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A critical appraisal of appendage disparity and homology in fishes

Running title: Fin disparity and homology in fishes

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Abstract

Fishes are both extremely diverse and morphologically disparate. Part of this disparity can be observed in the numerous possible fin configurations that may differ in terms of the number of fins as well as fin shapes, sizes and relative positions on the body. Here we thoroughly review the major patterns of disparity in fin configurations for each major group of fishes and discuss how median and paired fin homologies have been interpreted over time. When taking into account the entire span of fish diversity, including both extant and fossil taxa, the disparity in fin

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morphologies greatly complicates inferring homologies for individual fins. Given the phylogenetic scope of this review, structural and topological criteria appear to be the most useful indicators of fin identity. We further suggest that it may be useful to consider some of these fin homologies as nested within the larger framework of homologous fin-forming morphogenetic fields. We also discuss scenarios of appendage evolution and suggest that modularity may have played a key role in appendage disparification. Fin modules re-expressed within the boundaries of fin-forming fields could explain how some fins may have evolved numerous times independently in separate lineages (e.g. adipose fin), or how new fins may have evolved over time (e.g. anterior and posterior dorsal fins, pectoral and pelvic fins). We favour an evolutionary scenario whereby median appendages appeared from a unique field of competence first positioned throughout the dorsal and ventral midlines, which was then redeployed laterally leading to paired appendages.

KEYWORDS

Appendage evolution, fin-forming fields, homology, median and paired fins, modularity, morphological disparity

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1 INTRODUCTION

Homology is a fundamental concept in biological sciences (Hall, 1994a). Homologous characters are quintessential for phylogenetic analyses, while also providing traits that can be used to identify taxa for taxonomists, and traits that can be compared among clades for evolutionary biologists. However, there is a lack of consensus among biologists as to the criteria that should be used to establish homology (e.g. similarity through topographical correspondence and/or ontogenetic transformation, congruence or anatomical singularity, shared developmental processes, common evolutionary origins) (Hall, 1994b; Patterson, 1982; 1988). All this considered, identifying homologies of morphological traits across large phylogenetic scales is not always straightforward, as many structures are likely to have accrued changes in morphology and function over evolutionary time.

Fish appendages represent one such case where homologies have historically been difficult to interpret. Among the factors that complicate inferring fin homologies are that fishes are both extremely diverse [ranging from between ~32 000 to ~35 000 valid species according to current estimates (Fricke, Eschmeyer & Fong, 2018; Nelson, Grande & Wilson, 2016)] and morphologically disparate. One aspect of this disparity concerns the numerous possible fin configurations differing in the number of fins, fin shapes and sizes, fin positions on the body and types of skeletal support (Larouche, Zelditch & Cloutier, 2017). Additionally, fishes also have a rich fossil record. This is particularly relevant for the jawless fishes, or agnathans, as it is largely within this paraphyletic group that median and paired fins sequentially appeared. Extant agnathans comprise only hagfishes (Myxiniformes) and lampreys (Petromyzontiformes), neither of which can be considered as exhibiting primitive morphologies: both groups possess combinations of some apomorphic traits and others that have been transformed or lost from the ancestral condition (Furlong & Holland, 2002; Ota, Fujimoto, Oisi & Kuratani, 2011; 2013; Shimeld & Donoghue, 2012). Hagfishes and lampreys have well-developed median fins but lack paired fins. Fin configurations are much more diversified in fossil jawless fishes, some of which also have paired appendages (Larouche, Zelditch & Cloutier, 2017). However, the quality and completeness of preservation for fossilized agnathans is variable, which complicates interpretations of homologies for their appendages. Yet another aspect that complicates interpreting fin homologies is that in some taxa, median and paired fins have diverged and/or been co-opted towards a number of specialized functions. Examples include fins modified as sensory organs (e.g. adipose fins in salmonids), as suctorial apparatuses used to cling to hard surfaces or to other organisms (e.g. lumpsuckers, clingfishes, remoras and some gobies), and as lures used to attract prey (e.g. anglerfishes).

Fins are functionally important for locomotion, yet they are also evolutionarily labile structures that can generate high levels of morphological disparity, notably among ray-finned fishes (Larouche, Zelditch & Cloutier, 2018). The morphological and functional disparity of fish appendages, the quality of the fossil record, and the paraphyly of fishes all complicate inferring homologies of fins. With this in mind, our main objective is to review the major patterns of fin configuration disparity throughout the phylogeny of fishes and discuss how fin homologies have historically been interpreted. We begin by demonstrating that a clear definition even of what constitutes a fin is difficult to find in the scientific literature and propose a set of defining characteristics for the term. We then provide an exhaustive review of fin-like structures in all major clades of both jawless (agnathans) and jawed fishes (gnathostomes) and discuss proposed homologies for these appendages across the different groups. To our knowledge, this is the first thorough review of disparity and suggested homologies for both the median and paired fins performed with such a large macroevolutionary scope.

2 THE INHERENT COMPLEXITIES OF SIMPLY DEFINING THE TERM “FIN”

In this section, we begin by providing a historical account of how median and paired fin identities have been interpreted by previous authors. In doing so, we wish to emphasize the array of arguments that have been used to discuss fin homologies, including structural, topological, functional and developmental considerations. We conclude this section by summarizing the set of criteria that we find most informative in defining fins and their identities.

It may be surprising to find that a clear definition of what constitutes a "fin" is uncommon (even inexistent) in recent literature. Perhaps this can be attributed to the morphological and functional diversity of these appendages, precluding an all-encompassing definition of the term. Nonetheless, for centuries, it has been recognized that a common character of fishes is that they generally have fins (Table 1). For example, although Aristotle did not clearly define "fins", he observed that these were essentially organs of locomotion and that fishes displayed much disparity in their fin configurations (Aristotle & Barthélémy-Saint-Hilaire, 1883; Aristotle, Cresswell & Schneider, 1878). Antoine Goüan defined "fins" as parts composed of a series of rays or spines, covered and united by a membrane, that project from the body and are used to accomplish all of the different movements necessary for swimming; he further distinguished what he considered were "true fins" from appendages that he designated as "false fins," the latter being simple folds of skin without spines or rays (Goüan, 1770). Bernard Germain de Lacépède used a similar definition while adding that some fishes possess membranes without rays or rays without membranes and that these should nonetheless be termed fins owing to their position and/or function (Lacépède, 1798; Lacépède, Cuvier & Desmarest, 1853).

Notwithstanding the difficulties of defining "fins" in general, fish appendages can be further separated into two categories: median (or unpaired) and paired fins. Despite their opposing views on many topics, both Owen (1854) and Huxley (1871) considered that, from a morphological and structural standpoint, median fins consist of skin folds that are supported by dermal bones termed rays or spines. However, these authors interpreted the low median folds of integument present in the dorsal and caudal regions of cephalochordates as homologous to the median fin system of other fishes despite the absence of rays or spines. Goodrich (1909, p. 71) described the median fins as "*longitudinal median structures, internally segmented like the body itself, and involving many segments*." The preceding definitions of median fins focused on morphological or anatomical criteria, but other authors instead provided functional definitions of the median fins comparing them to the keels or rudders of boats (Cuvier, 1849; Cuvier & Valenciennes, 1828; Lacépède, 1798; Lacépède, Cuvier & Desmarest, 1853).

Median fins can further be categorized by their position on the body. Dorsal fins are located on the dorsal midline between the head and the tail, the anal fins are located along the ventral midline between the anus (or cloaca) and the tail, and the caudal fin is located at the extremity of the tail (Goüan, 1770; Günther, 1880; Huxley, 1871; Lacépède, 1798; Lacépède, Cuvier & Desmarest, 1853). Some taxa bear additional fins along the midline. Dorsally, a number of actinopterygians have an adipose fin. Günther (1880) used the term “fatty fin” and defined it as a dorsal rayless fold of skin in which fat is deposited. More recently, the adipose fin has been described as a small non-rayed fin usually located medially between the dorsal and caudal fins, and variably present among several groups of basal euteleosts (Reimchen & Temple, 2004). Although the fin-rays are generally absent, the adipose fin-web is nonetheless supported by proximo-distally oriented rods of collagen, termed actinotrichia (Stewart & Hale, 2013; Stewart, Smith & Coates, 2014). Two additional forms of dermal skeleton can be found in the adipose fin of some Siluriformes and Characiformes: anterior spines derived from modified scutes, and true fin-rays (Stewart, 2015; Stewart, Smith & Coates, 2014). In some euteleosts, a ventral adipose fin is also described (Fischer & Bianchi, 1984; Greenwood, Rosen, Weitzman & Myers, 1966). Furthermore, in some agnathans, a median ventral fin-fold can be found, positioned anteriorly to the cloaca and of variable extent.

Paired fins have a lateral rather than a median insertion along the body. In gnathostomes, the paired fins comprise the pectoral and pelvic fins. As with the median fins, some authors have used topological criteria to distinguish both sets of paired fins: the pectoral fins are located closely behind the gill openings, whereas the pelvic or ventral fins, even though they display more disparity in their position, are inserted on the abdomen and always anteriorly to the anus (Cuvier, 1849; Cuvier & Duméril, 1835; Cuvier & Valenciennes, 1828; Goüan, 1770; Günther, 1880). Paired fins have also been defined in light of their homology with the fore- and hindlimbs of tetrapods (Cuvier, 1849; Cuvier & Duméril, 1835; Cuvier & Valenciennes, 1828; Günther, 1880; Huxley, 1871; Owen, 1846; 1849; 1854). Owen (1849) considered that both the anterior and posterior members are structures supported by inverted arches: the pectoral fins are supported by the scapular arch (i.e. pectoral girdle) and the pelvic fins by the pelvic arch (i.e. pelvic girdle). Owen’s definitions of pectoral and pelvic appendages are thus strongly based on the nature of the appendicular skeleton and its relative positioning, even though he acknowledged that the position is frequently variable (Owen, 1854). Huxley (1871, p. 2) did not define the paired fins *per se* but stated that vertebrate paired limbs “*are always provided with an internal skeleton, to which the muscles moving the limbs are attached*.” Reflecting Owen and Huxley’s definitions of paired limbs, numerous recent authors consider that to qualify as homologs of pectoral or pelvic fins, paired fins must be inserted on an endoskeletal girdle and they must be supported by a series of endoskeletal (basals and radials) and exoskeletal (fin-rays) elements (Janvier, 1996a; Wilson, Hanke & Märss, 2007). Johanson (2010) added that, at least in gnathostomes, the paired fins are generally narrow-based and their movement is under muscular control. Other authors have emphasized functional considerations to define the paired fins. For example, Belon (1551) and Rondelet (1558) characterized the pectoral and pelvic fins as "wings" that fishes use to "fly" through the water. Howell (1933) suggested that the pectoral fins were owing to a requirement of voluntary movement for progression, whereas the pelvic fins evolved mainly for involuntary static action for support or balance.

Although so far we have only mentioned pectoral and pelvic fins, some taxa, among them many fossil agnathans, possess paired appendages that do not strictly conform to the definitions of pectoral and pelvic fins provided above. These appendages, which can be found in some anaspids and thelodonts, have variously been described using terms such as (ventro-)lateral fins or fin-folds (e.g. Blom, 2008; Blom, Märss & Miller, 2002; Ritchie, 1964; Ritchie, 1968a; 1980), paired anteroventral fins (Chevrinais et al., 2018), pectoral swimming appendages (Stensiö, 1964), paired or pectoral flaps (e.g. Dineley & Loeffler, 1976; Donoghue & Smith, 2001; Märss, Turner & Karatajūtē-Talimaa, 2007; Turner, 1982; 1991) and suprabranchial fins (e.g. Johanson, 2010; Wilson, Hanke & Märss, 2007).

For the purpose of this review, and to account for the structural and functional disparity in fin configurations, we propose a few defining characteristics of fins that can be applied across both extant and extinct taxa. Fins are (1) anatomical structures that project externally from the body outline, (2) and that are generally composed of a membrane supported by endo- and exoskeletal elements, although either of these can be absent. Thus, as did Lacépède (Lacépède, 1798; Lacépède, Cuvier & Desmarest, 1853), we consider that fin-folds without endoskeletal support or serial rays or spines without webbing should also be considered as fins. However, ridges that form along angular regions of the body and that contain neither membranes nor skeletal supports do not qualify as fins. As for the identity of the fins, we emphasize the utility of positional criteria: dorsal fins are located on the dorsal side, anal fins are on the ventral side between the anus and the tail, and the caudal fin is at the extremity of the tail. Some species present additional unpaired fin-folds that can be inserted either anteriorly (e.g. some Myxiniformes) or posteriorly to the cloaca (e.g. some Paralepididae): these will be termed "median ventral (or preanal) fins." As for the paired appendages, we will consider that pectoral fins are inserted on the thorax close to the gill openings, pelvic fins are ventrally inserted anteriorly to the cloaca, and both fins must have narrow bases. Other paired structures, either in the form of long ribbon-like folds or serially repeated fin supports, will be termed “ventrolateral paired fins.”

