The characters of Palaeozoic jawed vertebrates

MARTIN D. BRAZEAU[1]* and MATT FRIEDMAN[2]

[1]*Naturalis Biodiversity Center, P.O. Box 9514, 2300 RA Leiden, The Netherlands*
[2]*Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3AN, UK*

Newly discovered fossils from the Silurian and Devonian periods are beginning to challenge embedded perceptions about the origin and early diversification of jawed vertebrates (gnathostomes). Nevertheless, an explicit cladistic framework for the relationships of these fossils relative to the principal crown lineages of the jawed vertebrates (osteichthyans: bony fishes and tetrapods; chondrichthyans: sharks, batoids, and chimaeras) remains elusive. We critically review the systematics and character distributions of early gnathostomes and provide a clearly stated hierarchy of synapomorphies covering the jaw-bearing stem gnathostomes and osteichthyan and chondrichthyan stem groups. We show that character lists, designed to support the monophyly of putative groups, tend to overstate their strength and lack cladistic corroboration. By contrast, synapomorphic hierarchies are more open to refutation and must explicitly confront conflicting evidence. Our proposed synapomorphy scheme is used to evaluate the status of the problematic fossil groups Acanthodii and Placodermi, and suggest profitable avenues for future research. We interpret placoderms as a paraphyletic array of stem-group gnathostomes, and suggest what we regard as two equally plausible placements of acanthodians: exclusively on the chondrichthyan stem, or distributed on both the chondrichthyan and osteichthyan stems.

[T]he evidence from all useful characters must be weighed impartially, and unbiased comparisons must be made with all potentially related groups.

R. Denison (1979: 19).

INTRODUCTION

The phylogenetic relationships of early fossil gnathostomes (jawed vertebrates) remains one of the most significant but under-researched problems in vertebrate palaeontology. Unlike many other areas of vertebrate systematics, the debates do not concern how fossils might illuminate the inter-relationships of living taxa. Instead, the problems surround the placement of fossil taxa with respect to the modern groups. Gnathostomes are divided into two extant lineages: the Chondrichthyes (sharks, rays and skates, and chimaeras) and much more diverse Osteichthyes (bony fishes and tetrapods). That these are sister groups and reciprocally monophyletic is not greatly disputed, and is well supported by both molecular and morphological studies (Nelson, 1969; Wiley, 1979; Maisey, 1986; Takezaki *et al*., 2003; Blair & Hedges, 2005; Chen *et al*., 2012). Debate currently concerns the phylogenetic placement and monophyly of two exclusively fossil assemblages: the placoderms, armoured fishes with simple jaws and dental structures that are hotly debated homologues of teeth, and the acanthodians, shark-like fishes with numerous bony spines preceding their fins. When gnathostome fossils cannot be placed in either of the extant groups

*Corresponding author. Current address: Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK.
E-mail: martin.brazeau@gmail.com

they have typically been assigned to either of these extinct categories. From a phylogenetic perspective, that leaves few fossil branches that can be used to infer sequences of character acquisition in important parts of the gnathostome tree, such as those that document the origin of jaws and the unique anatomical attributes of chondrichthyans and osteichthyans.

Although fossils of Devonian and Silurian fishes that challenge old perceptions are frequently coming to light (Zhu, Yu & Janvier, 1999; Maisey, 2001; Maisey & Anderson, 2001; Miller, Cloutier & Turner, 2003; Hanke & Wilson, 2004, 2006, 2010; Brazeau, 2009; Maisey, Miller & Turner, 2009; Zhu et al., 2009, 2012a, 2013), comparatively little effort has been spent to investigate their phylogenetic relationships. In addition to this, the record of even the earliest jawed vertebrates is characterized by considerable anatomical disparity (Anderson et al., 2011; Davis, Finarelli & Coates, 2012). Currently, placoderms are the only group of widely accepted stem-group gnathostomes that are known to exhibit jaws (Young, 1986). Acanthodians have been placed in this position at one time or another (Watson, 1937; Rosen et al., 1981; Brazeau, 2009; Davis et al., 2012), but this has rarely been consistent and the character support is unclear. Meanwhile, fossils that branch between placoderms and their nearest jawless relatives have yet to be discovered or identified. Consequently no anatomical intermediates are known to punctuate this conspicuous gap. The number of stem osteichthyans and stem chondrichthyans identified with any confidence is similarly limited, with candidates usually sourced from the acanthodians. Nevertheless, the fossils of early gnathostomes are sometimes used as background for hypotheses of character and developmental evolution, even though these relationships and character transformations remain unclear (e.g. Beverdam et al., 2002; Koentges & Matsuoka, 2002; Gillis et al., 2011).

Over the past three decades, pioneering cladistic work has made it clear that Palaeozoic armoured jawless fishes, sometimes called 'ostracoderms', are a paraphyletic array of stem gnathostomes (Janvier, 1981a, 1984; Forey & Janvier, 1993). This brought an end to decades of work that considered the 'ostracoderms' almost exclusively in light of themselves (see review in Janvier, 1996b), and introduced a computational framework for studying stem gnathostome relationships (Donoghue, Forey & Aldridge, 2000). Although uncertainty and disagreement remains about the precise relationships of jawless stem gnathostomes, debates on the topic have proved highly fruitful. The resulting synapomorphic hierarchies have elucidated the step-wise acquisition of a suite of anatomical features that distinguish gnathostomes from their living jawless relatives.

These include the relative order of appearance of features such as an epicercal tail, paired pectoral appendages, and perichondral bone (Forey & Janvier, 1993; Janvier, 1996a; Donoghue et al., 2000; Janvier, 2001; Gai et al., 2011).

By comparison, the application of cladistic methods to the early gnathostome problem is in a state of infancy. This relative lack of progress is paradoxical: early gnathostome fossils are similarly diverse as their jawless counterparts and almost certainly richer in characters. Only a few numerical cladistic analyses have had the taxonomic scope to test such fundamental phylogenetic questions as the monophyly of placoderms and acanthodians, and evaluate competing placements for stem members of Osteichthyes, Chondrichthyes, and Gnathostomata (Friedman, 2007a; Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013). In this paper, we elaborate on the body of character information emerging from these recent analyses. We explore conflicting data, and frame the relevant systematic questions, as we see them, with greater explicitness, and set clear avenues for future research. To do this, we address three fundamental problems:

1. How might previous palaeontological collection, research, and analysis have failed to populate the naked stem-group branches of the chondrichthyan, osteichthyan, and crownward parts of the gnathostome stem (Fig. 1)?
2. What are the principal characters describing the hierarchy of these three gnathostome branches incident to the gnathostome crown node?
3. What are the implications of the resulting scheme for interpreting problematic or unusual taxa?

To address these questions, we need to re-evaluate the phylogenetic status of the two main extinct groups, placoderms and acanthodians, through a critical examination of their characters. As in our previous work on osteichthyans (Friedman & Brazeau, 2010), we can assess whether our current systematic traditions may be causing us to misidentify or misinterpret fossils. We feel the best approach to the problem is captured by Denison's (1979) quote in the epigraph. Denison invites us to make comparisons not just within the groups that we have inherited by the traditions of our discipline, but to compare each one objectively and across the perceived taxonomic boundaries as though they did not exist at all. In this way, we can better establish the quality of evidence that forms the basis of our current systematics of early gnathostomes.

A HISTORY OF THE 'PLACODERM PROBLEM'

The taxonomic history of Placodermi includes two major eras, each spanning nearly a century (Obruchev,

1964; Goujet, 1984b). The first of these corresponds to the initial identification of the taxon, followed by serial rejections of its coherence and redistribution of its constituent members to a range of vertebrate groups. The second period began with the rapid reunion of most original members along with newly discovered groups, followed by a long period of stasis in the concept of Placodermi that continues to the present.

M'Coy (1848) erected Placodermi to include members of Agassiz' (1844) Cephalaspides minus *Cephalaspis* with some additions: the heterostracan *Psammosteus* and a series of other genera (e.g. the ptyctodont *Chelyophorus*) previously aligned with coelacanths. These taxa, M'Coy argued, were united by the presence of large, tuberculated plates covering the head and trunk. Pander (1857), Kade (1858), and Traquair (1888) maintained a taxon closely corresponding to M'Coy's Placodermi. Then as now, arthrodires were interpreted largely in the light of living gnathostomes. Huxley (1861: 37) argued that *Coccosteus* was allied with catfishes, and in asserting that 'wherever *Coccosteus* goes, *Pterichthys* must follow . . . though the structure of the last-named fish is . . . more difficult of interpretation', inaugurated a new tradition: the investigation of poorly known or unusual placoderms through an arthrodire model with closer correspondences to modern gnathostomes (e.g. Young, 2010: fig. 1).

Huxley was not unique in aligning placoderms with osteichthyans; Newberry (1875), Crane (1877), Cope (1889, 1892), and Regan (1904) championed links between arthrodires and sarcopterygians. However, Huxley's enthusiasm to brush aside the differences between arthrodires and antiarchs was not universal. The latter were banished to Agnatha by Cope (1889, 1892), who remarked 'there is a wide gap between these forms and any of the fishes' (1892: 281). Others simply ignored placoderms in their classifications (e.g. Gill, 1872) or declared the assemblage *incertae sedis* (Lutken, 1871).

Thus within decades of its formulation, Placodermi lay in tatters. Woodward's (1891) classification captures prevailing sentiments at the close of the 19th century. *Coccosteus* and other arthrodires, along with *Chelyophorus*, were lungfishes, *Pterichthyodes* and other antiarchs were allied with 'ostracoderms', and *Psammosteus* was compared with sharks. Ptyctodonts (exclusive of *Chelyophorus*) had yet to be associated with placoderms, and were placed with holocephalans. Woodward's scheme persisted largely unscathed in textbooks well into the 20th century (Woodward, 1932).

The modern concept of Placodermi is often attributed to Stensiö (1925, 1931), Gross (1931, 1937), and Heintz (1932) (Obruchev, 1964; Goujet, 1984b), but key steps in reuniting the placoderms had already taken place in the first decade of the 20th century. Hussakof, who had earlier (1905, 1906) reiterated Dean's (1899, 1901) arguments that arthrodires were unrelated to lungfishes, rejected the link between antiarchs and 'ostracoderms'. Hussakof (1906: 134) asserted that these groups were 'united on negative evidence . . . rather than for the possession of a series of common characters'. Critical to Hussakof's thesis was Patten's (1904) discovery of mouthparts in *Bothriolepis* comparable to but 'inferior in development to [those] of the Arthrodira' (Hussakof, 1906: 135). As antiarchs could no longer be dismissed as jawless, Hussakof argued that correspondences between the dermal carapace of this group and arthrodires were evidence of a close relationship. Hussakof (1906) came to another prescient conclusion: placoderms are not members of the extant gnathostome radiation.

By the 1930s the construction of a modern concept of Placodermi was effectively complete. The content of the group varied over the coming years, including the temporary embrace of acanthodians (Watson, 1937; Moy-Thomas, 1939; Romer, 1945, 1966) and invocations of placoderm paraphyly with respect to chondrichthyans (e.g. Ørvig, 1962; Stensiö, 1963,
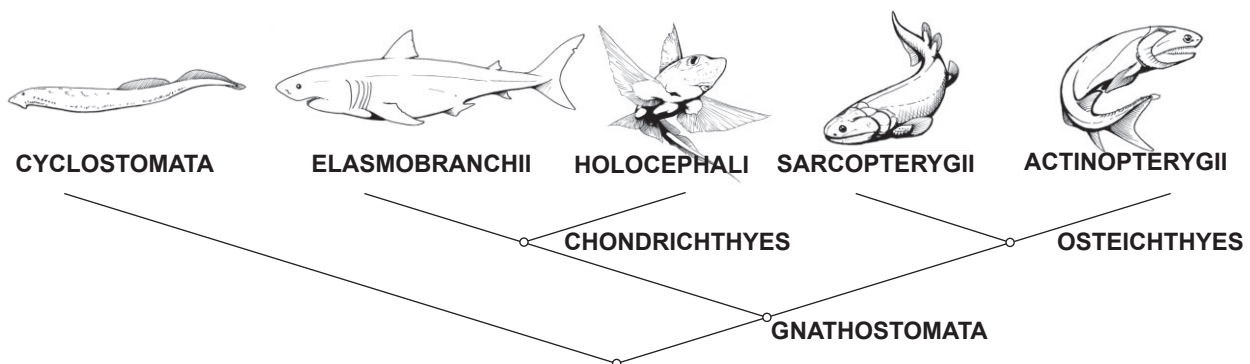
Figure 1. Assumed phylogenetic framework for the principal extant clades of vertebrates used in this analysis.

1969; Jarvik, 1980), but the concept of Placodermi that stabilized prior to the Second World War remains effectively indistinguishable from that which has persisted to the present day. It is important to recognize that workers of the time were comfortable with the notion of paraphyletic assemblages as legitimate taxonomic groups, and many authors understood that placoderms might be 'united' by shared primitive characters rather than any specializations of their own. This sentiment was clearly stated by Moy-Thomas (1939: 29) in his influential *Palaeozoic Fishes*: 'the more knowledge of them [placoderms] has increased the more certain it has become, that they represent a large early gnathostome group, probably containing the ancestors of all modern fishes'.

The modern era of placoderm systematics began with Denison's (1975: 9) character-based review of placoderm intrarelationships. He concluded that the group could be recognized on the basis of: an anteriorly placed gill chamber, lying beneath the neurocranium; a neck joint between the neurocranium and synarcual; and dermal bones covering the head and shoulder girdle. The first and last of these features are demonstrably plesiomorphic based on outgroup comparison, whereas the second is, as Denison himself admitted, possibly homoplastic. Miles & Young (1977) built upon Denison's (1975) efforts at inferring placoderm intrarelationships, but the placement of placoderms as a whole to other groups of gnathostomes was their primary preoccupation. Like Denison, Miles & Young (1977) did not focus on the question of placoderm monophyly, and instead worked under the assumption that placoderms formed a clade to the exclusion of other gnathostomes. These formative works set the agenda for subsequent investigation: the relationships within placoderms (e.g. Young, 1980, 1986; Gardiner, 1984a; Goujet, 1984b; Forey & Gardiner, 1986; Goujet & Young, 1995), and the relationships of placoderms to other vertebrates were topics for research (e.g. Goujet, 1982, 1984b; Gardiner, 1984a; Young, 1986), but placoderm monophyly was not subject to critical testing.

The most explicit arguments for placoderm monophyly (Goujet, 1984b, 2001; Young, 2010) share a common pedigree, tracing their ancestry to Goujet's (1982: 29) list of synapomorphies. These are summarized here based on our own translation:

[1] dermal skeleton formed of plates contributing to a head and trunk shield, with the latter forming a complete ring and supporting the pectoral fins; [2] the presence of a double cervical joint with an endoskeletal component (between occipital condyles and a synarcual) and a dermal component (the posterolateral part of the skull overlapping the front margin of the anterior dorsolateral plate); [3] a specific pattern of dermal plates contributing to the head and trunk shields; [4] the

presence of semidentine, a specific kind of hard tissue; [5] an omega-shaped palatoquadrate, with adductor muscles inserting on the ventral surface of this structure and the internal face of the suborbital plate; [6] fusion between dorsal elements of the mandibular and hyoid arches with dermal plates of the cheek.

Goujet (1984b: 237) was later able to expand his list of placoderm synapomorphies, which had grown from six to 11. These additional characters were:

[7] endocranium composed of two ossifications (rhinocapsular and postethmo-occipital) separated by a fissure, unless secondarily fused; [8] long ethmoid region of the endocranium with terminal nasal capsules and a long subnasal shelf; [9] lateral orbits; [10] variable skull pattern, with numerous plates; [11] cheek covered by three plates, including a large submarginal.

Subsequent studies regarded many of these characters as uninformative for the usual reasons: they were either primitive, or their polarity could not be determined through outgroup comparison. Not long after Goujet's argument for placoderm monophyly, Maisey (1986: 225) concluded that support for Placodermi might be more apparent than real, and that '[c]haracterization of placoderms as a monophyletic group . . . is problematical'.

Goujet (2001: 210) later produced a list of five synapomorphies [their equivalent(s) from Goujet, 1984b are given in parentheses]: a dermal shoulder girdle encircling the trunk and making an articulation with the skull through a joint (a partial combination of characters 1 and 2); a distinctive pattern of dermal bones contributing to the skull roof and cheek (a combination of characters 3 and 11); simple jaws bearing two or three pairs of bony plates (a new character); direct connection between the dermal operculum and braincase via a hyoid arch cartilage (a subset of character 6); and the presence of semidentine (character 4). In response to cladistic analyses rooted on jawless vertebrates that can test – but have failed to support – placoderm monophyly (Friedman, 2007a; Brazeau, 2009; a similar pattern has been found subsequently by Davis *et al.*, 2012 and Zhu *et al.*, 2013), Young (2010) more than trebled Goujet's most recent list. As the most recent argument favouring a classical Placodermi, we provide a detailed review of this synapomorphy scheme in a later section.

A HISTORY OF THE 'ACANTHODIAN PROBLEM'

The concept of acanthodians as a coherent assemblage can be traced to the mid-19th century (reviewed by Heyler, 1969; Miles, 1973b; Denison, 1979). Agassiz described spines of fishes now called acanthodians in his *Recherches* (1833–1844), but it was only in his

monograph on fishes from the Old Red Sandstone that he recognized a taxon with links to the modern concept of the group (Agassiz, 1844). Agassiz' Acanthodiens contained *Acanthodes*, *Cheiracanthus*, and *Diplacanthus*. Within this group, which clearly presages modern concepts of Acanthodii, Agassiz included an outlier: *Cheirolepis*. This actinopterygian, which was later recognized as such by Traquair (1875), was not the only crown osteichthyan to be interpreted as an acanthodian; the sarcopterygian *Onychodus* was assigned to this assemblage by some workers well into the 20th century (e.g. Romer, 1933, 1945).

Although Agassiz regarded acanthodians as distinct from both 'ganoids' and sharks, the next 150 years of research on acanthodian relationships can be summarized as a series of competing hypotheses aligning this group with either chondrichthyans (Roemer, 1857; Fritsch, 1890; Woodward, 1891; Dean, 1895, 1907, 1909; Reis, 1895, 1896; Nielsen, 1932; Woodward, 1932; Holmgren, 1942; Ørvig, 1957; Nelson, 1968, 1969; Jarvik, 1977, 1980) or osteichthyans (Kner, 1868; Zittel, 1893; Huxley in Davis, 1894; Nielsen, 1949; Heyler, 1958, 1962; Romer, 1968; Schaeffer, 1968, 1969; Miles, 1973a; Gardiner, 1984a; Maisey, 1986), plus rare proposals drawing links with placoderms (Watson, 1937; Romer, 1945, 1966) or placing acanthodians on the gnathostome stem (Rosen *et al*., 1981).

Despite debate concerning the position of acanthodians relative to other fishes, acanthodian monophyly has gone largely uninterrogated. One of the few explicit arguments was outlined by Maisey (1986: 225), who presented two 'admittedly weak' characters supporting the group. With their status as a clade accepted despite a lack of compelling anatomical evidence, most modern cladistic investigation of Acanthodii has concerned inter-relationships of its supposed members (Denison, 1979; Long, 1986; Maisey, 1986; Hanke & Wilson, 2004; Burrow & Turner, 2010).

The discovery of well-characterized chondrichthyans (Miller, Cloutier & Turner, 2003) and osteichthyans (Zhu *et al*., 2009) with paired fin spines, as well as diverse array of spiny early gnathostomes from the Early Devonian Man on the Hill (MOTH) locality (Bernacsek & Dineley, 1977; Gagnier & Wilson, 1996; Gagnier, Hanke & Wilson, 1999; Hanke, Davis & Wilson, 2001; Hanke, 2002, 2008; Hanke & Wilson, 2004, 2006, 2010; Hanke & Davis, 2008, 2012) have reinvigorated debate on the monophyly and relationships of the acanthodians. Some analyses have proposed acanthodian monophyly and focused on the question of inter-relationships within this group (Hanke & Wilson, 2004; Burrow & Turner, 2010), whereas analyses with broader taxon samples have generally rejected the status of this assemblage of

extinct gnathostomes as a clade (Brazeau, 2009; Davis *et al*., 2012; Zhu *et al*., 2013).

NAKED STEMS REVISITED

This paper seeks to address the long-standing failure to populate naked stem branches of the Osteichthyes, the Chondrichthyes, and crownward parts of the gnathostome stem. There are two possible explanations for this problem: the appropriate fossils are either unpreserved or undiscovered; or the fossils have been incorrectly identified when found (Friedman & Brazeau, 2010). In the second case, we are confronted with two further possible causes: that the data are misleading or that we have misidentified candidates through error. Although Acanthodii and Placodermi are stalwarts of historical classification schemes, the persistence of both assemblages does not necessarily reflect strong or even explicit evidence for their monophyly. We contend that their longevity reflects a combination of convention and convenience, partnered with a lack of decisive phylogenetic tests of their proposed synapomorphies. This contributes not only to their persistence, but also to the positive and systematic misidentification of newly discovered fossils.

