many (but not all) osteichthyan branchiostegal rays. Here we code taxa bearing other ossifications associated with the hyoid arch (e.g. submandibulars, gulars, suboperculars) as '1' for this character.

0. absent
1. present

63. [DFC 28] Branchiostegal plate series along ventral margin of lower jaw:

Davis et al. (2012) score for this character in some taxa is changed from '0' to '?' to reflect the lack of knowledge of this character in any figured specimens, or in any specimens cited by the authors. Scores for *Acanthodes* and *Homalacanthus* are changed from '-' to '1' in accordance with the re-evaluation of the hyoidean gill cover series.

0. absent
1. present

64. [DFC 29] Branchiostegal ossifications:

Score for *Ischnacanthus* changed to 1 based on figures presented in Blais et al. (2011).

0. plate-like
1. narrow and ribbon-like
2. filamentous

65. [DFC 30] Branchiostegal ossifications:

0. ornamented
1. unornamented

66. [DFC 31] Imbricated branchiostegal ossifications:

Davis et al. (2012) changed this character to a different definition from Brazeau (2009). It is here reinstated to the original meaning, reflecting the presence of proximal imbrication. *Mesacanthus* is restored to a score of '1'.

0. absent
1. present

67. Median gular:

Lund et al. (1995: character 64), Cloutier & Ahlberg (1996: character 66), Forey (1998: character 45), Coates (1999: character 11), Lund (2000: character 49), Schultze & Cumbaa (2001: character 84), Zhu & Schultze (2001: character 109), Zhu et al. (2001: character 85), Zhu & Yu (2002: character 85), Lund & Poplin (2002: character 47), Cloutier & Arratia (2004: character 115), Zhu et al. (2006: character 67), Friedman (2007: character 73), Zhu et al. 2009 (character 102), Zhu et al. (2013: character 196).

0. absent
1. present

68. Lateral gular:

0. absent
1. present

69. [DFC 33] Opercular (submarginal) ossification:

0. absent
1. present

70. [DFC 34] Shape of opercular (submarginal) ossification:

0. broad plate that tapers towards its proximal end
1. narrow, rod-shaped

71. [DFC 36] Size of lateral gular plates:

0. extending most of length of the lower jaw
1. restricted to the anterior third of the jaw (no longer than the width of three or four branchiostegals)

Ventral hyoid arch and gill skeleton

72. Gill arches:

Scores for certain placoderms without preserved or mineralized gill arch and braincase skeletons are based on the outline of the braincase on the visceral surface of the skull roofing bones and the postition of the postbranchial lamina on the shoulder girdle. In placoderms, there is no room for the gill chamber to be extended behind the skull, and must therefore have been placed in a sub-cranial position.

0. largely restricted to region under braincase
1. extend far posterior to braincase

73. [DFC 37] Basihyal:

The coding for chondrichthyans has been revised following Pradel et al. (2014).

0. present
1. absent

74. [DFC 38] Interhyal:

We agree with Davis et al. (2012) that the evidence for an interhyal in *Acanthodes* is weak. We retain their coding of '?' here. On the basis of an articulated hyoid arch of *Ischnacanthus* (NHMUK P.7000), we can confirm the absence of the interhyal in that genus and revise the code to '0'.

0. absent
1. present

75. Hypohyal:

The coding for chondrichthyans has been revised following Pradel et al. (2014). Gardiner (1984: character 27), Maisey (1986: character K11), Friedman & Brazeau (2010: character 12). The hypohyal is a cartilage that lies at the anterior end of the ceratohyal, and links the ventral half of the hyoid arch with the ventral gill skeleton. This character has been considered an osteichthyan synapomorphy (see Friedman & Brazeau 2010 for a review). Davis et al. (2012: 43, supplementary material) query—but do not test—the status of the hypohyal as an osteichthyan synapomorphy, noting occurrences in the chondrichthyans *Debeerius* (Lund & Grogan, 2000: fig. 7) and *Cobelodus* (Zangerl & Case, 1976: fig. 13). The putative example in *Debeerius* is peculiar, as it articulates with the anterolateral margin of the median basal element, rather than linking the ceratohyal with this basal cartilage. We consider the condition of the mesial hyoid arch in *Cobelodus* to be unclear.

0. absent
1. present

76. Endoskeletal urohyal:

Friedman (2007: character 164).

0. absent

1. present

Dentition and jaw bones

77. [DFC 39] Oral dermal tubercles borne on jaw cartilages or at margins of the mouth:

The original meaning of this character, as formulated by Brazeau (2009) is clarified by an elaborated formulation. Davis et al. (2012) have changed Brazeau's (2009) coding for *Obtusacanthus* from '1' to '0'. This taxon clearly has oral dermal tubercles, manifest as scales on the outer face of the Meckelian cartilage. Here we restore a score of '1' for this genus. We also code *Bothriolepis* as '1', based on the presence of the denticulated inferognathals described by Young (1984). The score for *Euthacanthus* is changed to ‘0’, contra Davis et al. (2012), as we have not observed teeth in any specimen.

0. absent
1. present

78. [DFC 39] Oral dermal tubercles patterned in organised rows (teeth):

Teeth are here defined as tubercles borne on the jaw cartilages exhibiting distinct, non-random cusps in serially organised rows.

0. absent
1. present

79. Enamel(oid) on teeth:

Modified from Rosen et al. (1981: 26), Lauder & Liem (1983: fig. 1, character 17), Gardiner (1984: character 36), Schultze & Cumbaa (2001: character 104), Zhu &

Schultze (2001: character 212), Zhu et al. (2001: character 156), Zhu & Yu (2002: character 156), Zhu et al. (2006: character 123), Friedman (2007: character 139), Zhu et al. (2009: character 153). Previous authors have restricted consideration to the presence of 'true' enamel only, a putative synapomorphy of sarcopterygians. Given the ambiguity in differentiating enamel and enameloid in many fossil vertebrates, we adopt a more general formulation of this character.

0. absent
1. present

80. Cap of enameloid restricted to upper part of teeth (acrodin):

Modified from Patterson (1982: character 12), Gardiner (1984: character 13), Maisey (1986: character N6), Gardiner & Schaeffer (1989: character B1), Cloutier & Ahlberg (1996: character 7), Taverne (1997: character 7), Coates (1999: character 1), Poplin & Lund (2000: character 21), Schultze & Cumbaa (2001: character 35), Zhu & Schultze (2001: character 210), Zhu et al. (2001: character 154), Zhu & Yu (2002: character 154), Cloutier & Arratia (2004: character 32), Gardiner et al. (2005: character 15), Friedman & Blom (2006: character 25), Zhu et al. (2006: character 120), Friedman (2007: character 137), Zhu et al. (2009: character 151), Friedman & Brazeau (2010: character 140), Zhu et al. (2013: character 140). Acrodin tooth caps are widely cited as character uniting most actinopterygians to the exclusion of *Cheirolepis* (Patterson, 1982; Gardiner, 1984). The presence or absence of acrodin is not well documented for most early actinopterygians, but is clearly present in both *Mimipiscis* and *Moythomasia* (Gardiner, 1984).

0. absent
1. present

81. [DFC 40] Tooth whorls:

We have restored a code of '1' for *Debeerius*, which bears teeth in families corresponding to the definition of whorls applied by Brazeau (2009). The parasymphysial tooth families of this genus align with a more restrictive view of whorls in having joined bases (Grogan & Lund, 2000: 226).

0. absent
1. present

82. [DFC 41] Bases of tooth whorls:

Doliodus is coded here as '0', reflecting the fact that the teeth described by Turner (2004) represent multiple tooth bases united by thin sheets of bone. It seems probable that seemingly 'isolated' teeth of this genus represent broken whorls (Maisey et al. in press).

0. single, continuous plate
1. some or all whorls consist of separate tooth units

83. [DFC42] Distribution of tooth whorls:

Dialipina (Schultze and Cumbaa, 2001), *Eusthenopteron* (Jarvik, 1980), *Euthacanthus*, *Gogonasus* (Long et al., 1997), *Mimipiscis* (Gardiner, 1984), *Rhamphodopsis* (Miles, 1967), and *Tetanopsyrus* (Gagnier et al., 1999) lack tooth whorls, and so are recoded as inapplicable for this character.

0. entire length of tooth row
1. restricted to symphysial region

84. Distribution of tooth whorls:

0. upper and lower jaws

1. lower jaws only

2. upper jaws only

85. [DFC 43] Teeth ankylosed to dermal bones:

Davis et al. (2012) revised the coding provided by Brazeau (2009) for this character to '1' for *Dicksonosteus*. By the same token, we revise the coding of *Buchanosteus* from '0' to '1' based on the account and figures provided by Young et al. (2001).

0. absent

1. present

86. Plicidentine:

Cloutier & Ahlberg (1996: character 14), Ahlberg & Johanson (1998: character 14), Schultze & Cumbaa (2001: characters 102-103), Zhu & Schultze (2001: characters 213-215), Zhu et al. (2001: character 157), Zhu & Yu (2002: character 157), Zhu & Ahlberg (2004: character 14), Daeschler et al. (2006: character 10), Long et al. (2006: character 21), Zhu et al. (2006: characters 124-125), Friedman (2007: character 150), Zhu et al. (2009: character 152), Zhu et al. (2009: character 152), Zhu et al. (2013: character 141).

0. absent

1. present

87. [DFC44] Dermal jaw plates on biting surface of jaw cartilages:

0. absent

1. present

88. [DFC 45] Maxillary and dentary marginal bones of mouth:

Modified from Brazeau (2009) and Davis et al. (2012) to omit reference to teeth.

0. absent

1. present

89. Premaxilla:

Friedman (2007: character 150).

0. extends under orbit

1. restricted anterior to orbit

90. Maxilla shape:

Lund et al. (1995: character 52), Lund (2000: character 31), Poplin & Lund (2000: character 18), Schultze & Cumbaa (2001: character 31), Zhu & Schultze (2001: character 54), Zhu et al. (2001: character 42), Zhu & Yu (2002: character 42), Lund & Poplin (2002: character 30), Cloutier & Arratia (2004: character 18), Zhu et al. (2006: character 43), Friedman (2007: character 39), Zhu et al. (2009: character 79), Zhu et al. (2013: character 180).

0. splint-shaped

1. cleaver-shaped

91. Pair of tooth plates (anterior supragnathals or vomers) on ethmoidal plate:

0. absent

1. present

92. Strong posterior flexion of dentary symphysis:

Friedman (2007: character 155).

0. absent

1. present

93. Extent of infradentaries:

0. along much of ventral margin of dentary
1. restricted to posterior half of dentary

94. Coronoid fangs:

Ahlberg et al. (2000: character 15), Zhu & Schultze (2001: character 90), Zhu et al. (2001: character 69), Zhu & Yu (2002: character 69), Zhu et al. (2006: character 59), Daeschler et al. (2006: character 71), Long et al. (2006: character 18), Friedman (2007: character 57), Zhu et al. (2009: character 94), Zhu et al. (2013: character 202).

0. absent
1. present

95. Position of upper mandibular arch cartilage (and associated cheek plate where present):

0. entirely suborbital
1. with a postorbital extension

96. Position of mandibular arch articulations:

Refers to whether the anteriormost mandibular arch articulations are anterior to the nasal capsules, or immediately below or posterior to them.

0. terminal
1. subterminal

97. Autopalatine and quadrate:

Miles & Dennis (1979: character 22); Dennis & Miles (1981: character 22).

0. comineralized
1. separate mineralizations

98. [DFC 46] Large otic process of the palatoquadrate:

We have revised the codes for *Poracanthodes* and *Pucapampella* to '1' based on Valiukevicius (1992) and Janvier & Maisey (2010), respectively.

0. absent
1. present

99. [DFC 47] Insertion area for jaw adductor muscles on palatoquadrate:

We accept the arguments outlined by Davis et al. (2012) for the lateral insertion of the adductor musculature in ptyctodonts.

0. ventral or medial
1. lateral

100. Palatoquadrate relationship to dermal cheek bones:

0. broad articulation
1. articulation narrow and restricted

101. Palatoquadrate fused with neurocranium:

0. absent
1. present

102. [DFC 48] Oblique ridge or groove along medial face of palatoquadrate:

Relative to the codings provided by Davis et al. (2012), here we change scores for taxa without an expanded posterodorsal region of the palatoquadrate (e.g. 'placoderms') to logical inapplicability.

0. absent
1. present

103. [DFC 49] Fenestration of palatoquadrate at basipterygoid articulation:

0. absent
1. present

104. [DFC 50] Perforate or fenestrate anterodorsal (metapterygoid) portion of palatoquadrate:

0. absent
1. present

105. [DFC 51] Pronounced dorsal process on Meckelian bone or cartilage:

Contrary to the formulation proposed by Davis et al. (2012), the pronounced dorsal process on the lower jaw of 'acanthodians' like *Gladiobranchus* issues from a dermal plate associated with the mandible rather than the Meckel's cartilage. Consequently, we re-code all taxa lacking dermal lower jaw plates as inapplicable for this character. Burrow & Young (2012: fig. 4b) have recently shown that a similar process is present in *Culmacanthus*, but we find evidence for such a feature lacking in *Diplacanthus* (contra Davis et al. 2012). *Tetanopsyrus* has a high dorsal process of the jaw that seems to be part of the Meckel's cartilage rather than a separate dermal plate like that found in *Gladiobranchus* and *Culmacanthus*. However, we conservatively code this taxon as '?'.

0. absent

1. present

106. Number of coronoids:

Ahlberg & Clack (1998: character 4), Daeschler et al. (2006: character 5), Long et al. (2006: character 11), Friedman (2007: character 158), Zhu et al. (2009: character 93), Zhu et al. (2013: character 201).

0. four or more

1. three or fewer

107. [DFC 52] Preglenoid process:

Onychodus and *Poracanthodes* are re-coded as '0'. This structure is not figured in the reconstruction of *Pucapampella* by Janvier & Maisey (2010: fig. 8), but a specimen photograph suggests there is a modest process. A conservative scoring of '?' is nevertheless retained.

0. absent

1. present

108. [DFC 53] Jaw articulation located on rearmost extremity of mandible:

Previously coded as of uncertain condition, *Tetanopsyrus*, *Pucapampella*, *Poracanthodes*, and *Ptomacanthus* are scored as '0'.

0. absent

1. present

Neurocranium and associated dermal ossifications

109. [DFC 54] Precerebral fontanelle:

0. absent

1. present

110. [DFC 55] Median dermal bone of palate (parasphenoid):

Parasphenoids are not preserved for '*Ligualepis'* (Basden and Young 2001), *Pucapampella* (Maisey 2001), or *Janusiscus*. We follow the convention, applied to other taxa in our analysis known from well-preserved neurocrania lacking parasphenoids, and code these genera as '0'.

0. absent

1. present

111. Parasphenoid:

Friedman (2007: character 168), Zhu et al. (2009: character 68).

0. lozenge-shaped

1. splint-shaped

112. [Z13 241] Multifid anterior margin of parasphenoid denticle plate:

Friedman (2007: character 167), Zhu et al. (2009: character 69), Zhu et al. (2013: character 241).

0. absent

1. present

113. Enlarged ascending processes of parasphenoid:

Modified from Patterson (1982: character 9), Dietze (2000: character 54); Schultze & Cumbaa (2001: character 52), Zhu and Schultze (2001: character 125), Cloutier &

Arratia (2004: character 123), Friedman & Blom (2006: character 28), Zhu et al. (2006: character 70), Zhu et al. (2009: character 67), Zhu et al. (2013: character 239).

0. absent
1. present

114. Buccohypophysial canal in parasphenoid:

0. single
1. paired

115. [DFC 56] Nasal opening(s):

The score for *Austroptyctodus* is changed to '?'. The opening is a dermal structure, and there is no dermal preservation around the nostrils of *Austroptyctodus* (Long 1997).

0. dorsal, placed between orbits
1. ventral and anterior to orbit

116. Posterior nostril:

Cloutier & Ahlberg (1996: character 46), Schultze & Cumbaa (2001: character 23); Zhu & Schultze (2001: character 40), Zhu et al. (2001: character 27), Zhu & Yu (2002: character 27), Friedman & Blom (2006: character 6), Zhu et al. (2006: character 31), Friedman (2007: character 25), Zhu et al. (2009: character 8), Zhu et al. (2013: character 152).

0. separated from orbital fenestra
1. confluent with orbital fenestra

117. [DFC 57] Olfactory tracts:

Reflecting incomplete neurocranial data, the code for *Austroptyctodus* is changed to '?'. Zhu et al. (2013) report short olfactory tracts in *Psarolepis* (IVPP V11490.2), and we revise the coding of this genus to '0'. We also accept their revision of the state in *Onychodus* to '?'.

0. short, with olfactory capsules situated close to telencephalon cavity
1. elongate and tubular (much longer than wide)

118. [DFC 58] Prominent pre-orbital rostral expansion of the neurocranium:

Chondrenchelys and *Debeerius* changed to '0', contra Davis et al. (2012). There is a prominent pre-orbital expansion in these taxa.

0. present
1. absent

119. [DFC 59] Pronounced sub-ethmoidal keel:

Here we revise scores presented by Davis et al. (2012) for *Debeerius*, *Chondrenchelys*, and *Tamiobatis* to '?'. There are no satisfactory published ventral views of the neurocranium in *Debeerius* (Grogan & Lund, 2000) and *Chondrenchelys* (Moy-Thomas, 1935). *Tamiobatis* preserves part of a structure that might be part of a sub-ethmoidal keel, but this is damaged and we adopt a more agnostic stance on the condition in this taxon.

0. absent
1. present

120. Internasal vacuities:

Zhu & Schultze (2001: character 139), Zhu et al. (2001: character 105), Zhu & Yu

(2002: character 105), Friedman (2007: character 91).

0. absent

1. present

121. Discrete division of the ethmoid and more posterior braincase at the level of the optic tract canal:

The intracranial division has been dismissed as a potential placoderm synapomorphy on the basis that it is a primitive vertebrate character (Goujet, 2001). It was therefore omitted by Brazeau (2009). However, the character is reinstated here because the belief that it is a primitive feature based on comparisons with taxa such as lamprey and embryos, which have no perichondral lining of the braincase, are not relevant to the question of adult conditions in either ingroup or outgroup taxa. A division as observed in nearly all placoderm taxa for which a braincase has been described is demonstrably and equivalently absent in galeaspids, osteostracans, osteichthyans, chondrichthyans, and *Ptomacanthus*. The condition in *Acanthodes* is unknown.

0. absent

1. present

122. [DFC 60] Position of myodome for superior oblique eye muscles:

0. posterior and dorsal to foramen for nerve II

1. anterior and dorsal to foramen

123. [DFC 61] Endoskeletal intracranial joint:

0. absent

1. present

124. [DFC 62] Spiracular groove on basicranial surface:

Contra Davis et al. (2012), Yu (1998) identifies a "prespiracular groove" in *Psarolepis*. Available figures of *Guiyu* are unclear, and the specimens quite distorted from one individual to another, especially in this region. This renders interpretation very difficult. However, Davis et al. (2012) scored these taxa and the braincase referred to *Ligulalepis* conservatively as '?'. We provisionally retain this scoring, except for *Psarolepis*, where we accept the interpetation provided by Yu (1998) and code this taxon as '1'.

0. absent
1. present

125. Transverse otic process :

Schaeffer (1981), Coates & Sequeira (1998). This character refers to the presence of a transverse wall or process of the otic region that supports the hyomandibular articulation. Such a structure is present in many placoderms (the anterior postorbital process of traditional nomenclature), chondrichthyans (the lateral otic process), and osteichthyans (the lateral commisure sensu lato). There is some variability in the structure (pierced by jugular canal versus imperforate) and location (level with the anterior or posterior of the otic capsule) of transverse otic processes among early gnathostomes. We describe these patterns of variability in characters 126 and 164.

0. present
1. absent

126. Jugular canal:

This character is modified from DFC characters 76 and 93. In part, this character describes patterns of variation among transverse otic processes that bear the hyomandibular facet (see characters 125 and 164). Transverse otic processes that lack a canal for the jugular are characteristic of many chondrichthyans (e.g. *Tamiobatis*, *Orthacanthus*). In cases where taxa lack a jugular canal and have a posteriorly positioned transverse otic process, this structure is typically called a lateral otic process (e.g. Schaeffer, 1981: figs. 6, 21; Coates & Sequeira, 1998: fig. 6). This character is composed as a compound because there are no further dependent characters. Mathematically, this should be equivalent to atomizing and using inapplicability.