3 APPENDAGE DISPARITY IN CHORDATES

In this section, we review which appendages are present/absent across the phylogeny from basal chordates to piscine sarcopterygians (Figure 1). For every major group of fishes, we highlight which fins contribute most to the patterns of disparity in appendage configurations and we discuss suggested homologies. Our characterization of fin configurations focuses on adult morphologies, and thus fin-folds that are only present during the early stages of development are not taken into consideration. Throughout this section, we refer to some groups as “basal” or “advanced”, and as “stem” or “crown.” Wherever applicable, we have prioritized the use of “stem” and “crown” groups, as defined by Jefferies (1979) based on the conceptual framework from Hennig (1969). More precisely, a crown group is a clade, nested within a larger “total group,” that includes all extant representatives of that total group. The stem group refers to the paraphyletic assemblage of exclusively fossil taxa that are part of the total group but basal to the crown group. For extant taxa, we will use “basal” when referring to those taxa that are closer to the stem and that display plesiomorphic character combinations for their respective crown group (*sensu* Trueb & Cloutier, 1991). Accordingly, by “advanced” we are referring to the taxa that are further from the stem and exhibit derived characteristics of the crown group. Because phylogenetic relationships among some of these groups remain unresolved and that this can have a bearing on how homologies are interpreted, we also call attention to the hypotheses of interrelationships that have been proposed.

3.1 Non-vertebrate chordates

Chordates comprise three subphyla: Cephalochordata, Tunicata and Craniata (including Vertebrata). Based on shared morphological characters, the cephalochordates have long been considered as the sister-group to craniates (e.g. Garstang, 1928; Herdman, 1904; Maisey, 1986; Rowe, 2004; Schaeffer, 1987; Shimeld & Holland, 2000). However, an alternative hypothesis has also been proposed whereby tunicates, and not cephalochordates, are the sister group to craniates (Jefferies, 1973; 1979; 1986; Jefferies & Lewis, 1978), a view that is well supported by many recent molecular-based phylogenetic analyses (e.g. Blair & Hedges, 2005; Bourlat et al., 2006; Delsuc, Brinkmann, Chourrout & Philippe, 2006; Delsuc, Tsagkogeorga, Lartillot & Philippe, 2008; Dunn et al., 2008; Heimberg, Cowper-Sallari, Semon, Donoghue & Peterson, 2010; Philippe, Lartillot & Brinkmann, 2005; Putnam et al., 2008; Singh et al., 2009).

The extant representatives of the Cephalochordata are the Amphioxiformes, or lancelets, which include between 30 and 35 species divided into two genera (Hubbs, 1922; Poss & Boschung, 1996; Satoh, Rokhsar & Nishikawa, 2014; Stokes & Holland, 1998). Lancelets possess a fin-fold along the dorsal and ventral midlines of the body that is continuous around the tip of the tail, as well as along the anterior tip of the notochord, where it forms a “rostral fin” (Andrews, 1893; Bigelow & Farfante, 1948; Goodrich, 1930; Herdman, 1904; Holland & Holland, 1991; Jefferies, 1986; Jordan & Evermann, 1896; Jordan & Gilbert, 1882; Jordan & Snyder, 1901; Kirkaldy, 1895; Lankester, 1889; Rice, 1880; Wiley, 1894). Schaeffer (1987) suggested the median fin-fold of lancelets to be homologous with the larval median fin-fold of developing vertebrates. Some authors describe the postero-ventral part of the median fin-fold as an anal fin (e.g. Goodsir, 1844; Jordan & Evermann, 1896; Jordan & Snyder, 1901) despite that its anterior insertion is in front of the anus, while others use the term preanal fin (e.g. Hubbs, 1922; Xu, Ma & Wang, 2005). Rod-like structures along the dorsal and ventral fins have sometimes been interpreted as fin-rays (e.g. Andrews, 1893; Bigelow & Farfante, 1948; Goodrich, 1930; Jefferies, 1986; Lankester, 1889; Wiley, 1894; Yarrell, 1836). It is now clear that these so-called fin-rays of lancelets are not homologous to the radials or dermal rays of vertebrates (Holland & Chen, 2001; Holland & Holland, 1991). They are in fact retroperitoneal accumulations of haemal fluid containing nutritional reserves that project into coeloms along the median fin-folds; they shrink and disappear during gametogenesis or if the individuals are subjected to starvation (Azariah, 1965; Holland & Holland, 1991; Stokes, 1996). Paired structures, termed metapleural folds, arise posteriorly to the oral hood, extending ventro-laterally under the branchial region and atrial cavity (Andrews, 1893; Goodrich, 1930; Goodsir, 1844; Herdman, 1904; Jefferies, 1986; Kirkaldy, 1895; Lankester, 1875; 1889; Rice, 1880; Wiley, 1894). Posteriorly, the left metapleural fold is continuous with the median ventral fin in *Epigonichthys*, whereas both metapleural folds are interrupted behind the atriopore in *Branchiostoma* (Kirkaldy, 1895; Poss & Boschung, 1996). Thacher (1877) suggested that the metapleural folds were homologous to the continuous lateral fin-folds from which pectoral and pelvic fins are hypothesized to have evolved. However, these are hollow structures that are filled with fluid and they become flattened and inconspicuous during the spawning season when the atrial cavity is distended owing to the increasing space occupied by the developing gonads (Lankester, 1875; 1889; Rice, 1880; Wiley, 1894). Therefore, metapleural folds are neither structured, nor are they functionally used as fins in cephalochordates (Wiley, 1894).

Tunicates, or urochordates, comprise three classes and about 3000 species (Satoh, Rokhsar & Nishikawa, 2014; Shenkar & Swalla, 2011). As adults, they are sac-like marine filter-feeding organisms, yet a post-anal tail and fin-fold is present during the larval stage in two of the classes, the Ascidiacea and Thaliacea, and persists during the entire life cycle in representatives of the third class, the Appendicularia (Cloney, 1982; Herdman, 1904; Nishino & Satoh, 2001). The tail includes the notochordal axis, muscle fibers, as well as dorsal and ventral fin-folds that are continuous around the posterior tip of the notochord (Berrill, 1930; Cloney, 1982; Herdman, 1904; Kowalevsky, 1866; McHenry, 2005). Tunicates are hypothesized to have arisen during or even before the Cambrian diversification, however their fossil record is very poor owing to the absence of mineralized parts; the only undisputed fossil tunicate is from the Lower Cambrian of China (Chen et al., 2003).

The fossil record also contains a few forms that have variously been interpreted as stem deuterostomes, cephalochordates, stem chordates, or stem craniates (i.e. *Yunnanozoon lividum*, *Haikouella lanceolata*, *H. jianshanensis*, *Pikaia gracilens*, *Cathaymyrus diadexus*). *Yunnanozoon,* from the Lower Cambrian of southern China, was originally interpreted as a worm-like animal bearing a segmented cuticle (Hou, Ramskold & Bergstrom, 1991). Although some authors have suggested cephalochordate affinity (e.g. Chen, Dzik, Edgecombe, Ramsköld & Zhou, 1995; Stokes & Holland, 1998), it seems more likely that *Yunnanozoon* is a stem deuterostome that is nested neither in craniates or vertebrates (e.g. Bergström, Naumann, Viehweg & Martí- Mus, 1998; Shu, 2003; 2008; Shu, Morris, Zhang & Han, 2010). Dorsal and ventral dark bands extending along the midline (Chen, Dzik, Edgecombe, Ramsköld & Zhou, 1995; Dzik, 1995) have been interpreted as dorsal and ventral fin-folds (Chen, Dzik, Edgecombe, Ramsköld & Zhou, 1995). Shu, Zhang & Chen (1996) interpreted the existence of a much larger sclerotized and segmented dorsal fin, a view which has been disputed based on recent evidence from the closely allied *Haikouella* suggesting that the segments are actually myomeres (Mallatt

& Chen, 2003; Mallatt, Chen & Holland, 2003). Paired ventrolateral folds are observable on many specimens (Chen & Li, 1997; Dzik, 1995) and have been compared to the metapleural folds of cephalochordates (Chen & Li, 1997). Based on the morphology of *Haikouella*, *Y. lividum* has occasionally been reconstructed as having a caudal process bearing a fin-web (e.g. Chen & Huang, 2006; Chen & Huang, 2008). However, Chen & Huang (2008) acknowledge that this structure has not been observed in any of the *Yunnanozoon* specimens.

Haikouella is known from hundreds of complete specimens from the Lower Cambrian of southern China (Chen, Huang & Li, 1999). Some specimens of *Haikouella* present a post-anal tail (referred to as a “caudal process”) posteriorly to the anus; its absence in other individuals is thought to be a result of breaking off during fossilization (Chen, Huang & Li, 1999; Mallatt & Chen, 2003). An alternate view is that the caudal process is a taphonomic artefact brought about by folding and compaction of the posterior part of the body (Shu & Morris, 2003). Medially, there are also dorsal and ventral fins but lateral appendages are entirely absent (Holland & Chen, 2001). The fins in *Haikouella* do not contain rays (Mallatt & Chen, 2003). Similarly to *Yunnanozoon*, the phylogenetic position of *Haikouella* is debated. On the one hand, this taxon might be a stem deuterostome (Shu, 2003; 2008; Shu & Morris, 2003; Shu, Morris, Zhang & Han, 2010; Shu et al., 2003b). Alternatively, it might be a stem craniate if the interpretation of structures identified as a brain, eyes, a post-anal tail and median fins are correct (Chen, Huang & Li, 1999; Mallatt & Chen, 2003; Mallatt, Chen & Holland, 2003). Some phylogenetic analyses have resolved *Haikouella* at the base of craniates (Holland & Chen, 2001; Mallatt & Chen, 2003), suggesting that yunnanozoans (i.e. *Yunnanozoon* + *Haikouella*) may be the sister group of all other craniates. Based on a more recent investigation of over 700 specimens, Cong, Hou, Aldridge, Purnell & Li (2015) argued that yunnanozoan characters can be open to alternative interpretations and that their affinities to other groups should conservatively be considered within a wider bilaterian context. Notwithstanding the uncertain phylogenetic position of yunnanozoans, it is generally agreed that *Yunnanozoon* and *Haikouella* are either close relatives (Mallatt & Chen, 2003; Mallatt, Chen & Holland, 2003; Shu & Morris, 2003; Shu et al., 2003b), or even possibly synonyms (Cong, Hou, Aldridge, Purnell & Li, 2015; Turner et al., 2010).

Pikaia, from the Middle Cambrian Burgess Shale of western Canada, was originally interpreted as a polychaete owing to the presence of curious lateral appendages in the branchial area (Walcott, 1911; 1931). Subsequent investigations of the material revealed chordate-like characters (Insom, Pucci & Simonetta, 1995; Morris, 1979; Morris & Whittington, 1979), and *Pikaia* has since been interpreted as closely related to cephalochordates (e.g. Shu et al., 1999; Smith, Sansom & Cochrane, 2001; Stokes & Holland, 1998) or to yunnanozoans (Morris & Caron, 2012). Following a thorough re-examination of the *Pikaia* material, the only appendages described are a dorsal fin-fold without fin-rays and a series of nine bilaterally arranged appendages with possible pharyngeal pores near their insertions (Morris & Caron, 2012). There is also a ventral keel extending from just behind the last of the lateral appendages and becoming less distinct posteriorly which might have represented a median ventral fin, or possibly a gonadal structure (Morris & Caron, 2012). Mallatt & Holland (2013, p. 268) argued that the ventral keel and posterior ventral area are most definitively a fin because they "*look fin-like and seem to be homologues of a fin.*" Although a tail-fin devoid of fin-rays has been mentioned in some descriptions (Briggs & Kear, 1994; Insom, Pucci & Simonetta, 1995; Smith, Sansom & Cochrane, 2001), this feature is absent in Morris & Caron (2012)'s detailed revision of the material.

Cathaymyrus was originally described based on a single specimen from the Lower Cambrian of southern China (Shu, Morris & Zhang, 1996). *Cathaymyrus* has been interpreted as lacking any evidence for fins or fin-rays (Shu, Morris & Zhang, 1996; Smith, Sansom & Cochrane, 2001), although a dorsal fin is explicitly mentioned in Shu (2003). It has been suggested that *Cathaymyrus* might actually be a crushed specimen of *Yunnanozoon*, however this hypothesis was later discredited (Luo, Hu & Chen, 2001; Shu, Chen, Zhang, Han & Li, 2001; Shu, Morris, Zhang & Han, 2010). *Cathaymyrus* is generally interpreted as belonging to cephalochordates (Mallatt & Holland, 2013; Morris, 2006; Shu, 2008; Stokes & Holland, 1998).

3.2 Stem vertebrates

Four Cambrian representatives of stem vertebrates (*Zhongjianichthys rostratus*, *Myllokunmingia fengjiaoa*, *Haikouichthys ercaicunensis, Metaspriggina walcotti*) are sufficiently well known to permit discussion of their fin configurations. Common to all four species is the absence of paired fins. Median ventral and dorsal fins are present in *Zhongjianichthys* (Shu, 2003), *Myllokunmingia* (Holland & Chen, 2001; Hou, Aldridge, Siveter & Feng, 2002; Shu, 2008; Shu et al., 1999) and *Haikouichthys* (Holland & Chen, 2001; Hou, Aldridge, Siveter & Feng, 2002; Shu, 2008; Shu et al., 1999; Shu et al., 2003a; Zhang & Hou, 2004). In the original descriptions of *Myllokunmingia* and *Haikouichthys*, doubts were expressed concerning the interpretation of a ventral structure that could have been either a median ventral fin-fold or paired ventrolateral fin-folds (Shu, Chen, Zhang, Han & Li, 2001; Shu et al., 1999). Subsequent discoveries and analyses of additional specimens of *Haikouichthys* provided no indications whatsoever that the ventral fin-fold is a paired structure (Hou, Aldridge, Siveter & Feng, 2002; Shu, 2008; Shu et al., 2003a; Zhang & Hou, 2004). A dorsal fin was originally considered to be absent in *Metaspriggina* (Simonetta & Insom, 1993). Later, a narrow area along the anterior trunk of the lectotype was interpreted as a possible dorsal fold or ridge (Morris, 2008). The most recent revision of the *Metaspriggina* material suggests that it was entirely finless although a keel-like structure is present along the ventral midline; Morris & Caron (2014) mentioned however that the absence of fins could be a taphonomic artefact. With the exception of *Zhongjianichthys* where the presence of an anal fin cannot be determined, a distinct anal fin is absent in all of these stem vertebrates. A caudal fin is present in *Haikouichthys* and absent in *Metaspriggina*; its presence cannot be assessed for *Zhongjianichthys* and *Myllokunmingia*.