METHODOLOGICAL OBSTACLES TO A COHERENT SYSTEMATICS OF EARLY GNATHOSTOMES

In this paper, we attempt to avoid a set of key problems that we perceive as common to many previous attempts to resolve early gnathostome relationships: self-referential assumptions of monophyly, assembly of character lists without accompanying phylogenetic tests, and the use of compound characters. Here we outline the effects of these approaches and show why we think they are misleading using concrete examples from the literature.

SELF-REFERENTIAL ASSUMPTIONS OF MONOPHYLY

The first problem arises from the way certain fossil groups are interpreted solely in light of themselves (e.g. Denison, 1975, 1978; Miles & Young, 1977; Goujet & Young, 1995). In instances where outgroup comparisons are used, procedures are inconsistent or inexplicit. The phylogenetic analysis of Goujet & Young (1995) was admittedly an exploratory investigation, but the results are routinely re-printed for use in comparative studies (Goujet, 2001; Smith & Johanson, 2003; Goujet & Young, 2004; Johanson & Smith, 2005; Carr, Lelièvre & Jackson, 2010). This analysis was rooted on a hypothetical all-zero ancestor. Of the 49 characters used, at least 32 of the presumed primitive states were conditions that

could only be observed in other placoderm taxa. That is, they had no relevant comparator in any non-placoderms. The assumed primitive characters of placoderms are thus largely based on the presupposition of monophyly and hypotheses about which placoderms can be viewed as primitive.

These problems were acknowledged by Goujet & Young (1995, 2004) who presented the work as a stimulus for future research. We have decided to apply a different approach modelled on our earlier investigation of osteichthyan characters (Friedman & Brazeau, 2010). We presented a list of characters for hierarchically ordered groups within the osteichthyan total group, based on reference to a fixed outgroup arrangement. The validity of these synapomorphies can therefore be challenged and refuted by: (1) the discovery of alternative outgroupings; and (2) the discovery of taxa that establish incongruent or conjunctive character distributions (cf. Patterson, 1982a; de Pinna, 1991).

Synapomorphy and its exaggeration

Vertebrates identified as placoderms and acanthodians exhibit distinctive features that might reasonably be offered as candidate synapomorphies. However, it is unclear that these resemblances reflect synapomorphies rather than symplesiomorphies or homoplasy. The task of systematists is resolution of these issues, but the construction of longer lists of 'confirming instances' is only a first step towards this goal. Phylogenetic relationships are not built on overall similarity, but on hierarchical character distributions; it is these that are actual synapomorphies. The construction of ever-longer lists of resemblances conflates similarity with synapomorphy, and ignores (or is at least inexplicit about) the key hierarchical component of the equation. This approach will tend to exaggerate the number of synapomorphies, even if the group does turn out to be a well-corroborated clade. Exaggerated lists of synapomorphies will ultimately lead to the systematic misidentification of newly discovered species.

Compound characters

Compound characters reflect a combination of character particles (conditions) assembled into one statement to give the appearance of one character. Morphologists understandably seek to give greater precision to their characters by composing multiple conditions to identify them. Unfortunately, this fails to distinguish compatibility from congruence, and leaves aside the possibility that the compounded conditions may individually have greater levels of phylogenetic generality. As it is the combination of conditions that defines them, compound characters imply all-or-nothing similarity in satisfying their criteria even though there is no biological or logical rule against homologues having partial resemblance. For example, Burrow, Trinajstic & Long (2012: 349) proposed, based on Burrow & Turner (2010), that 'the main synapomorphy of the group [Acanthodii] is a perichondrally ossified scapulocoracoid, with a slender dorsal shaft widening out basally to a blade that articulates with the pectoral fin spine'. This character can be decomposed into at least five separate variables: the presence of a scapulocoracoid (a general gnathostome character); perichondral ossification (a general gnathostome character); the presence of a dorsal shaft (a trait shared with chondrichthyans); a ventral widening of the basal part of the scapular blade (also seen in chondrichthyans); and its articulation with the fin spine (such as that found in placoderms and possibly spine-bearing chondrichthyans and osteichthyans). Under scrutiny, this character dissolves as an acanthodian synapomorphy (Fig. 2) as its individual parts can be shown to either have wider distribution or be simply irrelevant to many taxa (i.e. those where a spine is absent).

Placoderm characters of Young (2010): a review

In response to recent proposals of placoderm paraphyly, Young (2010) expanded the list of proposed placoderm synapomorphies to 16. Although we agree with some of Young's anatomical reappraisals (e.g. the supposed passage of the subclavian artery through the postbranchial lamina in antiarchs; Johanson, 2002), the list exhibits all of the issues described above, and results in an exaggeratedly long list of synapomorphies.

1. Distinctive pattern of dermal bones in skull roof, cheek, and operculum.

This is too vaguely stated to be subject to any specific test. However, it is indeed the case that the cranial bones of placoderms are identified in terms of those bones in other placoderm species under the assumption of a symplesiomorphic pattern. The resulting 'distinctive' pattern is therefore unsurprising, and this itself has recently been challenged directly (Zhu et al., 2013). Without an inferable plesiomorphic condition, the distinctiveness of placoderm skull bone patterns is moot. Only osteichthyans provide a possible outgroup condition, leaving the possible primitive condition equivocal.

2. Paired external openings of endolymphatic ducts linked to dermal bone ossification centres (nuchal
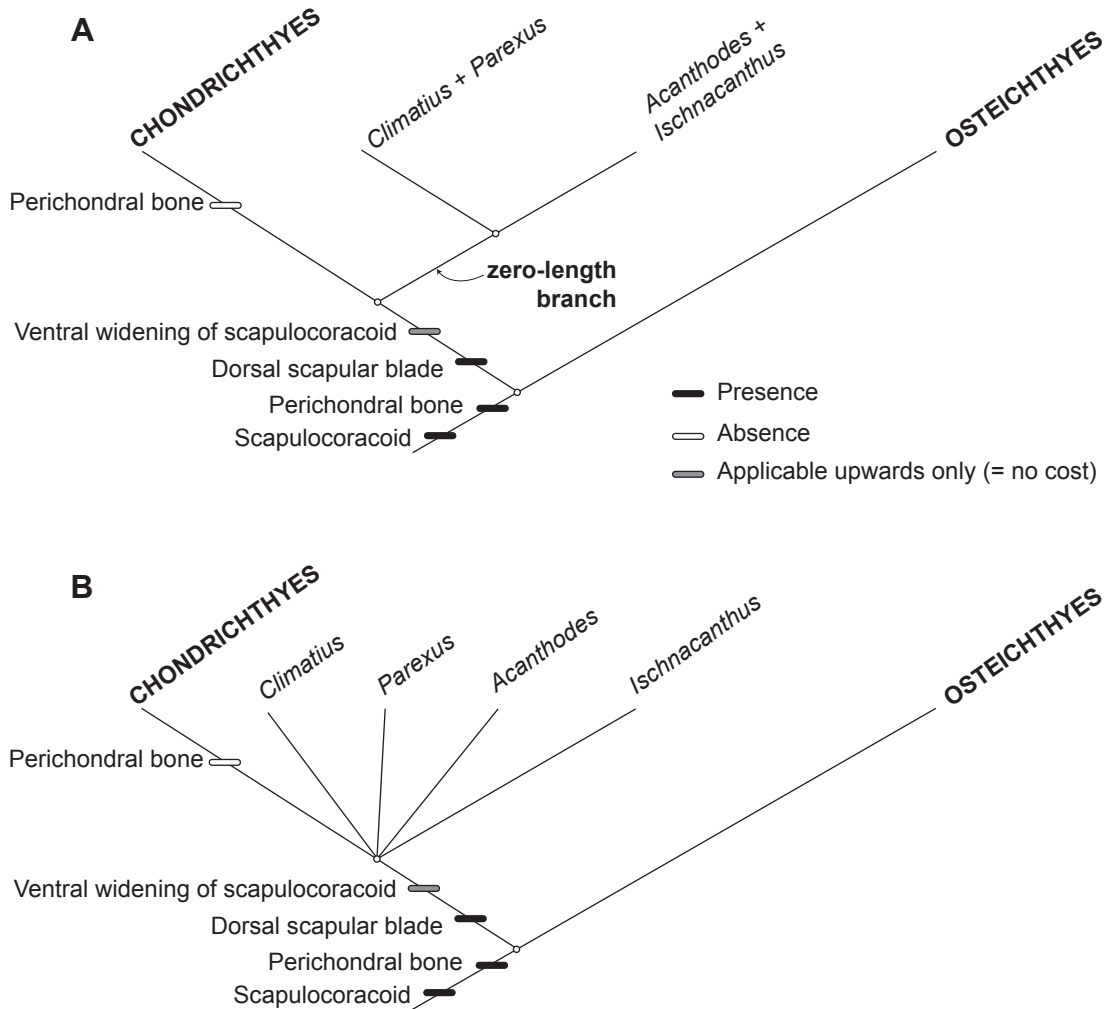
Figure 2. Decomposition of a compound character. The proposed synapomorphy of acanthodians (Burrow & Turner, 2010) can be decomposed into separate conditions each having greater levels of generality. A, acanthodians as a monophyletic group and the compound character of Burrow & Turner yields a zero-length branch. B, collapsed Acanthodii, showing true level of support for the individual character components.

or paranuchal plates) in posterior part of the skull roof.

This is a compound character that is conditioned on the following criteria: there are any endolymphatic openings in the skull roof at all; there are distinctive skull roofing bones identified as nuchals or paranuchals. This character cannot be considered independent evidence from character 1 because the identification of a nuchal plate is considered part of the distinctive placoderm skull roof condition. To condition this character on the passage of ducts through a nuchal or paranuchal plate would presuppose that some non-placoderms have nuchals or paranuchals. The only non-placoderms with macromeric skull roofing bones are osteichthyans, in which the endolymphatic ducts

do not pass through cranial plates. All non-placoderms in which there are endolymphatic openings in the skull roof are either tessellate, micromeric (osteostracans and acanthodians: Miles, 1973a; Sahney & Wilson, 2001), or bear a single large shield (some osteostracans and galeaspids; Janvier, 1985a, b, 1996a; Gai *et al.*, 2011), precluding any a priori attempt to resolve plesiomorphy from apomorphy.

3. Simple jaws with only two or three pairs of bony tooth plates.

There is no clear reason why simple jaws cannot (or should not) be a gnathostome symplesiomorphy. As with the pattern of skull roof bones, the variability of outgroups makes it difficult to establish whether this

condition is primitive or derived. Chondrichthyans and most acanthodians have no large tooth-bearing dermal bones, whereas osteichthyans have several. However, two pairs of bony plates (upper and lower) are found in the jaws of some acanthodians including *Tetanopsyrus* (Hanke *et al.*, 2001) and ischnacanthids (Burrow, 2004).

4. Omega-shaped upper-jaw cartilage (palatoquadrate), with deep ventral embayment for adductor mandibulae muscle (which was not enclosed mesially by dermal bone; see 6, 8).

Others (e.g. Schaeffer, 1975; Janvier, 1996a) have already noted that it is not possible to establish this character as a placoderm synapomorphy as opposed to a gnathostome symplesiomorphy without making the prior assumption that placoderms are crown-group gnathostomes.

5. Palatoquadrate enclosed by lateral attachment to one or two dermal bones (suborbital, postsuborbital plates), neither carrying socketed teeth (cf. maxilla, quadratojugal of osteichthyans).

This is not a feature shared by all placoderms (e.g. ptyctodonts, and possibly petalichthyids; Miles & Young, 1977; Long, 1997), and is contingent upon the presence of dermal cheek plates. Amongst non-placoderms, only osteichthyans and *Culmacanthus* (Long, 1983) have ossified cheek plates. The palatoquadrate and its relationship to the large cheek plate are unknown for the latter. In *Mimipiscis*, the palatoquadrate is fused to the preopercular plate (Gardiner, 1984b), meaning that this condition is also found outside of placoderms.

6. Mesial surface of palatoquadrate lacking dermal bone cover (cf. entopterygoid of osteichthyans).

This character only implies that placoderms are not crown-group osteichthyans.

7. Palatoquadrate carrying single dermal gnathal element (posterior supragnathal) (cf. dermopalatine, ectopterygoid of osteichthyans, both of which carry true teeth)

This character is a subcondition of Young's character 3, repeating some of the same information. Additionally, *Tetanopsyrus* and ischnacanthids show this putative placoderm trait.

8. No dermally enclosed adductor fossa in upper jaw.

See arguments on character 6.

9. Lower-jaw cartilage (Meckel's cartilage) carrying one dermal bone (infragnathal) with a primitive position on its dorsal face (cf. multiple coronoids of osteichthyans) and lacking external and internal cover of dermal bones (cf. dentary, prearticular of osteichthyans).

This arrangement is not unique to placoderms, because the same character state is apparent in *Tetanopsyrus* (Hanke *et al.*, 2001) and ischnacanthids (Burrow, 2004). In addition to being compound, this character repeats much of the information given in character 3, and therefore these two characters are not independent. Because all placoderms differ from the only specified outgroup (in this case, osteichthyans), then again, the polarity of the precise number of plates is unknown.

10. Adductor mandibulae muscle with broad lateral attachment to Meckel's cartilage (cf. posteriorly confined adductor fossa of osteichthyans).

This assertion about the comparative breadth of muscle insertion area in osteichthyans (or any other gnathostomes) and placoderms is misleading, conflating the area of attachment with the size of the adductor fossa (which is only known in fossil osteichthyans in which it is bounded by dermal bones). Although the adductor fossa in osteichthyans is restricted to a posterior position, this does not necessarily reflect the area of muscle attachment. In crown gnathostomes this insertion area is quite broad. In *Amia* (Allis, 1897) and *Chlamydoselachus* (Allis, 1923) the area of attachment spans nearly the entire length of Meckel's cartilage. The adductor narrows in lateral perspective at the level of the jaw joint where upper and lower members join at the mid-lateral raphe (Wilga, 2005).

11. A special type of opercular suspension, comprising a dermal submarginal plate connected directly to the braincase via a cartilage of presumed hyoid-arch derivation.

The hyoid system is known in few placoderms, and in those in which any aspects are known, it is usually incomplete (Young, 1986; Trinajstic *et al.*, 2012). Given the absence of any kind of opercular system in jawless fishes, this character can only be polarized on the assumption that placoderms are crown-group gnathostomes. Otherwise, it might simply be a gnathostome symplesiomorphy.

12. Extensive postorbital endocranial processes fused to the inner side of the dermal skull roof to delineate muscle attachments for operculum, visceral arches, and shoulder girdle.

This is an extremely elaborate compound character. It relies on conditions inapplicable to many possible

outgroups. The posterolateral vacuities identified by Young (e.g. 1978, 1980) as the cucullaris fossae may be alternatively interpreted as 'parabranchial fossae' (Elliott & Carr, 2010). Regardless, a cucullaris muscle is undefined for outgroups without a separation between the head and shoulders (e.g. osteostracans). Other ridges and processes are associated attachments of visceral arches, bringing the comparisons into line with the braincases of osteostracans (Janvier, 1985a, b).

13. Branchial chamber confined beneath braincase by anteroventrally sloping dermal postbranchial lamina

The branchial chamber lies beneath the braincase in osteostracans (Janvier, 1985a, b), galeaspids (Halstead, 1979; Gai et al., 2011), pituriaspids (Young, 1991), heterostracans (Janvier & Blieck, 1979), and at least partially in osteichthyans (Jarvik, 1980; Gardiner, 1984b). We see no alternative but to interpret this character as a primitive gnathostome trait (see also Zangerl, 1981). The remainder of this character description refers to compound features predicated on a series of conditions that can be atomized and treated independently. For instance, postbranchial laminae are found in osteichthyans, and also slope anteroventrally.

14. Exoskeletal shoulder girdle including one or two median dorsal elements overlapped with interlocking lateral and ventral plates to form a rigid ring encircling the trunk.

Median dorsal plates are known in at least one early osteichthyan, Guiyu (Zhu et al., 2009), whereas a rigid ring of dermal shoulder elements encircling the trunk is found in pituriaspids (Young, 1991) and many osteostracans (Janvier, 1985a), but there is some ambiguity in this latter group. Ateleaspis (Ritchie, 1967) and Superciliaspis (Adrain & Wilson, 1994) lack a significant ventral pectoral girdle, in contrast with what could be a more specialized condition (Janvier, 1985a; Sansom, 2009) in taxa such as Norselaspis (Janvier, 1981b). Nevertheless, there seems to be no way to establish this as a placoderm synapomorphy a priori.

15. Dermal articulation between skull and shoulder girdle localized to paired dermal neck-joint between anterior dorsolateral and paranuchal plates.

This character presupposes the macromeric condition as an outgroup state, and thus the only non-placoderms that might root this character are osteichthyans. However, if character 1 is accepted as a placoderm synapomorphy, then osteichthyans are precluded from comparison by definition. The character therefore has no clear polarity given any outgrouping for placoderms.

16. Special hard tissue (semidentine) in surface layer of dermal elements.

Like Davis et al. (2012), we retain this character below but note that it remains problematic. Semidentine is a tissue typology that can be further atomized into distinct traits: polarization of cells, and whether those cells are embedded in matrix. In effect, it is morphologically intermediate between meso- and orthodentine. There are also questions about the distribution of this tissue, as scales from Siberia attributed to the earliest known acanthodians (Karatajute-Talimaa & Smith, 2003) and a pteraspidomorph from the Ordovician of Australia (I. Sansom et al., 2013) bear semidentine-like tissue with polarized cell spaces.

Giles, Rücklin & Donoghue (2013) noted that not all placoderms exhibit a superficial dentinous layer. Semidentine therefore becomes a logically impossible trait variable for a large number of placoderm taxa. Nevertheless, the broad absence of dentinous tissue does not necessarily count against the status of semidentine as a placoderm synapomorphy. We have therefore provisionally kept this character as a potential placoderm synapomorphy.

In spite of this impressively long list of compatible similarities in placoderm taxa (Young, 2008, 2010), we cannot agree that they provide any a priori evidence of placoderm monophyly either collectively or individually. The status of all of these characters depends on their distribution in a cladogram that must be corroborated by other characters – a necessary background that has not been supplied.

METHODS AND ASSUMPTIONS

Here we justify our assumed phylogenetic backbone and outline the methods and assumptions used in this work. The goal is to list a series of highly congruent and easily identified characters that require the fewest number of phylogenetic assumptions in addition to our proposed phylogenetic backbone.

TAXONOMIC AND NOMENCLATURAL CONVENTIONS

In order to make our hypotheses about the interrelationships of early jawed vertebrates completely explicit, and therefore open them to direct testing and refutation, we adopt a standardized taxonomic terminology throughout this paper. Specifically, we apply crown-, total-, and stem-group conventions to avoid the systematic ambiguities that are sometimes associated with discussions of the affinities of fossil jawed vertebrates (e.g. the identification of some

acanthodians as 'putative chondrichthyans'; Sahney & Wilson, 2001; Hanke & Wilson, 2010; Hanke, Wilson & Saurette, 2013). Fig. 1 shows the nomenclatural and phylogenetic scheme. The osteichthyan crown group comprises the last common ancestor of living bony fishes, plus all of its descendants. The osteichthyan total group comprises the crown plus all fossil taxa more closely related to it than any other living group. The chondrichthyan crown group comprises the last common ancestor of Holocephali and Elasmobranchii. For the sake of precision, we choose to apply a restrictive use of the term Elasmobranchii, taking the elasmobranch crown group to include the last common ancestor of living sharks and rays, plus all of its descendants both fossil and living (see Maisey, 2012 for a historical review of the term elasmobranch). The elasmobranch total group is therefore the crown plus all taxa more closely related to it than to any other extant group. This stands in contrast to the way in which elasmobranch is sometimes applied as a term for any chondrichthyan with a shark-like body-plan. The chondrichthyan total group includes the chondrichthyan crown plus all fossil species more closely related to it than any other extant group. The gnathostome crown includes the last common ancestor of Chondrichthyes and Osteichthyes plus all of its descendants. The gnathostome total group includes the gnathostome crown plus all extinct taxa more closely related to it than any other living group. An important implication of this terminological scheme is that we regard many jawless vertebrates as members of the gnathostome total group because they are more closely related to living jawed vertebrates than they are to any other extant radiation (Forey & Janvier, 1993; Donoghue et al., 2000).

It is into this systematic framework that we introduce the two assemblages of extinct gnathostomes that are the focus of this contribution: acanthodians and placoderms. We apply these terms in their traditional capacity (e.g. Moy-Thomas & Miles, 1971; Denison, 1978, 1979; Janvier, 1996a). Our use of these terms should not be taken as an endorsement of the monophyly of the assemblages of species that they describe; they instead reflect hypotheses of monophyly that can be tested and potentially rejected. When these fossil groups are considered within the terminological framework proposed above, relevant questions concerning these assemblages are rendered clear. Are the placoderms or the acanthodians, as they are generally conceived, a clade? If yes, what are the specific attributes (i.e. synapomorphies) that unite their constituent taxa to the exclusion of all other species? Regardless of their status as a clade, to which stem do these assemblages belong: chondrichthyan, osteichthyan, gnathostome, or any and all of the three?