0. long (invested in otic region along length of skeletal labyrinth)
1. short (restricted to region anterior of skeletal labyrinth)
2. absent (jugular vein uninvested in otic region)

127. [DFC 63] Spiracular groove on lateral commissure:

Here we consider the relationship between the spiracular groove and the lateral commissure sensu lato (see Table 2 above). We have revised the coding given by Davis et al. (2012) for *Gogonasus* to '1', as this taxon shows a similar condition to *Eusthenopteron* (compare Long et al., 1997: fig. 22 and Jarvik, 1980: fig. 86). Osteostraci, Galeaspida, *Brindabellaspis*, and *Macropetalichthys* are scored as inapplicable for this character.

0. absent
1. present

128. [DFC 64] Subpituitary fenestra:

We have revised the score for *Gogonasus* to '0' following Long et al. (1997).

0. absent
1. present

129. [DFC 65] Supraorbital shelf broad with convex lateral margin:

Coding for *Doliodus* restored to '1', contra Davis et al. (2012). The broad supraorbital shelf with a convex lateral margin is clearly present in tomography renderings of *Doliodus* presented by Maisey et al. (2009). It is true that *Akmonistion* and *Cladoselache* exhibit a much more similar, highly pronounced condition, this being related to a much wider postorbital span in these taxa.

0. absent
1. present

130. [DFC 66] Orbit dorsal or facing dorsolaterally, surrounded laterally by endocranium:

Ptyctodonts are all scored as '?', contra Davis et al. (2012). Given the lack of complete endocranial data, the antorbital position for the hyomandibular articulation, and the presence of a suborbital lamina of the marginal bone of ptyctodonts, there is a distinct possibility that there is a comparable extension of the neurocranial wall as in *Brindabellaspis*, *Macropetalichthys*, and agnathan outgroups. We have therefore coded the condition in ptyctodonts as uncertain. Although rhenanids have dorsally facing orbits they lack any kind of posterior or ventral orbital processes. They are therefore coded as '1'.

0. present
1. absent

131. Eyestalk attachment area:

Zhu and Schultze (2001: character 147), Zhu et al. (2001: character 109), Zhu & Yu (2002: character 109), Zhu et al. (2006: character 83), Friedman (2007: character

95), Zhu et al, (2009: character 36), Zhu et al. (2013: character 222).

0. absent
1. present

132. Postorbital process:

Here we define the postorbital process as a dorsally positioned process at the rear margin of the orbit. The postorbital process is known by a variety of names in different groups: suprapterygoid process (sarcopterygians: Jarvik, 1980); supraorbital process (placoderms: Stensio, 1969; Jarvik, 1980); postorbital pila (in part; identified in some early sarcopterygians and *Entelognathus*, where a bridge encloses the jugular vein: Yu, 1998; Zhu et al., 2013); lateral commissure (in part; identified in early actinopterygians and *Ligulalepis*; Zhu et al., 2013). Rudimentary postorbital processes are present in the rhenanid *Jagorina* (Stensio, 1969: fig. 90) and the porolepiforms *Porolepis* and *Glyptolepis* (Jarvik, 1972: figs 20-21). Taxa in which the orbit is completely enclosed by the neurocranium (e.g. *Macropetalichthys*) or where the palatoquadrate is fused to the neurocranium (e.g. *Helodus*) are coded as uncertain for this character.

0. absent
1. present

133. Canal for jugular in postorbital process:

0. absent
1. present

134. Series of perforations for innervation of supraorbital sensory canal in supraorbital shelf:

This character is coded as inapplicable in taxa lacking well-developed supraorbital shelves.

0. absent
1. present

135. [DFC 67] Extended prehypophysial portion of sphenoid:

0. absent
1. present

136. [DFC 68] Narrow interorbital septum:

Davis et al. (2012) code this character as '1' in ptyctodonts based on Long's (1997) interpretation, but cite it as tentative. Because this relies on a reconstruction of medio-laterally flattened fossils, these scores are changed to '?'. The interorbital space in *Gogonasus* and *Eusthenopteron* is quite narrow, and this is recoded as '1' for these taxa. *Acanthodes* and *Howqualepis* are scored '?' because the interorbital space can only be inferred.

0. absent
1. present

137. [DFC 69] The main trunk of facial nerve (N. VII):

The braincase referred to *Ligulalepis* is scored '?' due to variable interpretations of the position and identity of the jugular canal in this taxon (Basden & Young, 2001; Friedman & Brazeau, 2010; Davis et al., 2012).

0. elongate and passes anterolaterally through orbital floor
1. stout, divides within otic capsule at the level of the transverse otic wall

138. [DFC 70] Course of hyoid ramus of facial nerve (N. VII) relative to jugular canal:

This character is coded as inapplicable for taxa that lack skeletal enclosure of the jugular vein within the otic capsule, as well as in osteostracans and galeaspids where the hyoid ramus of the facial nerve exits in the orbit (see previous character).

0. traverses jugular canal, with separate exit in otic region
1. intersects jugular canal, with exit through posterior jugular foramen

139. [DFC 71] Glossopharyngeal nerve (N. IX) exit:

The case for the placement of N. IX in *Acanthodes* by Davis et al. (2012) is problematic. The groove interpreted as the passage of the glossopharyngeal nerve in *Acanthodes* is also present in the braincase referred to *Ligulalepis*. So, either we must reinterpret the course of its glossopharyngeal nerve, or consider that this groove has no significance for the course of the glossopharyngeal nerve. We adopt a conservative approach, and code the condition in *Acanthodes* as '?'.

0. foramen situated posteroventral to otic capsule and anterior to metotic fissure
1. through metotic fissure

140. [DFC 74] Relationship of cranial endocavity to basisphenoid:

Reformulated from Brazeau (2009) and Davis et al. (2012). Formerly a distinction between tropibasy and platybasy, this character has been revised to use more descriptive terms and avoid embryological baggage and typology. The condition referring to the precise proportions of this feature (i.e. as septate or broad) are accounted for in character 135. Taxa for which this cannot be directly observed have been recoded to '?'. Acanthodes has been scored similarly because this region is not mineralised.

0. endocavity occupies full depth of sphenoid
1. enodcavity dorsally restricted

141. Subcranial ridges:

Subcranial ridges were first described in *Doliodus* by Maisey et al. (2009). These ridges extend along the ventrolateral corner of the basicranium from the level of the hypophysis up to the hyomandibular articulation. These ridges have not previously been recognized in other early gnathostomes prior to our observations in *Janusiscus*. It is apparent from our revised comparative anatomy of early gnathostome braincases that subcranial ridges are present in the braincase referred to *Ligulalepis*, where they are manifest as downturned margins of the ventral surface of the sphenoid (Basden & Young, 2001), and *Mimipiscis* (Gardiner, 1984: fig. 50), where they greatly reduced in length.

0. absent
1. present

142. [DFC 75] Ascending basisphenoid pillar pierced by common internal carotid:

There is ambiguity in assessing this character for any taxon for which the endocast has not been described in detail. Scores for *Guiyu*, *Psarolepis*, *Porolepis*, *Tristychius* and *Gogonasus* are changed to '?' as there is no adequate documentation of the endocranial cavity in these taxa.

0. absent
1. present

143. [DFC 77] Canal for lateral dorsal aorta within basicranial cartilage:

0. absent

1. present

144. [DFC 78] Entrance of internal carotids:

Zhu et al. (2013) propose revised codes of '0' for *Porolepis*, *Psarolepis*, and *Guiyu*. We accept these changes for *Porolepis* and *Psarolepis*, but retain a code of '?' for *Guiyu* owing to unclear conditions in published figures.

0. through separate openings flanking the hypophyseal opening or recess
1. through a common opening at the central midline of the basicranium

145. [DFC 79] Canal for efferent pseudobranchial artery within basicranial cartilage:

0. absent
1. present

146. [DFC 80] Position of basal/basipterygoid articulation:

Doliodus has been scored as polymorphic for this character because it represents a combination of both conditions. The orbital articulation appears to be coextensive with most of the length of the suborbital ridge (Maisey et al., 2009). The ridge is distinctly wider at the level of the hypophysial opening, which recalls the weak basipterygoid articulation in the braincase referred to *Ligulalepis* (Basden & Young, 2001; MDB pers. obs. 2007).

0. same anteroposterior level as hypophysial opening
1. anterior to hypophysial opening

147. [DFC: 81] Articulation between neurocanium and palatoquadrate posterodorsal to orbit (suprapterygoid articulation):

We reformulate this character to consider articulations between the palatoquadrate and dorsal regions of the neurocranium, regardless of whether the latter features are generally called 'postorbital processes' or not. This effectively represents a restoration of character 82 of Brazeau (2009). Outside of chondrichthyans and some acanthodians, articulations between the dorsal portion of the palatoquadrate and neurocranium are present in many sarcopterygian osteichthyans. Both *Eusthenopteron* (Jarvik, 1980: fig. 86) and *Porolepis* (Jarvik, 1972: fig. 20) bear clear facets on the neurocranium for a suprapterygoid articulation, and are recoded as '1'. Conditions of the neurocranium of *Gogonasus* are unclear, but the processus ascendens of the palatoquadrate in this genus appears to bear a clear articular facet (Long, 1997: 30). We therefore recode this taxon as '1'.

0. absent
1. present

148. [DFC 82] Labyrinth cavity:

Davis et al. (2012) code *Austroptyctodus* with state '1', citing Long (1997), Miles & Young (1977), and personal communication from K. Trinajstic (citing no date and no specimen numbers) in support of the statement "the basicranial ossifications include no evidence of the base of a medial capsular wall". This is a highly equivocal statement. The basicranial ossifications show no compelling evidence of the skeletal labyrinth or even the cranial cavity. They are highly incomplete in the extent of their ossification. *Austroptyctodus*, and other ptyctodonts, must be scored indicating missing data.

0. separated from the main neurocranial cavity by a cartilaginous or ossified capsular wall
1. skeletal capsular wall absent

149. [DFC 83] Basipterygoid process (basal articulation) with vertically oriented component:

0. absent
1. present

150. [DFC 84] Pituitary vein canal:

0. dorsal to level of basipterygoid process
1. flanked posteriorly by basipterygoid process

151. [DFC 85] External (horizontal) semicircular canal:

0. absent
1. present

152. [DFC 86] Sinus superior:

0. absent or indistinguishable from union of anterior and posterior canals with saccular chamber
1. present

153. [DFC 87] External (horizontal) semicircular canal:

0. joins the vestibular region dorsal to posterior ampulla
1. joins level with posterior ampulla

154. Horizontal semicircular canal in dorsal view:

This character captures the variable relationship between the course of the jugular vein and the horizontal semicircular canal. In placoderms, the jugular canal extends lateral to the horizontal canal in dorsal view, whereas most crown gnathostomes show a contrasting condition where the vein is overlapped by the canal. Galeaspids and osteostracans are lack a horizontal canal, and are coded as inapplicable for this character.

0. medial to path of jugular vein
1. dorsal to jugular vein

155. Lateral cranial canal:

Gardiner (1984: character 19), Gardiner & Schaeffer (1989: character 5, C1), Coates (1999: character 32), Cloutier & Arratia (2004: character 1), Gardiner et al. (2005: character 5), Zhu et al. (2006: character 91), Zhu et al. (2009: character 55), Zhu et al. (2013: character 233).

0. absent
1. present

156. [DFC 88] Trigemino-facial recess:

0. absent
1. present

157. [DFC 89] Posterior dorsal fontanelle:

Stensiö (1969: fig. 25) figures a posterior dorsal fontanelle in *Jagorina*, but examination of MB.f.510.5-6 shows that this part of the braincase was covered by skull roofing bones. It is therefore not possible to confirm Stensiö's reconstruction, and we consider it here to be inferential. However, we do note that he figured a similar opening for *Asterosteus* (Stensiö, 1969: figs. 30C, 92-93).

0. absent

1. present

158. [DFC 90] Shape of posterior dorsal fontanelle:

0. approximately as long as broad
1. much longer than wide, slot-shaped

159. Synotic tectum:

Coates & Sequeira (1998: character 9).

0. absent
1. present

160. [DFC 91] Dorsal ridge:

Like other dorsal ridges present in fish skulls, the dorsal ridge of the endocranium found in some chondrichthyans and acanthodians likely marks the division between the insertion of paired epaxial musculature. Because this arrangement is contingent upon the presence of such insertions on the dorsal surface of the neurocranium, we have coded this character as inapplicable for taxa with dermal skull roofs.

0. absent
1. present

161. Shape of median dorsal ridge anterior to endolymphatic fossa:

Modified from Coates & Sequeira (1999: character 11), Coates & Sequeira (2001a: character 75), Coates & Sequeira (2001b: character 9) and Maisey (2001: character 9).

0. developed as a squared-off ridge or otherwise ungrooved
1. bears a midline groove

162. [DFC 92] Endolymphatic ducts in neurocranium:

Zhu et al. (2013) revised the coding for *Cowralepis* to '0', citing the arrangement of impressions on the visceral surface of the dermal skull roof in this taxon. However, no endocranium is preserved in *Cowralepis*, and the present character refers explicitly to the course of these ducts within the neurocranium. We therefore restore a code of '?'.

0. posteriodorsally angled tubes
1. tubes oriented vertically through median endolymphatic fossa

163. [DFC 95] Position of hyomandibula articulation on neurocranium:

0. below or anterior to orbit, on ventrolateral angle of braincase
1. on otic capsule, posterior to orbit

164. [DFC 93, in part] Position of hyomandibula articulation relative to structure of skeletal labyrinth:

This character can be coded for taxa that either lack or bear a transverse otic process. We consider this a more precise statement of the relative placement of the hyomandibular articulation in most chondrichthyans by comparison with other gnathostomes. This character also captures whether the transverse otic process is level with the anterior part of the otic region, as is placoderms and osteichthyans, or is more posteriorly placed, as in chondrichthyans.

0. anterior or lateral to skeletal labyrinth
1. at level of posterior semicircular canal

165. [Z13: 227] Hyoid arch articulation on braincase:

Cloutier & Ahlberg (1998: character 88), Zhu & Schultze (2001: character 128), Schultze & Cumbaa (2001: character 53), Zhu et al. (2001: character 96), Zhu & Yu (2002: character 96), Zhu et al. (2006: character 73), Friedman (2007: character 84), Zhu et al. (2009: character 44), Zhu et al. (2013: character 228).

0. single
1. double

166. Branchial ridges:

Here we define the vagal process as a lateral extension (or extensions) of the posterior otic region that are associated with foramina for branches of the vagus (X) nerve and bear facets for the branchial arches. They can also be pierced by the jugular canal. Vagal processes are well developed in placoderms (e.g. *Dicksonosteus*; Goujet, 1984: fig 6). A complete account of vagal processes is provided above in section 3 ('Lateral Processes of Early Gnathostome Neurocrania').

0. present
1. reduced to vagal process
2. absent (articulation made with bare cranial wall)

167. Craniospinal process:

The craniospinal process forms the posterolateral corner of the braincase and is often involved with or supports the cranio-thoracic joint. A complete account of the craniospinal process is provided above in section 3 ('Lateral Processes of Early Gnathostome Neurocrania').

0. absent
1. present

168. [DFC 96] Ventral cranial fissure:

0. absent

1. present

169. Basicranial fenestra:

Ahlberg & Johanson (1998: character 76), Zhu et al. (2001: character 114), Zhu and Yu (2002: character 114), Zhu & Ahlberg (2004: character 76), Daeschler et al. (2006: character 52), Long et al. (2006: character 34), Friedman (2007: character 100), Zhu et al. (2009: character 52), Zhu et al. (2013: character 231).

0. absent

1. present

170. [DFC 97] Metotic (otic-occipital) fissure:

0. absent

1. present

171. [DFC 98] Vestibular fontanelle:

0. absent

1. present

172. [DFC 99] Occipital arch wedged in between otic capsules:

0. absent

1. present

173. [DFC 100] Spino-occipital nerve foramina:

0. two or more, aligned horizontally

1. one or two, dorsoventrally offset

174. [DFC 101] Ventral notch between parachordals:

This is changed to '?' for galeaspids as the notochordal space is unindicated by Gai et al. (2011). *Cowralepis* is changed to '0' as the parachordal plates are unfused, even though they are closely adpressed.

0. present or entirely unfused
1. absent

175. [DFC 102] Parachordal shape:

Modified from Brazeau (2009). Previous formulation was: "Parachordal shape: broad, flat (0); keeled with sloping lateral margins (1)." The parachordals might not necessarily slope, but they may be considerably narrower than the otic capsules; the base of the parachordals might be considerably more ventral than the otic capsules.

0. forming a broad, flat surface as wide as the otic capsules
1. mediolaterally constricted relative to the otic capsules

176. Stalk-shaped parachordal/occipital region:

In petalichthyids such as *Macropetalichthys*, the occiput is flanked by large cucullaris fossae, resulting in a very elongage and narrow occipital region (Stensiö, 1969; Young, 1978). Although the endocranium of *Lunaspis* is not known in any external preparations, the stalked occiput is clearly visible in a radiograph prepared by W. Stürmer (SMF WS 10825) of an isolated skull from the Hunsrück Slate.

0. absent
1. present

177. Paired occipital facets:

0. absent
1. present

178. Size of aperture to notochordal canal:

0. much smaller than foramen magnum
1. as large, or larger, than foramen magnum

179. Canal for median dorsal aorta within basicranium:

Coates & Sequeira (1998: character 3), Coates & Sequeira (2001a: character 68), Coates & Sequiera (2001b: character 68), Friedman (2007: character 183), Zhu et al. (2009: character 51), Friedman & Brazeau (2010: character 38), Zhu et al. (2013: character 234).

0. absent
1. present

180. [DFC 103] Hypotic lamina (and dorsally directed glossopharyngeal canal):

Presence of a hypotic lamina is contingent on the retention of an otoccipital fissure between the parachordals and otic capsule. We therefore code all taxa lacking a persistent fissure as inapplicable. Although Davis et al. (2012) argue for the presence of a hypotic lamina in *Chondrenchelys*, its condition cannot be assessed. We therefore recode this taxon as '?'.

0. absent
1. present

Paired fins and girdles

181. [DFC 104] Macromeric dermal shoulder girdle:

0. present
1. absent

182. [DFC 105] Dermal shoulder girdle composition:

0. ventral and dorsal (scapular) components
1. ventral components only

183. [CA96: 115] Shape of dorsal blade of dermal shoulder girdle (either cleithrum or anterolateral plate):

Cloutier & Ahlberg (1996: character 115), Schultze & Cumbaa (2001: character 94), Zhu & Schultze (2001: character 164), Zhu et al. (2001: character 122), Zhu & Yu (2002: character 122), Cloutier & Arratia (2004: character 148), Zhu et al. (2006: character 96), Friedman (2007: character 107), Zhu et al. (2009: character 124).

0. spatulate
1. pointed

184. [DFC 106] Dermal shoulder girdle forming a complete ring around the trunk:

0. present
1. absent

185. [DFC 107] Pectoral fenestra completely encircled by dermal shoulder armour:

0. present
1. absent

186. [DFC 108] Median dorsal plate:

0. absent
1. present

187. Posterior dorsolateral (PDL) plate or equivalent:

0. absent
1. present

188. [DFC 109] Pronounced internal crista (keel) on median dorsal surface of shoulder girdle:

0. absent
1. present

189. [DFC 109] Crista internalis of dermal shoulder girdle:

0. absent
1. present

190. Scapular infundibulum:

This character refers to the dermal opening for the scapulocoracoid. In antiarchs, the scapula is situated within an infundibulum, rather than a fenestration.

0. absent
1. present

191. [DFC 110] Scapular process of shoulder endoskeleton:

0. absent
1. present

192. [DFC 111] Ventral margin of separate scapular ossification:

0. horizontal
1. deeply angled

193. [DFC 112] Cross sectional shape of scapular process:

0. flattened or strongly ovate
1. subcircular

194. [DFC 113] Flange on trailing edge of scapulocoracoid:

0. absent
1. present

195. [DFC 114] Scapular process with posterodorsal angle:

Culmacanthus is scored as '?' because scapulocoracoids associated with a specimen of this taxon shows an inflection resembling a posterodorsal angle (Burrow & Young, 2012: fig. 2 f, g). However, this is not seen in other specimens. *Onychoselache* and *Hamiltonichthys* are re-coded '1' based on photographs and specimen illustrations (Maisey, 1989: fig. 14; Coates & Gess, 2007: fig. 5).

0. absent
1. present

196. [DFC 115] Endoskeletal postbranchial lamina on scapular process:

We have revised the coding for *Austroptyctodus* to '0' (Long, 1997).