Myllokunmingia, *Haikouichthys* and *Zhongjianichthys* are considered as close relatives and have been assigned to the order Myllokunmingiida (Shu, 2003). They are either interpreted as stem craniates (Shu, 2003; Shu et al., 2003a) or stem vertebrates (Shu, 2005; Shu, Chen, Zhang, Han & Li, 2001). It has been suggested that *Myllokunmingia* and *Haikouichthys* might be synonyms (e.g. Blieck, 2011; Hou, Aldridge, Siveter & Feng, 2002; Janvier, 2007; Turner et al., 2010; Žigaitė & Blieck, 2013), while other authors consider that these taxa are correctly identified as separate species (Morris, 2006; Morris & Caron, 2012; Shimeld & Holland, 2000). *Zhongjianichthys* has also been proposed as a possible synonym and badly preserved specimen of *Myllokunmingia* (Blieck, 2011; Janvier, 2007; Žigaitė & Blieck, 2013) or *Haikouichthys* (Morris & Caron, 2012). Recently, Morris & Caron (2014) supported *Metaspriggina*'s vertebrate affinity based on the presence of a notochord, camerular eyes, paired nasal sacs, a possible cranium, possible arcualia, W-shaped myomeres and a post-anal tail.

3.3 Myxiniformes

Myxines, or hagfishes, are either the most basal of extant craniates or they are basal vertebrates (see next sub-section for hypothesized interrelationships among hagfishes, lampreys and gnathostomes) and comprise a single order, with about 79 extant species (Zintzen et al., 2015).

Their fossil record extends at least to the Upper Carboniferous [but possibly as far as the Middle Devonian if *Palaeospondylus gunni* is confirmed as a primitive hagfish as suggested by Hirasawa, Oisi & Kuratani (2016)] and includes five extinct species, three of which are only tentatively assigned to the Myxiniformes (Bardack, 1991; 1998; Bardack & Richardson, 1977; Germain, Sanchez, Janvier & Tafforeau, 2014; Hirasawa, Oisi & Kuratani, 2016; Miyashita et al., 2019; Poplin, Sotty & Janvier, 2001). Hagfishes have a simple fin configuration that comprises a caudal fin supported by cartilaginous fin-rays (Adam & Strahan, 1963; Ota, Fujimoto, Oisi & Kuratani, 2011; 2013; Wright, Keeley & DeMont, 1998) and a median preanal fin-fold (Fernholm, 1998). The caudal fin can be absent in some extant species. For instance in *Myxine formosana*, the caudal fin is described as vestigial or absent (McMillan & Wisner, 2004; Mok & Kuo, 2001). Hagfishes generally lack a distinct dorsal fin, although in the Carboniferous *Myxinikela siroka*, a dorsal fin arises somewhat anterior to the mid-body and is continuous with the caudal fin posteriorly (Bardack, 1991; 1998). However, Bardack (1991; 1998) mentioned that the specimen might represent a juvenile stage of development.

The preanal fin-fold of hagfishes is devoid of skeletal supports (Hardisty, 1979) and is in fact a band of thin fleshy tissue found along the ventral midline starting from the cloaca and differing among species in its anterior extent (Wisner & McMillan, 1995). The preanal fin-fold is reported absent in the extant *Myxine debueni* (Fernholm, 1998; Wisner & McMillan, 1995) as well as in the Carboniferous *Gilpichthys greenei*, a fossil species that lacks all types of fins including the caudal fin (Bardack & Richardson, 1977). It should be mentioned that *Gilpichthys* is known from a single specimen and its assignment to Myxiniformes has been debated: it might in fact constitute an immature organism (Bardack, 1998; Bardack & Richardson, 1977). However, a recent phylogenetic analysis reaffirmed its position as a stem hagfish (McCoy et al., 2016). The presence and conspicuity of the preanal fin-fold can also vary intraspecifically; in some species, it is reported either as weakly-developed, vestigial or absent (e.g. Kuo, Huang & Mok, 1994; McMillan & Wisner, 2004; Wisner & McMillan, 1988; 1990).

Paired fins are generally considered as entirely absent in Myxiniformes although both species of *Neomyxine* present lateral folds of skin located immediately above the gill openings (Richardson, 1953; 1958; Zintzen et al., 2015). Contrary to the paired fins found in most other craniates, these “ventrolateral branchial fin-folds” are located dorsally to the branchial openings and do not seem to be used in swimming but rather as support when individuals settle on substrate (Adam & Strahan, 1963; Janvier, 1978; Richardson, 1953). Furthermore, there are no traces of internal skeletal support or of an associated specialized musculature (Forey, 1984). Because *Neomyxine* is not resolved as the most basal taxon among Myxiniformes (Zintzen et al., 2015), this structure is unlikely to be homologous to the paired fins of other vertebrates (Donoghue, Forey & Aldridge, 2000).

3.4 Petromyzontiformes

Petromyzontiformes, or lampreys, also comprise a single order including 43 extant species and five fossil species (Chang, Wu, Miao & Zhang, 2014; Hume, Bean & Adams, 2014; Renaud, 2011). The oldest fossil lamprey is *Priscomyzon riniensis* from the Upper Devonian of South Africa (Gess, Coates & Rubidge, 2006). The caudal fin is always present in extant lampreys, with the exception of a single specimen of *Lampetra planeri* that was described as having an incompletely formed caudal fin (Hume, Bean & Adams, 2014). Among fossil lampreys, the caudal fin is absent only in *Pipiscius zangerli* (Bardack & Richardson, 1977). However, the affinity of *Pipiscius* to the petromyzontids has been questioned (Bardack, 1998; Janvier & Lund, 1983). Recent phylogenetic analyses have resolved this taxon's position either as a stem lamprey (McCoy et al., 2016; Sallan et al., 2017) or as a stem cyclostome (Miyashita et al., 2019). Furthermore, a yolk sac might be present, suggesting that *Pipiscius* could represent a larval organism (Bardack & Richardson, 1977).

Most extant lampreys have two dorsal fins, with the exception of all species belonging to *Ichthyomyzon* that have a single dorsal fin (Renaud, 2011). As for fossil lampreys, most species have a single dorsal fin (Bardack & Zangerl, 1968; Chang, Wu, Miao & Zhang, 2014; Chang, Zhang & Miao, 2006; Gess, Coates & Rubidge, 2006; McCoy et al., 2016), excepting *Hardistiella montanensis* that has two dorsal fins (Janvier & Lund, 1983; Janvier, Lund & Grogan, 2004). A median preanal fin-fold, such as was described for hagfishes, is absent in lampreys. In extant species, an anal fin with skeletal support is typically absent although two specimens of *Petromyzon marinus* have been found with an anal fin with cartilaginous fin-rays, a condition interpreted as an atavism (Janvier, 1996a; 2007; 2008; Vladykov, 1973; Vladykov & Kott, 1980). Hume, Bean & Adams (2014) also reported the presence of an anal fin supported by five or six fin-rays in a single specimen of the extant *L. planeri*. Additionally, female lampreys preparing to spawn develop fleshy pre- and post-anal fin-like folds (Hardisty & Potter, 1971;

Janvier & Lund, 1983; Kott, Renaud & Vladykov, 1988; Pletcher, 1963; Renaud, 2011; Vladykov, 1973; Vladykov & Kott, 1980). Similarly, in males and females of Petromyzontidae, the bases of the dorsal fins become swollen prior to reproduction in a way that makes them appear united (Hardisty & Potter, 1971; Kott, Renaud & Vladykov, 1988; Renaud, 2011). Anal fins have been described in two fossil species, *H. montanensis* (Janvier & Lund, 1983) and *Mayomyzon pieckoensis* (Bardack & Zangerl, 1968). In *Hardistiella*, a small notch separates the chordal lobe of the caudal fin from the anal fin (Janvier & Lund, 1983). Later, Janvier & Arsenault (2007) expressed that the presence of an anal fin required confirmation in this species. As for *Mayomyzon*, the dorsal, anal and caudal fins are continuous along the body, the latter being separated from the first two by small notches (Bardack & Zangerl, 1968). Janvier & Lund (1983) questioned the presence of a true anal fin in *Mayomyzon* and suggested that this might instead be the typical anal fin-like fold found in spawning female lampreys.

Paired fins are entirely lacking in all fossil and extant lampreys. Janvier (1981b) suggested that the absence of paired fins is most likely secondary in the Petromyzontiformes based on their being present in closely related groups (e.g. anaspids). In support of this palaeontological hypothesis, it has been shown that the absence of paired fins in lampreys can be traced back to ventrally migrating extensions of the dermomyotome, effectively separating the lateral plate mesoderm from the overlying ectoderm (Tulenko et al., 2013). In tetrapods, the proper development of many elements of the paired limbs and girdles are known to require signaling between the ectoderm and the lateral plate mesoderm (Capdevila & Izpesúa Belmonte, 2001; Ehehalt, Wang, Christ, Patel & Huang, 2004; Malashichev, Borkhvardt, Christ & Scaal, 2005; Malashichev, Christ & Prols, 2008; Wang et al., 2005). Tulenko et al. (2013) further suggest that the persistence of somatic lateral plate mesoderm external to the myotomes was a key step towards the development of paired fins in gnathostomes.

A final representative of the Petromyzontiformes requires separate mention owing to its uncharacteristic morphology, *Tullimonstrum gregarium*. *Tullimonstrum,* from the Upper Carboniferous of Illinois, USA, was originally described as a worm-like animal (Richardson, 1966), and its relationship to annelids, molluscs or arthropods have been considered [see Turner et al. (2010) for a review of these hypothesized relationships]. Based on a re-examination of over 1200 specimens and the inclusion of the reinterpreted characters into a phylogenetic analysis, *Tullimonstrum* has recently been resolved as a stem lamprey (McCoy et al., 2016). However, Sallan et al. (2017) have raised issues concerning some biological, functional and taphonomical interpretations of the data that were used to establish vertebrate identity, as well as with the use of an all-chordate dataset for the phylogenetic analyses. Based on a reanalysis of the character matrix from McCoy et al. (2016) with some characters rescored, Sallan et al. (2017) suggest that a non-vertebrate assignment for *Tullimonstrum* is more likely. Notwithstanding the uncertainty in its phylogenetic placement among stem lampreys, *Tullimonstrum* possesses a single long and low dorsal fin, as well as an asymmetrical oblanceolate caudal fin (Clements et al., 2016; McCoy et al., 2016).

The interrelationships among lampreys, hagfishes and gnathostomes have been debated for many years and two competing hypotheses have been proposed: (1) either lampreys and hagfishes form a clade called the cyclostomes (Duméril, 1806; Schaeffer & Thomson, 1980; Shimeld & Donoghue, 2012), (2) or hagfishes are craniates while lampreys are vertebrates, making the "cyclostomes" paraphyletic relative to the gnathostomes (Dingerkus, 1979; Forey, 1984; Forey & Janvier, 1993; Hardisty, 1979; Janvier, 1978; 1981b; 1996b; Janvier & Blieck, 1979; Jefferies, 1986; Løvtrup, 1977). Cyclostome monophyly was initially suggested based on morphological arguments (e.g. Schaeffer & Thomson, 1980; Yalden, 1985) and is well supported by molecular phylogenetic analyses (Delarbre, Gallut, Barriel, Janvier & Gachelin, 2002; Furlong & Holland, 2002; Hedges, 2001; Heimberg, Cowper-Sallari, Semon, Donoghue & Peterson, 2010; Mallatt & Sullivan, 1998; Mallatt, Sullivan & Winchell, 2001; Stock & Whitt, 1992). In contrast, analyses based on morphological datasets and incorporating fossil taxa have generally resolved "cyclostomes" as paraphyletic relative to gnathostomes (Donoghue, Forey & Aldridge, 2000; Donoghue & Smith, 2001; Forey, 1995; Gess, Coates & Rubidge, 2006; Janvier, 1996a; Khonsari, Li, Vernier, Northcutt & Janvier, 2009; Miyashita, 2012; Turner et al., 2010). However, one such recently published phylogenetic analysis incorporating a newly discovered undisputed fossil hagfish has now recovered the cyclostomes as monophyletic (Miyashita et al., 2019). Moreover, Miyashita et al. (2019) found that anaspids and conodonts are resolved as stem cyclostomes using maximum parsimony, whereas anaspids are stem cyclostomes while conodonts are stem hagfishes using Bayesian inference. If this hypothesis gains additional support in future analyses, this would have major implications concerning the evolution of paired fins in jawless fishes. Because anaspids have paired appendages, if they are indeed stem cyclostomes, this would support the hypothesis that the absence of paired fins is owing to secondary loss not only in lampreys (Janvier, 1981b; Tulenko et al., 2013), but also in hagfishes and possibly conodonts.