CHARACTER ARGUMENTATION AND HOMOLOGY

Although we base many of our conclusions on the outcomes of recent cladistic analyses (Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013), this paper derives a verbal character list without an associated tree search. Our choice of characters to list here is guided by the same criteria as those used by Friedman & Brazeau (2010). We are using a strictly outgroup-based approach and have limited our characters to those with clear binary symmetry or for which we can resolve ambiguity with reference to the assumed backbone phylogeny (discussed below). We have argued synapomorphies in terms of the transformational hypotheses on which they depend. This is left opaque, or at best implicit, in most character lists that are not associated with a computer-based tree search. We have therefore paired all arguments of synapomorphy with an explicit transformational hypothesis from a particular plesiomorphic starting condition to another specific derived condition.

We apply two complementary approaches to homology argumentation in this paper. The first is that all hypotheses of homology are conditional (Bock, 1969). The second is that congruence constitutes the only real test of homology (see Patterson, 1982a). By 'real test' we mean that the test of congruence provides explicit, objective criteria for deciding when a character shared between two or more species should be considered nonhomologous. We leave aside hopeless arguments that appeal to the overall similarity of traits to establish the supposed 'strength' of a homology hypothesis. They have neither explicit nor implicit criteria for when a hypothesis of homology should be considered disconfirmed. They arise from failure to explicitly express the conditions of a homology proposition and rest on arbitrary essentialistic definitions of terms (cf. debates on the homology of teeth). As noted by Bock (1969), degrees of similarity can reflect degrees of relatedness. For that reason, we employ the conditional specifier 'homologous as . . .' whenever there is ambiguity about the taxonomic and comparative level of a hypothesis of homology. In that way, homologues can be proposed and refuted on different levels (e.g. wings of birds and bats: they are homologous as tetrapod limbs; nonhomologous as kinds of wings).

An exception to our reliance on congruence is when characters fail the logical test of conjunction (see Patterson, 1982a). Young (2008, 2010) provided a clear example of such a refutation for the passage of the subclavian artery as a character excluding antiarchs from placoderms and all other mandibulate gnathostomes. This character was first proposed by Johanson (2002), and then uncritically recycled in data

matrices by Friedman (2007a) and later Brazeau (2009) in modified form. Young (2008) showed that the brachial vascularization of antiarchs does not in fact pierce the postbranchial lamina, but instead a secondary ridge termed the crista internalis. The crista internalis cannot be interpreted ad hoc as a postbranchial lamina to save this homology, because the two occur in conjunction. The character can thus be eliminated from further consideration in this work and as a potential refutation for placoderm monophyly.

### THE JAWLESS SISTER GROUP OF MANDIBULATE GNATHOSTOMES

Identification of the immediate outgroup to jawed vertebrates is the first step to addressing the placement and testing the monophyly of problematic assemblages of early gnathostomes. We regard osteostracans as the jawless sister group of mandibulate gnathostomes. This is supported by the presence of: (1) paired appendages (Fig. 3); (2) an epicercal tail (Fig. 4); (3) perichondral mineralization; and (4) cellular bone (Donoghue, Sansom & Downs, 2006). Characters 1, 2, and 3 are found in all mandibulate gnathostome lineages and therefore unequivocally plesiomorphic for the crown-group node. Cellular bone is absent in chondrichthyans (see discussion below) but found in osteichthyans, placoderms, and acanthodians. This pattern is explained as a loss in chondrichthyans, with cellular bone representing a synapomorphy of mandibulate gnathostomes and osteostracans.

Outside of osteostracans, the most cited alternatives for the closest jawless relatives of gnathostomes are anaspids and thelodonts. Thelodonts have been proposed as a gnathostome sister group (Turner, 1991), or even a grade with respect to jawed vertebrates (Wilson & Caldwell, 1998). This hypothesis emphasizes their monocuspid, 'placoid-like' scales with a basal pore: morphology evocative of that found in chondrichthyans. Thelodonts have paired appendages that have a controversial interpretation. The most conservative approach for our present investigation is to accept these structures as primary homologues (*sensu* De Pinna, 1991) of gnathostome and osteostracan paired appendages (i.e. they should be coded the same way in cladistic matrices; see also Wilson, Hanke & Märss, 2007). Thelodonts, like gnathostomes, also bear pharyngeal denticles (Van der Brugghen & Janvier, 1993; Smith & Coates, 2000, 2001; Rücklin *et al.*, 2011). However, the small size of these structures, the state of preservation of many early vertebrate fossils, and the quality of preparation needed to reveal them suggests that determining absence of this trait is difficult (Brazeau, 2012).
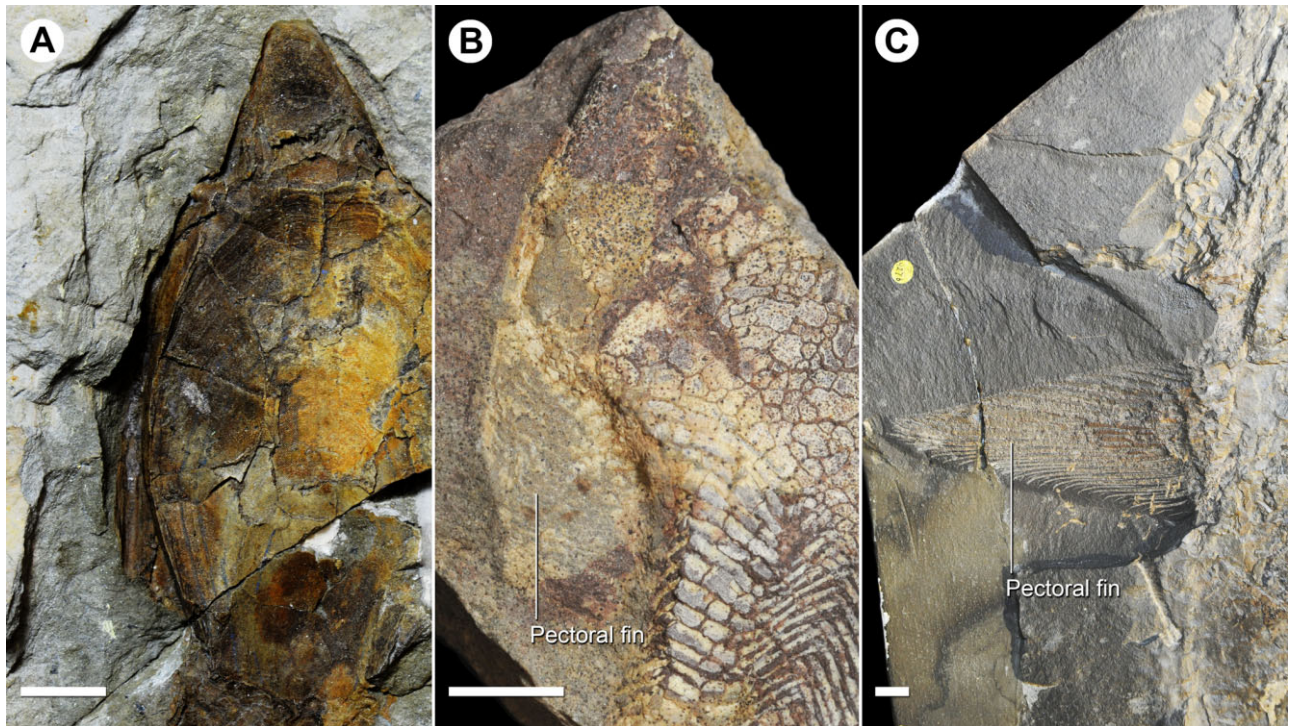
Figure 3. Pectoral fins of stem and crown gnathostomes. A, *Errivaspis waynensis*, NHMUK P.17477, a heterostracan lacking paired fins. B, *Hemicyclaspis murchisoni*, NHMUK P.8816, an osteostracan with paired fins. C, *Cladoselache* sp., NHMUK P.9276, a crown gnathostome and chondrichthyan with paired fins. Scale bars = 10 mm.
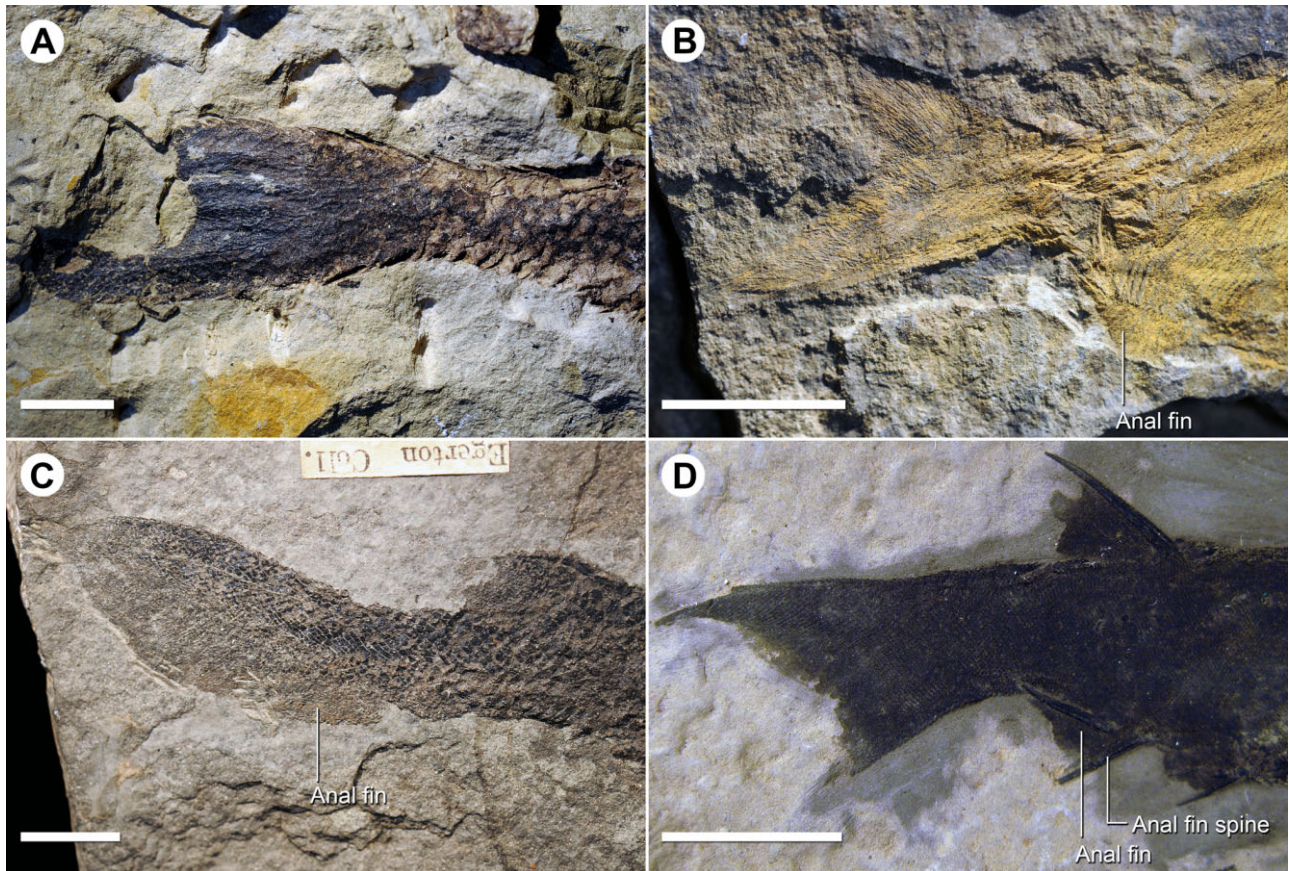
Figure 4. Tail geometry of stem and crown gnathostomes. A, *Errivaspis waynensis*, NHMUK P.17477, a heterostracan. B, *Birkenia* sp., NHMUK P.42020 (image reversed), an anaspid. C, '*Cephalaspis*' *powriei*, NHMUK P.670, an osteostracan. D, *Promesacanthus eppleri*, UALVP 42652, an acanthodian. Scale bars = 10 mm.

Most phylogenetic analyses do not recover sister-group relationships between thelodonts and mandibulate gnathostomes (Forey & Janvier, 1993; Donoghue *et al*., 2000; Donoghue & Smith, 2001; Shu *et al*., 2003; Gess, Coates & Rubidge, 2006), as they share few features that cannot be shown to be generalized traits of the gnathostome total group. We are concerned that thelodont/gnathostome sister-group hypotheses arise from characters given a privileged status because they are found in some shark-like chondrichthyans, perhaps under the supposition that a shark-like form is primitive for jawed vertebrates as a whole (Friedman & Brazeau, 2013).

Maisey (1986) alternatively outlined characters uniting anaspids and mandibulate gnathostomes to the exclusion of osteostracans. Most of these characters are either indirect proxies for other characters (horizontal septum, fin radials), are not generally found in gnathostomes (gular plates, dermal fin rays; Friedman & Brazeau, 2010), or do not exclude other jawless fishes such as osteostracans (circumorbital plates; e.g. *Superciliaspis*, Dineley & Loeffler, 1976; Adrain & Wilson, 1994).

Two other groups of jawless fishes must also be considered here: Galeaspida and Pituriaspida. Galeaspids resemble osteostracans in overall appearance, but have paired nasal capsules (amphirhini) and a buccohypophyseal opening in the mouth (Gai *et al*., 2011). In these respects, they resemble gnathostomes to the exclusion of other jawless fishes (but see evidence for paired nasal capsules in pteraspidomorphs; Janvier & Blieck, 1979; Gagnier, 1993), including osteostracans. They are an important complement to osteostracans and we consider their morphology where possible. Nevertheless, galeaspids lack cellular bone (although the endocranium is mineralized) and paired pectoral fins. Pituriaspids (Young, 1991) also resemble osteostracans, particularly in having paired postbranchial fenestrae, most reasonably interpreted as articulation sites for pectoral fins. Paired posterior ventrolateral projections of the carapace of pituriaspids even hint at the possibility of pelvic fins.

Unfortunately, pituriaspids are known only as natural moulds and so no precise details of their hard tissues can be considered. Aspects of their endocranial anatomy arepreserved in the moulds, but there is some uncertainty of interpretation.

We are not dismissing the importance of any agnathan group for understanding the characters of early gnathostomes. Furthermore, we emphasize that none of the 'ostracoderms' – including our selected outgroup – can serve as a surrogate ancestor for jawed vertebrates. Each group of armoured agnathans contributes to our understanding of this problem in complementary and significant ways. Nevertheless, preference for alternative, non-osteostracan sister groups seems to stem from dissatisfaction with osteostracans as proxy gnathostome ancestors. For instance, Goujet & Young (1995) considered but dismissed osteostracans as a useful placoderm outgroup, arguing that these taxa are so divergent as to preclude sound comparative study. However, subsequent authors (Janvier, 1996a, b; Brazeau, 2009) have shown that this is not the case. As Janvier (1996b: 269) noted, it is remarkable that Stensiö (1925, 1969) was unimpressed by the similarities between the placoderm *Macropetalichthys* and osteostracans, possibly dismissing shared characteristics as general craniate features. We elaborate on the importance of these shared similarities below.

PHYLOGENETIC BACKBONE ASSUMPTIONS

We can combine the above information with progress on the cladistic relationships of modern gnathostomes. We see broad agreement between molecular and morphological studies of early gnathostome interrelationships (Nelson, 1969; Wiley, 1979; Maisey, 1986; Takezaki *et al.*, 2003; Blair & Hedges, 2005; Chen *et al.*, 2012) as an ideal starting point for debating the relationships of problematic fossils. We therefore posit the following assumptions in order to derive our conclusions (Fig. 1).

1. Gnathostomata is a monophyletic group and its crown group comprises Osteichthyes and Chondrichthyes.
2. Chondrichthyes (comprising total groups Elasmobranchii and Holocephali) and Osteichthyes (comprising total groups Sarcopterygii and Actinopterygii) are reciprocally monophyletic, and thus constitute each others' extant sister groups. Neither is 'more basal' than the other.
3. Osteostracans are the sister group of all mandibulate gnathostomes. We consider conclusions drawn in this paper to be robust to an alternative scenario in which galeaspids and

osteostracans are sister groups. All other jawless vertebrates are taken to be more distant relatives of crown gnathostomes.

INSTITUTIONAL ABBREVIATIONS

NMS, National Museums of Scotland; NHMUK, Natural History Museum, UK; UALVP, University of Alberta Laboratory of Vertebrate Paleontology.

THE CHARACTERS OF GNATHOSTOMES

CHARACTERS THAT CAN PLACE A TOTAL GROUP MEMBER CROWNWARD OF SOME 'OSTRACODERMS'

The following characters place a vertebrate within the gnathostome total group, to the exclusion of a series of jawless groups: anaspids, heterostracans, and thelodonts. In practice, these features unite galeaspids, osteostracans, and possibly pituriaspids, or some subset of these, with jawed vertebrates.

Primary skeleton

Endoskeletal mineralization is widely distributed amongst vertebrates, including jawed forms (Donoghue *et al.*, 2006) and several jawless groups: *Eriptychius* (Denison, 1967; Smith & Hall, 1990), *Euphanerops* (Janvier & Arsenault, 2002), osteostracans (Janvier, 1985a, b), galeaspids (Halstead, 1979; Zhu & Janvier, 1998, Wang *et al.*, 2005), and quite possibly pituriaspids (Young, 1991). Extensive mineralization of the braincase is, however, limited to the latter three agnathan groups plus jawed vertebrates.

Perichondral ossification (Fig. 5) of the endoskeleton is a feature shared by osteostracans and jawed vertebrates (Donoghue *et al.*, 2006). The extensive endoskeletal mineralization of galeaspids appears to be composed of calcified cartilage, a more generalized tissue within vertebrates (Wang *et al.*, 2005). Pituriaspids are only known as mouldic fossils (Young, 1991), so the nature of the hard tissues surrounding the neurocranium in this group remains unknown. However, impressions of structures that are at least partially interpretable in terms of an endocast suggest that there was probably some endocranial mineralization in pituriaspids as well.

Osteostracans and jawed vertebrates share, to the exclusion of galeaspids and all other agnathans, perichondral mineralization of the sclerotic capsule. Within jawed vertebrates, the ossified capsule is most clearly present in some placoderms (e.g. Burrow, Jones & Young, 2005; Young, 2008). The 'sclerotic rings' of actinopterygian osteichthyans also appear to represent endoskeletal mineralization of the cartilaginous sclerotic capsule (Gardiner, 1984b; Franz-Odendaal, 2011). Outside of osteostracans and
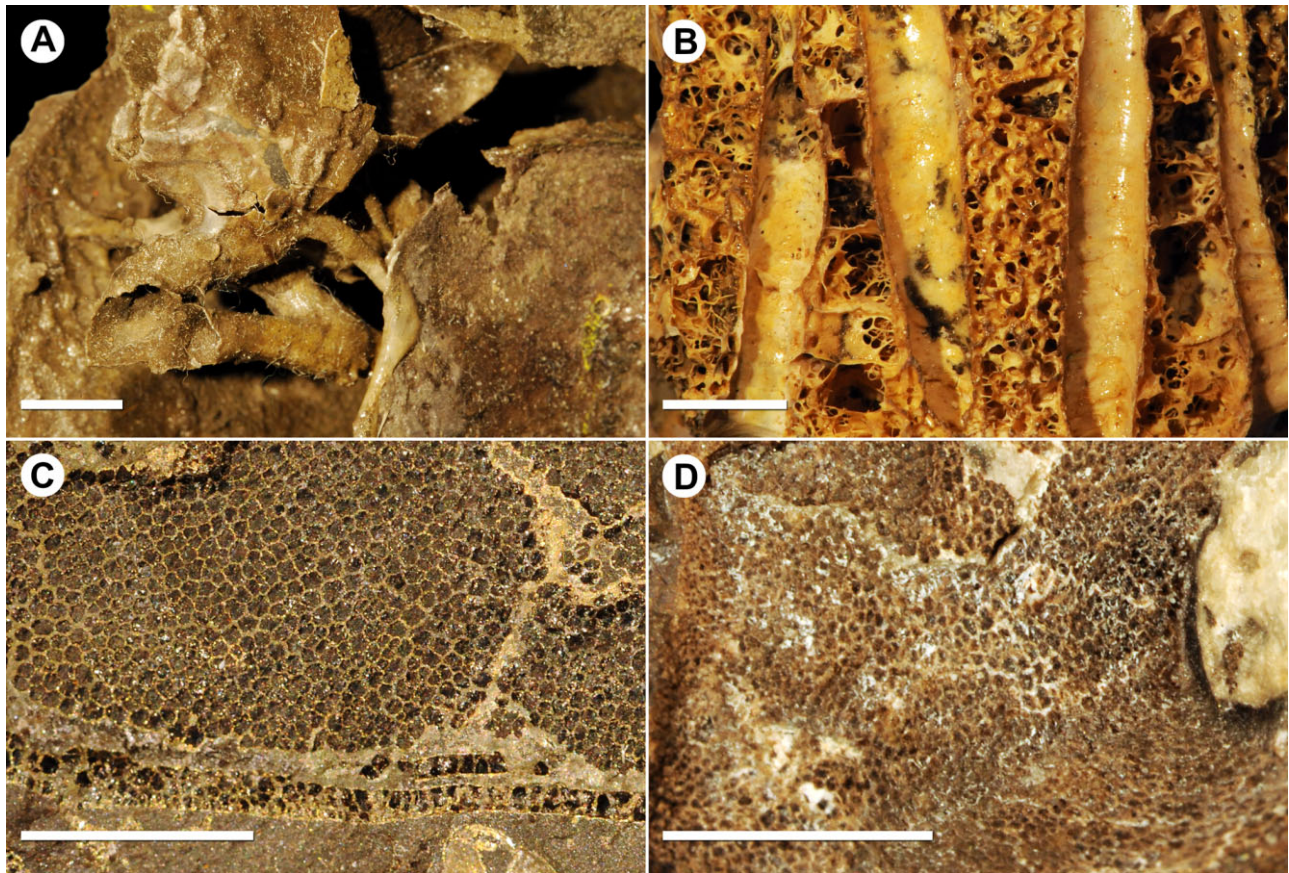
Figure 5. Endoskeletal mineralization of gnathostomes. A, *Buchanosteus confertituberculatus*, NHMUK P.48675, an arthrodire placoderm. Fractured postorbital process/lateral commissure showing perichondral lining of canals, but absence of endochondral ossification. B, *Griphognathus whitei*, NHMUK P.52574, a crown osteichthyan and crown sarcopterygian. Ethmoid region showing perichondrally lined canals for olfactory tracts, surrounded by endochondral ossification. C, *Tristychius arcuatus*, NHMUK P.57305/6, a crown chondrichthyan and stem elasmobranch. Fragment of cranial skeleton showing prismatic calcified cartilage. D, *Helodus simplex*, NHMUK P.8212, a crown chondrichthyan and stem holocephalan. Basicranial region showing prismatic calcified cartilage. Scale bars = 5 mm.

jawed vertebrates, mineralized sclerotic capsules are present in the Ordovician arandapsid *Sacabambaspis* (Gagnier, 1993), a taxon generally allied with heterostracans (Sansom, Donoghue & Albanesi, 2005). If placements of arandaspids as amongst the most distant stem gnathostomes from the gnathostome crown are correct, the mineralized sclerotic capsules of *Sacabambaspis* and jawed vertebrates plus osteostracans are most parsimoniously interpreted as convergent.