0. present
1. absent

197. [DFC 116] Mineralisation of internal surface of scapular blade:

0. mineralised all around
1. unmineralised on internal face forming a hemicylindrical cross-section

198. [DFC 117] Coracoid process:

0. absent
1. present

199. [DFC 118] Procoracoid mineralisation:

0. absent
1. present

200. [DFC 119] Fin base articulation on scapulocoracoid:

Guiyu and *Psarolepis* re-scored as '1'. *Acanthodes* scored '1'. Conditions in ptyctodonts are uncertain, but there is clearly more than one position for fin basals, often broadly separated (Miles & Young, 1977; Trinajstic et al., 2012). *Debeerius* is scored '1' as the articulation is indicated as being quite broad (Grogan & Lund, 2000).

0. deeper than wide (stenobasal)
1. wider than deep (eurybasal)

201. Pectoral fin articulation:

Zhu & Schultze (2001: character 175), Zhu et al. (2001: character 129), Zhu & Yu (2002: character 129), Zhu et al. (2006: character 104), Friedman (2007: character 113), Zhu et al. (2009: character 130), Zhu et al. (2013: character 130).

0. monobasal

1. polybasal

202. Number of basals in polybasal pectoral fins:

0. three or more

1. two

203. Branching radials in paired fins:

Complex patterns of branching radials are ubiquitous in the paired fins of crown gnathostomes. This branching is typically associated with the posterior margin of rear fins generally and the metapterygium specifically. By contrast, the basal support of osteostracan paired appendages consist of unbranched plates, while those of many placoderms appear to be constructed of parrallel rows of simpled, unbranched radials.

0. absent

1. present

204. Number of mesomeres in metapterygial axis:

Cloutier & Ahlberg (1996: character 123), Zhu & Schultze (2001: character 180), Zhu & Yu (2001: character 132), Zhu & Yu (2002: character 132), Friedman (2007: character 115).

0. five or fewer

1. seven or more

205. Biserial pectoral fin endoskeleton:

0. absent

1. present

206. [DFC 120] Perforate propterygium:

0. absent

1. present

207. Filamentous extension of pectoral fin from axillary region:

0. absent

1. present

208. [DFC 121] Pelvic fins:

0. absent

1. present

209. [DFC 122] Pelvic claspers:

Cladoselache is coded as '1' based on the clasper-like appendage figured by Hussakof & Bryant (1916) (cf. Maisey, 2008). Long et al. (2009) argue for the presence of claspers in *Cowralepis*, so we revise the code of this taxon to '1'.

0. absent

1. present

210. [DFC 123] Dermal pelvic clasper ossifications:

The presence of dermal pelvic clasper ossifications is contingent on the presence of claspers. We therefore code all taxa lacking claspers as inapplicable for the present character. All taxa for which the presence of claspers cannot be determined are coded as '?'.

0. absent
1. present

211. [DFC 124] Pectoral fins covered in macromeric dermal armour:

0. absent
1. present

212. [DFC 125] Pectoral fin base has large, hemispherical dermal component:

0. absent
1. present

Axial skeleton including median fins and their supports

213. [DFC 126] Dorsal fin spines:

A spine-like midline ossification is present at the anterior margin of the dorsal fin of *Ptericthyodes* (Hemmings, 1978), so we code this taxon as '1'.

0. absent
1. present

214. [DFC 127] Anal fin spine:

0. absent
1. present

215. [DFC 128] Paired fin spines:

0. absent
1. present

216. [DFC 129] Median fin spine insertion:

0. shallow, not greatly deeper than dermal bones/scales
1. deep

217. [DFC 130] Intermediate fin spines:

0. absent
1. present

218. Fin spine cross-section:

Early gnathostome fin spines have at least two distinctive profiles in cross-section. Generally, the profile is gently curving or parabolic. Taxa such as acanthodids and ischnacanthids exhibit a condition in which the cross-section is more rectangular, and the sides of the spine are flatter and closer to parallel (Denison, 1979; Gagnier & Wilson, 1996).

0. Round or horseshoe shaped
1. Flat-sided, with rectangular profile

219. Intermediate spines when present:

0. one pair
1. multiple pairs

220. [DFC 131] Prepectoral fin spines:

0. absent
1. present

221. [DFC 132] Fin spines with ridges:

0. absent
1. present

222. [DFC 133] Fin spines with nodes:

0. absent
1. present

223. [DFC 134] Fin spines with rows of large retrorse denticles:

0. absent
1. present

224. Expanded spine rib on leading edge of spine:

This character is common to acanthodids and their proximal relations. It is variably present in *Kathemacanthus*.

0. absent
1. present

225. Spine ridges:

0. converging at the distal apex of the spine
1. converging on leading edge of spine

226. [DFC 135] Synarcual:

0. absent
1. present

227. Series of thoracic supraneurals:

Cloutier & Ahlberg (1996: character 137), Ahlberg & Johanson (1998: character 99), Zhu & Ahlberg (2004: character 99), Zhu & Yu (2001: character 142), Zhu & Yu (2001: character 142), Friedman (2007: character 125).

0. absent
1. present

228. [DFC 136] Number of dorsal fins, if present:

0. one
1. two

229. Posterior dorsal fin shape:

This is admittedly a compound character. This owes to the problems of rendering ratio-scale continuous characters as a discrete character. Our conceptualisation of this character is intended to capture the distinctively broad or ribbon-shaped second dorsal fins that are differentiated from any of the other median fins, and the generalized triangular shape of many gnathostomes and their relatives. In taxa possessing only a single dorsal fin, we have scored taxa where we think the observed fin is equivalent to a posterior dorsal fin. This is based on the postition of the posterior dorsal fin behind or at the level of the posterior limit of the posterior wall of the body cavity (as indicated by the position of the pelvic girdle and/or anal fin, or evidence of the body cavity present as an infill). We have reinterpreted the vertebral column of *Cowralepis*, arguing that Ritchie's (2005) reconstruction inverts the dorsoventral orientation. Ritchie's sub-haemal spines are here interpreted as dorsal or caudal fin radials. This is evidenced by the fact that the series bearing these epi-spinal elements continues under the dermal shoulder armour, while the opposing series terminates at the level of the pelvic fins (based on AMF9764, Ritchie, 2005, fig. 16 A, B). This also better explains the direction of the gentle sigmoid bend seen in several specimens (Ritchie, 2005, figs.16B, 17A, C). In photographs of specimen AMF103767 (Ritchie, 2005, fig. 1A-D, the orientation of the collapsed vertebral column can be observed. In the specimen showing the dorsal surface, the chordal surface the series lacking the accessory elements is observed, suggesting this was their ventral surface rather than dorsal.

0. base approximately as broad as tall, not broader than all of other median fins
1. base much longer than the height of the fin, substantially longer than any of the other dorsal fins

230. Basal plate in dorsal fin:

Friedman & Brazeau (2010: character 42).

0. absent
1. present

231. Branching radial structure articulating with dorsal fin basal plate:

0. absent
1. present

232. [DFC 137] Anal fin:

0. absent
1. present

233. Basal plate in anal fin:

Friedman & Brazeau (2010: character 42).

0. absent

1. present

234. [DFC 138] Caudal radials:

0. extend beyond level of body wall and deep into hypochordal lobe

1. radials restricted to axial lobe

235. Supraneurals in axial lobe of caudal fin:

0. absent

1. present

236. Epichordal lepidotrichia in caudal fin:

Cloutier & Ahlberg (1996: character 134), Schultze & Cumbaa (2001: character 101), Zhu & Schultze (2001: character 191), Zhu et al. (2001: character 140), Zhu & Yu (2002: character 140), Cloutier & Arratia (2004: character 173), Zhu et al. (2006: character 110), Friedman (2007: character 123), Zhu et al. (2009: character 142), Zhu et al. (2013: character 146).

0. absent

1. present

Eliminated characters:

[DFC 32] Opercular cover of branchial chamber complete or partial (0); separate gill covers and gill slits (1).

Character description from Davis et al. (2012): “Modified from Hanke and Wilson

> (2004): a series of gill slits (with individual covers rather than pores, as in jawless fishes), none of which is overlain partly or completely by an enlarged hyoidean gill cover, represents a possible synapomorphy of certain acanthodians and certain, but not all Chondrichthyes. Notable exceptions include the Chimaeroids, as well as *Tristychius* (Dick 1978), and the symmoriid *Falcatus* (Lund 1985), as exhibited in specimen CM 41049. With regard to the present study, species of *Acanthodes* (Heidtke 1993; Beznosov 2009) consistently exhibit a long pharyngeal region separating the pectoral girdle from the occipital region, mandibular and hyoid arches. In several A. bronni specimens the gill skeleton is barely disturbed. The gill arch series preserved in specimen NHM P49979 (Supplementary Figure 12 e) especially resembles conditions in *Akmonistion* and *Cladoselache*, although overlain by an impression of skin with scales (these chondrichthyan exemplars are mostly scale-free). Although the skin impression in NHM P49979 is incomplete, the simplest interpretation is of a series of gill slits and flaps. Crucially, there is no evidence of a substantial, hyoid supported, opercular cover."

This character is deleted because it is requires too much subjective judgment and is highly vulnerable to taphonomic distortions resulting from compression of material.

[DFC 73] Ethmoid region elongate with dorsoventrally deep lateral walls: absent (0); present (1).

> Character description from Davis et al. (2012): "Holocephalan synapomorphy: in extant species the pre-orbital walls of the ethmoid region provide anchorage for most of the jaw adductor muscles (Didier 1995). This is a likely synapomorphy of a larger

> clade including non-holocephalan members of the chimaeroid total group (Stahl 1999; Grogan & Lund 2000). Although coded as uncertain in the vast majority of acanthodians, orbit and snout proportions indicate that all could be scored as ‘0’.”

This character is deleted because whether or not the ethmoid region is ‘elongate’ is highly dependent on the proportions of the braincase as a whole.

[DFC 72] Short otico-occipital region of braincase: absent (0); present (1). Schaeffer (1981); Coates & Sequeira (1998, 2001); Maisey (2001); Brazeau (2009); Davis et al. (2012).

This character is also deleted as it is highly dependent on individual braincase proportions.

[DFC 94] Process forming part or complete wall of jugular groove or canal projecting from otic capsule wall: absent (0); present (1).

> Character description from Davis et al. (2012): “The anterolateral otic process of *Acanthodes* (‘Alop’, Figure 2b and d, Supplementary Figures 9 and 15) is here suggested as a possible homologue of the thickened margin and posterior postorbital process of placoderm neurocrania (Stensio 1963; Goujet 1984; Young 1980). Topographically, these processes are near-equivalents: each projects laterally from the otic wall, situated between or surrounding the jugular passage and the exit of the glossopharyngeal nerve. However, the polarity of this character is admittedly difficult to judge, relative to conditions in jawless outgroups.”

This character is deleted because the presence of a process enclosing the jugular canal is accounted for in other characters.

8.1.2.2 List of Taxa

Taxa included in the analyses with associated references and specimen numbers.

Taxon	References	Specimens
Galeaspida	Donoghue et al., 2000; Wang et al., 2005; Gai et al., 2011.	
Osteostraci	Denison, 1947; Janvier, 1985; Janvier, 1996; Sansom, 2009.	
Acanthodes	Gross, 1947; Miles, 1968; Miles, 1973a, b; Coates, 1994; Valiukevicius, 1995; Davis et al., 2012.	
Akmonistion	Coates & Sequiera, 1998; Coates et al., 1998; Coates & Sequeira, 2001.	
Austroptyctodus	Long, 1997; Miles & Young, 1977.	
Bothriolepis	Denison, 1978; Young, 1984; Young, 1988.	
Brachyacanthus	Watson, 1937; Denison, 1979.	NHMUK P.6959, P.9595
Brindabellaspis	Young, 1980; Young, 1986; Burrow & Turner, 1998, 1999.	
Brochoadmones	Bernacsek & Dineley, 1977; Gagnier & Wilson, 1996b; Hanke & Wilson, 2006.	UALVP 41495
Buchanosteus	Young, 1979, 1986; Young et al., 2001.	
Campbellodus	Miles & Young, 1977; Long, 1997.	
Cassidiceps	Gagnier & Wilson, 1996a.	UALVP 32454
Cheiracanthus	Watson, 1937; Miles, 1973a; Denison, 1979.	
Cheirolepis	Ørvig, 1967; Pearson & Westoll, 1979; Arratia & Cloutier, 1996.	NHMUK P.62908; RSM 1877.30.5
Chondrenchelys	Moy-Thomas, 1935; Lund, 1982.	
Cladodoides	Gross, 1937, 1938; Maisey, 2005.	
Cladoselache	Hussakof & Bryant, 1916; Woodward & White, 1938; Bendix-Almgreen, 1975; Schaeffer, 1981; Zangerl, 1981; Maisey, 2007, 2008.	
Climatius	Watson, 1937; Ørvig, 1967; Miles, 1973a, b.	
Cobelodus	Zangerl & Case, 1976; Maisey,	

	2007.	
Coccosteus	Stensiö, 1963; Miles & Westoll, 1968.	
Cowralepis	Ritchie, 2005; Carr et al., 2009; Long et al., 2009.	
Culmacanthus	Long, 1983; Burrow & Young, 2012.	
Debeerius	Grogan & Lund, 2000.	
Dialipina	Schultze, 1968; Schultze and Cumbaa, 2001.	
Dicksonosteus	Goujet, 1975; Goujet, 1984.	
Diplacanthus	Watson, 1937; Miles, 1973a; Gagnier, 1996.	
Doliodus	Miller et al., 2003; Turner, 2004; Maisey et al., 2009; Maisey et al., in press.	
Entelognathus	Zhu et al., 2013.	
Eurycaraspis	Liu, 1991.	
Eusthenopteron	Jarvik, 1980.	
Euthacanthus	Watson, 1937; Newman et al., 2011.	
Gemuendina	Broili, 1930; Gross, 1963.	
Gladiobranchus	Bernacsek and Dineley, 1977; Hanke & Davis, 2008; Newman et al., 2012.	
Glyptolepis	Andrews & Westoll, 1970; Jarvik, 1972; Cloutier & Schultze, 1996; Ahlberg, 1989.	
Gogonasus	Long et al., 1997; Long et al., 2006.	
Guiyu	Zhu et al., 2009.	
Gyracanthides	Warren et al., 2000; Turner et al., 2005.	
Hamiltonichthys	Maisey, 1989b.	
Helodus	Moy-Thomas, 1936.	
Homalacanthus	Watson, 1937; Gagnier, 1996.	
Howqualepis	Long, 1988.	AMF65495
Incisoscutum	Johanson & Smith 2005, Ahlberg et al., 2009.	
Ischnacanthus	Watson, 1937; Gross, 1947; Miles, 1973a.	NHMUK P.7000
Jagorina	Stensiö, 1969.	MB.f.510.5-6
Kathemacanthus	Gagnier & Wilson, 1996a; Hanke & Wilson, 2010.	
Kentuckia	Rayner, 1951; Giles and Friedman, 2014.	
Kujdanowiaspis	Stensiö, 1969; Dupret, 2010.	
Latviacanthus	Schultze & Zidek, 1982.	
"*Ligulalepis*"	Basden et al., 2000; Basden and Young, 2001.	
Lunaspis	Heintz, 1937; Gross, 1961	SMF WS 10825
Lupopsyrus	Bernacsek & Dineley, 1977; Hanke & Davis, 2012.	
Macropetalichthys	Stensiö, 1925; Gross, 1935; Stensiö,	

	1969; Denison, 1978; Young, 1978.	
Mesacanthus	Watson, 1937; Gross, 1947; Miles, 1973a.	
Mimipiscis	Gardiner & Bartram, 1977; Gardiner, 1984; Giles & Friedman, 2014.	
Moythomasia	Gardiner, 1984.	
Obtusacanthus	Hanke & Wilson, 2004.	UALVP 41488
Onychodus	Andrews et al., 2006.	
Onychoselache	Dick & Maisey, 1980; Coates & Gess, 2007.	
Orthacanthus	Schaeffer, 1981; Maisey, 1983.	
Parayunnanolepis	Zhang et al., 2001; Zhu et al., 2012.	
Parexus	Watson, 1937; Miles, 1973a.	NHMUK P.130, P.38593
Poracanthodes	Valiukevicius, 1992; Denison, 1979.	
Porolepis	Jarvik, 1972; Clement, 2004.	
Promesacanthus	Hanke, 2008.	UALVP 42652
Psarolepis	Zhu & Schultze, 1997; Yu, 1998; Zhu et al., 1999; Qu et al., 2013; Zhu et al., 2013.	
Pterichthyodes	Hemmings, 1978.	
Ptomacanthus	Miles, 1973a; Denison, 1979; Brazeau, 2009; Brazeau, 2012.	
Pucapampella	Maisey, 2001; Maisey & Anderson, 2001; Janvier & Maisey, 2010; Maisey & Lane, 2010.	
Ramirosuarezia	Pradel et al., 2009.	
Rhamphodopsis	Miles, 1967; Long, 1997; Miles & Young, 1977.	
Romundina	Goujet & Young, 2004; Giles et al., 2013.	
Styloichthys	Zhu & Yu, 2002; Zhu & Yu, 2004; Friedman, 2007.	
Tamiobatis	Schaeffer, 1981; Williams, 1998.	
Tetanopsyrus	Gagnier & Wilson, 1995; Gagnier et al., 1999; Hanke et al., 2001.	UALVP 32571, 42512, 43246
Tristychius	Dick, 1978; Coates and Gess, 2007.	
Vernicomacanthus waynensis	Miles, 1973a.	NHM P.16614, 16615, 24938a, 52441a, 52443
Yunnanolepis	Zhu, 1996; Chang, 1980; Giles et al., 2013.	

Institutional Abbreviations

AMF, Australian Museum, Sydney

MB, Museum für Naturkunde, Berlin

NHMUK, Natural History Museum, London

SMF, Senckenberg Museum, Frankfurt

UALVP, University of Alberta Laboratory of Vertebrate Palaeontology, Alberta

RSM, National Museums of Scotland, Edinburgh

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8.1.4 Legends for electronic appendices

8.1.4.1 Data matrix. (electronic).

8.1.4.2 Character state optimisation tree showing all unambiguous character state transformations on one of the shortest trees. (electronic).