3.5 Conodonta

The conodont fossil record extends from the Upper Cambrian to the Upper Triassic (Aldridge & Smith, 1993). Depending on classifications, conodonts comprise between five and seven orders, most of which are known only from remains of the oral apparatus (Aldridge, Purnell, Gabbott & Theron, 1995; Aldridge & Smith, 1993; Dzik, 1991; Sweet, 1988). Although there are close to 5000 named species, Sweet (1988) estimated that 1446 species in 246 genera represents a more conservative figure. Only a few species are known from articulated specimens, exceptionally showing preservation of some of the soft tissues anatomy: one of these is *Promissum pulchrum*, known only from well-preserved material from the anterior portion of the animal (Aldridge & Theron, 1993; Gabbott, Aldridge & Theron, 1995), and two others belong to the genus *Clydagnathus* [*C. windsorensis* and *Clydagnathus*? sp. (*C.*? sp. cf. *C. cavusformis*)] (Aldridge, Briggs, Clarkson & Smith, 1986; Aldridge, Briggs, Smith, Clarkson & Clark, 1993; Briggs, Clarkson & Aldridge, 1983). In the latter species, the elements of the oral apparatus most useful for identification purposes remain for the most part buried in the sediment: Briggs, Clarkson & Aldridge (1983) tentatively assigned the material to *C. cavusformis* on the basis of general similarities, while expressing their uncertainty in that respect.

Because there are so few well-preserved specimens with postcranial material preserved, little is known concerning the fin configurations in conodonts. The tail region is preserved in some of the *Clydagnathus* material and shows a well-developed caudal fin supported by fin-rays (Aldridge, Briggs, Clarkson & Smith, 1986; Aldridge, Briggs, Smith, Clarkson & Clark, 1993; Aldridge & Purnell, 1996; Briggs, 1992; Briggs, Clarkson & Aldridge, 1983; Pridmore, Barwick & Nicoll, 1997). In *C. cavusformis*, there is a gap in the fin-rays along the dorsal midline, followed anteriorly by a second series that is interpreted as a dorsal fin (Aldridge, Briggs, Clarkson & Smith, 1986; Briggs, Clarkson & Aldridge, 1983). Indications as to the presence of other median or paired fins have not been found.

The affinity of conodonts is still strongly debated. Until the discovery of some specimens with elements of the soft anatomy preserved (Aldridge, 1987; Aldridge, Briggs, Clarkson & Smith, 1986; Briggs, Clarkson & Aldridge, 1983; Gabbott, Aldridge & Theron, 1995), they had been interpreted as belonging to a number of invertebrate and vertebrate groups [see Aldridge, Briggs, Smith, Clarkson & Clark (1993) for a review of previously hypothesized conodont interrelationships], or assigned to a separate phylum (Sweet, 1988). Current suggestions include (1) that they are chordates lying outside of craniates/vertebrates (Aldridge, 1987; Aldridge & Briggs, 1990; Aldridge, Briggs, Clarkson & Smith, 1986; Blieck et al., 2010; Pridmore, Barwick & Nicoll, 1997; Turner et al., 2010), (2) that they occupy a basal position among crown vertebrates (Aldridge & Purnell, 1996; Aldridge & Theron, 1993; Briggs, 1992; Briggs & Kear, 1994; Donoghue, Forey & Aldridge, 2000; Donoghue, Purnell & Aldridge, 1998; Gabbott, Aldridge & Theron, 1995; Purnell, 1995; Schubert, Escriva, Xavier-Neto & Laudet, 2006; Sweet & Donoghue, 2001), or (3) that they are stem cyclostomes (Miyashita et al., 2019).

3.6 Anaspida

The stratigraphic range of the Anaspida extends from the Lower Silurian to the Upper Devonian (Blom, Märss & Miller, 2002; Janvier, 1996b). Anaspids comprise two or three orders depending on classifications, and about 25 genera. Some authors consider that true anaspids are only those taxa that possess tri-radiate post-branchial spines: this includes the scaled anaspids, or birkeniids, and members of the genus *Lasanius* (Arsenault & Janvier, 1991; Blom, 2012; Blom, Märss & Miller, 2002; Janvier, 1996b; c). We favour the more inclusive view whereby the "naked-anaspids" or Jamoytiiformes, a group that shares with other anaspids the possession of a strongly hypocercal tail, are nested within the Anaspida (Blom & Märss, 2010; Chevrinais et al., 2018; Keating & Donoghue, 2016; Kiaer, 1924; Robertson, 1941; Stensiö, 1939; von Zittel & Woodward, 1902).

Anaspids present some challenges as to the interpretation of their fin configurations. All sufficiently known anaspids possess at least a caudal fin and an anal fin. These fins were supported by radials that were most likely under muscular control (Jarvik, 1959). A few species (e.g. *Birkenia elegans, Kerreralepis carinata, Pterygolepis nitida*) possess a series of plates or spines inserted anteriorly to the anus, which Blom (2012) interpreted as a possible median preanal fin. A long and low dorsal fin has been described for *Achanarella trewini* (Newman, 2002), *Endeiolepis aneri* (Arsenault & Janvier, 1991; Janvier, 1996b; Newman & Trewin, 2001; Robertson, 1941; Stensiö, 1939; White, 1946) and *Jamoytius kerwoodi* (Janvier, 1981b; Ritchie, 1968a; White, 1946). In *Euphanerops longaevus*, a dorsal fin has been reported either as present

(Arsenault & Janvier, 1991; Stensiö, 1939; Woodward, 1900a) or absent (Janvier & Arsenault, 2007; Sansom, Gabbott & Purnell, 2013). A recent re-investigation of the *Euphanerops* material confirms that a long and low dorsal fin is indeed present (Chevrinais et al., 2018). Furthermore, it has been proposed that *En. aneri* might actually represent a junior synonym for *Eu. longaevus* (Janvier, 2008; Janvier & Arsenault, 2007; Janvier, Desbiens, Willett & Arsenault, 2006; Sansom, Gabbott & Purnell, 2013), however this hypothesis has not yet been the subject of a thorough investigation. In other anaspids, a dorsal fin is generally absent although some consider that the series of dorsal and/or ventral scutes represent reductions of what was originally dorsal or ventral fin-folds (Forey, 1995; Moy-Thomas & Miles, 1971; Ritchie, 1964; 1968a; Stensiö, 1939; 1964). Another interpretation is that the large epichordal lobe of the caudal fin is homologous to the second dorsal fin found in lampreys, osteostracans and gnathostomes (Arsenault & Janvier, 1991; Blom & Märss, 2010; Janvier, 1981b; 1996b; 2007; 2008; Jarvik, 1959), a hypothesis that seems unlikely but that cannot be rejected given that it has not been formally tested.

Many anaspids have paired ventrolateral fin-folds and/or triradiate spines that have been considered as possibly homologous to either the pectoral fins (Gagnier, 1993b; Kiaer, 1924; Robertson, 1938a; 1941; Stensiö, 1927; 1932), the pelvic fins (Janvier & Arsenault, 2007; Moy-Thomas & Miles, 1971; Wilson, Hanke & Märss, 2007), or both paired fins (Stensiö, 1939). Homology of the paired ventrolateral fin-folds of anaspids with the metapleural folds of lancelets has also been suggested (Gagnier, 1993b; Westoll, 1958; Wickstead, 1969). Yet another hypothesis is that they represent independently derived structures (Coates, 2003; Hopson, 1974; Janvier, 1987; Ritchie, 1964; Robertson, 1941). Anaspid paired fins are found in a post-branchial position and there are traces of endoskeletal supports for the fin-web (Gagnier, 1993b; Ritchie, 1964; Stensiö, 1964; Wilson, Hanke & Märss, 2007). Some also consider that they were likely moveable structures under muscular control (Janvier, 1981b; 1984; 1987; 1996b; Ritchie, 1964; Wilson, Hanke & Märss, 2007; contra Westoll, 1958). The “pectoral spines” are generally interpreted as forming the leading edge of the ventrolateral fin-folds (e.g. Blom, 2008; Gagnier, 1993b; Janvier, 1996b; Kiaer, 1924; Moy-Thomas & Miles, 1971; Ritchie, 1964; 1980). In most species, the paired fins are unconstricted and ribbon-like, with the exception of *Pharyngolepis heintzii* and *Rhyncholepis parvulus* (Blom, Märss & Miller, 2002; Janvier, 1981b; 1984; Moy-Thomas & Miles, 1971; Ritchie, 1964; 1980) where they are much shorter. Blom (2012) argued that the evidence in favour of the paired lateral fin-folds described for *Jamoytius* and *Euphanerops* is inconclusive, and that an alternative hypothesis is that these might actually be unpaired median structures. Based on a thorough examination of the *Euphanerops* material (Chevrinais et al., 2018), paired ventrolateral fins are indeed found to be present in euphaneropids, as suggested by Stensiö (1939) and Janvier & Arsenault (2007). Furthermore, these ventrolateral paired fins are subdivided into a series of finlets, each composed of a radial, a meso- or metapterygial-like element and several fin-rays (Chevrinais et al., 2018). Janvier (1996b) suggested that the posterior extent of the paired fins in anaspids may have been constrained by the position of the anus. However, it has recently been found that the structure originally described as an anal fin in *Euphanerops* is in fact a paired fin (Sansom, Gabbott & Purnell, 2013). Paired anal fins are unique to *Euphanerops* among vertebrates, with the exception of some mutations in goldfish (*Carassius auratus*) and zebrafish (*Danio rerio*) that lead to duplicated anal and/or caudal fin structures (Abe et al., 2014; Abe & Ota, 2017).

3.7 Pteraspidomorphi

The extinct Pteraspidomorphi comprise four orders (Astraspidiformes, Arandaspidiformes, Cyathaspidiformes and Pteraspidiformes), most of which are known only from the remains of the cephalothoracic shield. The Astraspidiformes currently include only two species from the Ordovician of North America and Siberia (Janvier, 1996a; b), among which *Astraspis desiderata* is the best known. *Astraspis* has a caudal fin but no other median or paired fins (Elliott, 1987; Gagnier, 1993a; b; Lehtola, 1983; Sansom, Smith, Smith & Turner, 1997; Soehn & Wilson, 1990). Some of the earliest undisputed vertebrate remains, from the Lower Ordovician of Australia, have been assigned to the arandaspid genus *Porophoraspis* (Young, 1997). However, articulated postcranial material is known only for two species of Arandaspidiformes, *Sacabambaspis janvieri* from the Middle-Upper Ordovician of Bolivia (Gagnier, 1989; 1993b; Gagnier & Blieck, 1992; Gagnier, Blieck & Rodrigo, 1986; Pradel, Sansom, Gagnier, Cespedes & Janvier, 2007) and *Arandaspis prionotolepis* from the Lower-Middle Ordovician of Australia (Ritchie, 1985; Ritchie & Gilbert-Tomlinson, 1977). In *Sacabambaspis*, a caudal fin is present and there are dorsal and preanal crests and ridge scales along the dorsal and ventral midlines (Gagnier, 1993a; b; Gagnier & Blieck, 1992). As for *Arandaspis*, even in the best-preserved specimen, only a small part of the body posteriorly to the cephalothoracic shield is preserved so that nothing can be said concerning the shapes and arrangement of the fins (Ritchie, 1985; Ritchie & Gilbert-Tomlinson, 1977).

The Cyathaspidiformes and Pteraspidiformes are generally referred to as heterostracans. Heterostracans appeared during the Lower Silurian and their stratigraphic range extends to the Upper Devonian (Janvier, 1996b; Žigaitė & Blieck, 2013). They are extremely conservative in terms of fin configurations: all median and paired fins are absent with the exception of the caudal fin (Stensiö, 1964; White, 1935). Lateral extensions of the shield are present in some taxa and would have served as an aid in stability (the cornual plates of pteraspids and branchial plates of psammosteids) but these structures were generally not moveable (Halstead, 1973; Halstead & Turner, 1973; Janvier & Blieck, 1979; Westoll, 1958), with the possible exception of the branchial plates in *Psammosteus kiaeri* (Tarlo, 1964; 1965). Some authors have suggested that heterostracans retain a median ventral fin-fold in the form of a ventral crest composed of scales (Blieck, 1984; Janvier & Blieck, 1979; Stensiö, 1964). Stensiö (1964) also interpreted the median dorsal crest scales as representing a dorsal fin-fold. We consider these interpretations unlikely since scales or scutes arranged along the midline are present in other taxa and they are unquestionably not considered as fins [e.g. sturgeons (Acipenseriformes) and lumpsuckers (Cyclopteridae) have dorsal scutes; anchovies, herrings and sardines (Clupeiformes) generally have ventral scutes].

3.8 "Thelodonti"

The stratigraphic range of the "Thelodonti" [6 orders, ~132 described species (Märss, Turner & Karatajūtē-Talimaa, 2007)] extends from the Middle Ordovician to the Upper Devonian (Märss, Turner & Karatajūtē-Talimaa, 2007). All thelodonts so far described possess a caudal fin. A dorsal fin is generally present, but can be lacking in some Thelodontiformes and Furcacaudiformes. Some authors have also speculated that the epichordal lobe of at least some thelodonts could be homologous to the second dorsal fin of osteostracans and gnathostomes (Janvier, 1981b; van der Brugghen, 1994). An anal fin has been identified in all thelodonts where this region of the body is sufficiently well preserved, with the exception of the Furcacaudiformes where it is entirely absent (Märss, Turner & Karatajūtē-Talimaa, 2007). A possible preanal fin has been suggested for *Furcacauda fredholmae*, in the form of a rounded fin-like extension immediately anterior to the anal opening (Wilson & Caldwell, 1998). However, this feature has been observed in a single specimen and the authors expressed doubt in its interpretation as a median ventral fin (Wilson & Caldwell, 1998).