Dermal skeleton
Dermal sclerotic rings are found in osteostracans (e.g. Ritchie, 1967; Janvier, 1985a, b) and representatives of all traditional divisions of jawed vertebrates (placoderms: Denison, 1978; acanthodians: Denison, 1979; Burrow *et al*., 2011; chondrichthyans: Maisey, 2007; osteichthyans: Jarvik; 1980), and have been

interpreted as a character uniting these groups (Janvier, 1984, 2001). Such ossifications are absent in anaspids (Blom & Märss, 2010), thelodonts (Märss, Turner & Karatajute-Talimaa, 2007), galeaspids (Gai *et al*., 2011), and heterostracans (Janvier, 1996a). Outside of jawed vertebrates and osteostracans, sclerotic rings have only been reported in *Sacabambaspis* (Gagnier, 1993). As with the presence of perichondral mineralization of the sclerotic capsule, the presence of a dermal sclerotic ring in *Sacabambaspis* is possibly convergent with examples in jawed vertebrates and osteostracans.

Cellular bone is characterized by spaces for osteoblasts within the bony matrix. It is present in osteichthyans, acanthodians, placoderms, and osteostracans (Donoghue *et al*., 2006; Sire, Donoghue & Vickaryous, 2009), but absent in chondrichthyans (see Sire *et al*., 2009; Giles *et al*., 2013). Cellular

bone is usually absent in anaspids, thelodonts, and pteraspidomorphs. However, I. Sansom *et al.* (2013) recently described cellular dentine in isolated micro-vertebrate remains attributed to pteraspidomorphs. Perichondral bone identified in the Carboniferous chondrichthyan *Akmonistion* is described as acellular (Coates *et al.*, 1998). Bone has been identified in *Scyliorhinus* (Peignoux-Devill, Lallier & Vidal, 1982) and described as acellular. However, these same studies mention the presence of osteocytes within the bone matrix. Nevertheless, some doubts have been raised about the identification of these tissues in extant chondrichthyans as bone (Clement, 1992). If the identification of bone in chondrichthyans is correct, the acellularity of bone in chondrichthyans would be an anatomically generalized trait, not limited to the exoskeleton.

Fins
Hypocercal tails (Fig. 4) are found in most jawless fishes: lampreys (Marinelli & Strenger, 1954), euconodonts (Donoghue *et al.*, 2000), anaspids (Blom & Märss, 2010), heterostracans (Pradel *et al.*, 2007; Mark-Kurik & Botella, 2009), and thelodonts (Märss *et al.*, 2007) (for a review, see Pradel *et al.*, 2007). Caudal-fin structure remains unknown in pituriaspids and in galeaspids; it is unclear whether the hetero-cercal tails of galeaspids (e.g. *Sanqiaspis*, Liu, 1975) are are hypo- or epicercal. Osteostracans are the only agnathans in which an epicercal tail has been reliably identified, and it is therefore a feature that unites them with mandibulate gnathostomes (Fig. 4).

Complementing the epicercal caudal fin of jawed vertebrates is the anal fin (Fig. 4). In osteostracans, a narrow lobe that is closely applied to the caudal lobe is comparable to the anal fin of jawed verte-brates. In jawed vertebrates, these fins are separated by a broad gap or a deep notch. However, notable exceptions include certain 'acanthodians', such as *Brochoadmones* (Hanke & Wilson, 2006). Outside of these two groups, anal fins are only known in anaspids and *Euphanerops*, in which they are combined with a hypocercal caudal fin (Blom & Märss, 2010). There is no evidence of anal fins in heterostracans (Janvier, 1996a) or arandaspids (Pradel *et al.*, 2007). Extant agnathans are frequently considered as lacking anal fins (Marinelli & Strenger, 1954, 1956), but anal fins in specimens of lamprey have been reported (Vladykov, 1973; Vladykov & Kott, 1980). The condition in pituriaspids and galeaspids cannot be assessed owing to a lack of suitable postcranial material, whereas anal fins are variably present in thelodonts (Märss *et al.*, 2007). Dorsal fins are characterized by a similar pattern of distribution, being found in early representatives of all groups of jawed vertebrates (Denison, 1978, 1979; Jarvik,

1980; Zangerl, 1981), as well as many osteostracans (Heintz, 1967; Ritchie, 1967; Adrain & Wilson, 1994; Keating, Sansom & Purnell, 2012) and thelodonts (Caldwell & Wilson, 1995). However, the polarity of this character is complicated by the presence of dorsal fins in lampreys (Marinelli & Strenger, 1954).

An additional fin character unites some agnathans with jaw-bearing forms to the exclusion of other vertebrates: paired pectoral appendages (Fig. 3). Amongst jawless fishes, pectoral fins and their inter-nal skeletons are best known in osteostracans (Janvier, Arsenault & Desbiens, 2004; the absence of such structures in tremataspids is generally inter-preted as secondary; Janvier, 1996a; Sansom, 2009). Large fenestrations in the dermal carapace, located in a position comparable to the pectoral fins of osteostracans and bounded anteriorly by spine-like projections, represent circumstantial evidence for similar appendages in pituriaspids (Young, 1991). Remains of the fins themselves, however, are unknown.

Paired fins are also present in *Euphanerops*, anaspids, and some thelodonts. *Euphanerops* is unique in having what appears to be a paired anal fin, or at least an anal fin supported by paired cartilages (R. Sansom *et al.*, 2013). Anaspid paired fins differ considerably from the short-based appendages common to pituriaspids, osteostracans, and jawed vertebrates. The long-based anaspid examples extend the length of the flank from their anterior insertion at the rear of a triradiate postbranchial spine to their posterior termination near the level of the anal fin (Blom & Märss, 2010). By contrast, the paired appendages of the thelodont *Turinia* (see Donoghue & Smith, 2001) do not differ appreciably in either gross form or position from those found in early osteostracans (e.g. *Ateleaspis*; Ritchie, 1967). Character-mapping exercises using most hypotheses of agnathan inter-relationships (Donoghue *et al.*, 2000; Gess *et al.*, 2006) indicate that the paired appendages of anaspids are convergent with those of osteostracans and jawed vertebrates, but are equivo-cal concerning the status of thelodont pectoral fins relative to those found in gnathostomes.

Summary
We regard the following as features that unite some groups of armoured jawless vertebrates with jawed vertebrates to the exclusion of other 'ostracoderms'.

1. Perichondral bone (Fig. 5A, B).
2. Endoskeletal mineralization of sclerotic capsule.
3. Epicercal caudal fin (Fig. 4C, D).
4. Anal fin (Fig. 4B–D).
5. Paired fins (Fig. 3B, C).
6. Dermal sclerotic ring.

Neurocranium

Jawed vertebrates share a series of neurocranial features unknown in proximate agnathan outgroups. In shark-like chondrichthyans (Maisey, 2005, 2007; Maisey *et al.*, 2009), actinopterygians (Gardiner, 1984b), and *Acanthodes* (Miles, 1973b; Davis *et al.*, 2012), the neurocranium exhibits a well-developed lateral projection where the orbits meet the otic capsules (Figs 6, 7), termed the postorbital process. The process termed an 'anterior postorbital process' in arthrodires (Goujet, 1984a) and some other placoderms (Stensiö, 1969; Ørvig, 1975) supports the hyoid arch articulation. Its anterior surface therefore delimits the posterior boundary of the spiracular chamber and it cannot be interpreted as a postorbital process equivalent to those of osteichthyans and chondrichthyans, in which the extension is anterior to the spiracular space. Rather, we see the 'supraorbital

process' of certain arthrodires (e.g. *Kujdanowiaspis*, see Stensiö, 1963; Goujet, 1984a) as potentially equivalent. A postorbital process is apparently absent in most sarcopterygians (Jarvik, 1980). The equivalent position in most fish-like sarcopterygians excluding dipnoans (Miles, 1977; Friedman, 2007b) is marked by the intracranial joint. A structure termed the postorbital pillar is described in some stem sarcopterygians and *Styloichthys* (Yu, 1998; Zhu, Yu & Ahlberg, 2001; Zhu & Yu, 2002). Although not as pronounced as in other gnathostomes, the postorbital pillar is a projection anterior to the spiracular region that forms a posterior boundary to the orbit, straddles the jugular vein, and joins the basipterygoid articulation ventrally. It can be related to the postorbital process on the basis of multiple conditions. We therefore consider the postorbital process a generalized feature of crown-group gnathostomes. This argument echoes the identification of a postorbital pillar in *Entelognathus* by Zhu *et al.* (2013).

Orbital morphology of most crown gnathostomes contrasts with the condition in osteostracans, in
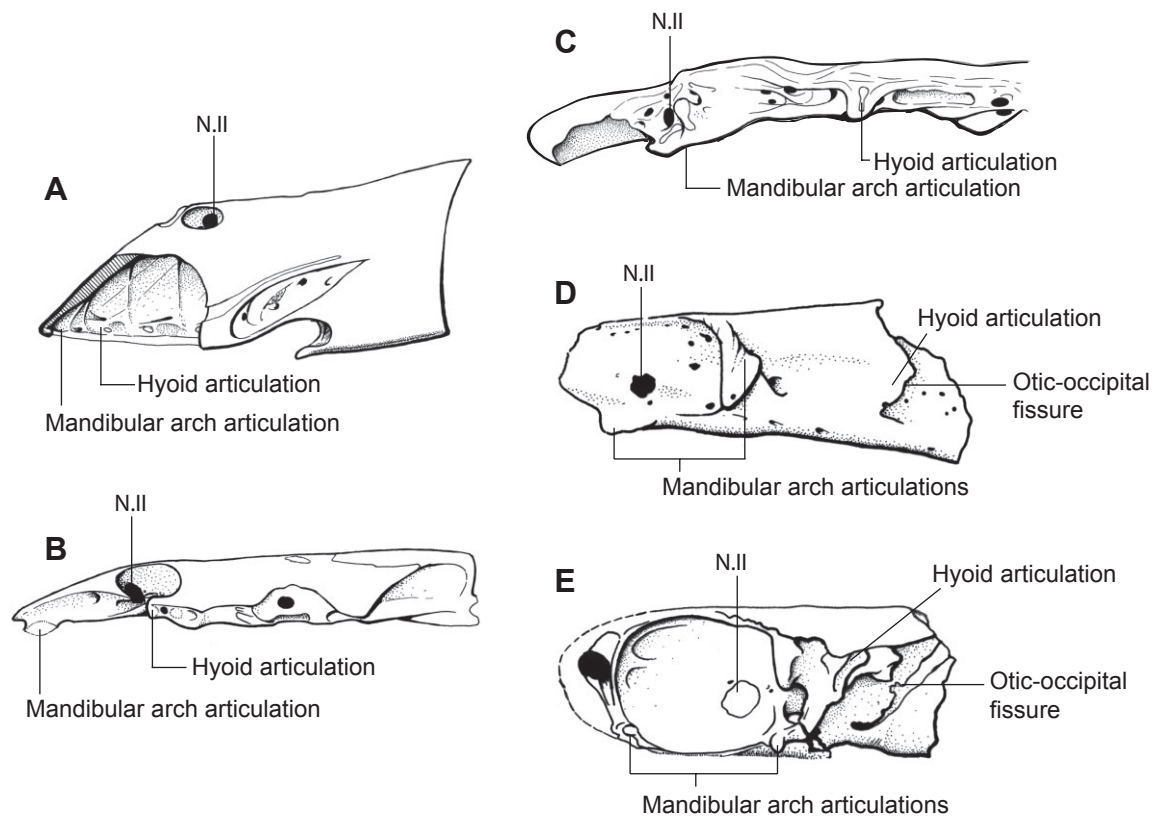
Figure 6. External neurocranial anatomy in lateral view. A, *Norselaspis*, an osteostracan (after Janvier, 1981b). B, *Macropetalichthys*, a petalichthyid placoderm (after Stensiö, 1969; Young, 1980). C, *Dicksonosteus*, an arthrodire placoderm (after Goujet, 1984a). D, *Cladodoides*, a chondrichthyan (after Maisey, 2005). E, *Mimpiscis*, a crown osteichthyan and actinopterygian (after Gardiner, 1984b). Abbreviation: N.II, opening for the optic tract (second cranial nerve). Not drawn to scale.
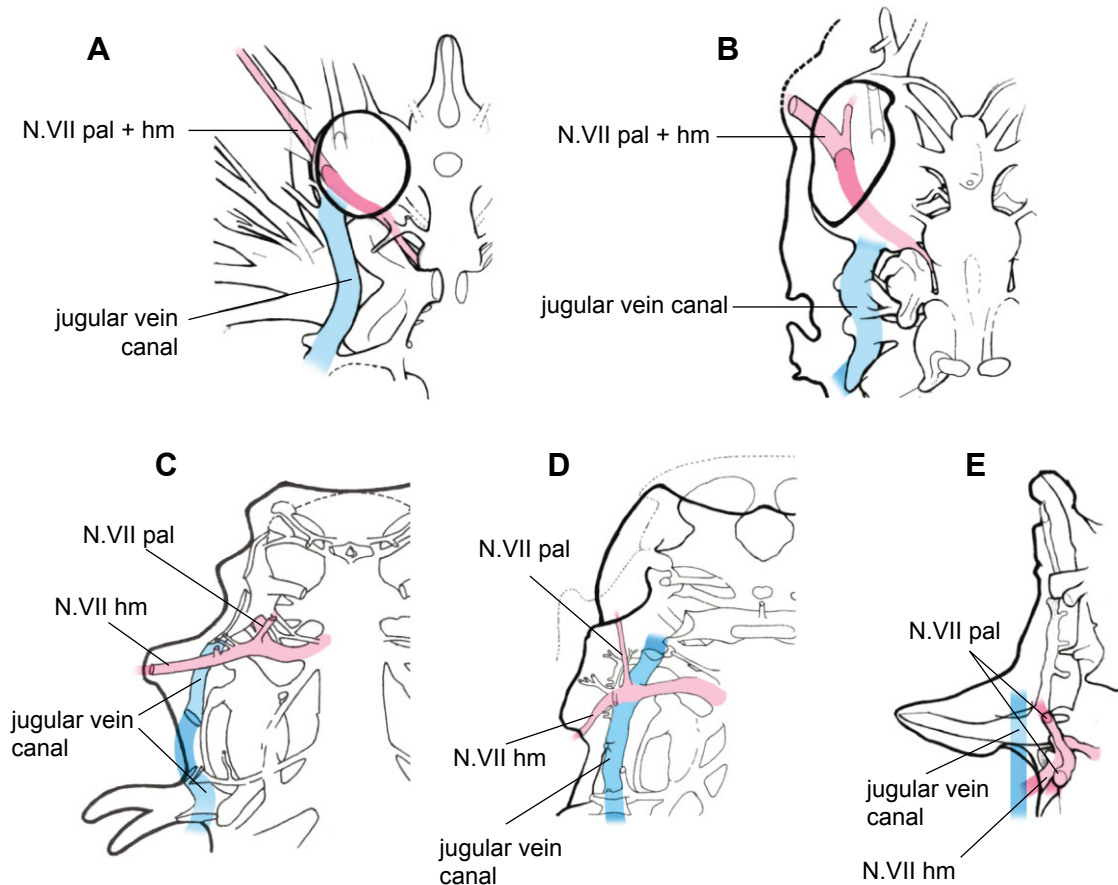
Figure 7. Endocranial cavities of various gnathostomes. A, *Benneviaspis*, an osteostracan (after Janvier, 1985a). B, *Brindabellaspis*, a placoderm (after Young, 1980). C, *Kujdanowiaspis*, an arthrodire placoderm (after Goujet, 1984a). D, *Buchanosteus*, an arthrodire placoderm (after Young, 1979). E, *Cladodoides*, a crown gnathostome and chondrichthyan (after Maisey, 2005). A, B, in dorsal view. C, D, E, in ventral view. Abbreviations: N.VII, canal or openings for the facial nerve (seventh cranial nerve); hm, hyomandibular branch; pal, palatine branch. Not drawn to scale.

which the orbit is surrounded by a broad lateral expansion of the braincase (Fig. 7). As noted by Janvier (1996b) and Brazeau (2009), a similar condition is seen in *Macropetalichthys* (Stensiö, 1925, 1969) and petalichthyid-like forms such as *Brindabellaspis* (Young, 1980) amongst presumed mandibulate gnathostomes. A notable non-placoderm example is the early chondrichthyan *Doliodus* (Maisey *et al.*, 2009). However, given the fact that these expansions are not seen in any other crown gnathostome, we consider the condition in *Doliodus* to be secondarily derived. The phylogenetic interpretation of petalichthyid-like gnathostomes is less clear, and the condition found in such taxa could easily be interpreted as a plesiomorphy shared primitively with osteostracans (Janvier, 1996b; Brazeau, 2009).

The facial nerve (nerve VII) of vertebrates has several branches, including a somatic sensory hyomandibular branch and a visceral sensory pala-

tine branch. Canals accommodating this division can be seen in the cranial endocasts of a number of Palaeozoic vertebrates: chondrichthyans (Schaeffer, 1981; Maisey, 2005, 2007), osteichthyans (Jarvik, 1980; Gardiner, 1984b), and arthrodires (Stensiö, 1963; Young, 1979; Goujet, 1984a). In these forms, the facial nerve divides into its several branches behind the orbit, deep to the postorbital process (Fig. 7C–E). This contrasts with the condition in osteostracans (Janvier, 1981b, 1985a), in which the facial nerve is undivided as it passes into the orbit and along or beneath the orbital floor (Fig. 7A). Its division, consistent with the placement of the hyoid arch (Fig. 6), is outside of the postorbital region. The condition is somewhat different in galeaspids (Gai *et al.*, 2011), but the precise position of the facial nerve division is not clear. It does not appear to have been medial to the passage of the jugular vein (as it is in crown gnathostomes). However, the hyoid arch is positioned

immediately posteroventral to the orbit. Thus, the branching of the facial nerve may be more posteriorly placed than in osteostracans.

Amongst presumed mandibulate gnathostomes, the facial nerve of *Brindabellaspis* (Young, 1980) and *Macropetalichthys* (Stensiö, 1925, 1969) passes through the orbital floor (Fig. 7B), with the hyomandibular branch exiting through the lateral wall of the orbit. In *Brindabellaspis*, the division is within the orbital floor. In *Macropetalichthys*, it appears to have been within the orbit itself. This closely resembles conditions in osteostracans, and contrasts with the arrangement found in arthrodires, *Romundina*, and all known crown-group gnathostomes, in which the division is as described above (Janvier, 1996b; Brazeau, 2009). We regard division of the facial nerve deep to the postorbital process as a probable synapomorphy uniting a subset of jawed vertebrates.

Potentially related to the above characters is the position for the articulation of the hyoid arch on the braincase (Fig. 6). In osteostracans, the hyoid and mandibular arches articulate in the anterior region of a broad rostral expansion of the braincase and cranial shield (Fig. 6A). A similar expansion is developed in some placoderms to a varying degree. The hyoid arch of galeaspids attaches in a mostly sub- or postorbital position. The hyoid arch of *Macropetalichthys*, *Brindabellaspis*, and ptyctodont placoderms attaches to the braincase in a position that is either immediately lateral or anterior to the orbit (Fig. 6B). This position is anatomically intermediate between the condition seen in osteostracans and the condition apparent in crown-group gnathostomes and arthrodires, in which the hyoid arch attaches behind the orbit (Fig. 6C–E). Although we retain this character here, we caution that it may be directly linked to aspects of orbital morphology and facial nerve orientation.