8.2 APPENDIX 2

8.2.1 Legends for electronic appendices

8.2.1.1 | PLY file of the otico-occipital portion of the braincase of *Cheirolepis.* (electronic)

8.2.1.2 | PLY file of the ethmoid portion of the braincase of *Cheirolepis.* (electronic)

8.2.1.3 | PLY file of the hyomandibula of *Cheirolepis.* (electronic)

8.2.1.4 | PLY file of the left pectoral fin endoskeleton of *Cheirolepis.* (electronic)

8.2.1.5 | PLY file of the mould of the braincase of *Howqualepis.* (electronic)

8.3 APPENDIX 3

Table of Contents

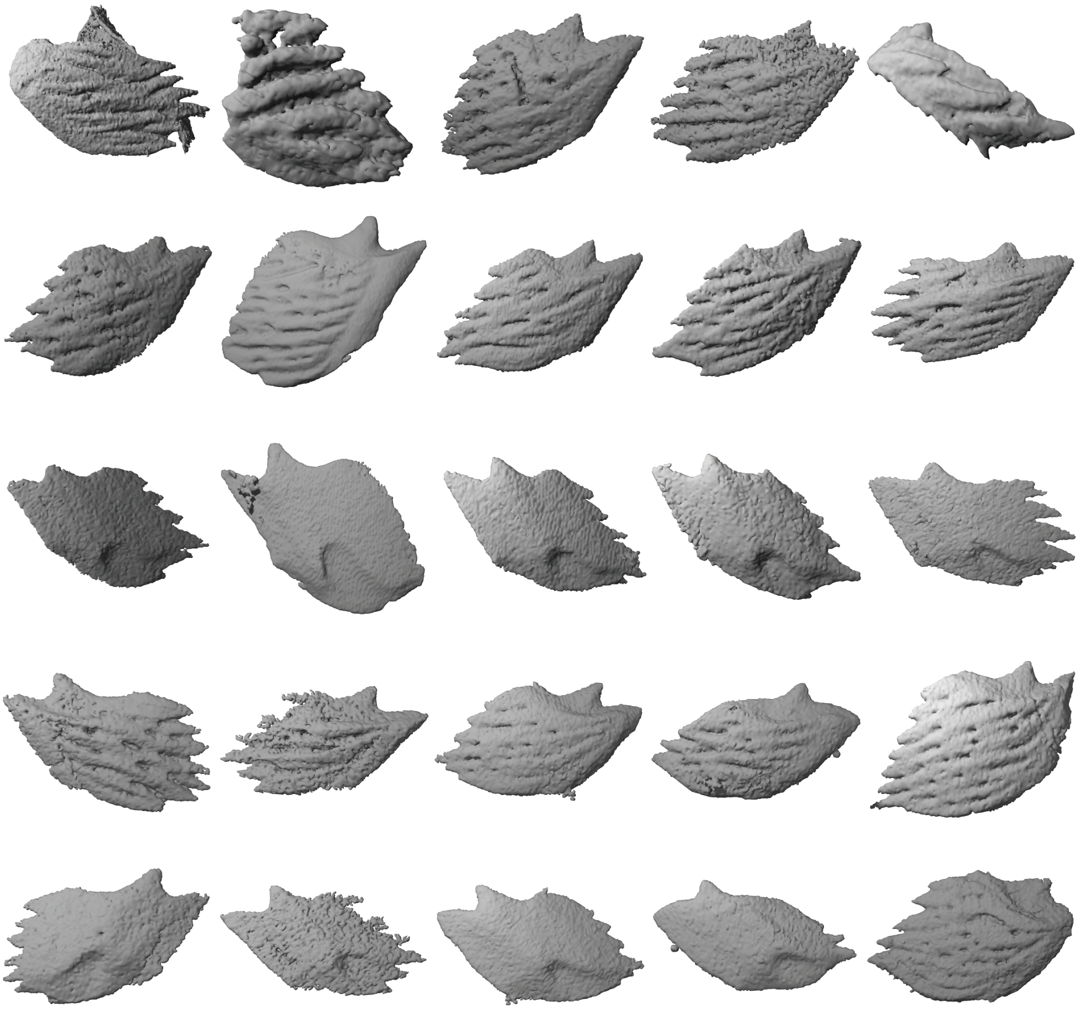
8.3.1 Supplementary Notes

8.3.1.1 Geological settings

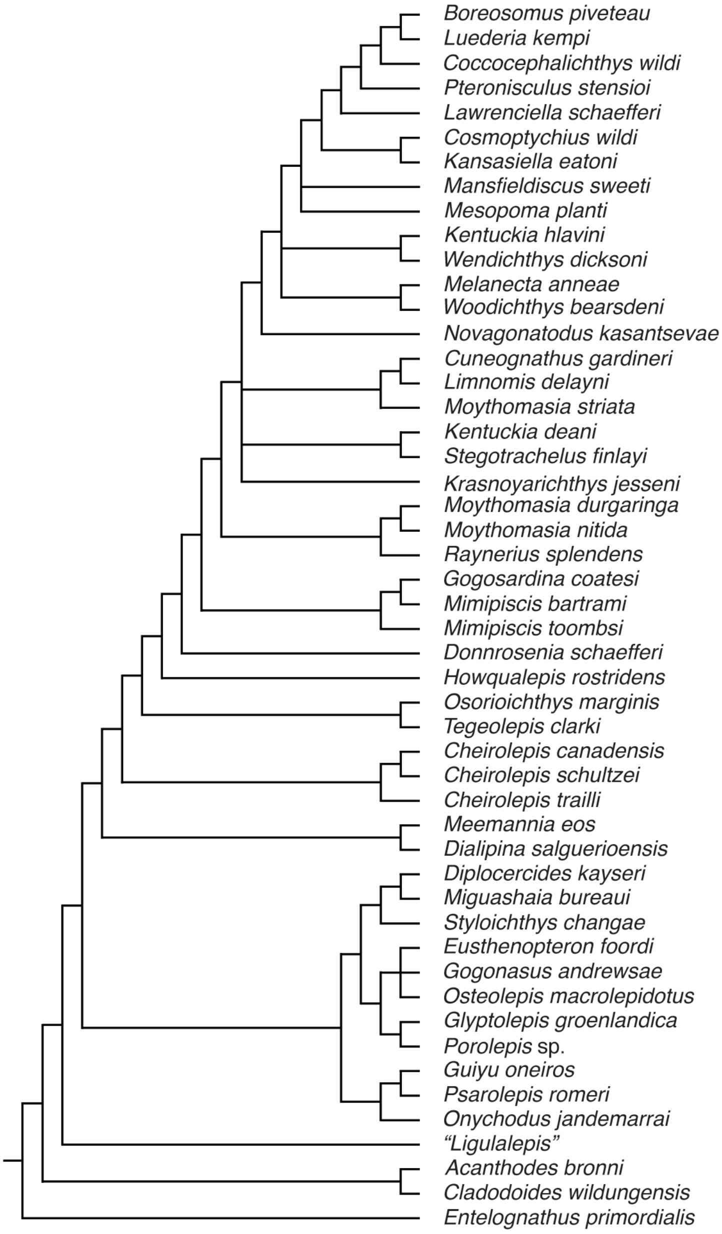
The specimen described in this paper (HGL 1245) was collected from the La Parisienne Member of the Ferques Formation, La Parisienne Quarry, Bas-Boulonais, France. Actinopterygian microremains, including scales and teeth, have also been collected from the Ferques region by a Palaeontological Association field meeting, and were described by Derycke et al. (1995). The Ferques Formation is associated with the upper *asymmetricus* and *triangularis* conodont zones (Derycke et al., 1995), corresponding to the earliest part of the Famennian (~372 Ma; Gradstein et al., 2012). Three of the scales (CVUL 38, CVUL 39, CVUL 40) were referred to *Moythomasia* sp., with a further scale (CVUL 44), a hemilepidotrichium (CVUL 46), a toothplate (CVUL 41) and an isolated tooth (CVUL 42) referred to Actinopterygii gen. et sp. indet. Additional material found in the Devonian of the Ferques region includes *Rhynchodus*? sp., *Symmorium*? sp., *Ctenacanthus* sp., Chondrichthyes gen. et sp. indet., *Ptomacanthus*? sp., *Acanthodes* sp., Acanthodii gen. et sp. indet., Onychodontida gen. et sp. indet., Porolepiformes gen. et sp. indet. and *Spodichthys*? sp.

Specimens CVUL 38, CVUL 39, CVUL 40 were referred to *Moythomasia* sp. due to similarities between them and those described by Jessen (1968). However, the scales of *Raynerius splendens* (Supplementary Fig. 1) also bear clear similarities with those of *Moythomasia*, most notably in the angled ganoin ridges and presence of open pores. As such, the scales described by Derycke et al. (1995) may well belong to *Raynerius splendens*, but due to a lack a clear association are not currently referred to the new genus.

8.3.1.2 Supplementary figures



Supplementary Figure 1 | Scale morphology of *Raynerius splendens*. Scales are not preserved in articulation, and so their original place on the body is not yet known. All specimens scaled to the same size.



Supplementary Figure 2 | Phylogenetic placement of *Raynerius splendens*.

Adams consensus of 336 most parsimonious trees.

8.3.2 Phylogenetic Analyses

8.3.2.1 Phylogenetic methods

Phylogenetic analysis was performed using a heuristic in PAUP* 4.0b10 (Swofford, 2003). The dataset was based on that of Choo (2011) with additional characters and taxa, to give a total of 182 characters and 50 taxa. A parsimony analysis was conducted using a heuristic search, with 1000 random addition sequences, 5 trees held at each step, maxtrees set to automatically increase, nchuck=10000, chuckscore=1, and the tree bisection and reconstruction strategy enabled. All characters were weighted equally, and 6 were ordered. Taxonomic equivalence (Wilkinson, 1995) was assessed using Claddis (Lloyd, 2014), and all taxa were found to comprise unique character combinations. The outgroup was constrained using the topology [*Entelognathus*[*Acanthodes, Cladodoides*[ingroup]]]. Bootstrap values were calculated using 1000 replicates of a heuristic search, with the tree branching and reconstruction strategy enabled, 25 replicates, 5 trees held at each step, rearrlimit = 50000000, limitprerep=yes, nchuck=10000, chuckscore=1. Bremer support values were calculated using PRAP2 (Müller, 2004). 336 most parsimonius trees of 506 steps were generated (consistency index = 0.379; homoplasy index = 0.621; retention index = 0.676; rescaled consistency index = 0.256). This relatively large number of MPTs resulted from varying relationships between three subsets of taxa: three sarcopterygians (*Eusthenopteron, Gogonasus* and *Osteolepis*), six actinopterygians (*Cuneognathus*, *Limnomis, Kentuckia deani, Stegotrachelus, Krasnoyarichthys* and *Moythomasia striata*), and four further actinopterygians (*Kentuckia hlavini*, *Wendichthys, Mansfieldiscus* and *Lawrenciella*).

8.3.2.2 Character List

The character list is based on that of Choo (2011), with substantial modifications in order to expand the analysis outside of actinopterygians. The source of additional characters is noted in the character descriptions. A number of characters have been deleted from Choo's (2011) matrix, and full justification for these deletions is given after the character list. Ordered characters are indicated by an asterisk ('*').

1. **Large dermal plates:**

   Forey, 1980; Gardiner, 1984; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau; 2010; Davis et al., 2012; Zhu et al., 2013; Brazeau & Friedman, 2014; Giles et al., 2015.

   0. absent
   1. present

2. **Sensory lines:**

   Brazeau, 2009; Zhu et al., 2013; Giles et al., 2015.

   0. preserved as open grooves
   1. pass through canals

3. **[CH 1] Premaxillae, contact at midline:**

   Cloutier & Ahlberg, 1996; Taverne, 1997; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Choo, 2011. The premaxillae in *Mansfieldiscus* (Long, 1988) are thought to have contacted at the midline but have not been observed, and so the coding for this taxon is conservatively changed from '0' to ‘?’. The snout is not preserved in *Novagonatodus* (Long, 1988; Holland et al., 2007), so the coding is changed from ‘1’ to ‘?’. Although a median dentigerous 'rostral' is preserved in *Luederia* (Schaeffer & Dalquest, 1978), the lack of associated bones means its identity is uncertain, and it may well represent fused premaxillae. This taxon is conservatively coded ‘?’. The premaxilla is absent in *Wendichthys* (Lund & Poplin, 1997), so the coding is revised from '0' to '-'.

0. present
1. absent

4. Premaxilla:

Friedman, 2007; Giles et al., 2015.

0. Reaches or extends past anterior margin of orbit
1. Confined to region anterior to orbit

5. Premaxilla contributes to orbital margin:

Cloutier & Ahlberg, 1996; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014. This character is coded as inapplicable in taxa where the premaxilla is restricted anterior to the orbit.

0. absent
1. present

6. [CH 3] Postrostrals (element[s] immediately anterior to frontals but not in

contact with premaxillae):

Cloutier & Ahlberg, 1996; Taverne, 1997; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. Choo's (2011) codes for this character appear reversed.

0. present
1. absent

7. [CH 4] Single median dermal bone capping snout:

Gardiner & Schaeffer, 1989; Taverne, 1997; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011.

0. absent
1. present

8. Pores for rostral organ:

Friedman, 2007.

0. absent
1. present

9. [CH 5] Transverse ornamentation of median rostral or dermal cover of ethmoid region:

Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The ornament in *Osorioichthys* (Taverne, 1997) is not preserved on the posterior portion of the rostral in sufficient detail to code this character (pers. obs. S.G.). As such, the coding is changed from ‘0’ to ‘?’.

0. absent

1. present

10. [CH 8] Nasal bone as single consolidated ossification (i.e. bone(s) carrying supraorbital canal between premaxilla and anterior margin of frontals):

Taverne, 1997; Schultze & Cumbaa, 2001; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011.

0. absent
1. present

11. [CH 57] Mesial margin of (anterior) nasal:

Lund et al., 1995; Ahlberg & Johanson, 1998; Ahlberg et al., 2000; Lund, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Zhu & Ahlberg, 2004; Daeschler et al., 2006; Long et al., 2006; Zhu et al., 2006; Zhu et al., 2009; Choo, 2011. The nasal is poorly preserved in *Cheirolepis canadensis* (Pearson & Westoll, 1979; Arratia & Cloutier, 1996), and coding for this taxon is revised from ‘0’ to ‘?’. The position of the nostrils is not clear in *Tegeolepis*, and the coding for this taxon is revised from '1' to '?'.

0. not notched
1. notched

12. [CH 6] Posterior nostril in complete communication with orbital fenestra:

Friedman & Blom, 2006; Long et al., 2008; Choo, 2011. The position of the nostrils is not clear in *Tegeolepis*, and the coding for this taxon is revised from '0' to '?'.

0. absent
1. present

13. **[CH 7] Posterior nostril – contribution to margin by premaxillae:**

Friedman & Blom, 2006; Long et al., 2008; Choo, 2011. The coding for *Howqualepis rostridens* (Long, 1988) and *Gogosardina* (Choo et al., 2009) is revised from ‘0’ to ‘1’. The premaxilla is not preserved in *Novagonatodus* (Long, 1988; Holland et al., 2007), so the coding is changed from ‘0’ to ‘?’. The premaxilla is absent in *Wendichthys* (Lund & Poplin, 1997), so the coding is revised from '0' to '-'. The position of the nostrils is not clear in *Tegeolepis*, and the coding for this taxon is revised from '0' to '?'.

0. absent
1. present

14. **Tectals (sensu Cloutier & Ahlberg 1996, not counting the posterior tectal of Jarvik):**

Lund et al., 1995; Cloutier & Ahlberg, 1996; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Lund & Poplin, 2002; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Swartz, 2009; Zhu et al., 2009; Zhu et al., 2013.

0. absent
1. present

15. **[CH 9] Pineal foramen:**

Cloutier & Ahlberg, 1996; Taverne, 1997; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu & Yu, 2002; Friedman & Blom, 2006; Friedman, 2007; Long et al., 2008; Brazeau, 2009; Swartz, 2009; Davis et al., 2012; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015. A pineal foramen is variably present in *Cheirolepis canadensis* (Pearson & Westoll, 1979; Arratia & Cloutier, 1996), C. trailli (Pearson

& Westoll, 1979), *Kentuckia deani* (Rayner, 1951) and *Meemannia* (Zhu et al., 2010), and these taxa are coded '0/1' to reflect this polymorphism.

0. present
1. absent

16. Pineal eminence:

Friedman, 2007; Zhu et al., 2009. Can only be coded in taxa that lack a pineal foramen.

0. absent
1. present

17. [CH 10] Shape of parietals (sarcopterygian postparietals):

Dietze, 2000; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. The coding for *Cuneognathus* (Friedman & Blom, 2006), *Kentuckia hlavini* (Dunkle, 1964) and *Stegotrachelus* (Swartz, 2009) is revised from ‘0’ to ‘1’. The coding for *Melanecta* (Coates, 1998) is revised from ‘1’ to ‘0’. *Wendichthys* (Lund & Poplin, 1997) was erroneously coded by Choo (2011) as state ‘2’, for which there is no description, and is recoded here as ‘1’.

0. rectangular, with long axis parallel to midline
1. quadrate

18. [CH 11] Relative lengths of frontals and parietals (sarcopterygian parietals and postparietals):

Lund et al., 1995; Taverne, 1997; Dietze, 2000; Lund, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Lund & Poplin, 2002; Cloutier & Arratia, 2004;

Friedman & Blom, 2006; Zhu et al., 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. The coding for *Mimipiscis toombsi* (Gardiner, 1984; Choo, 2011) is changed from ‘1’ to ‘2’.

0. frontal shorter than parietal
1. frontal approximately equal to parietal
2. frontal longer than parietal

19. Anterior pit line:

Giles et al., 2015. Although not figured, an anterior pit line is described for *Miguashaia* (Cloutier 1996).

0. absent
1. present

20. Otic canal extends through parietals:

0. absent
1. present

21. Tabular:

Lund et al., 1995; Cloutier & Ahlberg, 1996; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Cloutier & Arratia, 2004; Long et al., 2008; Swartz, 2009.

0. present
1. absent

22. Tabular pit line:

0. absent
1. present

23. [CH 12] Intertemporal – relative length:

Taverne, 1997; Friedman & Blom, 2006; Choo, 2011. The coding for *Moythomasia durgaringa* (Gardiner, 1984) and *Moythomasia nitida* (Jessen, 1968) is revised from '1' to '0'. The intertemporal appears to be absent in *Cheirolepis schultzei* (Arratia & Cloutier, 2004), so is coded '-'.

0. shorter than supratemporal
1. of similar length to supratemporal
2. longer than supratemporal

24. [CH 13] Intertemporal – contact with supratemporal anterior to that between frontal and parietal:

Friedman & Blom, 2006; Choo, 2011.

0. absent
1. present

25. [CH 54] Dermosphenotic with distinct posterior ramus:

Gardiner & Schaeffer, 1989; Coates, 1998; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Long et al., 2008; Zhu et al., 2009; Choo, 2011. The posterior limb of the dermosphenotic is exaggerated in Gardiner's (1984: fig 103) reconstruction of *Moythomasia durgaringa*. The illustration of the bone (Gardiner 1984, fig 69) makes it clear that the posterior limb is not developed, and the coding for this taxon is consequently revised from '1' to '0'. The shape of the dermosphenotic in *Cuneognathus* (Friedman & Blom, 2006) is inferred, and the coding is thus revised from '1' to '?'. The dermosphenotic of *Gogosardina* (Choo et al., 2009) was destroyed in prep, but is described as a ‘tripartite structure similar to the dermosphenotics of *Mimia* and *Moythomasia’*. However, as the dermosphenotic of *Moy. durgaringa* has been recoded as lacking a posterior limb, the condition in *Gogosardina* seems uncertain. As such, the coding for this taxon is revised from ‘1’ to ‘?’. The coding in *Melanecta* (Coates, 1998) is revised from ‘0’ to ‘?’. The posterior limb of the dermosphenotic is variably developed in *Mesopoma* (Coates, 1999), so this taxon is scored '0/1' to reflect this polymorphism.

0. absent
1. present

26. [CH 14] Dermosphenotic – contact with frontals blocked by intertemporal or dermopterotic:

Friedman & Blom, 2006; Choo, 2011.

0. absent
1. present

27. Intertemporal contacts nasal:

Xu & Gao, 2011; Xu et al., 2014.

0. absent
1. present

28. [CH 64] Number of bones carrying supraorbital canal between dermosphenotic and posterior edge of skull roof. :

Cloutier & Arratia, 2004; Choo, 2011. This character is reformulated from Choo's character 'Dermopterotic: present/absent'. The coding in *Melanecta* (Coates, 1998) has been revised from '0' to '1'. The coding in *Moythomasia nitida* (Jessen, 1968) has been revised from '1' to '0'.

0. at least two (i.e. intertemporal and supratemporal)

1. one (i.e. dermopterotic)

29. [CH 69] Supratemporal – narrow anterolateral flange forming ventral margin of spiracular opening:

Choo, 2011. The coding for *Mimipiscis bartrami* and *M. toombsi* (Gardiner, 1984; Choo, 2011) is revised from ‘0’ to ‘1’. The coding for *Moythomasia durgaringa* (Gardiner, 1984) and *Moy. nitida* (Jessen, 1968) is revised from ‘1’ to ‘0’. The position of the spiracular space in *Stegotrachelus* is uncertain, so this taxon is coded as ‘?’. The posterior and ventral borders of the supratemporal are poorly preserved in *Krasnoyarichthys* (Prokofiev, 2002), so the coding is changed from ‘0’ to ‘?’.

0. absent

1. present

30. [CH 15] Number of paired extrascapulars:

Gardiner & Schaeffer, 1989; Lund et al., 1995; Cloutier & Ahlberg, 1996; Coates, 1998; Lund, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Zhu et al., 2013.

0. one pair

1. two pairs

31. Extrascapular reaches lateral edge of skull roof:

New character. A complete skull roof of *Moythomasia durgaringa* is not figured by Gardiner (1984), but on the basis of his description (Gardiner, 1984: p. 318) it can be inferred that the extrascapular was blocked from reaching the lateral margin of the skull roof by the posterior flange of the supratemporal. This taxon is coded ‘0’. The extrascapular in *Cuneognathus* is incomplete laterally. However, the extensive posterolaterally extension of the supratemporal (Friedman & Blom, 2006: fig. 3) makes it unlikely that the extrascapular would have reached the lateral edge of the skull roof, and as such this character is coded ‘0’. This convention is also followed for *Tegeolepis* (Dunkle, 1964) and *Meemannia* (Zhu et al., 2006).

0. absent
1. present

32. [CH 71] Single median extrascapular:

Dietze, 2000; Cloutier & Arratia, 2004; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014. The coding in *Mimipiscis bartrami*, *M. toombsi* (Gardiner, 1984; Choo, 2011), *Stegotrachelus* (Swartz, 2009), *Cheirolepis canadensis* (Arratia & Cloutier, 1996), *C. schultzei* (Arratia & Cloutier, 2004), *C. trailli* (Pearson & Westoll, 1979), *Donnrosenia* (Long et al., 2008), *Howqualepis* (Long, 1988), Mansfieldiscus (Long, 1988) and *Woodichthys* (Coates, 1998) is revised from ‘0’ to ‘1’. The extrascapulars are not preserved in *Gogosardina* (Choo et al., 2009) and *Melanecta* (Coates, 1998), and the coding for these taxa is revised from ‘0’ to ‘?’. The median extrascapular in *Coccocephalichthys* has an anterior and posterior series, as well as being paired about the midline, and is coded as ‘0’ here.