With the exception of two species of Furcacaudiformes, *Sphenonectris turnerae* and *Pezopallichthys ritchiei* (Märss, Turner & Karatajūtē-Talimaa, 2007; Wilson & Caldwell, 1993; 1998), paired fins are generally present in thelodonts. However, the homology of these paired fins remains an open debate. Their insertion close to the branchial region prompted some authors to consider these paired fins as homologous to pectoral fins (e.g. Märss & Ritchie, 1998; Novitskaya & Turner, 1998; Powrie, 1870; Stensiö, 1927; Traquair, 1900; Turner, 1991; 1992; Turner & van der Brugghen, 1993; Turner & Young, 1992; Wilson & Märss, 2012). Other authors have been more cautious in their interpretation, while still recognizing the similarity in positioning by referring to these lateral expansions as "suprabranchial fins" (Johanson, 2010; Wilson, Hanke & Märss, 2007), "pectoral flaps" (Dineley & Loeffler, 1976; Donoghue & Smith, 2001; Märss, Turner & Karatajūtē-Talimaa, 2007; Ritchie, 1968b; Turner, 1982), "pectoral swimming appendages" (Stensiö, 1964), or "pectoral-level fins" (Coates, 2003). Wilson & Caldwell (1998) argued that the paired fins of traditional thelodonts (i.e. excluding the Furcacaudiformes) are inserted dorsally relative to the branchial openings making their homology to pectoral fins questionable. Another opinion is that these scale-covered lateral flaps should not be considered as "true fins" (Woodward, 1900b). Moy-Thomas & Miles (1971) expressed doubt regarding the mobility of these structures and instead considered them as possibly homologous to the cornual or branchial plates of heterostracans. Alternatively, Turner (1991; 1992) suggested that the triangular flaps were likely flexible, and that the linear arrangement of scales on their surface was indicative of an underlying cartilaginous or fibrous support, thus they would not have differed from true fins at least from a functional and structural standpoint.

Among thelodonts, the Furcacaudiformes have unusual morphologies, which does not simplify the issue of homology with the paired fins of other agnathans. In their initial description of the group, Wilson & Caldwell (1993) stated that the ventrally positioned paired fins of furcacaudids are inserted below the branchial row and are difficult to homologize to the paired fins of other fishes. The posterior limit of these paired flaps is near the anus so that homology to either pectoral or pelvic fins of gnathostomes cannot be ruled out (Wilson & Caldwell, 1998). Later, Wilson, Hanke & Märss (2007) proposed that the paired fins of most thelodonts have a suprabranchial insertion and could be precursors of pectoral fins, while the paired fins of furcacaudiforms (and of most anaspids) have a ventrolateral insertion and could be precursors of pelvic fins.

3.9 "Cephalaspidomorphi"

The extinct paraphyletic "Cephalaspidomorphi" comprise the Galeaspida, Pituriaspida and Osteostraci. All of these forms are characterized by the presence of a large cephalothoracic shield covering the head and branchial regions.

The stratigraphic range of the Galeaspida [3 orders, ~65 described species (Zhu & Gai, 2007)] extends from the Lower Silurian to the Upper Devonian, with all but one localities situated in China and northern Vietnam (Janvier, 1996b; Zhu & Gai, 2007; Žigaitė & Blieck, 2013). Galeaspids are known almost exclusively from their cephalic shields: articulated postcranial material is rare (Janvier, 1996b). So far, the trunk and caudal fin have been described only for *Sanqiaspis rostrata* (Liu, 1975). To our knowledge, there was never any evidence suggesting the presence of either dorsal [although the presence of two dorsal fins has been hypothesized for *Shuyu zhejiangensis* (Gai, Zhu & Zhao, 2005; Gai, Donoghue, Zhu, Janvier & Stampanoni, 2011)] or anal fins in galeaspids and most authors generally consider that they were absent (e.g. Janvier, 1996a; Turner et al., 2010). There is however a small dorsal spine which is fused to the cephalic shield (Pan, 1992). There is also no evidence that paired fins were present in galeaspids (Forey, 1995; Forey & Janvier, 1993; Janvier, 1981b; 1984; 1996b; 2007; 2008; Wilson, Hanke & Märss, 2007). No visible pectoral fin attachment area can be seen and there are no pectoral *fenestrae* in the postero-lateral part of the shield (Janvier, 1984; Zhu & Gai, 2007).

Pituriaspids are known from only two species (*Pituriaspis doylei* and *Neevambaspis enigmatica*) from a single Lower-Middle Devonian locality in Queensland, Australia (Janvier, 1996a; Young, 1991). Only *Pituriaspis* is sufficiently well preserved to allow interpretation of its general morphology, showing an attachment area for paired fins (Young, 1991). These fins can be interpreted as pectoral fins, owing to the positioning and morphology of the attachment area, which is shared with osteostracans, and to the close phylogenetic relationships between these two groups (Janvier, 2007; Young, 1991).

The Osteostraci [3 to 5 orders depending on recent classification, ~214 species (Janvier, 1981a; 1985a; 1996b; Sansom, 2008; 2009)] range from the Middle Silurian to the Upper

Devonian (Sansom, 2008; Žigaitė & Blieck, 2013). Osteostracans are the second most diverse jawless group, following conodonts. In all osteostracans in which the post-cephalic region is sufficiently well known, a caudal fin is present and there are no median ventral or anal fins, although many taxa do present a horizontal lobe lining the caudal fin ventrally (Heintz, 1939; 1967), which some have suggested might represent a modified anal fin (Forey, 1995; Janvier, 1981b; 1996a; b; 2007; Stensiö, 1932; 1964). Heintz (1939) considered that this horizontal lobe could not be homologized to the anal fin because the structure is distinctly paired, and that it could also not be homologized to the pelvic fins because it is inserted posteriorly to the anus; he concluded that it might be an independently derived structure. Of course, the argument that the horizontal lobe cannot be homologized to an anal fin owing to its paired nature may have to be revisited given that a paired anal fin has been described in *Euphanerops* (Sansom, Gabbott & Purnell, 2013). Westoll (1958) considered instead that the horizontal lobes of the caudal fin are posterior developments of the paired ventrolateral ridges lining the trunk (and also that the pectoral fins discussed below are anterior developments of these same ridges).

Most osteostracans have a single dorsal fin, although *Ateleaspis tessellata*, *Aceraspis robustus* and *Hirella gracilis* have anterior and posterior dorsal fins (Heintz, 1939; Ritchie, 1967). These species are considered as basal members of the Osteostraci (Blieck & Janvier, 1991; Janvier, 1985a; c; 1996b; Sansom, 2008; 2009) and the presence of two dorsal fins should thus be considered as plesiomorphic for the group (Janvier, 1981b). Osteostracans that have a single dorsal fin retain a series of median dorsal ridge scales along the trunk and tail (Heintz, 1967; Robertson, 1935b; Sansom, 2007; Stensiö, 1932; White, 1958), and the posterior end of the cephalic shield often presents a dorsal crest and/or a dorsal spine (Adrain & Wilson, 1994; Dineley, 1994; Heintz, 1967; Keating, Sansom & Purnell, 2012; Robertson, 1935a; b; Scott & Wilson, 2012; 2013; White, 1958). The dorsal crest and spine of the cephalic shield have frequently been interpreted as remnants of the anterior dorsal fin found in basal osteostracans (Heintz, 1939; 1967; Kiaer, 1911; Stensiö, 1927; 1932; 1964; Wängsjö, 1952). One hypothesis is that the dorsal crest is a modification of the cephalic shield to accommodate the reduced anterior dorsal fin, which has been drawn inwards into the cephalic shield (Heintz, 1939; Kiaer, 1911). Another hypothesis is that the dorsal spine constitutes the anterior termination of a dorsal fin-fold, which is represented along the trunk of osteostracans by the crest formed by the dorsal ridge scales (Stensiö, 1932; Wängsjö, 1952). As of yet, neither of these scenarios has been validated.

Paired fins are generally present in osteostracans, although they are lacking in the Tremataspididae (Denison, 1951; Halstead & Turner, 1973; Moy-Thomas & Miles, 1971; Robertson, 1938a; b; Stensiö, 1927; 1932). Tremataspids are derived members of the osteostracans, and so the absence of paired fins can be considered as a secondary loss rather than the plesiomorphic condition (Janvier, 1981a; 1985a; b; c; 1996b; Sansom, 2008; 2009; Stensiö, 1927; 1964; Wängsjö, 1952) (contra Denison, 1951; Halstead, 1982; Westoll, 1945a; 1958). Although the prevailing view is now that the paired fins of osteostracans are homologous to pectoral fins, this has not always been the case. Lankester (1870) hypothesized that the function of these "paired flaps" was to generate a current towards the branchial openings and that they were not involved in locomotion. Watson (1954) acknowledged the fin-like nature of these structures but considered that they were neomorphs and not homologous to the pectoral fins of gnathostomes. Concurring with Watson (1954), Janvier (1978; 1984) argued that the paired fins of osteostracans could not be considered as homologues of the gnathostome pectoral fins because they have an epibranchial insertion, whereas pectoral fins are always post-branchial structures. Osteostracan paired fins are anteriorly positioned, there are traces of muscular attachments and foramens for the passage of nerves and blood vessels (Janvier, 1978; 1996b; Janvier, Arsenault & Desbiens, 2004; Johanson, 2002), and there are endoskeletal supports (Janvier, 1996b; Janvier & Arsenault, 1996; Janvier, Arsenault & Desbiens, 2004). Furthermore, the endoskeletal shoulder girdle bears a strong resemblance to that of stem gnathostomes (scapulocoracoid with a monobasal articulation for the fin endoskeletal supports), most notably when compared to the shoulder girdle of antiarchs and various other placoderms (Goujet, 2001; Janvier, 2007; Janvier, Arsenault & Desbiens, 2004; Johanson, 2002; Wilson, Hanke & Märss, 2007). Based on these topological and structural observations, most authors agree that the paired fins of osteostracans are most likely homologous to the pectoral fins of gnathostomes (Forey, 1995; Forey & Janvier, 1993; 1994; Janvier, 2007; Janvier & Arsenault, 1996; Janvier, Arsenault & Desbiens, 2004; Johanson, 2002; Kiaer, 1924; Maisey, 1986; Sansom, 2009; Stensiö, 1927; 1932; 1964; Wängsjö, 1952; Westoll, 1958). Other paired fins are absent although the body is triangular in cross-section and the ventral angles expand into ventrolateral keels or ridges that extend posteriorly as far as the insertion of the tail (Adrain & Wilson, 1994; Heintz, 1939; Moy-Thomas & Miles, 1971; Ritchie, 1967; Stensiö, 1932; 1964; Westoll, 1958). These have been interpreted by some as remnants of ventrolateral fin-folds (Denison, 1951; Kiaer, 1924; Stensiö, 1932), or as rudimentary pelvic fins (Moy-Thomas & Miles, 1971; Stensiö, 1932; 1964).

3.10 “Placodermi”

The fossil record of placoderms [9 orders and 335 valid genera, most of which are monospecific (Denison, 1978; Young, 2010)] extends from the Lower Silurian to the end of the Devonian (Trinajstic, Boisvert, Long, Maksimenko & Johanson, 2014; Young, 2010). Common to all placoderms that are sufficiently known from their postcranial anatomy is the presence of pectoral fins and a caudal fin. There is some disparity in placoderms as to the presence of an anal fin, pelvic fins and the number of dorsal fins.

Most placoderms have a single dorsal fin, although in the antiarch *Remigolepis walkeri* it is absent (Johanson, 1997; Moloshnikov, 2008), and ptyctodontids have two dorsal fins. The antiarch *Bothriolepis canadensi*s was originally described as having two dorsal fins (e.g. Patten, 1904; Stensiö, 1948), but later reexaminations of the material revealed that a single dorsal fin is present (Arsenault, Desbiens, Janvier & Kerr, 2004; Béchard, Arsenault, Cloutier & Kerr, 2014; Vézina, 1996). It is uncertain whether the most primitive placoderms (Stensioellida, Pseudopetalichthyida) had one or two dorsal fins because of the scarcity of articulated material from behind the thoracic shield (Denison, 1978; Janvier, 1996b). An anal fin is generally considered as absent in placoderms, although this may be partly owing to preservation issues as an anal fin has recently been described for the Upper Devonian arthrodire *Africanaspis edmountaini* (Gess & Trinajstic, 2017). There are also some debates concerning the putative presence of an anal fin in two other arthrodires: in *Coccosteus cuspidatus* and *Plourdosteus canadensis*, a ventral bony plate has been described, facing the posterior limit of the dorsal fin (Heintz, 1931; Vézina, 1990; 1996; Watson, 1934). A possible interpretation is that it served as a basal plate supporting an anal fin (Carr, 1995; Heintz, 1938; Jarvik, 1960; Trinajstic, Boisvert, Long, Maksimenko & Johanson, 2014; John Long, pers. comm.). However, no traces of an anal fin-web, of skeletal supports of any kind other than this plate, or of an attachment area for radials have ever been found so that other authors consider unlikely that it served as endoskeletal support for an anal fin (Heintz, 1931; Miles & Westoll, 1968; Westoll, 1945b). Furthermore, Miles & Westoll (1968) postulated that this plate was too thin to provide support for a fin and considered instead that it most likely served as an area for an unspecified muscular attachment. Since the evidence is far from overwhelming in either case, the presence of an anal fin is dubious in *Coccosteus* and *Plourdosteus*.