The saccular cavity of the gnathostome skeletal labyrinth bears a diverticulum, termed the utricular recess, where the ampullar chambers of the anterior semicircular canal and the horizontal semicircular canal join it. This chamber is obvious in chondrichthyans (Schaeffer, 1981; Maisey, 2005, 2007), arthrodires (Stensiö, 1963, 1969), *Macropetalichthys* (Stensiö, 1925, 1969), *Acanthodes* (Davis *et al.*, 2012), and osteichthyans (Jarvik, 1980). There is no evidence of the utricular recess in either osteostracans (Janvier, 1981b, 1985a) or galeaspids (Gai *et al.*, 2011), and we regard this as the primitive gnathostome condition. The utricular recess was reported absent in *Brindabellaspis* and indistinct in *Jagorina* by Young (1980: 32). We submit that the utricular recess could be biologically related to the origin of a horizontal semicircular canal, which is absent in all known jawless vertebrates. However, we note that the identification of such a diverticulum of the anterior end of the saccular chamber is not dependent on the presence of both an anterior and horizontal canal. Thus, the diverticulum can be absent in a comparable manner in vertebrates with only two semicircular canals.

The jugular vein passes posteriorly from the orbit and laterally along the otic capsules. In crown-group gnathostomes and living agnathans, this vein is not invested in the neurocranium along the lateral sides of the otic capsules (Fig. 7E). However, in osteostracans (Janvier, 1981b, 1985a), galeaspids (Gai *et al.*, 2011), and certain placoderms (*Brindabellaspis*, Young, 1980; *Jagorina*, Stensiö, 1969; partially in *Macropetalichthys*, Stensiö, 1925, 1969; and *Buchanosteus*, Young, 1979), the jugular vein was completely invested in the otic sidewall (Fig. 7A, B, D). In many arthrodire placoderms (Stensiö, 1963, 1969; Goujet, 1984a) and in *Romundina* (Ørvig, 1975), the course of the jugular vein is uninvested laterally (Figs 6C, 7C), and situated in a deep groove in the otic side wall. We conclude that the invested condition of the jugular vein represents a transient condition along the gnathostome stem, with the presence of an exposed jugular vein representing a character uniting crown-group gnathostomes and some stem-group members.

Paired nasal capsules are a feature common to all jawed vertebrates, and thus merit some consideration here because modern outgroups lack this feature (see Janvier, 1993). Notably, osteostracans lack paired nasal openings and have a single, median, nasohypophyseal opening in the skull, resembling modern hagfish and lamprey. Recently, Gai *et al.* (2011) reported on the paired nasal capsules in a Siurian galeaspid from China. Placing osteostracans as the sister group of gnathostomes to the exclusion of galeaspids suggests an ambiguous distribution for this character. Either paired nasal capsules evolved twice (two steps) or were gained once and lost in osteostracans (two steps). Resolving this dichotomy is not simple because impressions of paired nasal capsules or paired openings are reported in pteraspidomorphs (e.g. Janvier & Blieck, 1979; Gagnier, 1993). Owing to the uncertain optimisation of this character, we have chosen to omit it from our list until future work resolves this issue.

Visceral arches, including palatoquadrate and Meckelian element

The most conspicuous synapomorphy of gnathostomes is dorsoventrally opposing jaws. This directional qualification is significant, given the presence of a lateral bite in living agnathans (Yalden, 1985; Clark & Summers, 2007) and conodonts (Purnell, 1994; Purnell & Donoghue, 1997; Donoghue & Purnell,

1999). The jaws of gnathostomes are further equipped with dermal ossifications bearing denticles.

Gnathostomes are also united by the presence of five or fewer gill arches. Exceptions to this pattern include hexanchiform neoselachians (six- and seven-gilled sharks), in which conditions are clearly secondary (Maisey, Naylor & Ward, 2004). Jawless fishes generally have higher numbers of gill arches, although counts vary considerably both amongst and within agnathan groups. Hagfishes bear between five and 15 gill arches, with some species showing variation in number, whereas lampreys have seven arches. Counts in extinct agnathans are less well constrained, and can often be estimated only for a few exemplars. In his review of gill-arch structure in vertebrates, Janvier (2004) reported the following values: 11 to 20 for arandaspids, eight for astraspids, six to 15 for anaspids, seven to nine for thelodonts, five to 45 for galeaspids, and eight to ten for osteostracans.

Fins
In addition to pectoral appendages, a more posteriorly placed set of paired appendages, pelvic fins, are known only in jawed vertebrates. Earlier authors (Johanson, 2002; Friedman, 2007a; Brazeau, 2009) have emphasized the absence of pelvic fins as excluding antiarchs from closer relationships between other placoderms and the gnathostome crown. Zhu *et al.* (2012b) subsequently reported a pelvic girdle in the Early Devonian antiarch *Parayunnanolepis*, suggesting that this structure may have been primitively present in the clade. Young (2010: 538) argued that

because most placoderms have pelvic girdles, the absence of these structures, even in non-antiarchs such as *Lunaspis*, 'can only be interpreted as secondary loss'. We do not find this persuasive, as it employs the specious argument that the most common character state within a group must be primitive (Watrous & Wheeler, 1981; Farris, 1982). Regardless of the precise optimization of this character, it is clear that the presence of pelvic fins unites the gnathostome crown group and its nearest sister taxa to the exclusion of agnathans.

Summary
The monophyly of jawed vertebrates is supported by the following hard-tissue characters. Dermal denticle plates on mandibular cartilages are discussed in a later section along with teeth. Many of these features would require homoplasy if the placoderms are treated as a clade (marked with a superscript 'P').

7. Dorsoventrally opposing jaws (Fig. 9).
8. Dermal denticle plates on mandibular cartilages (Fig. 9).
9. Pelvic fins.
10[P]. Postorbital process (Figs 7C–E, 8).
11[P]. Deep branching of nerve VII (Fig. 7C–E).
12[P]. Articulation of hyoid arch with neurocranium posterior to orbit (Fig. 6)
13[P]. Utricular recess.
14. Horizontal semicircular canal.
15[P]. Uninvested jugular canal lateral to otic capsule (i.e. discrete lateral commissure; Fig. 7C–E).
16. Five or fewer branchial arches.
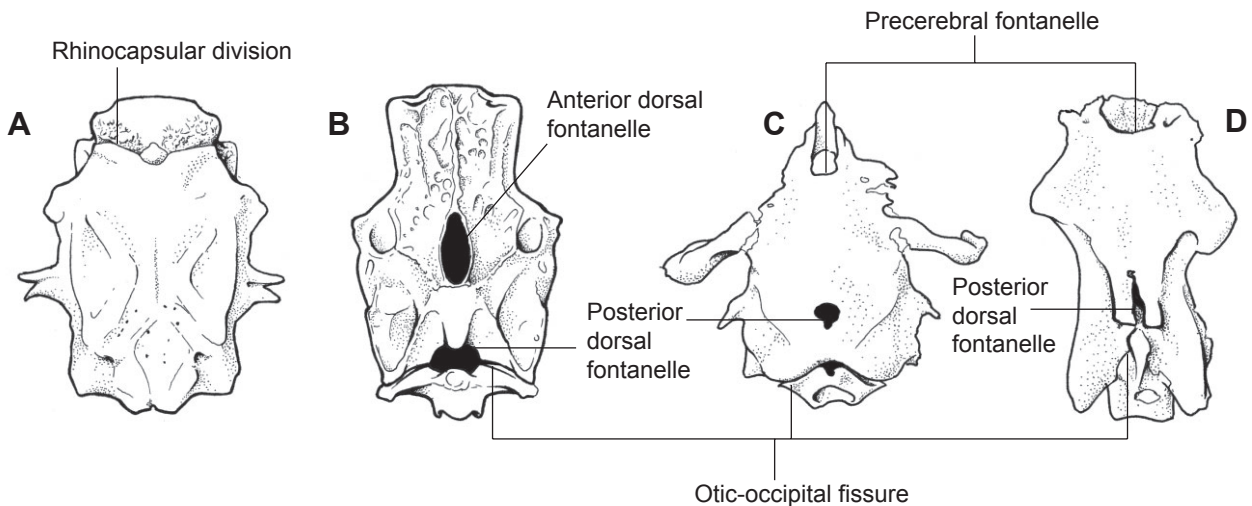
Figure 8. Gnathostome neurocrania in dorsal view. A, *Dicksonosteus*, an arthrodire placoderm (after Goujet, 1984a). B, *Lawrenciella*, a crown osteichthyan and crown actinopterygian (after Hamel & Poplin, 2008). C, cf. *Cobelodus*, a chondrichthyan and possible stem holocephalan (after Maisey, 2007). D, *Orthacanthus*, a chondrichthyan and possible stem elasmobranch (after Schaeffer, 1981).

CANDIDATE SYNAPOMORPHIES OF PLACODERMS

Two characters are unique to placoderms, irrespective of the relationships of other gnathostomes, and the osteostracan/galeaspid outgroup.

Neurocranium

In nearly all placoderms for which there is well-preserved neurocranial material, there is a discrete division between the rhinocapsular ossification and the rest of the braincase (Fig. 8A; Stensiö, 1963, 1969; Denison, 1978; Goujet, 1984a; Young, 1986). This contrasts with chondrichthyans (Schaeffer, 1981; Maisey, 2005, 2007; Maisey *et al*., 2009), osteichthyans (Jarvik, 1980; Gardiner, 1984b), osteostracans (Janvier, 1985a, b), and galeaspids (Gai *et al*., 2011), in which such a division is absent. Interestingly, this character has been dismissed as a placoderm synapomorphy in favour of being a generalized vertebrate character (Goujet, 2001). This argument is based on the separate chondrification of the nasal capsules in vertebrate embryos. However, in neither galeaspids, osteostracans, nor crown-group gnathostomes does such a discrete division persist in adult forms, and this persistence may itself be apomorphic. Nevertheless, the nasal capsules of many crown gnathostomes, such as *Acanthodes* (Miles, 1973b; Davis *et al*., 2012) and chondrichthyans, may be unmineralized or incompletely mineralized (Schaeffer, 1981). Thus, separate mineralization may be more generalized (Friedman, 2007a; Brazeau, 2009). However, we recommend that the specific placoderm condition be reinstated to future analyses of mandibulate gnathostomes because it is clear that the discrete, perichondrally lined division is absent in other non-placoderm gnathostomes, osteostracans, and galeaspids.

Dermal skeleton

We retain semidentine as a possible synapomorphy of Placodermi with some reservations. The presence of polarized, matrix-bound cell spaces in the dentinous tissues of placoderm dermal bones could be interpreted as intermediate in type between mesodentine, in which the cells are matrix bound but not polarized, and (ortho)dentine in which the cells are contained in a pulp cavity but have polarized canaliculi (cf. Ørvig, 1967; but see Sire *et al*., 2009). We note that work in progress on placoderm histology has found that characterization of semidentine in many taxa is problematic, and interpretations of this tissue type can vary depending on the orientation of histological sections and the methods used to visualize them (S. Giles, pers. comm., 2013; see also Giles *et al*., 2013: 639).

Summary

Two characters could most parsimoniously be interpreted as placoderm synapomorphies under our explicit, outgroup-based approach:

17. Perichondral division of orbitonasal unit (Fig. 8A).
18. Polarized, matrix-bound dentine cell spaces (semidentine).

CHARACTERS THAT CAN PLACE A FOSSIL IN THE GNATHOSTOME TOTAL GROUP, CROWNWARD OF ANY PLACODERM

Characters in this section concern traits found in both osteichthyans and chondrichthyans and which have logical alternatives in jawless vertebrates and placoderms. They therefore imply placement of a fossil crownward of any known mandibulate stem gnathostome.

Neurocranium

Several features of the braincase unite Osteichthyes and Chondrichthyes to the exclusion of placoderms and agnathans. Most of these have been covered in detail elsewhere (e.g. Schaeffer, 1981; Young, 1986: 50; Goujet, 2001: 213; Goujet & Young, 2004). Placoderms, along with lampreys and osteostracans (Janvier, 1975), have an extraocular muscle innervated by cranial nerve IV (trochlear) and which issues from a myodome posterior to the orbit (Young, 2008). Called the posterior oblique in these groups, this muscle appears to be the homologue of the trochlear-innervated superior oblique in crown-group gnathostomes. In living jawed vertebrates, this muscle inserts anterodorsal to the foramen for cranial nerve II (optic), a condition which we regard as derived (Young, 2008).

Placoderms (Stensiö, 1963, 1969; Young, 1980; Goujet, 1984a), osteostracans (Janvier, 1985a, b), galeaspids (Gai *et al*., 2011), and living agnathans share a condition in which the occipital and otic regions of the braincase are co-ossified. Osteichthyans and chondrichthyans are united by the presence of an oticoccipital fissure (Figs 6D, E, 8), which is apparent in early members of both groups (osteichthyans: Jarvik, 1980; Gardiner, 1984b; Yu, 1998; chondrichthyans: Schaeffer, 1981; Maisey, 2005; Maisey *et al*., 2009). This same condition characterizes *Acanthodes*, which has most recently been regarded as a total-group osteichthyan (Miles, 1973b; Friedman, 2007a; Brazeau, 2009; Friedman & Brazeau, 2010; Davis *et al*., 2012). These same taxa also bear a posterior dorsal fontanelle (Fig. 8), an unmineralized region on the posterodorsal surface of the braincase located dorsal to the foramen magnum, and which is intersected by the oticoccipital fissure (*Acanthodes*: Miles, 1973b; osteichthyans: Gardiner, 1984b; chondrichthyans: Schaeffer, 1981). No such structure is present in placoderms or any agnathan,

and might be related to the absence of a persistent fissure between the occipital arch and otic region.

For many decades, a persistent transverse fissure (termed the ventral cranial fissure; Fig. 9) separating the basisphenoid from the basioccipital was known only in fish-like osteichthyans and *Acanthodes*. Under outgroup-based cladistic investigation similar to the one presented here (Miles, 1973b), the ventral cranial fissure was listed amongst several synapomorphies of *Acanthodes* and crown-group Osteichthyes. The discovery of such a fissure in two Devonian chondrichthyans (*Pucapampella*, Janvier & Suarez-Riglos, 1986; Gagnier *et al.,* 1989; Maisey, 2001; and an unnamed form from South Africa, Maisey & Anderson, 2001) has challenged this interpretation. However, based on our assumed backbone tree the character distribution is ambiguous: it is not possible to distinguish between scenarios entailing the gain of a cranial fissure and its loss in crown chondrichthyans, or the independent acquisition of the cranial fissure in *Pucapampella* and Osteichthyes. The ambiguity could be resolved by

the placement of *Acanthodes* on the chondrichthyan stem, implying that the fissure is a crown-gnathostome symplesiomorphy. The braincase of *Ptomacanthus* is preserved as two sets of mineralizations: a basisphenoid region and parachordal plates. This taxon has been resolved to either the chondrichthyan stem (Brazeau, 2009) or the gnathostome stem (Brazeau, 2009; Davis *et al.*, 2012). However, it is unclear whether the separate mineralizations in *Ptomacanthus* are anatomical or a taphonomic artefact.

Placoderms (Stensiö, 1963, 1969; Goujet, 1984a), like osteostracans (Janvier, 1985a) and galeaspids (Gai *et al.*, 2011), have braincases that can be called 'thick walled'. In each of these groups, the perichondrally mineralized cavum cranii is widely separated from the external, mineralized surface of the braincase, with this gap indicating the presence of thick cartilaginous matrix (Fig. 7A–D; Zalc, Goujet & Colman, 2008). By contrast, the cavum cranii is separated from the external surface of the neurocranium by relatively thin walls in both chondrichthyans
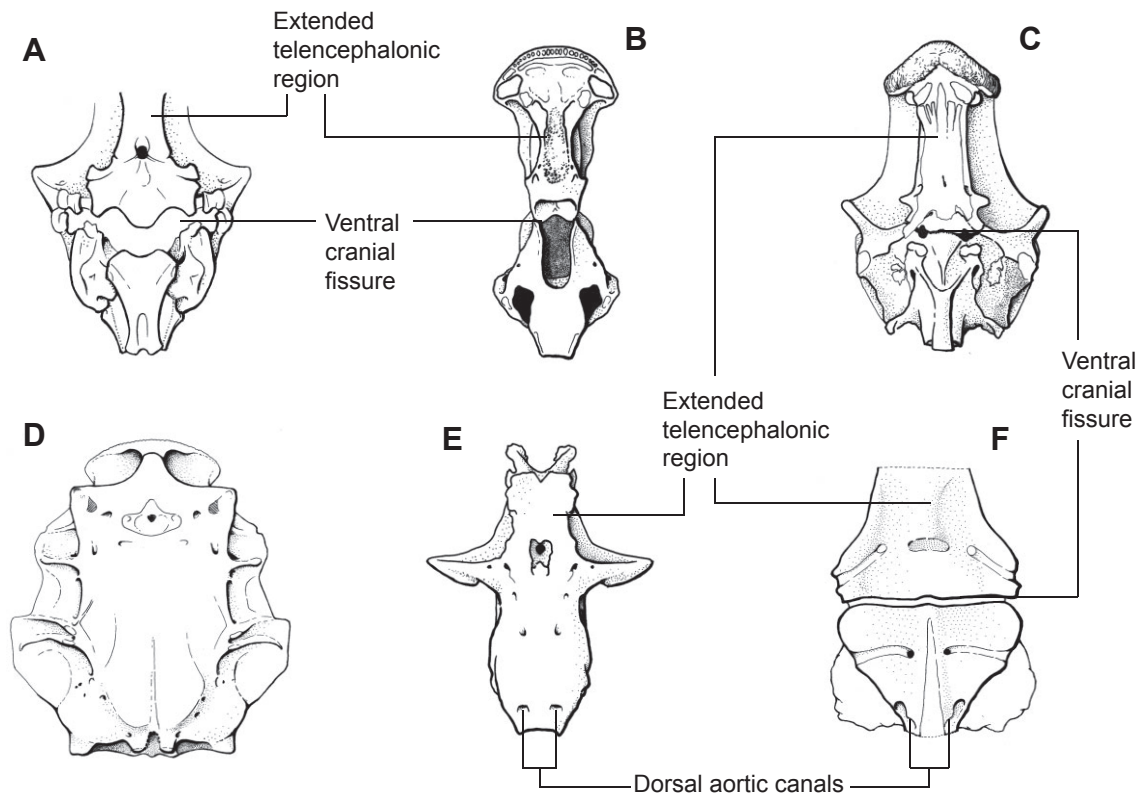
Figure 9. Gnathostome neurocrania in ventral view. A, *Acanthodes*, an acanthodian (after Davis *et al.*, 2012). B, *Gogonasus*, a crown osteichthyan and crown sarcopterygian (after Long, Barwick & Campbell, 1997). C, *Mimipiscis*, a crown osteichthyan and actinopterygian (after Gardiner, 1984b). D, *Dicksonosteus*, an arthrodire placoderm (after Goujet, 1984a). E, *Cladodoides*, a chondrichthyan and possible stem elasmobranch (after Maisey, 2005). F, *Pucapampella* sp. a probable stem chondrichthyan (after Maisey, 2001).

(Fig. 7E; Schaeffer, 1981; Maisey, 2005, 2007) and osteichthyans (Poplin, 1974; Jarvik, 1980; Gardiner, 1984b).

All jawed vertebrates are characterized by the presence of three semicircular canals (see above), but Davis *et al.* (2012, supplement) noted that the junction between the anterior and posterior canals of the bony labyrinth is represented by a well-developed sinus superior only in chondrichthyans (but see *Orthacanthus*; Schaeffer, 1981: fig. 14), osteichthyans, and *Acanthodes*. By contrast, the union of the anterior and posterior in all described placoderm endocasts is indistinguishable from their intersection with the saccular chamber (Stensiö, 1969; Young, 1980). The condition found in placoderms agrees with that in osteostracans (Janvier, 1985a), indicating that the absence of a sinus superior is a retained plesiomorphy whereas its presence represents a synapomorphy of crown-group gnathostomes. We note that an apparent sinus superior is present in the galeaspid *Shuyu* (Gai *et al.*, 2011: supplementary video 1). However, we consider this nonhomologous with that in extant jawed vertebrates based on the assumption that galeaspids are the sister group of osteostracans plus all mandibulate gnathostomes.

Davis *et al.* (2012: supplement) discussed an additional feature of the otic capsule that appears to be synapomorphic for crown gnathostomes: the absence of a skeletal capsular wall that separates the labyrinth cavity from the cavum cranii. Such a division is absent in early chondrichthyans (e.g. *Orthacanthus*: Schaeffer, 1981: fig. 14; *Cladodoides*: Maisey, 2005: fig. 7), osteichthyans (e.g. *Mimipiscis*: Gardiner, 1984b: fig. 26; *Psarolepis*: Yu, 1998: fig. 4), and *Acanthodes* (Davis *et al.*, 2012: supplementary fig. 10). By contrast, the labyrinth cavity is largely divided from the remainder of the endocranial cavity in osteostracans (Janvier, 1985a, b), galeaspids (Gai *et al.*, 2011), and a variety of placoderms (e.g. *Kujdanowiaspis*, *Tapinosteus*, *Macropetalichthys*, *Jagorina*: Stensiö, 1969: figs 44, 46, 48, 52; *Brindabellaspis*: Young, 1980: fig. 10; *Dicksonosteus*: Goujet, 1984a: fig. 26; possibly *Bolivosteus*, Goujet, Janvier & Suarez-Riglos, 1985: fig. 3), indicating that the condition apparent in crown gnathostomes is derived. Davis *et al.* (2012: supplement) argued that a capsular wall is absent in ptyctodonts. However, we regard the condition in this group as unclear, given uncertainties concerning neurocranial structure arising from the presence of multiple ossification centres.