0. present
1. absent

33. Extrascapulae contact each other at midline:

New character. This character is coded as inapplicable for taxa that possess a median extrascapular, as it is logically impossible for the lateral extrascapulae to meet in the midline. It is unclear whether the extrascapulae met at the midline in *Moythomasia durgaringa* (Gardiner, 1984) or *Cuneognathus* (Friedman & Blom, 2006), so these taxa are coded '?'.

0. absent
1. present

34. [CH 70] Medially-directed branch of sensory canal in extrascapulae:

Choo, 2011. The codings for *Mimipiscis bartrami*, *M. toombsi* (Gardiner, 1984; Choo, 2011), *Osorioichthys* (Taverne, 1997), *Cheirolepis canadensis* (Arratia & Cloutier, 1996), *C. trailli* (Pearson & Westoll, 1979), *Mansfieldiscus* (Long, 1988), *Woodichthys* (Coates, 1998) and *Wendichthys* (Lund & Poplin, 1997) are revised from ‘1’ to ‘0’. Although often figured as present in reconstructions, it is unclear whether these canals were present in *Howqualepis rostridens* (Long, 1988), *Cuneognathus* (Friedman & Blom, 2006), *Donnrosenia* (Long et al., 2008), *Kentuckia hlavini* (Dunkle, 1964), *Limnomis* (Daeschler, 2000), *Stegotrachelus* (Swartz, 2009) and *Krasnoyarichthys* (Prokofiev, 2002), and the coding for these taxa is revised from ‘1’ to ‘?’.

0. present
1. absent

35. Extratemporal:

Cloutier & Ahlberg, 1996; Ahlberg & Johanson, 1998; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu & Ahlberg, 2004; Daeschler et al., 2006; Long et al., 2006; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009.

0. absent

1. present

36. [CH 75] Dermal intracranial joint:

Cloutier & Ahlberg, 1996; Ahlberg & Johanson, 1998; Zhu & Ahlberg, 2004; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Daeschler et al., 2006; Long et al., 2006; Zhu et al., 2006; Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Choo, 2011; Davis et al., 2012; Zhu et al., 2013. Choo's coding for this character appears to be inaccurate, and codes have been changed where appropriate.

0. absent

1. present

37. [CH 60] Suborbital bones contributing to dorsal margin of orbit:

Choo, 2011.

0. absent

1. present

38. [CH 59] Antorbital bone:

Cloutier & Arratia, 2004; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014.

0. absent

1. present

39. [CH 61] Infraorbitals:

Cloutier & Arratia, 2004; Gardiner et al., 2005; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014. Choo's (2011) codes for this character appear reversed. The coding for *Gogosardina* (Choo et al., 2009) is revised from '0' to '?'. The coding for *Limnomis*

(Daeschler, 2000) is revised from '?' to '0'. The coding for *Tegeolepis* (Dunkle & Schaeffer, 1973) is revised from '0' 'to '?'.

0. two
1. more than two

40. [CH 16] Anterior expansion of lacrimal:

Taverne, 1997; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The coding for *Melanecta* (Coates, 1998) is revised from ‘0’ to ‘?’. The coding for *Miguashaia* (Cloutier, 1996) is revised from '1' to '?'.The coding for *Novagonatodus* (Long, 1988; Holland et al., 2007) and *Onychodus* (Andrews et al., 2006) is revised from ‘?’ to ‘1’. The coding for *Tegeolepis* (Dunkle & Schaeffer, 1973) is revised from '1' to '0'. The coding for *Wendichthys* (Lund & Poplin, 1997) is revised from '0' to '1'.

0. absent
1. present

41. [CH 17] Notch in anterior margin of jugal:

Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. Although the jugal of *Moythomasia durgaringa* is only faintly notched in its reconstruction (Gardiner, 1984: fig. 103), the notch is clearly visible on the medial face (Gardiner, 1984: fig. 73). As such the coding is revised from ‘0’ to ‘1’. The coding in *Cuneognathus* (Friedman & Blom, 2006) is revised from’0’ to ‘?’. The coding in *Novagonatodus* (Long, 1988; Holland et al., 2007) is changed from ‘1’ to ‘0’.The coding in *Wendichthys* (Lund & Poplin, 1997) is revised from '1' to '0'.

0. absent

1. present

42. [CH 18] Jugal and maxilla separated by non-canal bearing ossificatons (i.e. anamestic suborbitals):

Taverne, 1997; Schultze & Cumbaa, 2001; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011.

0. absent
1. present

43. Multiple rami of infraorbital canal in jugal:

New character. Multiple branches radiate from the infraorbital canal in the jugal of many Carboniferous actinopterygians.

0. absent
1. present

44. [CH 62] Jugal canal:

Patterson, 1982; Lauder & Liem, 1983; Gardiner, 1984; Cloutier & Arratia, 2004; Brazeau, 2009; Friedman & Brazeau, 2010; Choo, 2011; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015. Choo's (2011) codes may be reversed for this character, but it is unclear. The coding for *Cuneognathus* (Friedman & Blom, 2006), *Kentuckia hlavini*, *Krasnoyarichthys* and *Limnomis* is revised from '1' to ?'. The coding for *Donnrosenia*, *Gogosardina*, *Howqualepis*, *Masnfieldiscus*, *Melanecta*, *Mimipiscis bartrami*, *M. toombsi, Moythomasia durgaringa, Moy. nitida, Novagonatodus, Stegotrachelus* and *Woodichthys* is revisied from '1' to '0'. The coding for *Onychodus* is revised from '0' to '1'. The coding for *Miguashaia* is revised from '-' to '1'.

0. absent

1. present

45. [CH 53] Dermohyal:

Patterson, 1982; Gardiner & Schaeffer, 1989; Lund et al., 1995; Cloutier & Ahlberg, 1996; Coates, 1998; Dietze, 2000; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Lund & Poplin, 2002; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014. This region of the cheek is missing in *Coccocephalichthys* (Poplin, 1974; Poplin & Véran, 1996), and was presumably removed by Watson (1925) when he first described the specimen. It is unclear from the surviving cast whether a dermohyal and/or accessory operculum were present, and as such this taxon is coded as '?'. The presence of a dermohyal is only inferred in *Donnrosenia* (Long et al., 2008), and the coding for this taxon is revised from '1' to '?'.

0. absent
1. present

46. Head of dermohyal projects above dorsal margin of operculum:

New character. The dermohyal is not preserved in *Melanecta* (Coates, 1998), but it is clear from the surrounding bones that it would not have projected above the dorsal surface of the operculum.

0. absent
1. present

47. Dermohyal:

Gardiner et al., 2005; Coates, 1999; Xu & Gao, 2011; Xu et al., 2014. The relevant part of the cheek is not preserved in *Donnrosenia* (Long et al., 2008), so the coding for this taxon is changed from '1' to '?'.

0. fused to hyomandibular
1. separate from hyomandibular

48. [CH 58] Quadratojugal as distinct ossification:

Lund et al., 1995; Cloutier & Ahlberg, 1996; Dietze, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Cloutier & Arratia, 2004; Long et al., 2008; Swartz, 2009; Choo, 2011.The presence of a quadratojugal in *Stegotrachelus* (Swartz, 2009), *Moythomasia nitida* (Jessen, 1968) and *Limnomis* (Daeschler, 2000) is uncertain, and the coding for these taxa is revised from ‘1’ to ‘?’. The coding in *Cheirolepis canadensis* (Arratia & Cloutier, 1996) and *Wendichthys* (Lund & Poplin, 1997) is revised from ‘1’ to ‘0’.

0. present
1. absent

49. Complete enclosure of spiracle by bones bearing otic and infraorbital canals:

Friedman, 2007; Zhu et al., 2009. The position of the spiracular space in *Stegotrachelus* (Swartz, 2009) is uncertain, so this taxon is coded as '?'.

0. absent
1. present

50. [CH 19] Accessory operculum:

Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009. This region of the cheek was removed in

Coccocephalichthys (Poplin, 1974; Poplin & Véran, 1996), presumably by Watson (1925) when he first described the specimen. It is unclear from the surviving cast whether a dermohyal and/or accessory operculum were present, and as such this taxon is coded as '?'.

0. absent
1. present

51. [CH 67] Operculum - relative size :

Lund et al., 1995; Lund, 2000; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Long et al., 2008; Swartz, 2009; Choo, 2011. The coding in *Osorioichthys* (Taverne, 1997), *Mansfieldiscus* (Long, 1988), *Melanecta* (Coates, 1988), *Moythomasia nitida* (Jessen, 1968), *Novagonatodus* (Long, 1988; Holland et al., 2007), *Woodichthys* (Coates, 1998), *Cuneognathus* (Friedman & Blom, 1006) and *Krasnoyarichthys* (Prokofiev, 2002) is revised from '0' to '1'. The coding in *Howqualepis* (Long, 1988), *Donnrosenia* (Long et al., 2008) and *Limnomis* (Daeschler, 2000) is revised from '1' to '0'.

0. at least twice as high as suboperculum
1. less than twice as high as suboperculum

52. [CH 68] Anterodorsal process of suboperculum:

Long et al., 2008; Choo, 2011. The coding in *Howqualepis* (Long, 1988) and *Donnrosenia* (Long et al., 2008) is changed from '0' to '1'. The anterodorsal process is described as well developed in *Gogosardina* (Choo et al., 2009), and the coding for this taxon is revised from '?' to '1'.

0. absent
1. present

53. [CH 72] Branchiostegal rays - dorsal-most in series:

Lund et al., 1995; Cloutier & Arratia, 2004; Choo, 2011. The coding for *Mimipiscis bartrami, M. toombsi* (Gardiner, 1984, Choo, 2011), *Stegotrachelus* (Swartz, 2009), *Cheirolepis canadensis* (Arratia & Cloutier, 1996), *C. schulzei* (Arratia & Cloutier, 2004), *C. trailli* (Pearson & Westoll, 1979) *Donnrosenia* (Long et al., 2008), *Gogosardina* (Choo et al., 2009), *Howqualepis rostridens* (Long, 1988), *Novagonatodus* (Long, 1988; Holland et al., 2007), Mansfieldiscus (Long, 1988) and *Woodichthys* (Coates, 1998) is revised from '1' to '0'. The coding for *Cuneognathus* (Friedman & Blom, 2006), *Kentuckia hlavini* (Dunkle, 1964) and *Melanecta* (Coates, 1998) is revised from '1' to '?'. The coding for *Krasnoyarichthys* (Prokofiev, 2002) is changed from '?' to '1'.

0. of similar depth to adjacent branchiostegal ray
1. deeper than adjacent branchiostegal ray

54. [CH 20] Lateral gulars:

Gardiner & Schaeffer, 1989; Cloutier & Ahlberg, 1996; Taverne, 1997; Lund & Poplin, 1997; Coates, 1999; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Brazeau, 2009; Xu & Gao, 2011; Davis et al., 2012; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015. The coding for *Mansfieldiscus* (Long, 1988) is revised from '?' to '1'. The condition in *Boreosomus* (Nielsen, 1942) is unique: instead of lateral gulars flanking a median gular, there appears to be a second median gular. This may well represent a fusion of the two, longer lateral gulars, is coded as such.

0. extending most of the length of the lower jaw
1. restricted to the anterior third of the lower jaw (no longer than the width of

three branchiostegals)

55. **Median gular:**

Lund et al., 1995; Cloutier & Ahlberg, 1996; Coates, 1999; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001: Lund & Poplin, 2002; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015. Pearson & Westoll (1979: p. 365) state that a median gular is not known in *Cheirolepis canadensis*. Although a median gular is reconstructed by Cloutier & Arratia (1996: fig. 7), this bone is not present in any specimen photos and is not mentioned in the text. As such, this taxon is coded as '?'.

0. absent
1. present

56. **Relative length of median gular:**

New character. The condition in *Boreosomus* (Nielsen, 1942) is unique: instead of lateral gulars flanking a median gular, there appears to be a second median gular. This may well represent a fusion of the two, longer lateral gulars, and is coded as such.

0. shorter than lateral gulars
1. same length as or longer than lateral gulars

57. **Maxilla:**

Zhu & Yu, 2002; Friedman, 2007; Xu et al., 2014.

0. absent
1. present

58. Expanded dorsal lamina of maxilla:

Lund et al., 1995; Lund, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

59. [CH 63] Maxilla - posteroventral overlap of lower jaw:

Cloutier & Arratia, 2004; Choo, 2011.

0. posteroventral margin of maxilla largely straight with minimal overlap of lower jaw
1. posteroventral extension of maxilla with pronounced overlap of lower jaw

60. Contribution by maxilla to posterior margin of cheek:

Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

61. Sensory canal/pit line associated with maxilla:

Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013;

0. absent
1. present

62. Number of cheek bones bearing pre-opercular canal posterior to jugal:

Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013. .

0. one
1. two

63. [CH 21] Course of mandibular canal:

Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011.

0. traces ventral margin of jaw along entire length
1. arches dorsally in anterior half of jaw

64. Mandibular canal reaches anterior margin of mandible:

New character. The mandibular canal is reconstructed as reaching the anterior margin of the dentary in *Cuneognathus* (Friedman & Blom, 2006), but specimen photos appear to show it leaving through the dorsal margin. As such, this taxon is coded '1' for this character.

0. present
1. absent

65. [CH 74] Mandibular canal:

Patterson, 1982; Cloutier & Ahlberg, 1996; Coates, 1998; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Choo, 2011; Zhu et al., 2013.

0. primarily carried by infradentaries
1. primarily carried by dentary

66. Relative length of dentary:

Ahlberg & Johanson, 1998; Zhu et al., 2001; Zhu & Yu, 2002; Zhu & Ahlberg, 2004; Friedman, 2007; Zhu et al., 2009.

0. long (constitutes most of the length of the lower jaw)
1. short (constitutes less than half of jaw length)

67. [CH 22] Dentary with conspicuously reflexed distal tip:

Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The anterior extent of the dentary is not preserved in *Limnomis* (Daeschler, 2000), so the coding for this taxon is revised from '1' to '?'.

0. absent
1. present

68. [CH 24] Enlarged series of parasymphysial teeth on dentary:

Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. Choo's (2011) codes for this character appear reversed. The anterior extent of the dentary is not preserved in *Limnomis* (Daeschler, 2000), so the coding for this taxon is revised from '1' to '?'.

0. absent
1. present

69. [CH 73] Facet for parasymphysial tooth-whorl on anterior dentary:

Choo, 2011. The anterior extent of the dentary is not preserved in *Limnomis* (Daeschler, 2000), so the coding for this taxon is revised from '1' to '?'.

0. present
1. absent

70. **Teeth of outer dental arcade:**

Friedman, 2007. Long (1988) states that the maxilla of *Melanecta* bears large teeth interspersed with smaller teeth, but it is unclear how these teeth are arranged. As such, this taxon is coded '?'.

0. several rows of disorganized teeth
1. two rows, with large teeth lingually and small teeth labially
2. single row of teeth

71. **[CH 25] Acrodin caps on teeth:**

Patterson, 1982; Gardiner, 1984; Maisey, 1986; Gardiner & Schaeffer, 1989; Cloutier & Ahlberg, 1996; Taverne, 1997; Coates, 1999; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Zhu et al., 2009; Friedman & Brazeau, 2010; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015. The presence of acrodin in *Limnomis* (Daeschler, 2000), *Mansfieldiscus* (Long, 1988), *Melanecta* (Coates, 1998) and *Woodichthys* (Coates, 1998) is uncertain, and the coding for these taxa is revised from '1' to '?'.

0. absent
1. present

72. **[CH 26] Remodeled porous ganoine on lower jaw:**

Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. Although the dermal ornament is poorly preserved in Osorioichthys, faint ridges are visible on the dentary (Taverne, 1997: p.67; pers. obs. S.G.). As such, this character is coded as '0'.

0. absent

1. present

73. [CH 27] Ossification of mentomeckelian region:

Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014.

0. present
1. absent

74. Coronoids (sensu stricto, excluding parasymphysial tooth whorl or anterior coronoid):

Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009.

0. present
1. absent

75. Number of coronoids*:

Ahlberg & Clack, 1998; Daeschler et al., 2006; Long et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015. A single specimen of *Pteronisculus stensioi* has at least five or six coronoids anterior to the prearticular region. However, these appear to correspond to the three coronoids present in most specimens, so the taxon is coded here as '2'. Two coronoids are reported in *Boreosomus* (Nielsen, 1942).

0. five
1. four
2. three
3. two

76. **Posterior coronoid:**

0. morphologically similar to anterior coronoids
1. expanded

77. **[CH 23] Number of infradentaries*:**

Friedman & Blom, 2006; Friedman, 2007; Long et al., 2008; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014. The coding for *Kentuckia hlavini* (Dunkle, 1964) and *Guiyu* (Zhu et al., 2009) is revised from '0' to '?'. The coding for *Limnomis* (Daeschler, 2000) and *Stegotrachelus* (Swartz, 2009) is revised from '1' to '?'. The coding in *Mansfieldiscus* (Long, 1988) is revised from '0' to '2'.

0. more than two
1. two (angular and surangular)
2. one (angular only)

78. **Expanded crest on posterior infradentary:**

Zhu & Yu, 2002; Friedman, 2007.

0. absent
1. present

79. **Retroarticular process:**

Friedman, 2007.

0. present
1. absent

80. **Articular area for symplectic:**

Friedman, 2007.

0. present
1. absent

81. Number of dermopalatines:

Friedman, 2007.

0. multiple
1. single

82. Basipterygoid fenestra :

Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

83. Fenestra ventrolateralis:

Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013;

0. absent
1. present

84. Palatal opening surrounded by premaxilla, maxilla, dermopalatine and vomer (choana):

Zhu & Yu, 2002; Friedman, 2007. Character can only be coded in taxa that possess all of these bones.

0. absent

1. present

85. Internasal cavity:

Ahlberg & Johanson, 1998; Zhu & Yu, 2002; Zhu & Ahlberg, 2004; Daeschler et al., 2006; Long et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

86. Interorbital septum:

Friedman, 2007; Zhu et al., 2009; Brazeau, 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015. *Cheirolepis trailli* is coded '0' (Giles et al., in review).

0. broad
1. narrow

87. Pronounced median anterior crista on dorsal surface of braincase:

New character. Carboniferous and younger actinopterygians such as *Lawrenciella* (Hamel & Poplin, 2008) have a median crista anterior to the anterior dorsal fontanelle upon which the skull roof sits.

0. absent
1. present

88. Expanded anterior dorsal fontanelle:

New character. The anterior dorsal fontanelle of many Carboniferous and younger actinopterygians is greatly expanded, in contrast to the smaller fontanelle of

Devonian taxa such as *Mimipiscis* (Gardiner, 1984).

0. absent
1. present

89. Endoskeletal intracranial joint:

Cloutier & Ahlberg, 1996; Ahlberg & Johanson, 1998; Zhu & Ahlberg, 2004; Zhu et al., 2001; Zhu & Yu, 2002; Daeschler et al., 2006; Long et al., 2006; Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Davis et al., 2013; Zhu et al., 2013; Giles et al., 2015. *Cheirolepis trailli* is coded '0' (Giles et al., in review).

0. absent
1. present

90. Eye stalk or unfinished area for similar structure:

Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015. This character is coded as absent for taxa that possess a large interorbital fenestra (e.g. *Pteronisculus, Coccocephalichthys, Kentuckia deani*), as, if present, the eyestalk area would be visible posterior to the opening for the optic nerve.

0. absent
1. present

91. Roof of posterior myodome perforated by palatine branch of facial nerve (VII):

Coates, 1999.

0. absent
1. present

92. Foramen for abducens nerve (VI) dorsally positioned (level with optic foramen (II)):

Coates, 1999.

0. absent
1. present

93. Anterodorsal myodome:

Coates, 1999; Xu & Gao, 2011; Xu et al., 2014.

0. paired
1. single

94. Canal for pituitary vein:

Coates, 1999; Xu et al., 2014.

0. present
1. enlarged
2. obliterated

95. Pituitary vein foramen:

Ahlberg & Johanson, 1998; Zhu & Ahlberg, 2004; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. dorsal to basipterygoid process
1. anterior to basipterygoid process
2. posterior to basipterygoid process

96. Basicranial fenestra:

Ahlberg & Johanson, 1998; Zhu et al., 2001; Zhu & Yu, 2002; Zhu & Ahlberg, 2004; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015.

Cheirolepis trailli is coded '0' (Giles et al., in review).