Pelvic fins and/or girdles are known for most placoderm groups with the exception of petalichthyids, for which this feature has never been found, and antiarchs, where they were thought to be entirely absent (Arsenault, Desbiens, Janvier & Kerr, 2004; Trinajstic, Boisvert, Long, Maksimenko & Johanson, 2014; Young, 2010; Zhu, Yu, Choo, Wang & Jia, 2012). As a possible exception within antiarch placoderms, pelvic flaps or fins had been suggested in *B. canadensis* (Patten, 1904; Stensiö, 1948; Vézina, 1996), however, these structures are now considered as a taphonomic artefact (Arsenault, Desbiens, Janvier & Kerr, 2004; Béchard, Arsenault, Cloutier & Kerr, 2014). Recent findings by Zhu et al. (2012) suggest that the presence of pelvic fins might be plesiomorphic for the entire gnathostome clade, and that their absence in some placoderms is due to secondary loss, a view shared with Young (2010) and Charest, Johanson & Cloutier (2018).

3.11 "Acanthodii"

The fossil record of acanthodians, or "spiny sharks", extends as far as the Upper Silurian (Burrow & Rudkin, 2014; Hanke, 2008). Acanthodians comprise a little over 100 genera that have traditionally been divided into three orders: Acanthodiformes, Climatiiformes and Ischnacanthiformes (Denison, 1979; Janvier, 1996b; Miles, 1970; 1973; Moy-Thomas & Miles, 1971; Zajíc, 1995; 1998; Zidek, 1993). However, many authors consider that the Diplacanthiformes constitutes a fourth order closely related to the Climatiiformes (Burrow, den Blaauwen, Newman & Davidson, 2016; Burrow & Turner, 2010; Burrow & Young, 2012; Hairapetian, Valiukevičius & Burrow, 2006; Hanke, Davis & Wilson, 2001; Newman, Davidson, Den Blaauwen & Burrow, 2012). The monophyly of the Diplacanthiformes is well supported in recent phylogenetic analyses (e.g. Burrow, den Blaauwen, Newman & Davidson, 2016; Burrow & Turner, 2010; Davis, Finarelli & Coates, 2012; Dupret, Sanchez, Goujet, Tafforeau & Ahlberg, 2014; Hanke & Davis, 2012; Hanke & Wilson, 2004). It had been suggested by Gagnier & Wilson (1996) and Janvier (1996b) that the "Climatiiformes," if not the entire "Acanthodii," are paraphyletic, a hypothesis which is also well supported by recent phylogenetic investigations. Indeed, climatiiforms were resolved as paraphyletic by Burrow and Turner (2010) and Hanke and Wilson (2002; 2004). As for acanthodians, they have been resolved as either polyphyletic with some being stem chondrichthyans and others stem osteichthyans (Brazeau, 2009; Davis, Finarelli & Coates, 2012), or paraphyletic with respect to chondrichthyans (Brazeau & de Winter, 2015; Burrow, den Blaauwen, Newman & Davidson, 2016; Chevrinais, Sire & Cloutier, 2017; Giles, Friedman & Brazeau, 2015; Long et al., 2015; Qiao, King, Long, Ahlberg & Zhu, 2016; Zhu et al., 2013).

Acanthodians always have caudal, anal, dorsal and pectoral fins. Median and paired fins other than the caudal have spines at their leading edges, although a fin-web is not always present (Denison, 1979; Moy-Thomas & Miles, 1971; Watson, 1937). Acanthodiforms possess a single dorsal fin, whereas climatiiforms and ischnacanthiforms have two dorsal fins. The absence of an anterior dorsal fin is considered as a derived condition in acanthodiforms (Burrow, 2004; Denison, 1979; Hanke, 2002). Acanthodians generally have pelvic fins, although members of the Acanthodidae lack paired pelvic fin spines (Beznosov, 2009; Burrow & Young, 2005; Zajíc, 1995). Instead, *Acanthodes* species have a single ventral median spine inserted close behind the pectoral fins, often bearing a long and shallow fin-web (Beznosov, 2009; Heidtke, 1990; Zajíc, 1995; 1998). Despite that it is a median structure, Beznozov (2009) suggested a possible homology to the pelvic fin spines.

Many acanthodians also possess a series of up to six pairs of prepelvic (or intermediate) spines inserted ventrally between the pectoral and pelvic fins; prepelvic spines are generally small and only occasionally described as bearing a fin-web (Denison, 1979; Hanke, 2002; Hanke & Wilson, 2006; Watson, 1937). The prepelvic fin spines may have acted as cutwaters or as defensive organs (Moy-Thomas & Miles, 1971). It has also been suggested that such spines might have functioned as holdfasts in running waters (Gregory & Raven, 1941), although we feel that this last hypothesis is unlikely. The presence of paired prepelvic spines is considered plesiomorphic for acanthodians, while their absence is derived (Denison, 1979; Gagnier, Hanke & Wilson, 1999; Hanke, 2002; Hanke & Wilson, 2004; Moy-Thomas & Miles, 1971; Warren, Currie, Burrow & Turner, 2000; Watson, 1937; Westoll, 1945b; Westoll, 1958). Some authors have considered the hypothesis that the prepelvic fin spines were derived from an initially continuous lateral fin-fold: the fin-fold would have become divided and the spines would have subsequently developed (Dean, 1907; Kiaer, 1924; Ørvig, 1967; Watson, 1937; Westoll, 1945b). This scenario would be consistent with the lateral fin-fold hypothesis for the origin of paired fins

(Balfour, 1876; 1878; 1881; Mivart, 1879; Thacher, 1877; see Discussion). Others found that the prepelvic fin spines of acanthodians offer little to no support for the lateral fin-fold hypothesis and instead proposed that they are special developments of the ventrolateral body ridges found, for instance, in cephalaspids (Miles, 1970; 1973; Westoll, 1958), a hypothesis which is neither parsimonious, nor likely. Several diplacanthids and climatiids also possess spines that are positioned anteriorly to the prepelvic spines and medially to the pectoral fin spines (Burrow, 2007; Burrow, den Blaauwen, Newman & Davidson, 2016; Burrow, Newman, Davidson & den Blaauwen, 2013; Denison, 1979; Ørvig, 1967; Watson, 1937), termed admedian spines, and/or spines that are generally positioned anteromedially to the pectoral fin spines (Brazeau, 2012; Burrow, Newman, Davidson & den Blaauwen, 2013; Denison, 1979; Hanke & Davis, 2008; 2012; Miles, 1973; Newman, Davidson, Den Blaauwen & Burrow, 2012; Ørvig, 1967; Warren, Currie, Burrow & Turner, 2000), termed prepectoral spines. Miles (1973) suggested that the pelvic, prepelvic and prepectoral fin spines formed a continuous series. Miles (1973) further hypothesized that the pectoral fins would have initially arisen within this continuous series, but would have subsequently migrated laterally, possibly for functional reasons. Another hypothesis is that the pelvic and prepelvic spines are serial homologues (Gagnier & Wilson, 1996; Hanke & Wilson, 2006), whereas the prepectoral spines are serial homologues of the pectoral spines (Gagnier & Wilson, 1996). As for the admedian spines, they are generally considered as the most anterior elements of the prepelvic spine series (Gagnier & Wilson, 1996; Hanke & Davis, 2008; Hanke, Davis & Wilson, 2001; Miles, 1973).

3.12 Chondrichthyes

The fossil record of Chondrichthyes [~33 orders of which 13-14 still have extant representatives; ~3000 extinct species, ~1251 extant species (Compagno, Dando & Fowler, 2005; Klimley, 2013; Nelson, Grande & Wilson, 2016)] extends to the Lower Silurian, and possibly as far as the Upper or Middle Ordovician (Grogan, Lund & Greenfest-Allen, 2012; Hanke & Wilson, 2010; Maisey, Miller & Turner, 2009; Miller, Cloutier & Turner, 2003; Sansom, Smith & Smith, 1996; Turner, 2004; Young, 1997). Chondrichthyans include sharks, skates, rays and chimaeras and are considered to have retained fin characteristics that are plesiomorphic for crown gnathostomes (Coates, 2003; Freitas, Zhang & Cohn, 2007; Mabee, 2000). They are characterized by having a cartilaginous skeleton with prismatic endoskeletal calcification, and by males possessing modified myxopterygia, termed claspers, used for internal fertilization (Grogan & Lund, 2004; Grogan, Lund & Greenfest-Allen, 2012; Maisey, 1984a; Maisey, 1986; Schaeffer, 1981; Schaeffer & Williams, 1977). Two main evolutionary lineages are recognized, the Euchondrocephali and the Elasmobranchii, which have been traditionally considered as sister groups (Grogan & Lund, 2004; Grogan, Lund & Greenfest-Allen, 2012; Lund & Grogan, 1997; 2004; Schaeffer & Williams, 1977). This relationship is supported by most phylogenetic analyses (e.g. Grogan & Lund, 2000; 2004; Grogan & Lund, 2008; Inoue et al., 2010; Lund & Grogan, 1997), although the Euchondrocephali have been found occasionally to be nested within a paraphyletic assemblage of elasmobranchs (e.g. Coates & Sequeira, 2001a; b; Ginter, Hampe & Duffin, 2010). Furthermore, the phylogenetic position of the Iniopterygii, a clade of peculiar-looking fishes with enlarged pectoral fins that are inserted high along the side of the body (Grogan & Lund, 2009; Zangerl, 1997; Zangerl & Case, 1973), is unclear. The iniopterygians are either considered to be nested within the Euchondrocephali (Grogan & Lund, 2000; 2004; Lund & Grogan, 1997), or they are stem chondrichthyans that diverged prior to the Euchondrocephali-Elasmobranchii split (Grogan & Lund, 2009; Grogan, Lund & Greenfest-Allen, 2012; Lund, Grogan & Fath, 2014).

The Euchondrocephali include 12 orders among which only the Chimaeriformes contain extant species. They have a fossil record that extends to the Lower Carboniferous (Grogan & Lund, 2004; Grogan, Lund & Greenfest-Allen, 2012; Lund & Grogan, 1997). The more advanced forms, the Holocephali, are characterized by the presence of an erectile first dorsal fin spine that articulates, via a basal plate, with the dorsal process of the synarcual, a structure formed from the fusion of the anteriormost vertebrae (Didier, 1995; Didier, Kemper & Ebert, 2012; Maisey, 1986). The disparity in fin configurations observed in the Euchondrocephali results mostly from the dorsal fin(s), which can be present (either as a single fin or as two separate fins) or absent, and the presence/absence of the anal fin. The evidence as to the plesiomorphic number of dorsal fins in chondrichthyans is inconclusive. Lund (1985) wrote that arguments of equal weight could be made for the presence of a single dorsal fin, as in Xenacanthiformes, *Heteropetalus* and Chondrenchelyiformes, or two dorsal fins as in *Cladoselache*. Lund & Grogan (1997) later mentioned that the accumulated evidence seemed to support the elongation of the second dorsal fin into the single fin found in these taxa as a derived condition. The Euchondrocephali also include the Eugeneodontiformes, which is the only chondrichthyan order with pelvic fins absent.

The stem Elasmobranchii, ranging from the Devonian to the Cretaceous, comprise nine orders, but only four of these are represented by complete articulated postcranial material. Caudal, pectoral and pelvic fins are always present in these forms. Pectoral fin spines are known to occur in articulated specimens of *Doliodus latispinosus* (Omalodontiformes) from the Lower Devonian of Canada (Burrow, Turner, Maisey, Desbiens & Miller, 2017; Maisey et al., 2017; Miller, Cloutier & Turner, 2003; Turner & Miller, 2005) and *Wellerodus priscus* (Antarctilamniformes) from the Middle Devonian of the USA (Potvin-Leduc, 2017; Potvin-Leduc, Cloutier, Landing, VanAller Hernick & Mannolini, 2011). Based on the subsequent discovery of other putative chondrichthyans with pectoral fin-spines, it has also been suggested that a spine originally interpreted as forming the leading edge of a dorsal fin (Young, 1982; 1989) could be reinterpreted as a pectoral fin-spine in *Antarctilamna prisca* (Antarctilamniformes) from the Middle/Upper Devonian of Antarctica and Australia (Hanke & Wilson, 2010; Miller, Cloutier & Turner, 2003; Wilson, Hanke & Märss, 2007). There is some disparity as to the number of dorsal fins and the presence/absence of the anal fin. Additionally, the dorsal fin is described as entirely lacking in *Thrinacodus* (= *Thrinacoselache*) *gracia* (Phoebodontiformes) (Ginter & Turner, 2010; Grogan & Lund, 2008).

The crown group Elasmobranchii are the Neoselachii, which include the Selachii and the Batoidea. The Neoselachii have a fossil record that extends as far as the Lower Jurassic (Grogan, Lund & Greenfest-Allen, 2012; Maisey, 1984b; 2012). The Selachii, or modern sharks, are fairly homogeneous in terms of fin configurations. As with stem Elasmobranchii, the caudal, pectoral and pelvic fins are always present. There are generally two dorsal fins, but there is a single dorsal fin in Hexanchiformes, and in some species of Synechodontiformes and Carcharhiniformes. The anal fin is present in most orders, although it is generally absent in the Squalomorphii (i.e. an anal fin is absent in Squaliformes, Protospinaciformes, Pristiophoriformes and Squatiniformes, but is present in Hexanchiformes), a condition which is considered as derived relatively to other neoselachians (Compagno, 1977).