The sphenoid region and telencephalon of placoderms (Stensiö, 1963, 1969; Young, 1980; Goujet, 1984a) are comparatively much shorter than those of chondrichthyans (Schaeffer, 1981; Maisey, 2005, 2007) and osteichthyans (Jarvik, 1980; Gardiner, 1984b), with petalichthyids representing an important exception owing to their greatly elongated olfactory tracts (Stensiö, 1925). Conditions found in placoderms correspond most closely to those in galeaspids (Gai *et al.*, 2011) and osteostracans (Janvier, 1985a), suggesting this is the primitive geometry, whereas osteichthyans and chondrichthyans are united by a relatively elongated sphenoid (Brazeau, 2009).

Dermal skeleton
The nature of 'true' teeth has been a subject of considerable debate. There is general agreement that structures that may be described as teeth are present in both chondrichthyans and osteichthyans. Controversy centres on the naming of features present on the dermal jaw bones of placoderms (Smith & Johanson, 2003; Young, 2003; Johanson & Smith, 2005; Rücklin *et al.*, 2012). These debates have been clouded by the application of developmental-process definitions of teeth (e.g. Reif, 1982) that are unobservable in palaeontological material (e.g. the dental lamina), and by transformational scenarios that lack any phylogenetic reference (e.g. 'outside-in' vs. 'inside-out' hypothesis). The dental lamina – an epidermal invagination in which teeth are preformed – has featured prominently in debates about fossils. As it is a soft tissue structure, its presence can only be inferred through an interpretation of static osteological characters in fossils. The choice to interpret some of these characters as necessary and sufficient evidence for a dental lamina – and therefore teeth – is not germane to systematic debate as it does not constitute independent evidence.

We are primarily interested in the systematic relationships of problematic fossil taxa, and not with the definition of the word 'tooth'. We have therefore resolved teeth into hierarchical, conditional statements of homology. This reflects possible relationships at the levels of oral dermal tubercles alone, or variations on this condition including precise ordering/patterning, replacement, topology, or other conditions.

Amongst placoderm-grade fishes, some bear tubercles along their dermal jaw bones whereas others, so far as can be determined, do not. Regardless of any additional criteria, these tuberculations are acceptable primary homologues of teeth insofar as they are *kinds of dermal tubercle* borne on the biting surfaces of the jaws; this holds even if they do not satisfy essentialistic definitions of teeth. Such oral denticles may unite some placoderms with the gnathostome crown to the exclusion of others, support jawed vertebrate monophyly with losses in some placoderm groups, or represent unique derivations within particular placoderm clades.

It is only in a subset of arthrodire placoderms that these tubercles are manifest in a precisely patterned

arrangement that resembles that of the teeth of crown-group gnathostomes (Smith & Johanson, 2003; Johanson & Smith, 2005; Rücklin *et al.*, 2012). The question of whether or not the precise patterning of these structures is homologous to that apparent in the teeth of crown gnathostomes pivots on the systematic status of placoderms generally and arthrodires specifically. However, there seems to be no reason to regard arthrodire teeth (indeed, those of many placoderms) and those of crown gnathostomes as nonhomologous insofar as they are both *kinds of dental tubercles* forming biting plates on the mandibular arch, a feature optimized to the last common ancestor of both groups regardless of whether placoderms form a clade (e.g. Smith & Johanson, 2003; Johanson & Smith, 2005; Rücklin *et al.*, 2012) or grade (Friedman, 2007a; Brazeau, 2009; Davis *et al.*, 2012).

Given the broad distribution of whorl-like cusp files (Fig. 10) in chondrichthyans (Zangerl, 1981; Williams, 2001; Maisey *et al.*, 2009), many acanthodians (e.g. ischnacanthids: Watson, 1937; *Climatius*: Miles, 1973a; '*Protodus*': Burrow & Turner, 2010; *Ptomacanthus*: Brazeau, 2012; *Latviacanthus*: Schultze & Zidek, 1982), sarcopterygians (onychodonts: Andrews *et al.*, 2005; porolepiforms: Jarvik, 1972), we consider this to be the general pattern for crown-group gnathostome teeth. Contrasts are provided by most actinopterygians (Pearson & Westoll, 1979; Gardiner, 1984b; but see *Howqualepis*, in which anterior dentary teeth are arrayed in a whorl-like fashion: Long, 1988) and some probable stem osteichthyans (e.g. *Dialipina*; Schultze & Cumbaa, 2001), and we caution that our inference may be extremely sensitive to new osteichthyan data. Dentitions of crownward members of the osteichthyan stem remain effectively undocumented, following re-interpretation of putative teeth in the stem osteichthyan *Andreolepis* and *incertae sedis* taxon *Lophosteus* (Cunningham *et al.*, 2012).

The recent discovery of *Entelognathus* (Zhu *et al.*, 2013) a placoderm-grade fish with marginal jaw bones
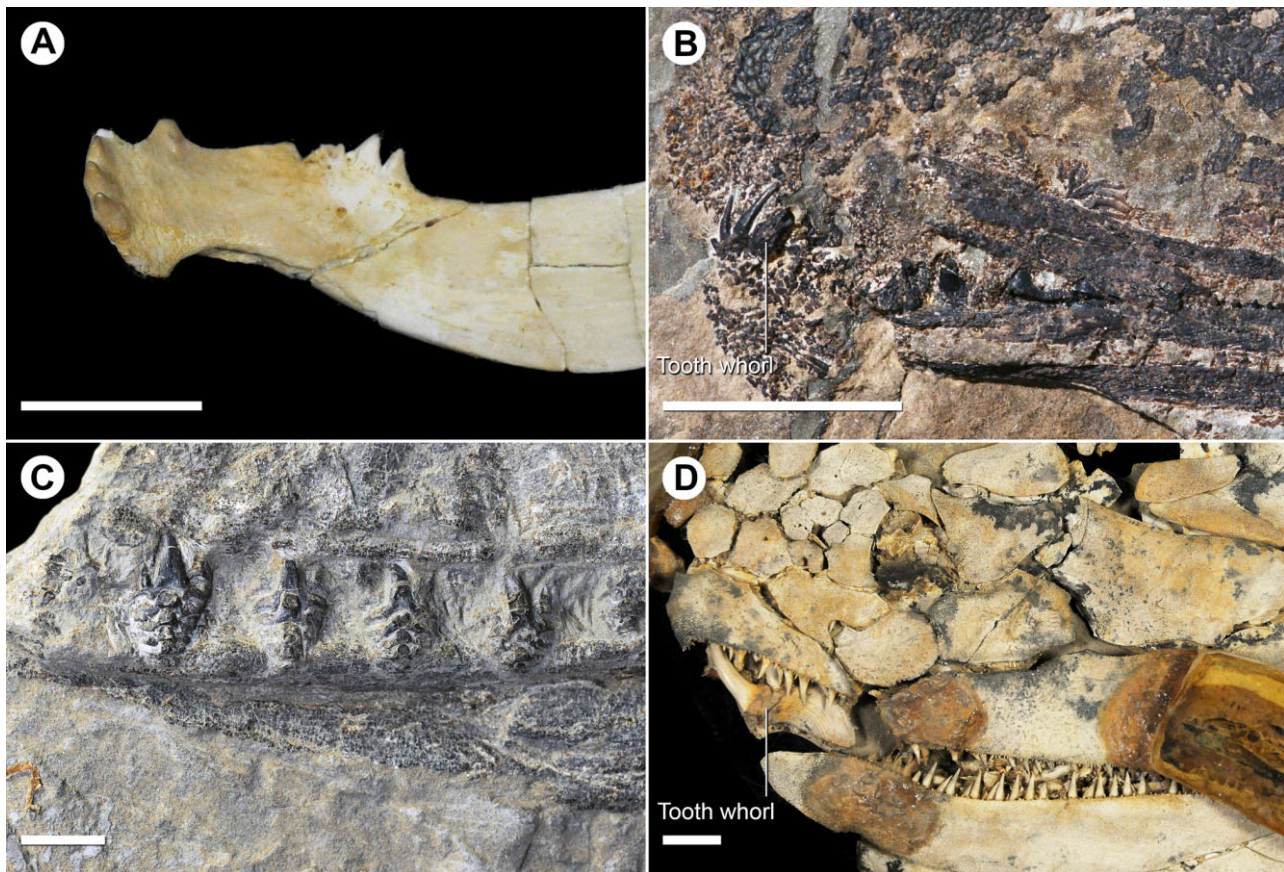
Figure 10. Gnathostome dental anatomy. A, *Torosteus pulchellus*, NHMUK P.50966, an arthrodire placoderm. B, *Ischnacanthus gracilis*, NMS 1887.35.2, an acanthodian. C, *Cladoselache* sp., NHMUK P.9272, a crown gnathostome and chondrichthyan. D, *Onychodus jandemarrai*, NHMUK P.63576 (image reversed), a crown osteichthyan and sarcopterygian. Scale bars = 10 mm.

and gular armour has raised questions about the phylogenetic distribution of these traits. In discussing osteichthyan characters, Friedman & Brazeau (2010) included 'differentiated branchiostegals (opercular, subopercular, lateral gulars)' in their list of osteichthyan synapomorphies. Their presence or absence was not considered contingent on the presence of more general macromery of the dermal skull. This is because branchiostegal plates are common in many acanthodian-type fishes that have micromeric skulls. In addition to being absent in chondrichthyans and all fishes assigned to the Acanthodii, they were absent in any placoderm-grade fishes prior to the discovery of *Entelognathus*.

Assuming that *Entelognathus* is a stem gnathostome (based on the apparent absence of cranial fissures, the absence of teeth, and lack of any specific apomorphies of either chondrichthyans or osteichthyans – except potentially the facial jaw bones and gulars), we envision two possible scenarios for the origin of facial jaw bones and gular plates. Either they were two independent gains or one gain and one loss. Owing to this uncertainty, we follow Zhu *et al.* (2013) in not placing *Entelognathus* in a resolved position with respect to arthrodires and the gnathostome crown.

Summary

The following are derived features that can place a fossil crownward of placoderms.

19. Extrinsic eye muscle innervated by the trochlear nerve (N.IV) originates anterodorsal to optic foramen.
20. Otico-occipital fissure.
21. Posterior dorsal fontanelle (Fig. 8B–D).
22. Ventral fissure (Fig. 9).
23. Thin endocranial wall.
24. Sinus superior.
25. Labyrinth cavity confluent with remainder of endocranial chamber (capsular wall absent).
26. Extended telencephalonic region (and/or correspondingly elongate sphenoid).
27. Teeth (possibly homoplasious in arthrodires; Fig. 10).

CANDIDATE SYNAPOMORPHIES OF ACANTHODIANS

We retain here all characters common to classically defined acanthodians. We exclude the proposed acanthodian synapomorphy concerning the shoulder girdle (Burrow & Turner, 2010; Hanke & Davis, 2012) for reasons given above in our discussion of compound characters.

Dermal skeleton

Acanthodians have been characterized as possessing scales with concentrically apposed generations –

giving rise to an 'onion skin' appearance when viewed in histological cross-section. This unique mode of development does appear to characterize a subset of spine-bearing early gnathostomes, in particular the acanthodiforms and diplacanthids. However, the term 'Acanthodii' is more broadly applied, and includes taxa such as *Parexus*, *Climatius*, and *Ptomacanthus*, which have been reported to have areally growing scales (Burrow & Turner, 2010; Brazeau, 2012; Burrow *et al.*, 2013). Ischnacanthids and *Brochoadmones* have unusual conditions in which odontode generations do not cover the entire crown (Valiukevicius, 1992; Hanke & Wilson, 2006). Owing to the patchy distribution of this character, we are omitting it from our list, but we accept that it probably identifies a monophyletic subset of taxa commonly referred to as acanthodians.

Fins

The presence of dermal projections associated with the pelvic girdle in placoderms (Long & Young, 1988), stem-group sarcopterygians (Zhu *et al.*, 2012a), and possibly early chondrichthyans (Miller *et al.*, 2003: 503) suggests that pelvic spines are not a synapomorphy uniting acanthodians. However, acanthodians do appear unique amongst vertebrates in bearing a well-developed spine in association with the anal fin (Fig. 4D; Maisey, 1986). This structure, which is absent in all known placoderms, chondrichthyans, and osteichthyans, is present in all classically recognized acanthodian orders (Denison, 1979). An anal fin spine is retained in the acanthodian *Paucicanthus*, which lacks spines in association with its paired fins (Hanke, 2002). A series of more complete body fossils bearing anal-fin spines has recently been attributed to either the Chonrichthyes or Teleostomi *incertae sedis* (Hanke & Wilson, 2004, 2010; Hanke *et al.*, 2013) on the basis of scale morphology. This implies several competing scenarios for anal fin spine distributions, which are discussed later in the text.

Summary

We recognize a single character as a potential synapomorphy of acanthodians:

28. Anal-fin spine present (Fig. 4D).

CHARACTERS THAT CAN PLACE A FOSSIL IN THE GNATHOSTOME CROWN GROUP: CHONDRICHTHYAN SYNAPOMORPHIES

Positively placing a taxon within the gnathostome crown requires uniting it with either Chondrichthyes or Osteichthyes. We provide an account of chondrichthyan characters here, along with an updated

synapomorphy scheme for osteichthyans from Friedman & Brazeau (2010) in the next section.

In spite of broad consensus on the monophyly of Chondrichthyes, highly inclusive total-group characters for chondrichthyans have been elusive and this group has generally been identified by the absence of osteichthyan features (Maisey, 1986: 216). Tessellate prismatic calcified cartilage (Fig. 5C, D) seems to be the only undisputed chondrichthyan synapomorphy. Many of the characters detailed below may well be elasmobranch synapomorphies, rather than more general chondrichthyan traits, but present evidence does not allow an unequivocal conclusion. We are concerned here with total-group membership rather than discriminating between stem and crown chondrichthyans; any feature that is a synapomorphy of Elasmobranchii (all crown-group chondrichthyans that are not members of total-group Holocephali) must also be evidence of membership within the chondrichthyan total group. This is an admittedly unsatisfactory situation, but the uncertain status of the characters reviewed below can be taken to indicate the current state of early chondrichthyan systematics. The discussion of potential chondrichthyan synapomorphies presented here is maximally inclusive, in the sense that it reviews those features supporting chondrichthyan monophyly if all acanthodians can be assigned to the total group. Such features, which are either gnathostome symplesiomorphies or of equivocal polarity when some or all acanthodians are placed on the osteichthyan stem, are indicated explicitly below and in the following character list.

Neurocranium
A broad anterodorsal opening of the cranial cavity between the nasal capsules (Fig. 8) is a remarkably stable feature of shark-like chondrichthyans and batoids from the Palaeozoic to the Recent (Schaeffer, 1981; Maisey, 2005, 2007; Maisey *et al.*, 2009). It is absent in adult holocephalans. De Beer & Moy-Thomas (1935) interpreted the ethmoid canal in embryos of *Callorhincus* as a corresponding structure, leading Schaeffer (1981) to propose this feature as a generalized trait of chondrichthyans. Maisey (2005: 288) retained the stricter interpretation of the precerebral fontanelle as an elasmobranch synapomorphy, because of differences in interpretation of the ethmoid canal. However, as noted by Maisey (2005), the hypothesis that some elasmobranch-like Palaeozoic chondrichthyans are stem holocephalans (e.g. Coates & Sequeira, 2001; Pradel *et al.*, 2011), as well as its presence in *Doliodus* (a probable stem-group chondrichthyan) invites the possibility that the absence of a precerebral fontanelle in holocephalans is secondary.

Amongst fossil chondrichthyans, many taxa exhibit a pair of canals for the lateral dorsal aortae within the basioccipital cartilage. This includes *Doliodus* and *Pucapampella* (Maisey, 2001; Maisey *et al.*, 2009), taxa that are reasonably interpreted as stem chondrichthyans, as well as forms that are routinely interpreted as members of the chondrichthyan crown group (Schaeffer, 1981; Coates & Sequeira, 1998). This contrasts with the condition seen in arthrodires and osteichthyans. A canal for the medial dorsal aorta is seen in early actinopterygians, but the divided portion of the artery is uninvested in cartilage (Gardiner, 1984b). This supports an interpretation of this feature as either an elasmobranch synapomorphy (Coates & Sequeira, 1998, 2001) or a chondrichthyan crown-group synapomorphy (Maisey, 2001). The absence of canals for the lateral dorsal aortae is not universal in placoderms, however. Paired canals are found in *Brindabellaspis*, and modest canals are seen in *Macropetalichthys* (see Young, 1980). We retain this character as evidence of chondrichthyan total-group membership, but note that the status of this character hinges on the phylogenetic interpretation of placoderms.

The hypotic lamina consists of a broad lateral extension of the parachordal plate that underlaps the otic capsules. This feature is present in a number of Palaeozoic chondrichthyans in which the relationship between the parachordal plate and the otic capsules can be inspected (Schaeffer, 1981; Maisey, 2005, 2007). Amongst chondrichthyans that lack a distinct metotic fissure, the presence or absence of the trait can be verified in embryonic stages showing distinct neurocranial divisions (De Beer, 1931). The feature is absent in either adult or embryonic specimens of *Callorhincus* (see De Beer & Moy-Thomas, 1935), a state that may be general to holocephalans. Embryonic information is lacking in fossil taxa, especially placoderms, making it difficult to assess the polarity of this character within crown-group gnathostomes. Although there is a clearly observable condition that is restricted to a subset of fossil chondrichthyans, we currently exclude this character from our list because of the uncertainty concerning outgroup conditions. Nevertheless, Maisey (2001) reported the hypotic lamina as absent in the probable stem chondrichthyan *Pucapampella*. It is therefore possible that this character is restricted to a more limited subset of the chondrichthyan crown or to total-group elasmobranchs. Resolution of this will be greatly assisted by improved documentation of the anatomy of *Pucapampella*.

A dorsal otic ridge has been proposed as a chondrichthyan synapomorphy (Maisey, 2001; this is mentioned, but not listed as a chondrichthyan synapomorphy, by Schaeffer, 1981). This consists of a

distinct, anteroposteriorly orientated, midline ridge situated in front of the endolymphatic fontanelle on the otic portion of the braincase (Fig. 8C, D). The ridge is flanked on either side by a pair of depressions, which were probably insertion areas for the epaxial muscles. A comparable ridge has not been observed in any placoderm (Stensiö, 1969), and is absent in Devonian osteichthyans (Gardiner, 1984b). The ridge was recently identified in *Acanthodes* by Davis *et al.* (2012). The placement of *Acanthodes* as a stem osteichthyan in recently published cladograms (Brazeau, 2009; Davis *et al.*, 2012) contradicts the interpretation of this feature as a synapomorphy of chondrichthyans, implying instead that it is a gnathostome symplesiomorphy. However, if we apply the logic used throughout this paper, then the absence of this feature in all outgroups (osteichthyans, all placoderms, and proximal jawless groups), then we must count this character as evidence against the osteichthyan placement of *Acanthodes*.

What is problematic about this character is its potential irrelevance to taxa with strongly attached skull roofing bones. Although the character is absent in chondrichthyan outgroups considered here, it appears in the actinopterygian *Lawrenciella* (see Fig. 8B; Hamel & Poplin, 2008), a taxon only known from isolated braincases for which associated roofing bones have not been recovered. The arrangement in *Lawrenciella* is very probably convergent on the chondrichthyan condition, but that is itself potentially significant because the presence of a ridge is associated with taxa without firmly attached skull roofing bones. We therefore caution that the absence of this feature in taxa with and without a tight association between the dermal skull roof and the neurocranium might not reflect the same state. Nevertheless, it is absent in some chondrichthyan groups. If it is not a chondrichthyan synapomorphy, it might be informative for chondrichthyan ingroup relationships.

Primary skeleton
The endoskeleton of chondrichthyans comprises one or more layers of tessellate prismatic calcified cartilage (Fig. 5C, D; Dean & Summers, 2006). The significance of this character as a chondrichthyan synapomorphy has been well established and corroborated by phylogenetic analysis (Goodrich, 1909; Schaeffer, 1981; Maisey, 1986; Brazeau, 2009; Davis *et al.*, 2012). Studies of living and fossil chondrichthyans have established its ubiquity in elasmobranchs, holocephalans, and the various Palaeozoic taxa within this dichotomy (e.g. Kemp & Westrin, 1979; Schaeffer, 1981; Stahl, 1999; Dean & Summers, 2006).