0. absent
1. present

97. Spiracular groove on lateral commissure:

Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

98. Spiracle housed in:

Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates, 1999; Gardiner et al., 2005; Xu & Gao, 2011; Xu et al., 2014. Taxa that lack a groove on the lateral commissure are coded as inapplicable for this character. Following Xu & Gao (2014), the spiracle in *Moythomasia durgaringa* is coded '1'. *Cheirolepis trailli* is coded '0' (Giles et al., in review).

0. groove
1. canal

99. Spiracular grooves extending onto basicranial surface:

Ahlberg & Johanson, 1998; Zhu & Ahlberg, 2004; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Daeschler et al., 2006; Long et al., 2006; Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Brazeau & Friedman, 2014; Giles et al., 2015.

Cheirolepis trailli is coded '1' (Giles et al., in review).

0. absent

1. present

100. Basipterygoid process:

Gardiner et al., 2005; Xu & Gao, 2011; Xu et al., 2014.

0. present

1. absent

101. Basipterygoid process with vertically oriented component:

Ahlberg & Johanson, 1998; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu & Ahlberg, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. absent

1. present

102. Dermal component to basipterygoid process:

Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates, 1999;

0. absent

1. present

103. Prespiracular fossa:

Poplin, 1984. *Cheirolepis trailli* is coded '0' (Giles et al., in review).

0. absent

1. present

104. Fossa bridgei:

Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates, 1999; Xu & Gao, 2011; Xu et al., 2014. Cheirolepis trailli is coded '0' (Giles et al., in review).

0. absent
1. present

105. Posttemporal fossae:

Zhu & Yu, 2002; Friedman, 2007.

0. absent
1. present

106. Vestibular fontanelle:

Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Brazeau & Friedman, 2014; Giles et al., 2015. *Cheirolepis trailli* is coded '1' (Giles et al., in review).

0. absent
1. present

107. Ventral cranial fissure and vestibular fontanelle:

Coates, 1999. We follow Coates (1999) in coding *Howqualepis* as '0' on the basis of Long 1988 fig. 16 and AMF65495 (pers. obs. S.G.), rather than the braincase reconstruction (Long, 1988: fig. 18). *Cheirolepis trailli* is coded '0' (Giles et al., in review).

0. separated by bridge of bone
1. conflent

108. Accessory fenestration in otic capsule :

Friedman, 2007; Zhu et al., 2009. *Cheirolepis trailli* is coded '0' (Giles et al., in review).

0. absent
1. present

109. Otoccipital fissure:

Friedman, 2007; Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015. *Cheirolepis trailli* is coded '1' (Giles et al., in review).

0. absent
1. present

110. Median projection overhanging posterior part of posterior dorsal fontanelle:

New character. Variable in *Boreosomus*: the posterior dorsal fontanelle is closed in the specimen figured in Nielsen (1942: plate 25F), but developed in the specimen figured in plate 28. This taxon is coded ‘0/1’ to reflect this polymorphism.

0. absent
1. present

111. Median projection overhanging anterior part of posterior dorsal fontanelle:

New character. This projection is somewhat reduced in *Pteronisculus* (Nielsen, 1942), but is coded '1' here. Variable in *Boreosomus*: the posterior dorsal fontanelle is closed in the specimen figured in Nielsen 1942 plate 25F, but developed in the specimen figured in plate 28. This taxon is coded ‘0/1’ to reflect this polymorphism. *Cheirolepis trailli* is coded '0' (Giles et al., in review).

0. absent

1. present

112. Dorsal aorta*:

Coates & Sequeira, 1998; Coates & Sequeira, 2001a, b; Coates, 1999; Friedman, 2007; Zhu et al., 2009; Friedman & Brazeau, 2010; Zhu et al., 2013; Giles et al., 2015. This character is coded as inapplicable in taxa that lack a canal for the dorsal aorta. *Cheirolepis trailli* is coded '0' (Giles et al., in review). The aortic canal of *Moythomasia* is not figured by Gardiner (1984), but a clear posterior notch in the aortic canal can be seen in Long & Trinajstic (2010:fig 5b). The neurocranium of *Gogosardina* is not yet described, but this character can be coded on the basis of Choo et al. (2009: fig. 9).

0. open in groove
1. notched posteriorly
2. enclosed in canal

113. Dorsal aorta pierced by canal/s for exit of eff.a.2:

New character. In *Mimipiscis bartrami* and *M. toombsi*, a groove for one of the efferent branchial arteries branches off from the lateral dorsal aorta immediately before the articular area for the first infrapharyngobranchial. However, it is uncertain which, so both taxa coded as '?' for these characters. The neurocranium of *Gogosardina* is not yet described, but this character can be coded on the basis of Choo et al. (2009: fig. 9).

0. absent
1. present

114. Dorsal aorta pierced by canal/s for exit of eff.a.1:

New character. In *Mimipiscis bartrami* and *M. toombsi*, a groove for one of the efferent branchial arteries branches off from the lateral dorsal aorta immediately before the articular area for the first infrapharyngobranchial. However, it is uncertain which, so both taxa coded as '?' for these characters. The neurocranium of *Gogosardina* is not yet described, but this character can be coded on the basis of Choo et al. (2009: fig. 9).

0. absent
1. present

115. Bifurcation of dorsal aorta:

Coates & Sequeira, 1998; Coates & Sequeira, 2001a, b; Coates, 1999; Friedman, 2007; Zhu et al., 2009; Friedman & Brazeau, 2010; Zhu et al., 2013; Giles et al., 2015.

0. posterior to occiput
1. anterior to occiput

116. Birfurcation of dorsal aorta into lateral dorsal aortae:

Coates, 1999. This character is coded as inapplicable in taxa that lack a canal for the dorsal aorta. In *Mimipiscis toombsi*, the bifurcation point of the dorsal aorta can be open (Giles & Friedman, 2014: fig. 2) or closed (Gardiner 1984: fig. 15). This taxon is coded '0/1' to reflect this polymorphism. The aortic canal of *Moythomasia* is not figured by Gardiner (1984), but the bifucation into the lateral dorsal aortae can be seen in Long & Trinajstic (2010:fig 5b).

0. open
1. enclosed in canal

117. **Parasphenoid:**

Gardiner, 1984; Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

118. **Parasphenoid:**

Coates, 1999; Zhu & Yu, 2002; Gardiner et al., 2005; Friedman, 2007, Xu & Gao, 2011; Xu et al., 2014. *Cheirolepis trailli* is coded '0' (Giles et al., in review).

0. terminates at/anterior to ventral otic fissure
1. extends across ventral otic fissure

119. **Parasphenoid protruding forwards into ethmoid region:**

Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013.

0. absent
1. present

120. **[CH 28] Ascending process of the parasphenoid:**

Patterson, 1982; Coates, 1999; Dietze, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Zhu et al., 2006; Zhu et al., 2009; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015. The coding in *Wendichthys* (Lund & Poplin, 1997) is revised from '?' to '1'.

0. absent
1. present

121. [CH 29] Parasphenoid with multifid anterior margin:

Friedman & Blom, 2006; Friedman, 2007; Zhu et al., 2009; Choo, 2011; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

122. Parasphenoid denticle field:

Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013.

0. terminates at, or anterior to, level of internal carotid arteries
1. extends posterior to foramina for internal carotid arteries

123. Denticulated field of parasphenoid:

Ahlberg & Johanson, 1998; Zhu & Ahlberg, 2004; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Daeschler et al., 2006; Zhu et al., 2006; Long et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013.

0. without spiracular groove
1. with spiracular groove

124. Buccohypophyseal canal pierces parasphenoid:

New character. The buccohypophyseal canal typically enters the dorsal surface of the parasphenoid, but whether it exits via the posterior surface is more variable, and this distribution is captured by this character.

0. present
1. absent

125. Anterolaterally divergent olfactory tracts:

Coates, 1999; Giles & Friedman, 2014. *Cheirolepis trailli* is coded '1' (Giles et al., in review).

0. absent
1. present

126. Elongate olfactory tract(s:

Brazeau, 2009; Friedman & Brazeau 2010; Davis et al., 2012; Zhu et al., 2013; Brazeau & Friedman, 2014; Giles & Friedman, 2014; Giles et al., 2015. *Cheirolepis trailli* is coded '0' (Giles et al., in review). The olfactory tracts of *Osorioichthys* are elongate (pers. obs. unpubl. scan data S.G.).

0. absent
1. present

127. Olfactory nerves carried in a single tract:

Coates, 1999; Giles & Friedman, 2014. *Cheirolepis trailli* is coded '1' (Giles et al., in review). The olfactory nerves are carried in separate tracts in *Osorioichthys* (pers. obs. unpubl. scan data S.G.).

0. present
1. absent

128. Hypophyseal chamber:

Coates, 1999; Xu & Gao, 2011; Xu et al., 2014.

0. projects posteroventrally
1. projects ventrally or anteroventrally

129. Optic lobes:

Giles & Friedman, 2014.

0. narrower than cerebellum
1. same width or wider than cerebellum

130. Optic tectum divided into bilateral halves:

Coates, 1999.

0. absent
1. present

131. Cerebellar corpus:

New character. The region posterior to the cerebellar auricles in *Lawrenciella* was considered to be the area octavolateralis by Hamel & Poplin (2008). However, we interpret it as the corpus cerebellum (see Giles & Friedman, 2014), and this taxon is coded '1'.

0. absent
1. present

132. Horizontal semicircular canal:

Davis et al., 2012; Zhu et al., 2013; Giles & Friedman, 2014; Giles et al., 2015.

0. joins vestibular region dorsal to ampulla for the posterior semicircular canal
1. joins vestibular region level with ampulla for the posterior semicircular canal

133. Junction between ampulla of posterior semicircular canal and cranial cavity:

New character. In certain primitive actinopterygians, such as *Mimipiscis* (Giles and Friedman, 2014), a short length of canal lies between the posterior ampulla and the remainder of the labyrinth.

0. separated by short length of canal

1. confluent

134. Crus commune of anterior and posterior semicircular canal:

Giles & Friedman, 2014.

0. dorsal to endocranial roof

1. ventral to endocranial roof

135. Lateral cranial canal:

Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Cloutier & Arratia, 2004; Gardiner et al., 2005; Zhu et al., 2006; Zhu et al., 2009; Zhu et al., 2013; Giles & Friedman, 2014; Xu et al., 2014; Giles et al., 2015. The presence of a lateral cranial canal in *Ligulalepis*, *Psarolepis* and *Meemannia* is uncertain. The fossae identified by Zhu et al. (2010) occupy a rather anterior position compared to the lateral cranial canal in actinopterygians, being situated lateral to the sacculus rather than posterior to it. As such, we regard the identity of these features as suspect, and these taxa are coded '?'.

0. absent

1. present

136. Ceratohyal:

Gardiner et al., 2005; Xu & Gao, 2011; Xu et al., 2014.

0. single ossification

1. two ossifications

137. Anterior ossification of ceratohyal:

Coates, 1999.

0. subcylindrical
1. hourglass-shaped

138. Anterior ceratohyal:

Coates, 1999. The groove for the afferent hyoidean artery in the ceratohyal of *Gogosardina* is visible in Choo et al. (2009: fig 6).

0. no groove
1. groove for afferent hyoidean artery

139. Double headed hyomandibular:

Cloutier & Ahlberg, 1996; Zhu & Schultze, 2001; Schultze & Cumbaa, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Friedman & Brazeau, 2010; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

140. Perforate hyomandibula:

Friedman, 2007; Zhu et al., 2009; Friedman & Brazeau, 2010; Xu & Gao, 2011; Zhu et al., 2013; Brazeau & Friedman, 2014; Xu et al., 2014. Although Long (1988: p.24) mentions the presence of a depression for the hyomandibular nerve in *Howqualepis*, it is unclear whether this perforated the hyomandibula. This taxon is conservatively coded as '?'. *Cheirolepis trailli* is coded '0' (Giles et al., in review). Following Friedman (2007), we code *Onychodus* as '0'.

0. absent

1. present

141. Opercular process on hyomandibula:

0. absent
1. present

142. Endoskeletal urohyal:

Friedman, 2007; Friedman & Brazeau, 2010; Giles et al., 2015.

0. absent
1. present

143. Basihyal:

Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

144. Interhyal:

Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

145. Hypohyal:

Friedman & Brazeau, 2010; Brazeau & Friedman, 2014; Giles et al., 2015.

0. absent
1. present

146. Gill arches:

Giles et al., 2015.

0. largely restricted to area under braincase
1. extend far posterior to braincase

147. [CH 30 in part] Enameloid on dermal bones and scales:

Characters 147-150 form part of an atomisation of the compound characters 'ganoine' (typically defined as a single or multilayer enamel covering) and 'cosmine' (typically defined as a single layer of enamel with a well defined pore canal network) (e.g. Cloutier & Ahlberg, 1996; Ahlberg & Johanson, 1998; Zhu & Ahlberg, 2004; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Daeschler et al., 2006; Long et al., 2006; Zhu et al., 2006; Zhu et al., 2009; Davis et al., 2012; Zhu et al., 2013). A similar approach to atomization was taken by Friedman (2007), Brazeau & Friedman (2010) and Giles et al. (2015). As detailed histological investigations have not been carried out for the majority of early actinopterygians (rather, they have simply been described as being covered in/bearing ridges of ganoine), many of these characters cannot be coded for a number of taxa. Histological data are only known for specimens of *Mimipiscis toombsi* (Gardiner, 1984; Choo, 2011), so this and the following characters are coded '?' for *Mimipiscis bartrami* (Gardiner, 1984; Choo, 2011).

0. absent
1. present

148. Extensive pore-canal network:

See notes above for c. 147.

0. absent

1. present

149. [CH 30 in part] Enamel:

See notes above for c. 147.

0. single-layered
1. multi-layered

150. [CH 30 in part] Enamel layers:

See notes above for c. 147.

0. applied directly to one another
1. separated by layers of dentine

151. [CH 34] Scales:

Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011.

0. micromeric
1. macromeric

152. [CH 32 in part] Scales with 'peg and socket articulation':

Maisey, 1986; Gardiner & Schaeffer, 1989; Cloutier & Ahlberg, 1996; Coates, 1999; Dietze, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Friedman, 2007; Long et al., 2008; Brazeau, 2009; Swartz, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Xu & Gao, 2011; Choo, 2011; Davis et al., 2012; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015. This character is coded only for taxa that possess rhombic scales. The coding for *Kentuckia hlavini* (Dunkle, 1964) is revised from '1' to '0', and the coding for

Limnomis (Daeschler, 2000) from ‘0’ to ‘1’. The coding for *Cheirolepis trailli* (Giles et al., in review) is revised from ‘0’ to ‘1’.

0. absent
1. present

153. [CH 32 in part] Peg on rhomboid scale:

Patterson, 1982; Cloutier & Ahlberg, 1996; Dietze, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001: Zhu & Yu, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009. Although peg-and-socket articulation of is present between the scales of *Limnomis* (Daeschler, 2000), the nature of the peg is not described. As such, this taxon is conservatively coded '?'. The coding for *Cheirolepis trailli* (Giles et al., in review) is revised from ‘?’ to ‘0’.

0. narrow
1. broad

154. [CH 33] Anterodorsal process on scale:

Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Zhu et al., 2013; Giles et al., 2015. The coding for *Limnomis* (Daeschler, 2000) and *Cheirolepis trailli* (Giles et al., in review) is revised from '0' to '1'.

0. absent
1. present

155. [CH 35] Scales with well developed pores on surface:

Friedman & Blom 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. Scale crowns of *Cheirolepis schultzei* (Arratia & Cloutier, 2004) are not preserved, so this and the following scale characters are coded as '?'. The coding for *Donnrosenia* (Long et al., 2008) is revised from '1' to '0'. Scales from the posterior half of the flank in *Wendichthys* bear pores on the enamel surface, whereas those from the anterior part of the flank lack these pores (Lund & Poplin, 1997: fig. 6). This taxon is scored '1'.

0. absent
1. present

156. [CH 36] Curved ridges along anterior margin of scales:

Friedman & Blom 2006; Long et al., 2008; Swartz, 2009; Choo, 2011.

0. absent
1. present

157. [CH 76] Scales – anastomosing linear ornament:

Choo, 2011. This character was proposed by Choo (2011), but no character description was provided. This character is interpreted here are referring to branching and anastomosing ridges on the scale surface, and taxa are recoded accordingly. Ridges often bifurcate on the scales of *Mimipiscis toombsi* (e.g. Gardiner 1984, fig. 140b) and *M. bartrami* (e.g. Choo, 2011, fig. 17a), and as such the coding for these taxa is revised from ‘0’ to ‘1’. Gardiner (1984: p. 387, fig. 141) describes the scale ornament of *Moythomasia durgaringa* as 'ridges of ganoine which branch and anastomose', and the coding is therefore revised from ‘0’ to ‘1’. The coding for *Mansfieldiscus* (Long, 1988) is also changed from ‘0’ to ‘1’. The coding for *Krasnoyarichthys* (Prokofiev, 2002) is revised from '?' to '1'. The coding for *Cheirolepis canadensis* (Arratia & Cloutier, 1996), C. trailli (Pearson & Westoll, 1979) and *Donnrosenia* (Long et al., 2008) is revised from '1' to '0'.

0. absent
1. present

158. Lepidotrichia:

Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Brazeau & Friedman, 2014; Giles et al., 2015.

0. absent
1. present

159. [CH 37] Fringing fulcra:

Patterson, 1982; Gardiner & Schaeffer, 1989; Coates, 1999; Dietze, 2000; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014.

0. absent
1. present

160. Dorsal margin of cleithrum:

Cloutier & Ahlberg, 1996; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Giles et al., 2015.

0. pointed
1. broad and rounded

161. Anocleithrum:

Gardiner & Schaeffer, 1989; Lund et al., 1995; Cloutier & Ahlberg, 1996; Dietze, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013.

0. bone developed as postcleithrum
1. bone developed as anocleithrum sensu stricto
2. bone absent

162. [CH 39] Presupracleithrum:

Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Lund & Poplin, 2002; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014. Presence of a presupracleithrum is only inferred in *Donnrosenia* (Long et al., 2008), *Gogosardina* (Choo et al., 2009) and *Kentuckia hlavini* (Dunkle, 1964), and the coding for these taxa is revised from ‘1’ to ‘?’. Similarly, absence is inferred in *Krasnoyarichthys* (Prokofiev, 2002) and *Novagonatodus* (Long, 1988; Holland et al., 2007), and the coding is thus changed from '0' to '?'. An elongate bone termed the 'anocleithrum' is variably present in *Wendichthys* (Lund & Poplin, 1997) in the position occupied by the presupracleithrum in other taxa. We regard this as a positional homologue, and code the taxon '0/1' to reflect this polymorphism. Coded as '?' in *C. trailli* following arguments in Friedman & Blom (2006). The coding is revised to '0' in *Osorioichthys* (Taverne, 1997).

0. absent
1. present

163. Perforate propterygium:

Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Rosen, 1989; Taverne, 1997; Coates, 1999; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Xu & Gao, 2011; Davis et al., 2012; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015.

0. absent
1. present

164. [CH 41] Anterior rays embrace propterygium:

Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates, 1999; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu & Gao, 2011. The radials are only described for *Mimipiscis toombsi*, so the coding for this character is revised from '1' to '?' for *M. bartrami* (Choo, 2011). The radials are not described in *Gogosardina* (Choo et al., 2009), so the coding is changed from '1' to '?'.

0. absent
1. present

165. [CH 42] Metapterygium elongated relative to preceding radials:

Taverne, 1997; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Xu & Gao, 2011; Xu et al., 2014. The endoskeletal shoulder girdle is only described for *Mimipiscis toombsi*, so the coding for this character is revised to '?' for *M. bartrami* (Gardiner, 1984; Choo, 2011). The metapterygium is not described in *Gogosardina*

(Choo et al., 2009), *Howqualepis* (Long, 1988) or *Moythomasia durgaringa* (Gardiner, 1984), so the coding is changed from ‘1’ to ‘?’. Although Swartz (2009) describes a series of endoskeletal radials in *Stegotrachelus*, the elements figured in fig. 17 have a scale-like morphology and appear to be made of dermal bone. As such, the coding in this taxon is revised from ‘1’ to ‘?’. The coding in *Cheirolepis trailli* is revised from ‘0’ to ‘1’ (Giles et al., in review).

0. absent
1. present

166. Pectoral fin radials:

Zhu & Yu, 2002; Friedman, 2007. Two series of pectoral fin radials are described (but not figured) for *Cheirolepis candensis* (Arratia & Cloutier, 2004). Although we consider this arrangement to be unlikely, for now this taxon is coded '1'. Although Swartz (2009) describes a series of endoskeletal radials in *Stegotrachelus*, the elements figured in fig. 17 have a scale-like morphology and appear to be made of dermal bone. As such, this taxon is coded '?'.