Batoids comprise four orders that include about 630 species, representing close to half of extant chondrichthyan biodiversity (Aschliman, Claeson & McEachran, 2012). The fossil record of batoids extends to the Lower Jurassic (Maisey, 2012). Batoids possess highly derived paired fin morphologies and are much more disparate in their fin configurations than the Selachii. Again, the pectoral and pelvic fins are always present in batoids. The pectoral fins are connected to the antorbital process of the cranium and are generally greatly enlarged to the point of frequently being referred to as wings (Franklin, Palmer & Dyke, 2014; Rosenberger, 2001; Schaefer & Summers, 2005). The number of dorsal fins differs among species: it can be absent, and when present there can be one or two dorsal fins. The anal fin is also frequently absent, and in many species of Rajiformes and Myliobatiformes, the tail is long, whip-like and devoid of a terminal caudal web. In Myliobatiformes, some species bear spines or barbs with a dorsal insertion along the tail: there are generally one or two spines, occasionally three, and rarely four or five (Amesbury & Snelson, 1997; Halstead, 1978; Lowe et al., 2007; Thorson, Langhammer & Oetinger, 1988). The caudal spines are composed of a vitrodentine core with an external layer of enameloid and are anchored in a dense collagenous network of the dermis on the dorsal side of the caudal appendage (Amesbury & Snelson, 1997; Halstead, 1978; Halstead, Ocampo & Modglin, 1955; Johansson, Douglass & Lowe, 2004). These caudal spines are thought to be modified placoid scales (Johansson, Douglass & Lowe, 2004; Kemp, 1999; Reif, 1982), and as such, they should not be considered as fins. Another issue concerning some Myliobatiformes pertains to the rostral or cephalic fins (Bigelow & Schroeder, 1953; Fowler, 1941; Garman, 1913; Jordan & Evermann, 1896; Smith, 1907; Tinker, 1944). These are extensions of the pectoral fins, which are interrupted on the sides of the head and reappear in front of the snout as fleshy protuberances (Garman, 1913; Meek & Hildebrand, 1923; Mulvany & Motta, 2013). Finally, a number of batoid taxa are also described as having lateral keels or ridges along the tail (e.g. Bean & Weed, 1909a; b; Bigelow & Schroeder, 1958). These should probably not be considered as paired fins owing to their location along the tail, behind the insertion of the pectoral and pelvic fins.

A final source of disparity in fin configurations should be mentioned as it relates to the “total group chondrichthyans.” This disparity concerns the presence of prepelvic fin spines between the pectoral and pelvic fins in at least two putative chondrichthyans, *Kathemacanthus rosulentus* and *Seretolepis elegans*, both from the Lower Devonian of the Northwest Territories, Canada (Gagnier & Wilson, 1996; Hanke & Wilson, 2010). A series of prepelvic spines have also recently been described in two stem elasmobranchs: *D. latispinosus*, which also possesses prepectoral and possibly admedian spines (Burrow, Turner, Maisey, Desbiens & Miller, 2017;

Maisey et al., 2017), and *W. priscus* (Potvin-Leduc, 2017). Notably, it has also been suggested based on the results of a phylogenetic analyses on cranial morphological characters that *D. latispinosus* may occupy a more stemward position in the chondrichthyan phylogeny, prior to the Euchondrocephali-Elasmobranchii split (Maisey, Turner, Naylor & Miller, 2014; Pradel, Tafforeau, Maisey & Janvier, 2011). If acanthodians are added to the total group chondrichthyans as suggested by recent investigations (e.g. Brazeau & de Winter, 2015; Burrow, den Blaauwen, Newman & Davidson, 2016; Chevrinais, Sire & Cloutier, 2017; Giles, Friedman & Brazeau, 2015; Long et al., 2015; Qiao, King, Long, Ahlberg & Zhu, 2016), the presence of prepelvic spines will become a common character of stem chondrichthyans.

3.13 Actinopterygii

Among fishes, actinopterygians, or ray-finned fishes, have achieved a remarkable ecological and evolutionary success (Lauder & Liem, 1983), resulting in over 30 500 species (Nelson, Grande & Wilson, 2016), as well as an abundant fossil record extending to the Upper Silurian (Cloutier & Arratia, 2004). The diversity of actinopterygians represents close to half of all described vertebrate species. Not only are actinopterygians impressively species-rich, but they are also extremely morphologically disparate, and part of this disparity can readily be observed in differences in fin configurations. Indeed, many changes in modes of feeding and locomotion are associated with modifications of the structure, size, number and position of fins (Lauder & Drucker, 2004; Lauder & Liem, 1983; Webb, 1982; 1984).

Basal actinopterygians (i.e. excluding neopterygians) comprise two extant orders [Polypteriformes (bichirs and reedfishes) and Acipenseriformes (sturgeons and paddlefishes)] and about ten extinct orders of fishes. The presence of a single dorsal fin has been considered as an actinopterygian synapomorphy (Cloutier & Arratia, 2004). *Dialipina salgueiroensis*, one of the oldest putative actinopterygians from the Lower Devonian of Canada, has two dorsal fins (Schultze & Cumbaa, 2001). However, since its description, phylogenetic investigations have placed *Dialipina* sometimes as a stem actinopterygian (Giles, Darras, Clement, Blieck & Friedman, 2015; Long et al., 2015; Schultze & Cumbaa, 2001; Taverne, 1997; Zhu & Schultze, 2001; Zhu, Yu, Wang, Zhao & Jia, 2006; Zhu et al., 2009), and other times as a stem osteichthyan (Brazeau, 2009; Brazeau & de Winter, 2015; Burrow, den Blaauwen, Newman & Davidson, 2016; Davis, Finarelli & Coates, 2012; Dupret, Sanchez, Goujet, Tafforeau &

Ahlberg, 2014; Friedman, 2007; Giles, Friedman & Brazeau, 2015; Lu, Giles, Friedman, den Blaauwen & Zhu, 2016; Qiao, King, Long, Ahlberg & Zhu, 2016). Other basal actinopterygians have a single dorsal fin, a single anal fin, a caudal fin and pectoral fins. The pelvic fins are sometimes lacking in a few species of Polypteriformes, "Palaeonisciformes" and Tarrasiiformes.

Basal neopterygians include two extant orders [Lepisosteiformes (gars) and Amiiformes (bowfins)] as well as a dozen extinct orders. Their fin configurations resemble those of basal actinopterygians although to our knowledge, the loss of pelvic fins has not been observed in any of the described taxa. However, a second dorsal fin has been described for *Placidichthys bidorsalis*, which belongs to the extinct order Ionoscopiformes (Brito, 2000).

The more advanced neopterygians are the teleosteans. Basal teleosteans are extremely diversified and include a number of very speciose marine and freshwater groups: notably the Osteoglossomorpha, Elopomorpha, Clupeomorpha and Ostariophysi. Among the Osteoglossomorpha (bony-tongues and their allies), the Osteoglossiformes comprises species that use a mode of locomotion based on undulations of the anal fin (Notopteridae), or of the dorsal fin in the case of the monotypic family Gymnarchidae (Lindsey, 1978; McNeill Alexander, 1967). The fin that is used for propulsion is elongated in these forms and in some species, the pelvic, dorsal, anal and/or caudal fins can be lost.

The Elopomorpha (eels and their allies) are mostly fishes with an elongated body shape, and many species have developed an anguilliform mode of locomotion whereby the entire body is used in undulations that produce thrust (Lindsey, 1978; Sfakiotakis, Lane & Davies, 1999; Webb, 1975). As such, the dorsal and anal fins are often well developed and continuous with the caudal fin, while the paired fins are reduced or lost. The most disparate elopomorphs in terms of fin configurations belong to the order Anguilliformes. In Anguilliformes, the pelvic fins are always absent and in many species, the pectoral fins are lost as well. Additionally, the median fins are frequently reduced to some extent or lost, and in some taxa, fins are entirely lacking in the adult (McCosker, 1977; 2004).

The Clupeomorpha (sardines and their allies) are comparatively far less disparate. The pelvic fins are frequently lost, and the reduction or loss of the dorsal fin is described for at least one species, *Raconda russeliana* (Gray, 1831). Furthermore, in species of *Sundasalanx*, a median ventral fin-fold is present, positioned between the pelvic and anal fins (Roberts, 1981; Siebert, 1997).

The Ostariophysi are extremely species-rich and are generally the group best represented in freshwater fish communities. Ostariophysans correspondingly present very disparate fin configurations, particularly in the Siluriformes (catfishes), and to a lesser extent in the Gymnotiformes (knifefishes and their allies). In Siluriformes, loss of the dorsal, anal and/or pelvic fins is observed in many species. In the Eel catfish, *Channallabes apus*, the presence of the pectoral and pelvic fins varies intraspecifically: in some specimens, both paired fins are present, in others both paired fins are absent, and yet in others only the pectoral fins are present (Adriaens, Devaere, Teugels, Dekegel & Verraes, 2002). In members of the Plotosidae, there is a second ray-supported dorsal fin which is confluent with the caudal and anal fins (Ferraris, 1999; Gormon, 1986; Jayaram, 1981; 1982; Nelson, Grande & Wilson, 2016); it seems likely that this second dorsal fin is supported by a series of anteriorly expanding and enlarged upper procurrent rays of the caudal fin (Allen, 1998; Ferraris, 1999; Gormon, 1986). Members of the Gymnotiformes use an anal fin-based mode of locomotion (de Santana, Vari & Wosiacki, 2013; Lindsey, 1978; McNeill Alexander, 1967; Sfakiotakis, Lane & Davies, 1999; Webb, 1975), as with the previously mentioned Notopteridae. These two groups are not closely related (Alves-Gomes, 1999; Lavoué et al., 2012; Near et al., 2012), thus their similarities in terms of body shape and anal fin based propulsion have been independently acquired. Pelvic fins and a ray-supported dorsal fin have been lost in all Gymnotiformes, and the caudal fin is absent in four of the five families of this order.

Another source of disparity in ostariophysan fin configurations is the presence/absence of the adipose fin, which is usually a small, primitively non-rayed fin located medially between the dorsal and caudal fins (Aiello, Stewart & Hale, 2016; Buckland-Nicks, Gillis & Reimchen, 2012; Reimchen & Temple, 2004; Stewart, 2015). The adipose fin first appears among the Ostariophysi (Characiformes and Siluriformes), but it is also found in several orders of more advanced Euteleostei (Argentiniformes, Salmoniformes and Osmeriformes) and Neoteleostei (Stomiiformes, Ateleopodiformes, Aulopiformes, Myctophiformes and Percopsiformes). These orders do not constitute a natural group, suggesting that the adipose fin might have evolved multiple times independently (Stewart, 2015; Stewart, Smith & Coates, 2014), or that it was secondarily lost in some groups (Esociformes, Lampridiformes). The adipose fin was hypothesized to be a degenerate appendage homologous to the posterior dorsal fin of basal gnathostomes (Bridge, 1904; Garstang, 1931). Later investigations suggested instead that the adipose fin is a novel structure and that its rudimentary appearance is the ancestral state for this appendage (Sandon, 1956; Stewart & Hale, 2013; Stewart, Smith & Coates, 2014). Some euteleosteans possess a median ventral keel or fin-fold, often termed a ventral adipose fin, which is positioned anteriorly to the anal fin: this ventral fin has been described in some Osmeriformes, Stomiiformes, Aulopiformes and Gasterosteiformes (Fischer & Bianchi, 1984; Froese & Pauly, 2016; Greenwood, Rosen, Weitzman & Myers, 1966; Nelson, Grande & Wilson, 2016). In the Apteronotidae, a fleshy dorsal electroreceptive organ (also called "dorsal filament" or "dorsal thong") is present. Some have suggested that it might constitute a modified adipose fin (Boulenger, 1898; Kaup, 1856). The dorsal organ of apteronotids and the adipose fins of other ostariophysans share a similar position along the dorsal midline, and are both scaleless and composed principally of connective and sensory tissues (Franchina & Hopkins, 1996). Despite these similarities, Franchina & Hopkins (1996) found that the hypothesis of an evolutionary modification of the adipose fin and the hypothesis of an evolutionary novelty should be considered as equally parsimonious. An elongated adipose fin has also been described for a single fossil representative of the Gymnotiformes, *Humboldtichthys kirschbaumi* from the Upper Miocene of Bolivia, although the authors acknowledged that it corresponds topologically to the apteronotid dorsal electroreceptive organ (Gayet & Meunier, 1991; Gayet, Meunier & Kirschbaum, 1994). Furthermore, it has been argued that the hypothesized adipose fin in *Humboldtichthys* could be a taphonomic artefact due to compression of the body outline (Albert, 2001; Albert & Fink, 2007).

The more advanced teleosteans are the Euteleostei and the Neoteleostei. In addition to the dorsal and ventral adipose fins, the most notable source of disparity in fin configurations among the orders of basal euteleosteans and neoteleosteans is the occasional absence of pelvic fins. Among the Stomiidae, the pectoral fins are absent in late juveniles and adults of *Photostomias*, *Idiacanthus* and *Tactostoma* (Bolin, 1939; Fink, 1985; Goodyear & Gibbs, 1986; Hulley, 1986; Kawaguchi & Moser, 1984; Kenaley & Hartel, 2005). In these genera, paddle-shaped pectoral fins are present in larvae and are gradually lost during metamorphosis (Kawaguchi & Moser, 1984; Kenaley & Hartel, 2005). Additionally, in the sexually dimorphic genus *Idiacanthus*, adult females only lack the pectoral fins, whereas males lack both pectoral and pelvic fins (Hulley, 1986). The reduction of the pectoral girdle and fins is an evolutionary trend among stomiids, which is partly owing to a co-option of some of the fin-rays as elements of a light-producing complex (Fink, 1985).