Dermal skeleton
Most Palaeozoic chondrichthyans lack any significant dermal skull plates (Zangerl, 1981; Stahl, 1999). A notable exception is found in some early holocephalans (Patterson, 1965; Stahl, 1999), but we consider this probably a derived state. Outgroup comparison with agnathans is equivocal, but osteostracan and galeaspid skull roofs appear to have been primitively composed of individual tesserae (Janvier, 1996a; Sansom, 2009). Placoderm and osteichthyan skull roofs, however, are generally macromeric, although tessellate conditions appear in certain placoderms. Under our outgrouping scheme, the status of micromery as a chondrichthyan apomorphy is ambiguous. We must assume at least two independent acquisitions of macromery (in osteichthyans and placoderms), or one gain of macromery and a subsequent reversal to micromery (in chondrichthyans and acanthodians). The resolution between these alternatives further depends upon the placement of acanthodians relative to the two crown gnathostome lineages. If the members of this assemblage branch from the osteichthyan, chondrichthyan, and gnathostome stems (Brazeau, 2009; Davis *et al.*, 2012), then micromery would map as the generalized condition for crown gnathostomes. However, if acanthodians are restricted to the chondrichthyan stem, then micromery would probably represent a synapomorphy of a subset of the chondrichthyan total group.

Isolated scales and teeth are the most commonly found fossil remains assigned to the Chondrichthyes. In spite of a dearth of articulated body fossils of Devonian and Silurian chondrichthyans, isolated material is routinely attributed to the group without contest. Scale-based taxa have thus seized the reins of debate to the degree that articulated specimens bearing superficially 'shark-like' scales, but otherwise lacking any obvious synapomorphies of either crown gnathostomes or jawed vertebrates more broadly, have been identified as chondrichthyans (Märss, Wilson & Thorsteinsson, 2002). Such interpretations are combined with the persistent identification of very early chondrichthyans based on 'shark-like' scales that cite overall similarity rather than distinct characters as evidence (e.g. Sansom *et al.*, 2012: 246). These conclusions are symptomatic of the hazy criteria for identifying early chondrichthyans on the basis of skeletal debris, and have the potential to substantially distort our understanding of the timing of evolutionary divergences within gnathostomes and vertebrates more generally. We regard these phenomena as especially problematic, given that the earliest body fossils that can be identified as chondrichthyans on the basis of unambiguous synapomorphies bear scales that have effectively gone unstudied (e.g.

Doliodus, *Protacrodus*; but see *Gladbachus*: Burrow & Turner, 2013).

Schemes for the attribution of microremains to chondrichthyans consist of abstracted descriptions of scale types, largely derived from isolated scales for which there is no additional anatomical information (Karatajute-Talimaa, 1998). No clear indications (i.e. synapomorphic hierarchy) are offered as to why these differing scale types might derive from chondrichthyans. Nevertheless, published accounts of scales derived from chondrichthyan skeletons clearly show areal growth patterns (e.g. Dick, 1981; Williams, 1998) – that is, growth comprising complexes of primarily appositionally joined odontodes (as opposed to burial and/or resorbtion). We have not seen evidence of this type of scale in skeletons of fishes that are demonstrably not chondrichthyans. Nevertheless, Palaeozoic chondrichthyans may exhibit a variety of scale morphologies, ranging from placoderm-like scales in *Gladbachus* (Burrow & Turner, 2013) to monodontode denticles (e.g. *Hamiltonichthys*; Maisey, 1989). Thus, areal scale growth is apparently unique to chondrichthyans, but it is uncertain whether it is the most inclusive synapomorphy so far identified.

We contend that derived features of early chondrichthyan dentitions can be more reliably isolated at present than those of scales. Based on their broad distribution amongst chondrichthyans, osteichthyans, and acanthodians, whorl-like tooth files would appear to be a general feature of crown gnathostomes. We consider individualized tooth bases in such whorls to be the specialized chondrichthyan trait based on its presence within elasmobranchs and some early holocephalans (e.g. *Helodus*; Moy-Thomas, 1936). It is notable that the bases of teeth assigned to *Doliodus problematicus* exhibit a thin lamina of bone joining them (Turner, 2004). This is consistent with a placement of *Doliodus* as the sister group of most other chondrichthyans (Brazeau, 2009; Davis *et al.*, 2012). It also suggests that individualized bases evolved somewhat later than the precerebral fontanelle and a more robustly mineralized endoskeleton, meaning that this will be of little value in resolving the acanthodian problem.

Many fossil chondrichthyans show the lateral line canal passing between flank scales (*Cladoselache*, *Ctenacanthus*: Dean, 1909; *Diademodus*: Harris, 1951; *Hamiltonichthys*: Maisey, 1989; *Gladbachus*: Friedman & Brazeau, 2010). This condition is seen in all acanthodians (Ørvig, 1972). In osteichthyans (Jarvik, 1980; Gardiner, 1984b), placoderms (see *Pterichthyodes*, Hemmings, 1978; *Sigaspis* Goujet, 1973; *Groenlandaspis*, Burrow & Turner, 1999: fig. 4i), and jawless stem gnathostomes (osteostracans: Sansom, Rodygin & Donoghue, 2008; thelodonts:

Gross, 1968; Märss, 1979, 1986; but see putative cranial sensory lines between scale rows in Wilson & Caldwell, 1998: 19), the lateral line canal of the trunk passes through a perforation or groove in a single scale, rather than between rows of scales. Skeletal signatures for sensory lines on the trunk are unknown in anaspids (Ørvig, 1972). Cephalic sensory lines that lie within grooves or canals on the head shields of pteraspidomorphs (Halstead, 1973; Sansom *et al.*, 1997), and pore-like openings in the scales of *Anglaspis heintzi* are described by Blieck & Heintz (1983). In *Sacabambaspis*, the ventral lateral line grooves extend onto the body scales.

The extension of the main lateral line between (rather than within or on) scales was initially interpreted as a gnathostome symplesiomorphy by Friedman & Brazeau (2010) on the basis of an assumed osteichthyan affinity for *Acanthodes*. However, using our outgroup-based approach here, the signal is clear: this character would be most parsimoniously interpreted as a synapomorphy uniting all acanthodians with the chondrichthyan total group. We therefore consider this evidence against an osteichthyan identity for all acanthodians, like the scapular blade discussed above, but note that both are incongruent with other apparently derived features shared between some acanthodians and osteichthyans (see below).
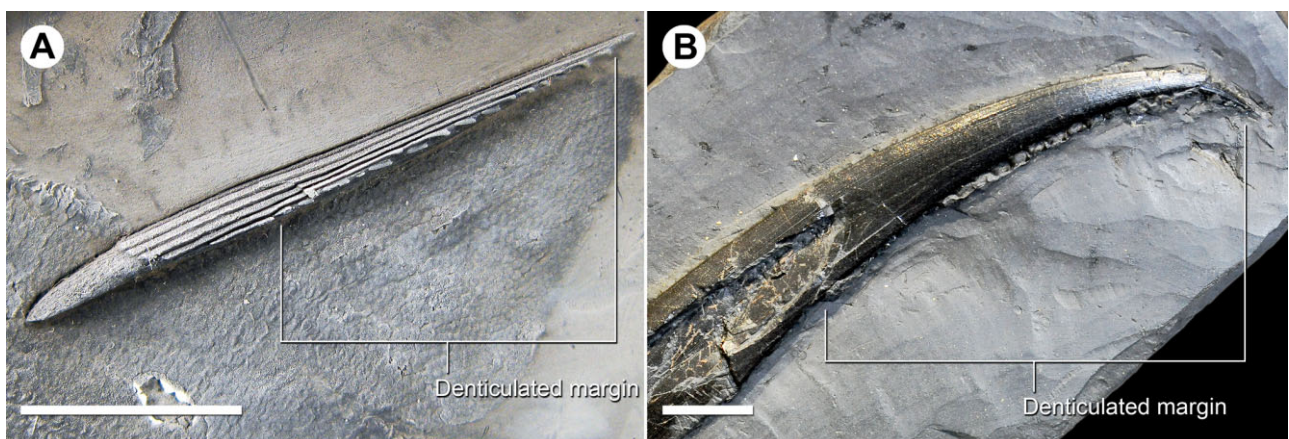
Fins

The gnathostome pectoral girdle comprises an endoskeletal component, the scapulocoracoid, which supports the pectoral fin skeleton and serves as an insertion for fin muscles. In chondrichthyans, the scapulocoracoid bears a tall blade or process that forms the posterior boundary of the gill chamber and provides an origin for the neck muscles and anterior trunk muscles (Zangerl, 1981; Liem & Summers, 1999; Stahl, 1999; Gudo & Homberger, 2002; Coates & Gess, 2007; Anderson, 2008). A similar process is observed in a large number of acanthodians (Miles, 1973a; Denison, 1979), and is only absent in taxa in which the whole pectoral endoskeleton is unpreserved. In osteichthyans and placoderms in which the scapulocoracoid is preserved, a pronounced scapular blade is absent (Jarvik, 1980; Gardiner, 1984b; Goujet, 1984a). Davis *et al.* (2012) scored a scapular process as present in ptyctodontids based on the figures in Miles & Young (1977). Although we are not rejecting characters based on overall similarity, this projection seems to have hardly anything in common with the scapular process of chondrichthyans and acanthodians. It appears to be quite removed from any participation in the posterior margin of the branchial chamber, or any likely origin for the neck muscles (Trinajstic *et al.*, 2012: fig. 4). It may be

homologous as a modest dorsal projection, but then it would lack the conditions that we have described above, and which we consider derived states. We also acknowledge that this character might be correlated with the absence of macromeric shoulder plates, with the scapular spine assuming the functional place of the cleithrum/anterolateral plate or vice versa. However, there is no logical reason why such a dermal plate and endoskeletal scapular blade could not co-exist (as they appear to in a limited way in some acanthodians: Miles, 1973a). Although previous placements of acanthodians on both the chondrichthyan and osteichthyan stems (Brazeau, 2009; Davis *et al.*, 2012) suggest that the presence of a scapular process is a general feature of crown gnathostomes, this feature is most parsimoniously interpreted as a synapomorphy of acanthodians and chondrichthyans under our approach. We therefore regard this feature as evidence against an osteichthyan identity for some acanthodians.

Several additional median- and paired-fin characters as synapomorphies of chondrichthyans (Maisey, 1986). Some of these are widely distributed (e.g. basal cartilages of the dorsal fin, which are also found in osteichthyans, acanthodians, and placoderms; Watson, 1937; Ørvig, 1960; Friedman & Brazeau, 2010), or do not appear to be characteristic of all or even most early members of the group (e.g. premetapterygial 'basals' present, with each articulating with multiple radials; Zangerl, 1981). From this list, we retain the presence of pelvic claspers as a chondrichthyan synapomorphy. Our assessment is complicated by the presence of claspers in ptyctodonts, as well as their recent discovery in arthrodires (Ahlberg *et al.*, 2009), which indicate

wider distribution of these structures within placoderms than previously realized. The presence of claspers in ptyctodonts has long been known (Ørvig, 1960), and these structures have generally been considered independently derived relative to chondrichthyan examples (e.g. Denison, 1978). The absence of pelvic claspers in osteichthyans, as well as all acanthodians (some of which are associated with the chondrichthyan and gnathostome stems in recent analyses; Brazeau, 2009; Davis *et al.*, 2012), suggests that chondrichthyan claspers are not homologous with those found in placoderms on the basis of character distribution.

Dorsal fin spines are recognized in chondrichthyans (Zangerl, 1981), acanthodians (Denison, 1979), osteichthyans (Zhu *et al.*, 1999, 2009), and placoderms (Denison, 1978). In most Palaeozoic chondrichthyans in which the dorsal spine is preserved, a series of denticles can be observed on the posterior or posterolateral margins (Fig. 11; Zangerl, 1981; Brazeau, 2009). This includes early holocephalans (Patterson, 1965; Stahl, 1999). Such denticles are also present on the dorsal fin spines of some acanthodians such as *Brochoadmones* (Fig. 11; Hanke & Wilson, 2006) and *Parexus* (Watson, 1937). Their precise location can be somewhat varied, being either at the margins of the posterior face of the spine or more medially aligned along this posterior surface. These variable placements might be individually apomorphous conditions, rather than suggesting nonhomology of these denticles. We note however that the distribution of such denticles is more sporadic in paired fin spines. We therefore emphasize that this character only supports chondrichthyan affinity when referring to dorsal fin spines.

Figure 11. Dorsal fin spines with trailing edge denticles, a potential synapomorphy of chondrichthyans. A, *Brochoadmones milesi*, UALVP 41495, an acanthodian. B, *Tristychius arcuatus*, NHMUK P.11378-79, a crown chondrichthyan and stem elasmobranch. Scale bars = 10 mm.

Summary
The following characters represent derived features that permit the placement of a fossil in the chondrichthyan total group. Characters marked with a superscript 'A' have potentially ambiguous distributions based on the placement of *Acanthodes* and its relations (e.g. other acanthodids such as *Homalacanthus* and *Cheiracanthus*, and probably also *Mesacanthus* and *Promesacanthus*):

29.   Precerebral fontanelle (Fig. 8C, D).
30.   Canals for lateral dorsal aortae in basioccipital.
31[A].   Dorsal otic ridge (Fig. 8C, D).
32.   Tessellate prismatic calcified cartilage (Fig. 5C, D).
33[A].   Micromeric skull.
34.   Scales with areally apposed odontodes.
35.   Tooth files with unfused bases (Fig. 10C).
36.   Denticles on fin side of dorsal-fin spines (Fig. 11).
37.   Pelvic claspers.
38[A].   Dorsal scapular blade.
39[A].   Lateral sensory line passing between flank scales.

CHARACTERS THAT CAN PLACE A FOSSIL IN
THE GNATHOSTOME CROWN GROUP:
OSTEICHTHYAN SYNAPOMORPHIES

Characters supporting the monophyly of Osteichthyes have already been discussed in detail by Friedman & Brazeau (2010). They will not be treated extensively here. We have made a few amendments based on recent publications (Maisey, 2007; Brazeau, 2009; Davis *et al.*, 2012; Zhu *et al.*, 2013).

Tropibasy has recently been clarified in terms of adult anatomical conditions by Maisey (2007). Three main anatomical conditions are observed in osteichthyans: a narrow or septate division between the orbits, that this septum or division consists of a deep endochondral floor between the cranial cavity at the ventral surface of the basisphenoid, and that it is pierced by the common internal carotid. The first two of these conditions are observed in a braincase comparable to *Cobelodus* (Maisey, 2007). Furthermore, it is doubtful whether many anatomically primitive osteichthyan braincases (e.g. *Ligulalepis*, *Guiyu*, *Psarolepis*, *Onychodus*) have a narrow interorbital space. What does appear to be limited to osteichthyans (and symmoriforms, which appear to be highly clustered within Chondrichthyes; Pradel *et al.*, 2011) is a dorsally restricted endocranial cavity in the sphenoid portion of the braincase – regardless of whether this region is mediolaterally narrow. We have further refined the osteichthyan condition to reflect this, rather than the complex character compound implied in 'tropibasy'.

The ascending basisphenoid pillar pierced by the common internal carotid is conditional on the presence of an anatomical structure comparable to a basisphenoid pillar. This is absent in platybasic taxa (which includes most non-osteichthyans). This makes this a highly contingent character that could, at best, identify only more crownward members of the osteichthyan stem, but by itself is not evidence independent of the presence of a dorsally restricted endocranial cavity in the braincase of osteichthyans. We eliminate this character in order to maintain consistency across the present contribution.

The presence of dorsal scutes has been regarded as a derived character of either osteichthyans (Friedman & Brazeau, 2010) or a subset of that group (Patterson, 1982b). However, ridge scales of some description are present in a wide variety of total-group gnathostomes, including acanthodians (e.g. *Brachyacanthus*: Watson, 1937), placoderms (e.g. *Lunaspis*: Gross, 1961; *Stensioella*, *Paraplesiobatis*: Gross, 1962; *Sigaspis*: Goujet, 1973; *Parayunnanolepis*: Zhang, Wang & Wang, 2001), and many osteostracans (Janvier, 1985b, 1996a). In light of this distribution and ambiguities surrounding the placement of acanthodians (see below), we no longer consider the presence of dorsal ridge scales a reliable osteichthyan synapomorphy. Similarly, the presence of gular plates in the probable stem gnathostome *Entelognathus* (Zhu *et al.*, 2013) casts doubt on prior claims that such structures are derived features of osteichthyans (Friedman & Brazeau, 2010).

As with our list of chondrichthyan synapomorphies, the list presented here is maximally inclusive. Here, our list reflects osteichthyan synapomorphies given placement of *Acanthodes* on the osteichthyan stem (Miles, 1973a; Friedman, 2007b; Brazeau, 2009; Friedman & Brazeau, 2010; Davis *et al.*, 2012). However, those characters that are no longer reconstructed as synapomorphic for Osteichthyes under alternative placements of *Acanthodes* and its immediate relations are indicated here with a superscript 'A'. An asterisk indicates that the character becomes ambiguous and unresolvable if *Acanthodes* is removed to the chondrichthyan stem (cf. Zhu *et al.*, 2013), owing to uncertainty in outgroups. Contrary to Zhu *et al.* (2013) and Friedman & Brazeau (2013), Friedman & Brazeau (2010) did not list the premaxilla, maxilla, and dentary bones as osteichthyan synapomorphies because they are contingent on the presence of macromeric skull roofing bones.

40[A].   Two or fewer spino-occipital nerve openings.
41.   Endocranial cavity dorsally restricted within sphenoid (i.e. between orbits).
42[A].   Ventral surface of otic capsules mediolaterally sloping.

43^A.   Spiracular grooves on basisphenoid.

44^A.   Vestibular fontanelles.

45.   Horizontal semicircular canal joins level with the posterior ampulla (Davis *et al.*, 2012).

46.   Absence of endolymphatic duct openings in dermal skull.

47^A.   Anterior dorsal fontanelle (Fig. 8B).

48^A.   Enamel.

49.   Endochondral bone (Fig. 5B).

50^A.   Hyomandibular articulates with lateral commissure/postorbital process.

51.   Hyomandibular branch of the facial (N.VII) nerve exits into jugular canal.

52.   Long canals for olfactory tracts.

53.   Ethmoid comineralized with sphenoid and completely encloses the nasal capsules.

54.   Hypohyal linking ceratohyal and basihyal.

55.   First two gill arches articulate with common basibranchial.

56.   Suprapharyngobranchials.

57^A*. Anteriorly directed infrapharyngobranchials.

58*.   Hyomandibular bears deep groove or canal for hyomandibular branch of facial nerve (possibly independently derived within the crown).

59.   Biconcave glenoid on lower jaw.

60^A.   Macromeric dermal skull.

61^A.   Pectoral girdle with substantial dermal component.

62.   Lepidotrichia.

63.   Proximally restricted radials supporting hypochordal lobe of caudal fin.

64.   Dermal bones lining palate and lower jaw (e.g. entopterygoid, prearticular).

IMPLICATIONS FOR CLASSICAL TAXONOMIES OF EARLY VERTEBRATES

PROBLEMS WITH PLACODERM MONOPHYLY

Our investigation identifies two candidate placoderm synapomorphies: a separate rhinocapsular ossification and the presence of semidentine. Nevertheless, we remain circumspect concerning placoderm monophyly. These two proposed synapomorphies are not unproblematic in their interpretation, nor have they been universally observed in placoderms (see discussions above). The separate rhinocapsular ossification can only be observed in taxa with mineralized neurocrania, although it is taxonomically widespread. However, it has even been dismissed as a placoderm synapomorphy by proponents of placoderm monophyly (Goujet, 2001), and is therefore absent from any of the recent lists of placoderm synapomorphies (e.g. Goujet & Young, 2004; Young, 2008, 2010). More important is that these characters are incongruent with a number of other features of

placoderm skulls, notably the architecture of the braincase of arthrodires plus *Romundina* relative to some or most other placoderms. Arthrodires and *Romundina* differ from osteostracans and some placoderms in the presence of laterally open orbits (i.e. the orbits open on the lateral, rather than dorsal, face of the dermal skull; Fig. 6), incompletely invested jugular vein lateral to the otic capsule (Fig. 7C), laterally open orbits possessing a suborbital shelf (Figs 6, 7), deep branching of the facial nerve (Fig. 7C, D), and a suborbital attachment of the mandibular arch (complemented by a postorbital attachment of the hyoid arch; Fig. 6). This suggests that even our proposed placoderm synapomorphies might also be considered gnathostome symplesiomorphies, a hypothesis we currently favour.

Arthrodires are quite reasonably interpreted in light of crown-group gnathostomes, with which they share many specializations. This is reflected in their frequent deployment as an outgroup in phylogenetic analyses of osteichthyans and chondrichthyans (e.g. Zhu *et al.*, 1999, 2001, 2006, 2009; Coates & Sequeira, 2001; Zhu & Yu, 2002). However, other placoderms are frequently, by extension, interpreted in light of arthrodires (e.g. Young, 1980) under the assumption that placoderms form a natural group to the exclusion of all other jawed vertebrates. We and others (e.g. Janvier, 1996b) have highlighted the deep division in placoderms between those with remarkably osteostracan-like braincase anatomy, and those, such as arthrodires, that closely resemble crown gnathostomes. As easy as it is to interpret arthrodires in terms of crown gnathostomes, so too is it easy to interpret *Brindabellaspis* and *Macropetalichthys* in terms of any given osteostracan or, potentially, galeaspid.