0. unjointed
1. jointed

167. [CH 40] Triradiate scapulocoracoid:

Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014. The endoskeletal shoulder girdle is only described for *Mimipiscis toombsi*, so the coding for this character is revised from '?' for *M. bartrami* (Gardiner, 1984; Choo, 2011). The precise morphology of the scapulocoracoid is not known for *Cheirolepis canadensis* (Arratia & Cloutier, 1996) or *Gogosardina* (Choo et al., 2009), and as such the coding for these taxa is changed from ‘0’ to ‘?’. *Cheirolepis trailli* is coded ‘0’ (Giles et al., in review).

0. absent
1. present

168. [CH 43] Pectoral fin endoskeleton:

Taverne, 1997; Coates, 1999; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Xu & Gao, 2011; Xu et al., 2014. The pectoral fin of *Cuneognathus* (Friedman & Blom, 2006) and *Kentuckia hlavini* (Dunkle, 1964) is unknown, and so the coding is revised from ‘1’ to ‘?’.

0. extends far beyond body wall (fins lobate)
1. barely extends beyond body wall (fins not lobate)

169. Fin articulation:

Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Friedman & Brazeau, 2010; Zhu et al., 2013; Giles et al., 2015.

0. monobasal
1. polybasal

170. Shape of pectoral fin:

0. [leaf-like]
1. (not leaf-like)

171. [CH 44] Pectoral fin-ray segmentation*:

Coates, 1999; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014. The pectoral fin in *Kentuckia hlavini* (Dunkle, 1964) is not preserved, so the coding for this taxon is revised from ‘1’ to ‘?’. The coding for *Osorioichthys* (Taverne, 1997) is revised from '0' to '1'. The segmentation of the pectoral fin is not described for *Limnomis* (Daeschler, 2000), so the coding for this taxon is revised from '0' to '?'.

0. roughly even segmentation to fin base
1. proximal segments elongate with terminal segmentation
2. no significant segmentation on pectoral fin

172. Paired fin spines:

Zhu et al., 2001; Zhu & Yu, 2002; Friedman, 2007; Zhu et al., 2009; Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. absent
1. present

173. [CH 38] Pelvic fins:

Friedman & Blom, 2006; Friedman, 2007; Brazeau, 2009; Choo, 2011; Davis et al., 2012; Zhu et al., 2013; Brazeau & Friedman, 2014; Giles et al., 2015. The pelvic fin is not figured or described for *Moythomasia durgaringa* (Gardiner, 1984), so the coding for this taxon is changed from '1' to '?'.

0. absent
1. present

174. [CH 45] Pelvic fin insertion:

Gardiner & Schaeffer, 1989; Coates, 1998; Coates, 1999; Lund, 2000; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006;

Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Xu et al., 2014. The pelvic fin is incomplete in *Novagonatodus* (Long, 1988; Holland et al., 2007), so this taxon is coded '?'.

0. shorter than fin depth (short based)
1. longer than fin depth (long based)

175. [CH 46] Epichordal lobe of caudal fin:

Patterson, 1982; Cloutier & Ahlberg, 1996; Coates, 1999; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The caudal fin is not figured or described for *Moythomasia durgaringa* (Gardiner, 1984), so the coding is revised from '1' to '?'.

0. present
1. absent

176. [CH 47] Fulcra along dorsal ridge of caudal fin:

Patterson, 1982; Taverne, 1997; Gardiner & Schaeffer, 1989; Gardiner et al., 2005; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011. Choo's (2011) codes for this character appear reversed.

0. absent
1. present

177. Basal scutes on fins:

Zhu & Yu, 2002; Friedman, 2007.

0. absent
1. present

178. [CH 48] Dorsal scutes anterior to dorsal fin*:

Lund, 2000; Poplin & Lund, 2000; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo; 2011. Choo's (2011) codes for this character appear reversed. The dorsal fin is not figured or described for *Moythomasia durgaringa*, so the coding for this taxon is changed to '?'.

0. absent
1. few limited to region immediately anterior to fin (basal fulcra only)
2. many, extending to posterior of skull roof (complete set of dorsal ridge scales)

179. [CH 49] Ventral scutes between hypochordal lobe of caudal fin and anal fin:

Patterson, 1982; Taverne, 1997; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011. The coding for *Howqualepis rostridens* (Long, 1988) and *Melanecta* (Coates, 1998) is revised from ‘0’ to ‘1’. This region is not figured or described for *Moythomasia durgaringa*, so the coding is changed from ‘1’ to ‘?’.

0. absent
1. present

180. [CH 50] Ventral scutes anterior to anal fin:

Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. Although not figured, Gardiner (1984: p 392) states that basal fulcra are not present anterior to the anal fin in *Moythomasia* durgaringa. As such, the coding in this taxon is revised from ‘1’ to ‘0’. The coding for *Gogosardina* (Choo et al., 2009) is revised from ‘1’ to ‘0’. *Cuneognathus* (Friedman & Blom, 2006) possesses several scutes immediately anterior to the anal fin, although it is unclear how far anteriorly they extend. As such, the coding is changed from ‘?’ to ‘1’. The coding in

Melanecta (Coates, 1998) is revised from '?' to '1'. Choo (2011) erroneously codes *Krasnoyarichthys* (Prokofiev, 2002) as state '2', which lacks a description; the coding is revised to '1'.

0. absent
1. present

181. [CH 52] Dorsal fin(s):

Gardiner & Schaeffer, 1989; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Brazeau, 2009; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015.

0. two
1. one

182. [CH 51] Relative positions of anal and (second) dorsal fin*:

Poplin & Lund, 2000; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The coding for *Moythomasia durgaringa* (Gardiner, 1984) is revised from '2' to '1'. The coding for *Stegotrachelus* is revised from '1' to '2'.

0. anal shifted anteriorly relative to dorsal
1. fins opposite one another
2. anal shifted posteriorly relative to dorsal

Deleted Characters

[CH 2] Premaxillae - shape of (0) wider than deep; (1) depth approximately equal to width.

This character is deleted as the premaxillae are often poorly preserved or distorted in early osteichthyans, with the result that the shape is highly vulnerable to taphonomic distortions.

[CH 31] Scale rows, number of (0) fewer than 60; (1) more than 60.

This character is deleted due to a difficultly in counting the number of scale rows in many taxa, and because the distinction between the two states relies on an arbitrary number.

[CH 55] Intertemporal - contact with parietal (0) no contact; (1) contacts parietal laterally; (2) contacts parietal posterolaterally.

This character is deleted due to the subjective judgement required when considering whether the contact is lateral or posterolateral.

[CH 56] Rostral - shape of (0) widens anteriorly; (1) equal anteriorly and posteriorly; (2) narrows anteriorly.

This character is deleted because the anteriormost portion of the snout, comprising the rostral, is often poorly preserved in actinopterygians, and distortion or poor preservation may cause the shape of the rostral to be midleading.

[CH 65] Preoperculum - vertical linear ornament (0) absent; (1) present.

This character is deleted because the ornament on the preoperculum is often hard to discern, and, even where preserved, distinction between different orientations can be difficult to judge.

[CH 66] Serrated linear ganoine ornament on skull roof (0) absent; (1) present.

This character was erected by Choo (2011) to account for the 'herringbone' ornament on the skull roof of *Moythomasia*. This character is difficult to assess. Furthermore, 'herringbone' ornament is identified only on the skull roof of *Moy. durgaringa* (Gardiner, 1984), and does not appear to be present on the skull roof of *Moy. nitida* or *Moy. perforata* (Jessen, 1968).

[CH 77] Maxilla - shape of anterior section (0) straight; (1) reflexed.

Although listed as a new character by Choo (2011), no description is given and this character is not coded in Choo's matrix.

8.3.2.3 List of taxa

Taxon	**Source**	**Specimens**
Acanthodes bronni	Miles, 1973; Davis et al., 2012.	
Boreosomus piveteaui	Nielsen, 1942.	
Cheirolepis canadensis	Arratia & Cloutier, 1996; Arratia, 2009.	
Cheirolepis schultzei	Arratia & Cloutier, 2004.	
Cheirolepis trailli	Pearson & Westoll, 1979; Giles et al., in review.	
Cladodoides wildungensis	Maisey, 2005.	
Coccocephalichthys wildi	Poplin, 1974; Poplin & Véran, 1996.	
Cosmoptychius wildi	Schaeffer, 1971; Coates, 1999	

Cuneognathus gardineri	Friedman & Blom, 2006.	
Dialipina salgueiroensis	Schultze, 1968; Schultze & Cumbaa, 2001.	
Diplocercides kayseri	Stensiö, 1922a,b; Forey, 1996.	
Donnrosenia schaefferi	Long et al., 2008.	
Entelognathus primordialis	Zhu et al., 2013.	
Eusthenopteron foordi	Jarvik, 1980.	
Gogonasus andrewsae	Long et al., 1997; Long et al., 2006; Holland, 2014.	
Gogosardina coatesi	Choo et al., 2009.	
Glyptolepis groenlandica	Jarvik, 1972; Jarvik, 1980.	
Guiyu oneiros	Zhu et al., 2009; Qiao & Zhu, 2010.	
Howqualepis rostridens	Long, 1988; Choo, 2009.	
Kansasiella eatoni	Poplin, 1974	
Kentuckia deani	Rayner, 1951; Giles & Friedman, 2014.	MCZ 8363, MCZ 5226
Kentuckia hlavini	Dunkle, 1964; Feldman, 1996.	
Krasnoyarichthys jesseni	Poplin, 1974.	
Lawrenciella schaefferi	Poplin, 1984; Hamel & Poplin, 2008.	
"Ligulalepis"	Basden et al., 2000;	

	Basden & Young, 2001.	
Limnomis delayni	Daeschler, 2000.	
Luederia kempi	Schaeffer & Dalquest, 1978.	
Mansfieldiscus sweeti	Long, 1988.	
Meemannia eos	Zhu et al., 2006, 2010.	
Melanecta anneae	Coates, 1998.	
Mesopoma planti	Coates, 1999.	
Miguashaia bureaui	Cloutier, 1996.	
Mimipiscis bartrami	Gardiner, 1984: Choo, 2011.	
Mimipiscis toombsi	Gardiner, 1984; Choo, 2011; Giles & Friedman, 2014.	
Moythomasia durgaringa	Gardiner, 1984; Long & Trinajstic, 2010.	
Moythomasia nitida	Jessen, 1968.	
Moythomasia striata	Jessen, 1968.	
Novagonatodus kasantsevae	Long, 1998; Holland et al., 2007.	
Osorioichthys marginis	Taverne, 1997.	IRSNB P.1340
Onychodus jandemarrai	Andrews et al., 2006.	
Osteolepis macrolepidotus	Jarvik 1948	
Porolepis sp.	Jarvik, 1972; Jarvik, 1980.	
Psarolepis romeri	Yu, 1998; Zhu et al.,	

	1999; Zhu & Yu, 2009; Qu et al., 2013.	
Pteronisculus stensioi	Nielsen 1942; Coates, 1998.	
Stegotrachelus finlayi	Gardiner, 1963; Swartz, 2009.	
Styloichthys changae	Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007.	
Tegeolepis clarki	Gardiner, 1963; Dunkle & Schaeffer, 1973.	TOOTH SPECIMEN
Wendichthys dicksoni	Lund & Poplin, 1997.	
Woodichthys bearsdeni	Coates, 1998.	

8.3.3 References

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8.3.4 Legends for electronic appendices

8.3.4.1 *Raynerius* video. (electronic).

8.3.4.2 Character state optimisation tree showing all unambiguous character state transformations on one of the shortest trees. (electronic).

8.4 APPENDIX 4

8.4.1 Previous descriptions of gnathostome endocasts in the literature

TAXON	AGE AND LOCALITY	DESCRIBED BY	DESCRIBED PORTION	METHOD
ACTINOPTERYGIANS				
Kansasiella eatoni Poplin, 1974	Pennsylvanian (Gzhelian-Kasimovian), Kansas, USA	Watson, 1925; Watson, 1928; Case, 1937; Eaton, 1939; Poplin, 1974	Endocast, natural internal mould of cranial cavity	Surface description, microtome sectioning, wax models
Kentuckia deani	Mississippian (Tournaisian-Visean), Kentucky, USA	Eastman, 1908; Moodie, 1915; Rayner, 1951; this contribution	Natural internal mould of cranial cavity, cranial cavity, endocast	Surface description, sagittal section through braincase, CT (computed tomography) scanning
Lawrenciella schaefferi Poplin, 1984	Pennsylvanian (Gzhelian-Kasimovian), Kansas, USA	Watson, 1925; Poplin, 1984; Hamel and Poplin, 2008	Natural internal mould of cranial cavity, endocast	Surface description, microtome sectioning, wax models
Luederia kempi Schaeffer and Dalquest, 1978	Permian (Cisuralian), Texas, USA	Schaeffer and Dalquest, 1978	Mid-sagittal section	Mechanical preparation, radiography, sagittal section through braincase
Mesopoma planti Traquair, 1890	Pennsylvanian (Moscovian), Lancashire, UK	Coates, 1999	Endocast	Minor mechanical preparation, casts
Mimipiscis toombsi	Late Devonian (Frasnian),	Gardiner, 1984; this contribution	Cranial cavity, endocast	Acid preparation, some sectioning,

	Western Australia, Australia			CT scanning
"Palaeoniscoid C"	Pennsylvanian, (Gzhelian-Kasimovian), Kansas, USA	Moodie, 1915; Rayner, 1951	Natural internal mould of cranial cavity, braincase	Surface description
Unnamed actinopterygian	Age unknown, ?Iowa	Moodie, 1929	Natural internal mould of cranial cavity	Surface description
SARCOPTERYGIANS				
"Chirodipterus" australis Miles, 1977	Late Devonian (Frasnian), Western Australia, Australia	Campbell et al., 2000; Miles, 1977	Semicircular canals	Acid preparation, radiography
Chirodipterus wildungensis Gross, 1933	Late Devonian (Frasnian), Wildungen, Germany	Säve-Söderbergh, 1952	Endocast, restoration of brain	Mechanical preparation
Diplocercides schmidti Stensiö, 1937	Late Devonian (Frasnian), Wildungen, Germany	Stensiö, 1937, Jarvik, 1942; Stensiö, 1963b; Jarvik, 1980	Endocast, sections through braincase	Sollas' grinding method, wax model
Dipnorhynchus sussmilchi Etheridge, 1906	Early Devonian (Emsian), New South Wales, Australia	Thomson and Campbell, 1971; Campbell and Barwick, 1982	Endocast	Mechanical and acid preparation
Dipnorhynchus kurikae Campbell and Barwick, 1985	Early Devonian (Emsian), New South Wales, Australia	Campbell and Barwick, 2000	Semicircular canals	Acid preparation
Ectosteorachis nitidus Cope, 1880	Permian (Cisuralian), Texas, USA	Romer, 1937	Endocast	Serial grinding, peel method, wax model

Euporosteus yunnanensis Zhu et al., 2012	Early Devonian (Pragian), Yunnan, China	Zhu et al., 2012	Semicircular canals	CT scanning
Eusthenopteron foordi Whiteaves, 1881	Late Devonian (Frasnian), Miguasha, Quebec, Canada	Bjerring, 1971; Jarvik, 1980	Endocast, restoration of brain	Sollas' grinding method, wax model
Glyptolepis groenlandica Jarvik, 1972	Middle Devonian (Eifelian), Greenland	Jarvik, 1972	Endocast	Sollas' grinding method, wax model
"Griphognathus" whitei Miles, 1977	Late Devonian (Frasnian), Western Australia, Australia	Miles, 1977	Partial endocast including semicircular canals	Acid preparation, radiography, sections
Gyroptychius sp. M'Coy, 1848	Middle Devonian (Eifelian), Morayshire, Scotland, UK	Thomson, 1964	Olfactory canals and capsules	Surface description
Onychodus jandemarrai Andrews et al., 2006	Late Devonian (Frasnian), Western Australia, Australia	Andrews et al., 2006	Cranial cavity (portion of otic region only)	Acid preparation
Orlovichthys limnatus Krupina, 1980	Late Devonian (Famennian), Orel, Russia	Krupina et al., 2001	Cranial cavity	Acid preparation
Osteolepis sp. Agassiz, 1843	Middle Devonian (Eifelian), Tynet Burn, Scotland, UK	Watson, 1926; Thomson, 1965	Endocast, restoration of brain	Casts
Powichthys spitsbergensis Clément and Janvier, 2004	Lower Devonian (Lochkovian-Pragian), Spitsbergen	Clément and Ahlberg, 2010	Anterior portion of endocast (in ethmosphenoid division only)	Acid preparation, CT scanning
Sengoerichthys ottoman	?Late Devonian	Janvier et al., 2007	Olfactory canals	Surface

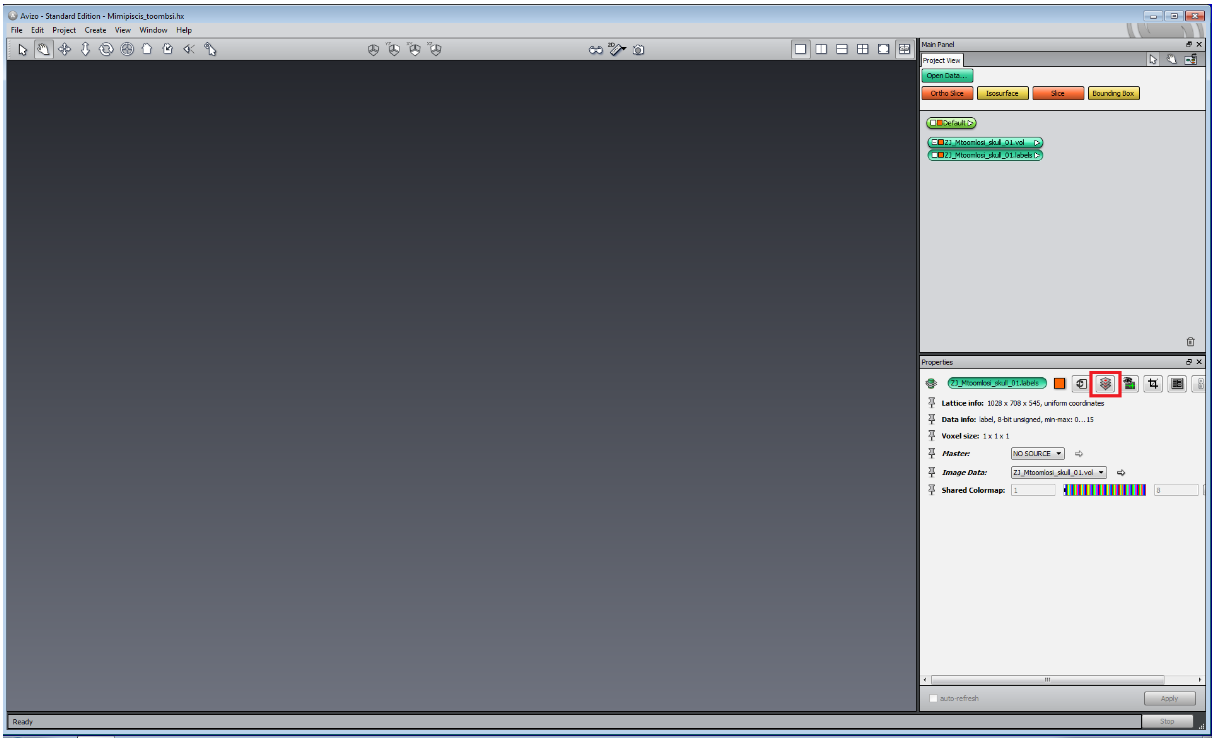
Janvier et al., 2007	(?Frasnian), Turkey		and capsules	description
Spodichthys buetleri Jarvik, 1985	Late Devonian (Frasnian), East Greenland	Snitting, 2008	Anterior portion of endocast (in ethmosphenoid region only)	CT scanning
Tungsenia paradoxa Lu et al., 2012	Early Devonian (Pragian), Yunnan	Lu et al., 2012	Anterior portion of endocast (in ethmosphenoid region only)	CT scanning
Youngolepis praecursor Chang and Yu, 1981	Early Devonian (Lochkovian), Yunnan, China	Chang, 1982	Endocast	Sollas' grinding method, wax model
CHONDRICHTHYANS				
Cladodoides wildungensis Gross, 1937	Late Devonian (Frasnian), Wildungen, Germany	Maisey, 2005; Maisey and Lane, 2010	Endocast	Mechanical prep, CT scanning
"*Cobelodus*" Zangerl, 1973	Pennsylvanian (Visean), Arkansas, USA	Maisey, 2005; Maisey, 2007; Maisey and Lane, 2010	Endocast	Mechanical prep, CT scanning
Kawichthys moodiei Pradel et al., 2011	Pennsylvanian (Kasimovian-Gzehelian), Kansas, USA	Pradel et al., 2011	Partial endocast including semicircular canals	SRμCT (synchrotron microtomography) scanning
Orthacanthus Agassiz, 1843	Permian (Cisuralian), Texas, USA	Schaeffer, 1981	Endocast	Serial grinding, peel method, wax model
Pucapampella sp. Janvier and Suárez-Riglos, 1986	Middle Devonian (Eifelian), Bolivia	Maisey 2001, Maisey and Lane, 2010	Semicircular canals	CT scanning, mechanical preparation
"*Pucapampella*" sp.	Early Devonian (Emsian), South	Maisey and Anderson, 2001; Maisey and Lane,	Semicircular canals	CT scanning

	Africa	2010		
Iniopera sp. Pradel et al., 2010	Pennsylvanian (Kasimovian-Gzehelian), Kansas and Oklahoma, USA	Pradel et al., 2009, Pradel, 2010.	Endocast, actual brain	Mechanical preparation, CT scanning, SRCT scanning
ACANTHODIANS				
Acanthodes bronni Agassiz, 1832	Permian (Cisuralian), Lebach, Germany	Heyler, 1962; Miles, 1973; Davis et al., 2012	Labyrinth	Acid preparation, casts
PLACODERMS				
Brindabellaspis stensioi Young, 1980	Early Devonian (Emsian), New South Wales, Australia	Young, 1980	Endocast	Acid preparation
Buchanosteus osseus Hills, 1936	Early Devonian (Emsian), New South Wales, Australia	Stensiö, 1962	Partial endocast	Acid preparation
Bryantolepis williamsi Elliott and Carr, 2010	Devonian (Emsian), Uta and Idaho, USA	Elliott and Carr, 2010	Endocast	Mechanical preparation
Dicksonosteus arcticus Goujet, 1975	Early Devonian (Pragian), Spitsbergen	Goujet, 1984	Endocast	Mechanical and acid preparation, microtome
Jagorina pandora Jaekel, 1921	Late Devonian (Frasnian), Wildungen, Germany	Stensiö, 1950	Endocast	Mechanical preparation
Kujdanowiaspis sp. Stensiö, 1942	Early Devonian (Lochkovian-Pragian), Ukraine	Stensiö, 1963a	Endocast, restoration of brain	Sollas' grinding method, wax model

Macropetalichthys rapheidolabis Norwood and Owen, 1846	Middle Devonian (Eifelian), New York, USA	Stensiö, 1925; Stensiö, 1963a, 1963b	Endocast, restoration of brain	Mechanical preparation
Tapinosteus heintzi Stensiö, 1963a	Late Devonian (Frasnian), Wildungen, Germany	Stensiö, 1963a	Endocast, restoration of brain	Sollas' grinding method, wax model

8.4.2 Workflow of segmentation method described for Avizo.

Step 1. After importing vol files into Avizo, a *new label field* is generated by selecting the *segmentation editor*.