The recent discovery of *Entelognathus* (Zhu *et al.*, 2013) highlights a further piece of evidence difficult to reconcile with placoderm monophyly. *Entelognathus* is an arthrodire-like fish that exhibits marginal jaw bones and a facial jaw and gular skeleton, previously unreported in any placoderm. Placoderms are not rare fossils, and a number of species are known from articulated specimens. *Entelognathus* therefore comes as something quite unexpected (Friedman & Brazeau, 2013). It provides strong corroboration for a crownward placement of arthrodire-like taxa, but not without implying that all acanthodians are total-group chondrichthyans.

PROBLEMS WITH PLACODERM PARAPHYLY

Although we currently favour a paraphyletic arrangement for placoderms, we do not contend that this is without problems. Recent proposals of placoderm paraphyly have highly pectinate arrangements, and

each disagrees in some significant details (Brazeau, 2009; Davis *et al*., 2012; Zhu *et al*., 2013). Common to all three hypotheses is that ptyctodonts and arthrodires do not form a clade, but there is disagreement over which is closest to the gnathostome crown. Exceptional evidence of both claspers and internal fertilization has recently been discovered in these two groups (Long *et al*., 2008; Ahlberg *et al*., 2009; Long, Trinajstic & Johanson, 2009). The phylogenetic hypotheses of Brazeau (2009), Davis *et al*. (2012), and Zhu *et al*. (2013) would therefore suggest that either this trait was acquired multiple times within the gnathostomes or that it was lost in the osteichthyan stem (see Ahlberg, 2009). It seems unparsimonious to imply three acquisitions of this trait when two are already implied (chondrichthyans and ptyctodonts). Furthermore, there is no precedent in vertebrates for a transition from internal fertilization to external fertilization (see Long *et al*., 2009). However, on present evidence, it may simply suffice to solve this dilemma by making arthrodires and ptyctodonts a clade – but this solution was not recovered by Brazeau (2009), Davis *et al*. (2012), or Zhu *et al*. (2013). Furthermore, it conflicts with the petalichthyid like cranial morphology of ptyctodonts.

Semidentine can be interpreted as intermediate in type between mesodentine and orthodentine. Semidentine shares polarization of the odontoblasts within the mineralized matrix. However, although orthodentine is found in chondrichthyans and osteichthyans (Sire *et al*., 2009), there may be reason on the basis of character distributions to see these as potentially independently derived, especially if acanthodians are not monophyletic. Placoderm paraphyly not only requires the independent acquisition of odontoblast polarization, but also the reversion to mesodentine-type tissue. It is for this reason that semidentine has been preserved, albeit with reservations, in our list of potential placoderm synapomorphies.

A further concern relates to the dermal bones of placoderms and osteichthyans and existing parsimony software. The matrices of Brazeau (2009) and Davis *et al*. (2012) employ a contingent coding (or reductive coding) technique (Hawkins, 2000). Although this limits the number of redundant states and spurious effects of other coding methods, it is prone to length overestimates because of the limitations of currently available parsimony software (Maddison, 1993). Even though the topologies arising from analyses of these two data sets imply nonhomology of placoderm and osteichthyan dermal cranial roofs, characters concerning this system (such as the rectilinear skull roof pattern of arthrodires and osteichthyans) may be attracting arthrodires towards the gnathostome crown. If placoderms are separated from osteichthyans by a paraphyletic array of micromeric/tessellate taxa, then the support for this placement of arthrodires is at least partially artefactual.

Resolving the question of placoderm monophyly will not come about through list-building projects with the objective of showing that Placodermi is a clade. As the only mandibulate stem gnathostomes, placoderms are morphologically peculiar and care must be taken not to confuse their peculiarities with synapomorphies. Furthermore, dismissing comparisons between placoderms and osteostracans, galeaspids, and pituriaspids is counterproductive. We see a more rigorous and careful comparative anatomy of placoderms and agnathans to be a potential avenue for resolving these problems.

THE 'ACANTHODIAN PROBLEM' AND CHARACTERS OF THE CHONDRICHTHYAN TOTAL GROUP

As with Placodermi, Acanthodii has been unsupported in nearly all published cladistic tests of its monophyly. However, there is some disagreement about the precise stem placement of all of the acanthodian genera included in published cladograms. Davis *et al*. (2012) and Brazeau (2009) placed *Acanthodes* and its nearest relations on the osteichthyan stem. However, the relationships of the *Climatius*-like acanthodians (*sensu* Brazeau, 2012) remain in conflict. Brazeau (2009) recovered most of these taxa as stem chondrichthyans, whereas Davis *et al*. (2012) resolved them as stem gnathostomes. This lability of placement has two likely causes. One is the small number of chondrichthyan total-group synapomorphies, the other is the small number of morphological characters that can be reliably scored for acanthodians owing to the incompleteness of their fossils.

Remarkably few characters consistently identify members of the chondrichthyan total group under alternative placements of acanthodians. Of the characters that we have listed above, tessellate prismatic calcified cartilage and the precerebral fontanelle are fairly uncontroversial. Neither has ever been observed in an acanthodian. The phylogenetically late appearance of individualized tooth bases relative to a robustly calcified endoskeleton and the precerebral fontanelle, as based on conditions in *Doliodus*, makes this character unlikely to help identify less crownward stem chondrichthyans. This leaves areally growing scales as the only feature unambiguously uniting any acanthodian-like fossils (e.g. *Kathemacanthus* and *Seretolepis* from the MOTH locality, Hanke & Wilson, 2010) with the chondrichthyan stem.

What phylogenetic conclusions can be drawn from this, and what are their implications in light of our synapomorphy scheme? Reports of areally growing scales in *Climatius* and *Parexus* (Burrow & Turner, 2010; Burrow *et al.*, 2013) have not been matched with stem-chondrichthyan identifications that have been offered for both fragmentary and articulated taxa showing the same characters (Hanke & Wilson, 2010). Instead, they have been united with other acanthodians on the basis of the scapulocoracoid characters that we consider spurious evidence of acanthodian monophyly. However, let us give benefit of the doubt to acanthodian monophyly and the identification of *Kathemacanthus* and articulated *Seretolepis* as chondrichthyans (Fig. 12). We might then assume that acanthodians are either stem osteichthyans or less crownward stem chondrichthyans (this is never explicitly stated by acanthodian workers, but we must assume that it is one of these). The anal fin spine (the potential synapomorphy that we retain above) could not be considered an acanthodian synapomorphy, but has two possible resolutions: either a gnathostome or chondrichthyan symplesiomorphy in these respective circumstances, or independently derived (Fig. 12A). The choice depends on whether taxa such as *Kathemacanthus* and *Seretolepis* are paraphyletic or monophyletic (Fig. 12 shows optimal situations). However, similar interpretations must then follow the pattern of areal scale growth (Fig. 12A–C).

Choosing between these hypotheses depends on the placement of a presumed monophyletic Acanthodii. If they are stem osteichthyans, then areally growing scales represent a generalized feature of the gnathostome crown (Fig. 12A–C), later modified higher on the osteichthyan stem and in acanthodians (where concentric superposition is acquired). The character therefore loses force as a chondrichthyan synapomorphy, and the placement of *Kathemacanthus* and *Seretolepis* is Gnathostomata *incertae sedis* (Fig. 12C).

If all acanthodians are stem chondrichthyans, this might imply that areally growing scales are actually a plesiomorphic trait of acanthodians, later substituted by the concentric appositional growth more 'typical' of acanthodian scales (Fig. 12D, E). All that ties *Seretolepis* and *Kathemacanthus* to the chondrichthyan stem in the hypothesis of Hanke & Wilson (2010) is simply this character ('*Seretolepis*-type' areal scale growth). However, we are then forced to propose the acquisition and subsequent loss of the anal fin and admedian fin spines along the chondrichthyan stem. This makes placing *Kathemacanthus* and *Seretolepis* as the immediate sister groups of all acanthodians the parsimonious solution for both characters (leaving us with only

the acquisition of the anal fin spines and no losses, Fig. 12E). In this hypothesis, *Kathemacanthus* and *Seretolepis* are chondrichthyans, but no more crownward than any other acanthodian.

This latter phylogenetic hypothesis could be rejected if, for example, the full spine complement of *Doliodus* or *Pucapampella* included anal fin spines. Nevertheless, if only the scale growth type and anal fin spine characters are considered, then the most parsimonious solution involving *Kathemacanthus* and *Seretolepis* as stem chondrichthyans also places them in a clade with all known acanthodians. However, we see no reason to separate some acanthodian-like taxa as 'putative chondrichthyans' to the exclusion of others on the basis of such a small character sample and without consideration of the diversity of outgroup conditions.

Acanthodian anatomy, and to a lesser extent early chondrichthyan anatomy, is very poorly known. What is known of acanthodians is mostly restricted to the dermal hard parts with few comparators in other gnathostome taxa. However, approximately half of the characters in our synapomorphy scheme concern some aspect of the endoskeleton, especially the neurocranium. What is known of acanthodian neurocrania reveals widely divergent morphologies, consistent with a nonmonophyletic Acanthodii (Brazeau, 2009). Phylogenetically significant axial skeleton characters are known only for a small number of acanthodids (e.g. Miles, 1970). This dearth of endoskeletal data leaves few traits that can be compared generally throughout the gnathostomes.

The acanthodian problem may be resolved in very limiting and incremental steps as palaeontologists mine the diversity and distribution of their hard tissue anatomy. This is a necessary step towards a stable systematics of early gnathostomes. However, by itself it will probably be insufficient. As new acanthodian fossils rarely reveal anatomical details of the endoskeleton, the rate of new taxonomic discoveries potentially outstrips the rate at which new characters with links to non-acanthodians are discovered. This means that it will become increasingly difficult to add significantly more phylogenetically informative characters, which are needed to resolve data sets with large amounts of missing data (Wiens, 2003a, b). Resolving the acanthodian problem will therefore require the discovery of uniquely well-preserved acanthodian and other early gnathostome endoskeletons.

CONCLUSIONS

We have created a nested hierarchical synapomorphy scheme for the deepest crown nodes of the Gnathostomata using an outgroup-based approach
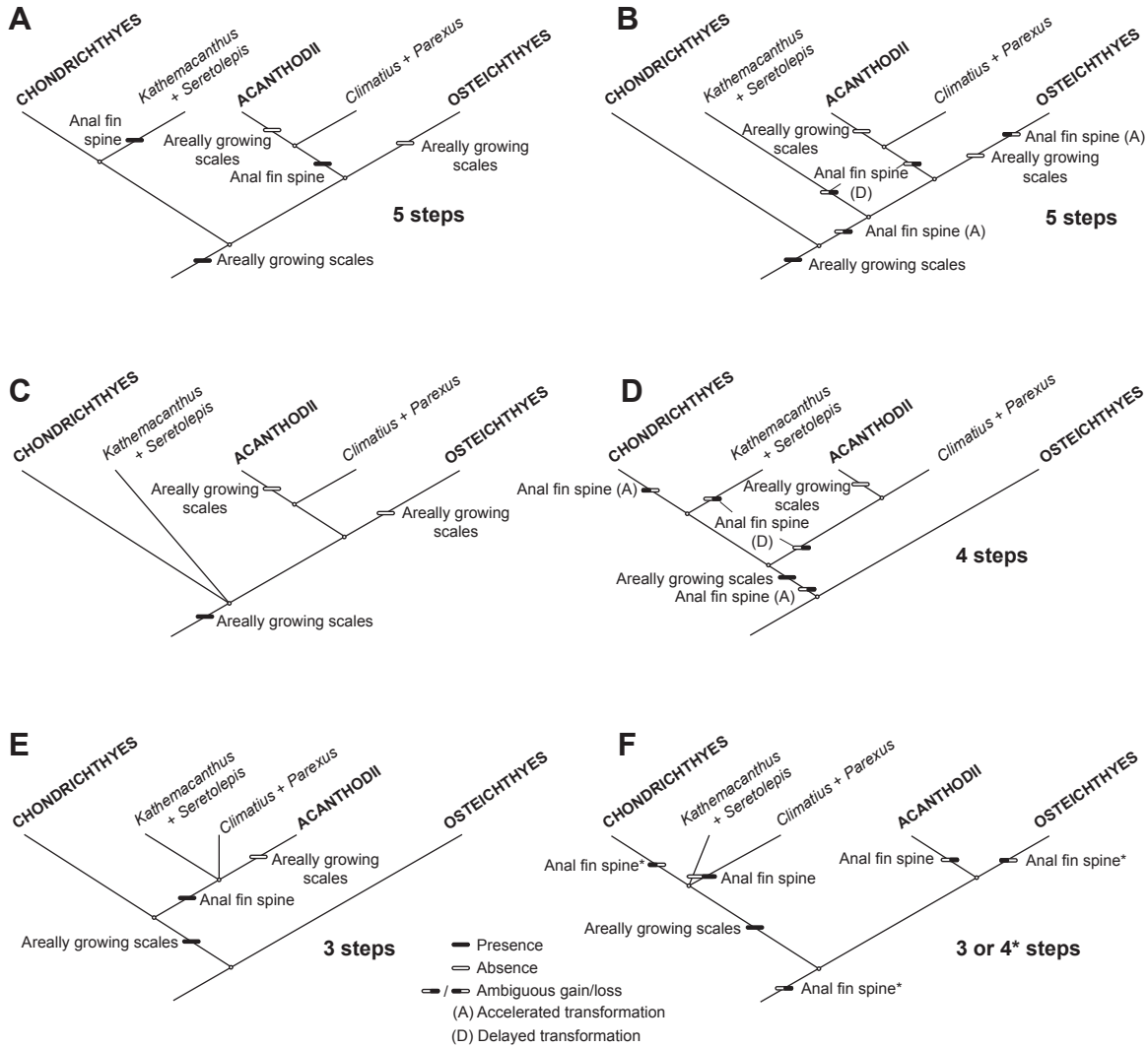
Figure 12. Alternative phylogenetic placements for problematic acanthodian-like taxa and their implications in light of two characters discussed in the text and assumptions of acanthodian monophyly. A, one of the hypotheses implied by placing only *Kathemacanthus* and *Seretolepis* on the chondrichthyan stem, independent of other acanthodians. B, equally parsimonious placement of *Kathemacanthus* and *Seretolepis* on osteichthyan stem. C, consensus tree showing that resolution of *Kathemacanthus* and *Seretolepis* to the chondrichthyan stem collapses if all other acanthodians are placed on the osteichthyan stem (areal scale growth is plesiomorphic). D–F, improvements to parsimony score if some or all acanthodians are moved to the chondrichthyan stem (restoration of areal scale growth as a chondrichthyan synapomorphy). D, hypothesis in which all acanthodians are stem chondrichthyans, but paraphyletic. E, hypothesis in which all acanthodians are stem chondrichthyans but monophyletic. F, hypothesis in which taxa with areally growing scales are stem chondrichthyans, whereas the remaining (assumed monophyletic) Acanthodii are stem osteichthyans. Ambiguities in character state distributions based on a soft polytomy may entail different lengths depending on their resolution. Note that loss of areal scale growth in Acanthodii and Osteichthyes reflects transitions to different, not identical, states and must therefore be treated as separate events. Asterisk indicates values derived from resolving stem chondrichthyan polytomy as a paraphylum with respect to the crown.

(Fig. 13). Our preferred solution places placoderms as a paraphyletic array of stem gnathostomes. We have omitted antiarchs, even though most phylogenetic analyses place them as the sister group of all other mandibulate gnathostomes (Brazeau, 2009; Davis *et al.*, 2012; Zhu *et al.*, 2013). This hinges on the absence of pelvic fins, which is likely to reflect a derived state in the group (Zhu *et al.*, 2012b). They might therefore act as a 'wildcard' taxon within the gnathostome stem. We suggest two
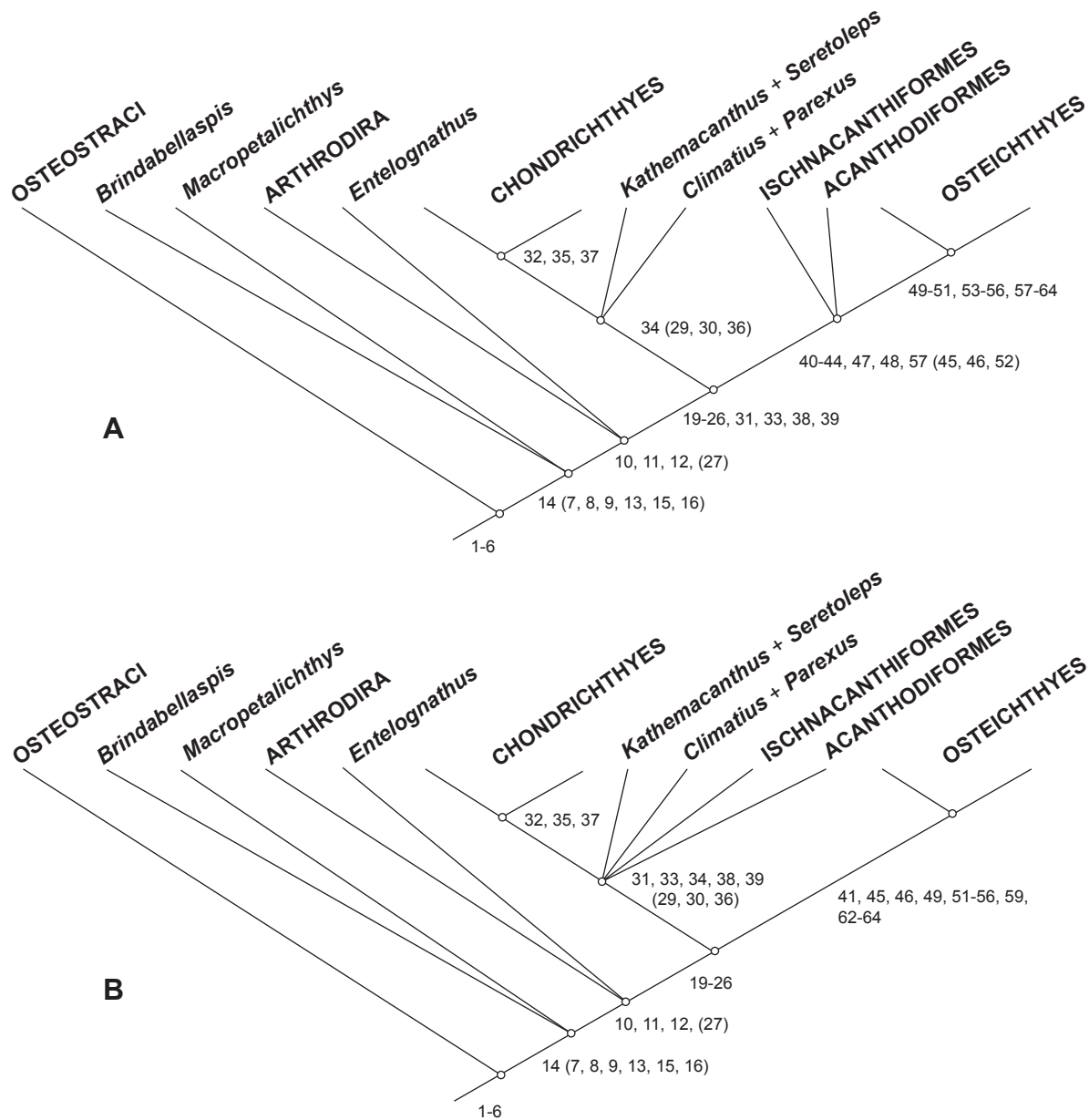
Figure 13. Summary cladograms of hypotheses of phylogenetic placements argued in this paper. A, cladogram depicting acanthodian genera distributed on the chondrichthyan and osteichthyan stems. B, cladogram depicting acanthodians restricted to chondrichthyan stem, but left unresolved. Character transformation labels at internal nodes correspond to those in the text. Numbers in parentheses reflect ambiguities that are resolved to their most inclusive level (i.e. 'accelerated transformation') and could have more restricted distributions.

alternative hypotheses concerning the placement of acanthodians. The first of these places most acanthodians on the chondrichthyan stem, with *Acanthodes* and its closest relatives representing members of the osteichthyan total group (Fig. 13A). The second hypothesis places all acanthodians as stem chondrichthyans (Fig. 13B). This latter hypothesis enjoys support from a number of dermal and endoskeletal characters, as well as some braincase characters in *Acanthodes* newly recognized by Davis *et al*. (2012) and evidence for the homology of placoderm and osteichthyan macromeric skull conditions described by Zhu *et al*. (2013). These alternatives differ from one another by only two steps under our synapomorphy scheme, and we regard this as insufficient to distinguish between them at present.

We have emphasized the importance of phylogenetic background assumptions in argumentation about the systematic significance of characters underwriting this set of tree topologies. This explicitness renders our proposals open to empirical refutation in the hope that this work will promote future research focused on testing these distributions in a methodologically consistent manner. We expect that many of these proposals will succumb to refutation, consistent with the current level of uncertainty in the study of early gnathostome phylogenetics. Because of this, we have not only emphasized our current preferred solution, but have explored a number of alternatives that could easily supplant our proposal with further study and new fossil data.

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