ZJ_Mtoomlosi_skull_01.labels

Lattice info: 1028 x 708 x 545, uniform coordinates

Data info: label, 8-bit unsigned, min-max: 0…15

Voxel size: 1 x 1 x 1

Master: NO SOURCE

Image Data: ZJ_Mtoomlosi_skull_01.vol

Shared Colormap: 1 8

Step 2. Bone material is selected using the *magic wand tool* and added to a new mask ('Bone').

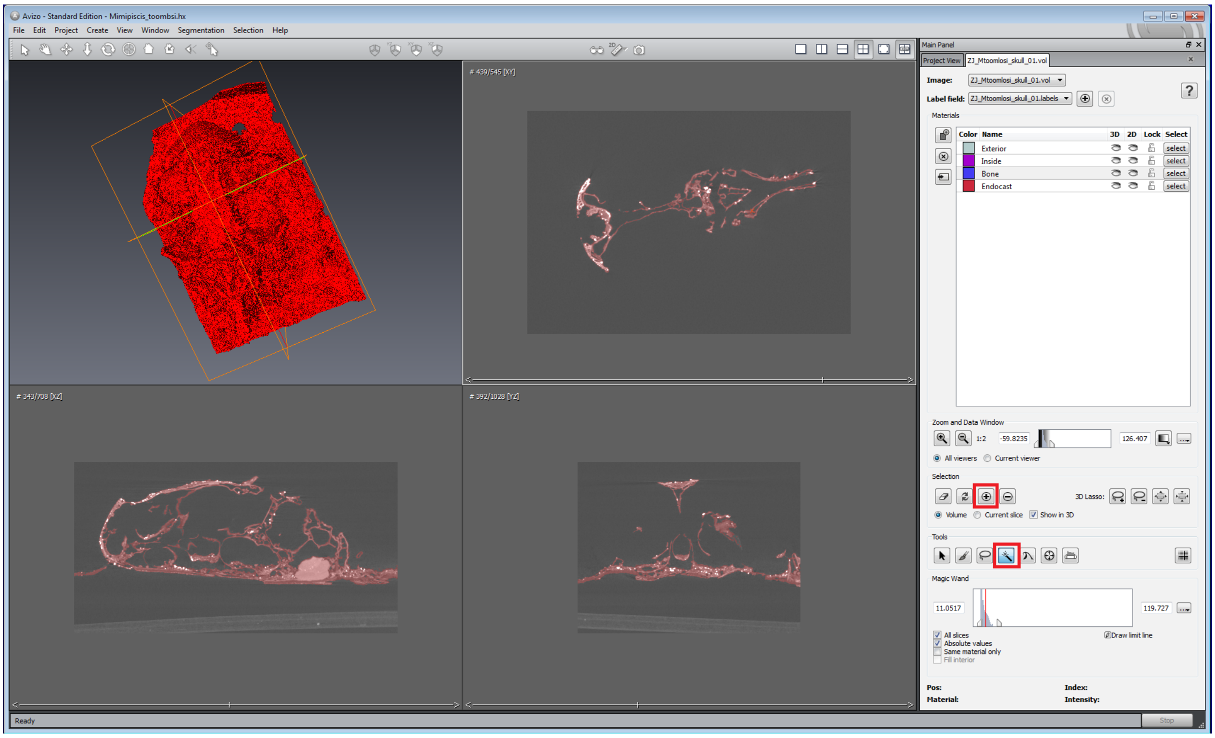


Image: ZJ_Mtoomlosi_skull_01.vol

Label field: ZJ_Mtoomlosi_skull_01.labels

Color	Name	3D	2D	Lock	Select
🟦	Exterior				select
🟪	Inside				select
🟦	Bone				select
🟥	Endocast				select

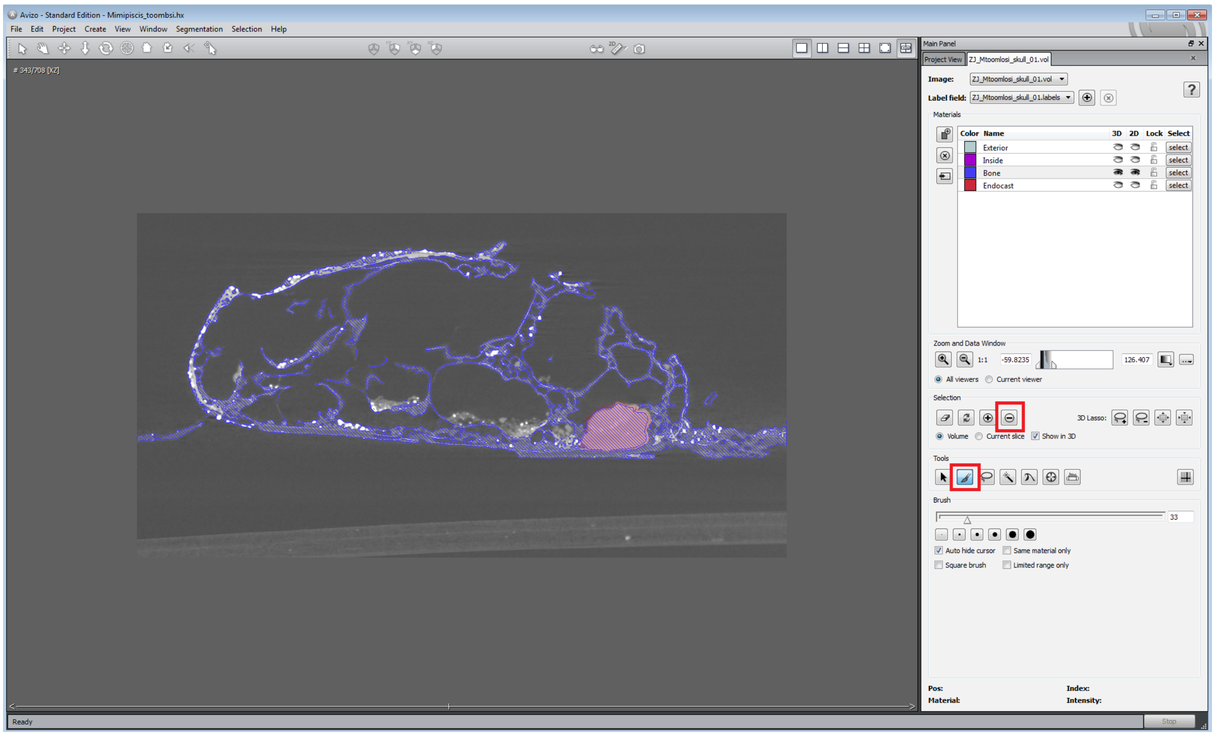
Zoom and Data Window: -59.8235 – 126.407

● Volume ○ Current slice ☑ Show in 3D

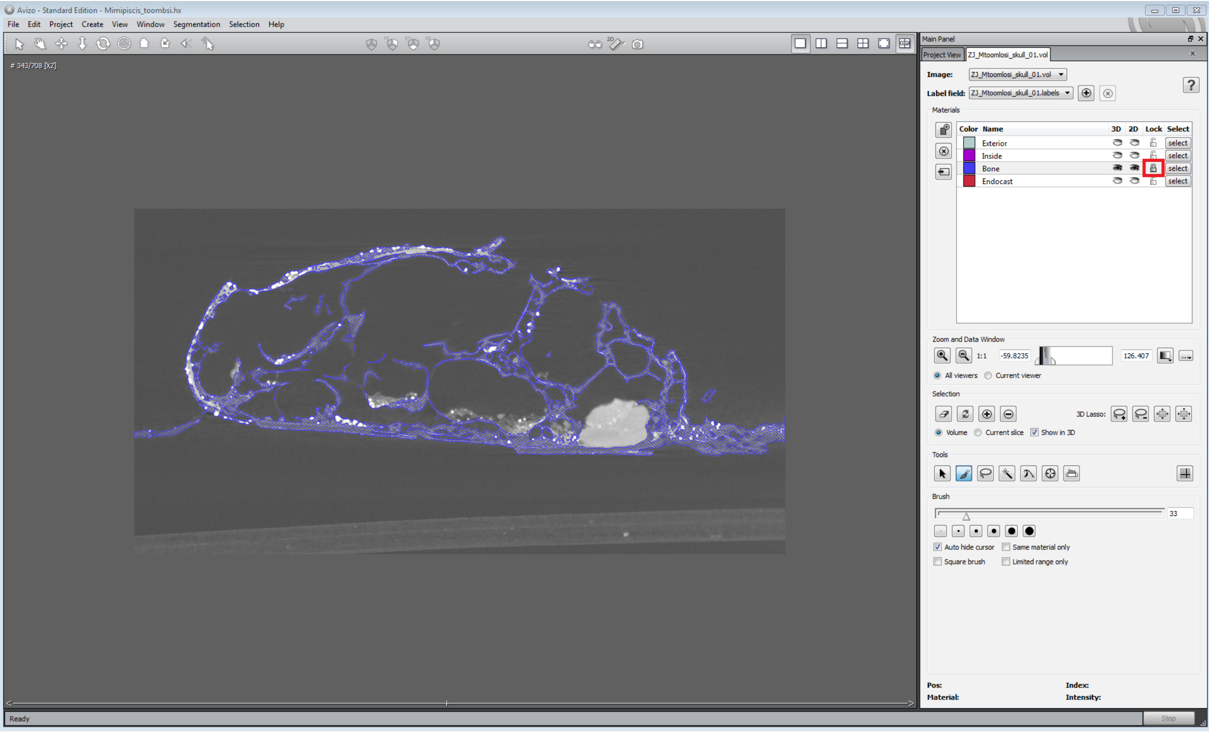
Magic Wand: 11.0517 – 119.727

☑ All slices
☑ Absolute values
☐ Same material only
☐ Fill interior
☑ Draw limit line

Step 3. Sediment with the same attenuation as the bone is manually selected using the *brush tool* and removed from the mask.



Step 4. The ‘bone’ mask is locked.



Step 5. The *blow tool* is used to select the void space, representing the cranial cavity. This tool propagates outwards until it reaches voxels of a sufficiently different grey value. Nb the propagation will also stop when sediment with a different attenuation to the air is reached. As this sediment represents infilling of the cranial cavity, it must be added to the selection manually using the *brush tool*.

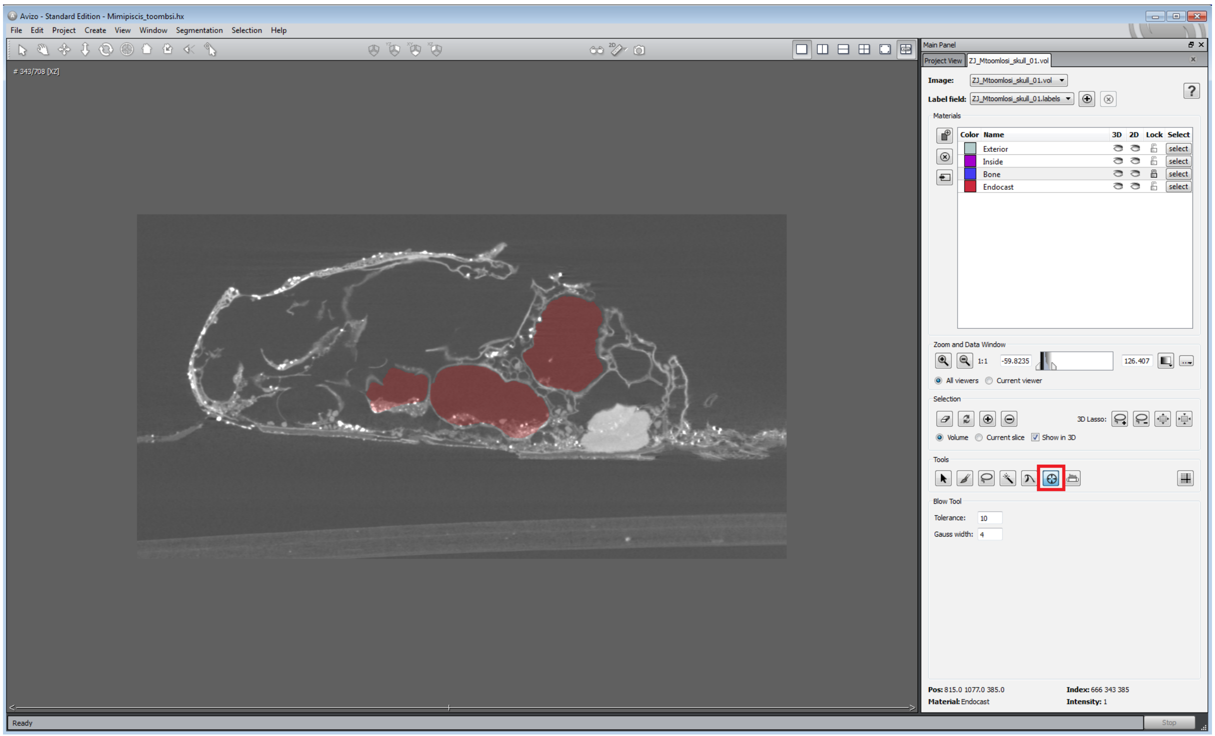


Image: ZJ_Mtoomlosi_skull_01.vol

Label field: ZJ_Mtoomlosi_skull_01.labels

Color	Name	3D	2D	Lock	Select
🟦	Exterior				select
🟪	Inside				select
🟦	Bone				select
🟥	Endocast				select

1:1 -59.8235 126.407

● All viewers ○ Current viewer

● Volume ○ Current slice ☑ Show in 3D

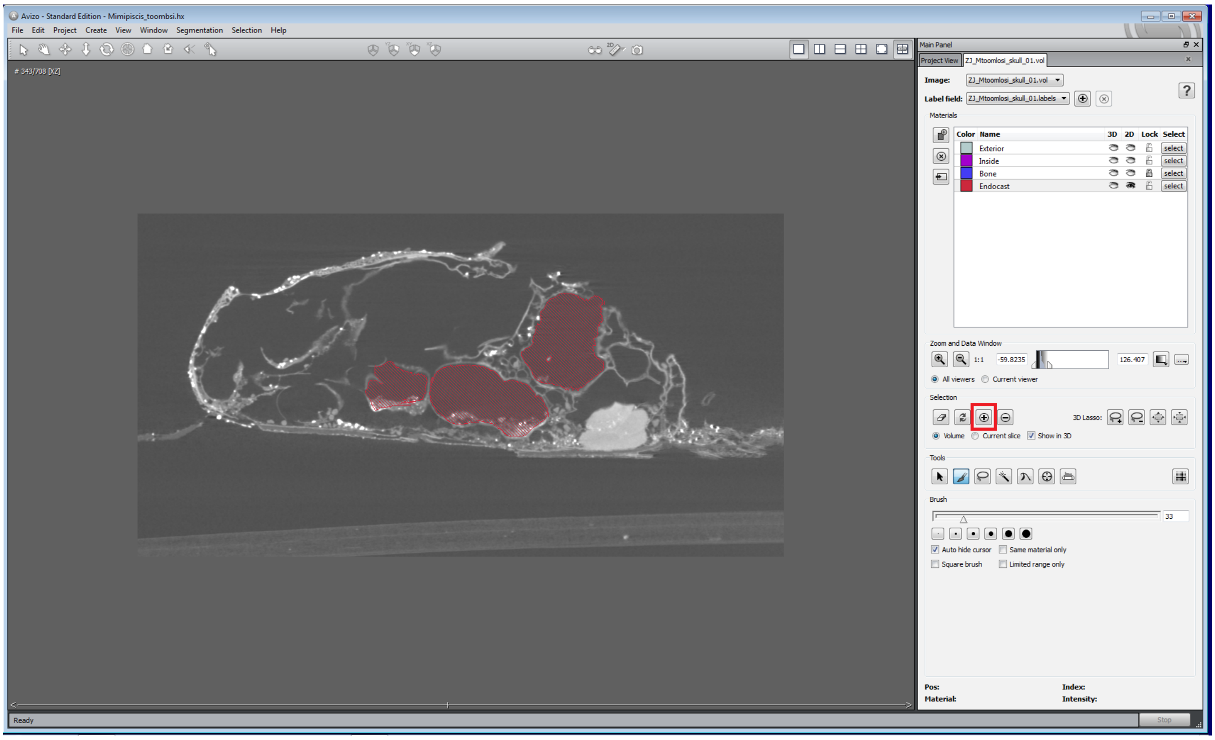
Tolerance: 10

Gauss width: 4

Pos: 815.0 1077.0 385.0 **Index:** 666 343 385

Material: Endocast **Intensity:** 1

Step 6. The selected void space is added to a new mask (‘Endocast’).



Avizo - Standard Edition - Mimipiscis_toombsi.hx

Image: ZJ_Mtoomlosi_skull_01.vol

Label field: ZJ_Mtoomlosi_skull_01.labels

Color	Name	3D	2D	Lock	Select
	Exterior				select
	Inside				select
	Bone				select
	Endocast				select

Zoom and Data Window: 1:1 -59.8235 126.407

● All viewers ○ Current viewer

● Volume ○ Current slice ☑ Show in 3D

Brush: 33

☑ Auto hide cursor ☐ Same material only

☐ Square brush ☐ Limited range only

8.4.3 References

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8.4.4 Legends for electronic appendices

8.4.4.1 Animation of the endocast of *Mimipiscis toombsi* NHMUK PV P.53247. (electronic)

8.4.4.2 Animation of the endocast of *Kentuckia deani* MCZ 8361. (electronic)

8.4.4.3 PLY 3D file of the endocast of *Mimipiscis toombsi* NHMUK PV P.53247. (electronic)

8.4.4.4 PLY 3D file of the endocast of of *Kentuckia deani* MCZ 8361. (electronic)

8.4.4.5 PLY 3D file of the partial endocast of of *Kentuckia deani* MCZ 5226. (electronic)