The more advanced Neoteleostei are the Acanthomorpha, which include the extremely species-rich Acanthopterygii. Acanthomorphs are characterized by the presence of spines in their dorsal and anal fins (Johnson & Patterson, 1993). A major source of disparity in fin configurations among acanthomorphs concerns the median fins: there are frequently two separate dorsal or anal fins, and even occasionally a third dorsal fin, for instance in some Gadiformes (cods and their allies). Mabee, Crotwell, Bird & Burke (2002) hypothesized that the spinous first dorsal fin of acanthomorphs may have arisen through duplication and divergence of the preexisting posterior dorsal fin module. The loss of fins also remains an important source of disparity in fin configurations in acanthomorphs. All of the median and paired fins can be lost, including the caudal fin in at least some species of six orders. Finally, in some groups, fins can be co-opted to serve novel functions. Examples include the co-option of the first dorsal fin into a fishing apparatus (spines of the plesiomorphic spinous dorsal fin are modified into an illicium which serves as the rod, and an esca which is the bait) in anglerfishes (Lophiiformes) (Lauder & Liem, 1983; Pietsch, 1984; Pietsch & Orr, 2007) or into a suctorial apparatus in remoras (Echeneidae, Perciformes) (Britz & Johnson, 2012; Friedman, Johanson, Harrington, Near & Graham, 2013; Fulcher & Motta, 2006; O'Toole, 2002; Storms, 1888), or the co-option of the pelvic fins into a suctorial disk in lumpsuckers and snailfishes (Cyclopteridae and Liparidae respectively, both belonging to the Scorpaeniformes) (Budney & Hall, 2010; Gill, 1890; Voskoboinikova & Kudryavtseva, 2014).

3.14 Sarcopterygii

Sarcopterygians are a monophyletic group that includes lobe-finned fishes as well as all tetrapods (Cloutier & Ahlberg, 1996; Janvier, 1996b; Schultze, 1986; 1993). For the purpose of this review, we will focus only on the piscine sarcopterygians [7 orders; 8 extant species; ~190 extinct genera (updated from Cloutier & Ahlberg, 1996)], which comprise only a few extant species but are nonetheless represented by a diversified fossil record extending as far as the Upper Silurian (Zhu & Schultze, 1997). Sarcopterygians are generally characterized by having paired fins that are supported by a monobasal endoskeleton (Cloutier & Ahlberg, 1996; Janvier, 1996b). However, the morphology of the pectoral girdle, and possibly also the pelvic girdle, in some stem sarcopterygians from China (i.e. *Guiyu oneiros* from the Upper Silurian and *Psarolepis romeri* from the Upper Silurian to Lower Devonian) suggests that the plesiomorphic condition for the group may have been a polybasal articulation (Zhu & Yu, 2009; Zhu et al., 2012a). *Guiyu*, *Psarolepis*, *Achoania*, and more recently *Sparalepis tingi*, have been resolved as forming a clade of stem sarcopterygians (Choo et al., 2017), yet they present a mosaic of characters found in actinopterygians, sarcopterygians and even non-osteichthyan taxa (Zhu, Yu & Ahlberg, 2001; Zhu et al., 2012a; Zhu, Yu & Janvier, 1999; Zhu et al., 2009). These psarolepids, *sensu* Choo et al. (2017), share the characteristic of having spines at the leading edges of their pectoral, pelvic and both dorsal fins (Choo et al., 2017; Zhu et al., 2012a; Zhu et al., 2009).

The most basal sarcopterygian groups are the Onychodontiformes and the Actinistia. Onychodontiformes are known from only six genera and their fossil record extends from the Lower to the Upper Devonian (Cloutier & Ahlberg, 1996; Lu & Zhu, 2010; Lu et al., 2016). Postcranial material is known only for a few species: they all have pectoral and pelvic fins, two dorsal fins, a single anal fin, and a caudal fin (Andrews, Long, Ahlberg, Barwick & Campbell, 2005; Jessen, 1966). Actinistians, or coelacanths, are known from two extant species and their fossil record extends from the Lower Devonian to the Upper Cretaceous (Arratia & Schultze, 2015; Cloutier & Ahlberg, 1996; Cloutier & Forey, 1991; Forey, 1998; Friedman, 2007; Johanson, Long, Talent, Janvier & Warren, 2006; Zhu et al., 2012b). Actinistians display little disparity in fin configurations, even in terms of the shape of individual fins with a few rare exceptions concerning caudal fin morphology (Cloutier, 1991; 1996; Forey, 1998; Wendruff & Wilson, 2012). The generalized fin configuration observed in the extant *Latimeria* species is considered to be an example of conservative evolution, because it does not differ importantly from the fin configuration found in Carboniferous (Cloutier, 1991) and even some Devonian actinistians [e.g. *Serenichthys kowiensis* from the Upper Devonian of South Africa (Gess & Coates, 2015), *Diplocercides heiligenstockiensis* (Jessen, 1966; 1973) and *Diplocercides kayseri* (Stensiö, 1937; von Koenen, 1895), the latter two from the Upper Devonian of Germany]. Most actinistians typically have a triphycercal caudal fin that consists of symmetrical dorsal and ventral lobes separated by a smaller supplementary lobe that differs in size among species. However, some species have highly asymmetrical caudal fins where either the epichordal (e.g. *Allenypterus*; *Piveteauia*) or the hypochordal lobes (e.g. *Miguashaia*) are more developed

(Cloutier, 1991; Forey, 1998). Uyeno (1991) suggested that what is considered as a trilobate caudal fin in *Latimeria* is actually a third dorsal and a second anal fin in which the rays are supported by pterygiophores, and these flank a small true caudal fin with rays unsupported by pterygiophores. However, this hypothesis does not hold with the evolution of caudal fin morphology in fossil actinistians. Actinistians are also characterized by the structural similarities between the endoskeleton of dorsal and anal fins, and that of the paired fins (Ahlberg, 1992; Forey, 1998; Schultze, 1986).

The Dipnomorpha include the Porolepiformes and the Dipnoiformes. The fossil record of porolepiforms includes about eight genera and extends from the Lower to the Upper Devonian (Cloutier & Ahlberg, 1996; Janvier, 1996b), although a possible Early Carboniferous occurrence has been recorded (Schultze, 1993). All porolepiforms have pectoral and pelvic fins, two dorsal fins, a single anal fin and a caudal fin. Porolepiforms are characterized as having widely differing paired fin morphologies: the pectoral fins are long, leaf-like and nearly symmetrical while the pelvic fins are shorter, rounded and asymmetrical (Ahlberg, 1989). Furthermore, in the Upper Devonian *Quebecius quebecensis,* only the pectoral fins are lobed, whereas the pelvic fins are not (Cloutier & Schultze, 1996). The Dipnoiformes, or lungfishes, include six living species and at least 81 genera with a fossil record extending to the Lower Devonian (Cloutier & Ahlberg, 1996; Schultze, 1992). All dipnoans have lobed pectoral and pelvic fins, but there is some disparity in the configurations of the median fins, which creates difficulties in the interpretation of dorsal, anal and caudal fin characters. The Early Devonian *Uranolophus wyomingensis* has two dorsal fins (Denison, 1968), which is considered as the plesiomorphic condition for the group (Ahlberg & Trewin, 1995; Schultze, 1986). The more derived dipnoans possess a single median fin that is continuous around the tail (Arratia, Schultze & Casciotta, 2001; Bemis, 1984; Friedman, 2010), and the caudal fin has changed from heterocercal to diphycercal (Johanson, Ericsson, Long, Evans & Joss, 2009). Friedman (2010) reviewed the evolutionary scenarios that have been proposed to explain the emergence of this continuous median fin in derived dipnoans, which he summarized as either: (1) reversal to a hypothetical ancestral protocercal condition (Bemis, 1984; Goodrich, 1930); (2) loss of the caudal and posterior expansion of the dorsal and anal fins (Abel, 1911; Arratia, Schultze & Casciotta, 2001; Balfour & Parker, 1882); (3) loss of dorsal and anal fins and anterior expansion of the caudal fin (Schmalhausen, 1913); (4) expansion of the plesiomorphic two narrow dorsal fins that fuse with the epichordal lobe of the caudal fin and loss of the anal fin (Dollo, 1895); (5) or consolidation of the dorsal, anal and caudal fins (Arratia, Schultze & Casciotta, 2001; Long & Clement, 2009; Westoll, 1949). Friedman (2010) concluded that hypotheses (1) through (3) were improbable, and argued that out of the two remaining hypotheses, the prevalence of a regionalized endoskeleton supporting the hypochordal lobe favored incorporation of the anal fin rather than its loss. Contrastingly, in a detailed study of the ontogeny of *Neoceratodus forsteri*, Johanson, Ericsson, Long, Evans & Joss (2009) found better support for hypothesis (4). These latter authors suggest that the dorsal part of the diphycercal fin of Carboniferous and extant lungfishes is formed by the confluence of the two dorsal fins found in more basal members with the epichordal lobe of the caudal fin, whereas the ventral part of the fin is formed only by the hypochordal lobe, and the anal fin is lost entirely (Johanson, Ericsson, Long, Evans & Joss, 2009).

The crown sarcopterygians are the Tetrapodomorpha. Piscine tetrapodomorphs include the Rhizodontiformes, "Osteolepiformes" and "Elpistostegalia." In tetrapodomorphs, the paired fins are composed of robust endochondral elements (i.e. humerus, radius, ulna, femur, tibia, fibula) that can be homologized to those of the tetrapod limbs (Boisvert, 2005; Boisvert, Mark-Kurik & Ahlberg, 2008; Shubin, Daeschler & Jenkins, 2006; 2014; Vorobyeva & Hinchliffe, 1996; Vorobyeva & Schultze, 1991). Rhizodontiformes range from the Upper Devonian to the Lower Carboniferous, while "Osteolepiformes" range from the lower Middle Devonian to the Lower Permian (Cloutier & Ahlberg, 1996; Janvier, 1996b). Rhizodontiforms and osteolepiforms present the fin combinations characteristic of most sarcopterygian taxa: presence of pectoral and pelvic fins, two dorsal fins, a single anal fin and a caudal fin. The paraphyletic elpistostegalians include the closest relatives to tetrapods and their fossil record extends from the Middle to the Upper Devonian (Cloutier & Ahlberg, 1995; Cloutier & Ahlberg, 1996; Daeschler, Shubin & Jenkins, 2006; Swartz, 2012). They are a poorly documented group and in the few taxa where postcranial material is preserved (e.g. *Panderichthys*, *Tiktaalik*, *Elpistostege*), there seems to be an evolutionary trend towards the loss of median fins other than the caudal fin (Daeschler, Shubin & Jenkins, 2006; Shubin, Daeschler & Jenkins, 2014).

4 DISCUSSION

In this paper, our main objectives were to summarize how fish appendages have historically been described in both fossil and extant taxa, and to discuss putative homologies with the fins of gnathostomes whenever possible. To our knowledge, this is the most exhaustive review of the literature on the distribution of median and paired fins across such a wide phylogenetic span. We found that, when taking into account the phenomenal biodiversity and morphological disparity in fishes, not only does it become extremely difficult to interpret fin homologies, it is also arduous even to formulate an all-encompassing definition as to what constitutes a fin.

Among the factors that complicate inferring fin homologies are that fishes have highly diversified fin configurations and that some fin morphologies are restricted to certain taxonomic groups (e.g. preanal fin-fold of hagfishes, admedian and intermediate spines in acanthodians and stem chondrichthyans, adipose fins in teleosteans). The debate about fin homologies is further complicated because median and paired fins first appeared among agnathans, and the only extant representatives of these jawless fishes are hagfishes and lampreys, both of which exhibit character combinations that are not plesiomorphic for vertebrates (Furlong & Holland, 2002; Janvier, 2008; Ota, Fujimoto, Oisi & Kuratani, 2013; Shimeld & Donoghue, 2012). Developmental studies on these extant agnathans have nonetheless provided useful information as to the evolutionary history of fish appendages. Indeed, recent studies have shown that the absence of paired fins in lampreys is likely secondarily derived (Onimaru & Kuraku, 2018; Tulenko et al., 2013). If anaspids continue to be well-supported as stem cyclostomes by future phylogenetic analyses, as suggested by Miyashita et al. (2019), this would provide additional weight to the hypothesis that the paired fins found in fossil agnathans (e.g. anaspids, thelodonts) can be homologized to the paired fins of gnathostomes, as opposed to structures that have independently evolved.

Despite the difficulties mentioned above, it is possible to construct a scenario whereby the different median and paired fins appeared in a stepwise manner (Larouche, Zelditch & Cloutier, 2017). For the median fins, developmental and palaeontological evidence suggest that they developed first as elongated structures before being modified into more constricted appendages. Indeed, median fins have been found to develop from a continuous fin-fold in lampreys (Freitas, Zhang & Cohn, 2006), chondrichthyans (Ballard, Mellinger & Lechenault, 1993) and actinopterygians (Abe, Ide & Tamura, 2007; Bemis & Grande, 1999; Richter & Moritz, 2017; van Eeden et al., 1996). However, this may not always be the case as Stewart, Bonilla, Ho & Hale (2019) have found that adipose fins in Characoidei develop from fin-buds that appear after the reduction of the median larval fin-fold. As for palaeontological evidence, the most basal vertebrates from the fossil record are described as having elongated median fins that extend over most of the dorsal and ventral aspects of the fish (Hou, Aldridge, Siveter & Feng, 2002; Shu et al., 1999; Shu et al., 2003a; Zhang & Hou, 2004). Lancelets also possess elongated median fin-folds that extend along the ventral and dorsal midlines leading to the hypothesis that these structures may be homologous (Schaeffer, 1987).

The situation is more difficult to interpret concerning the paired fins, and variants of two basic evolutionary scenarios have been proposed. One scenario is that the elongated paired fins described for many stem vertebrates (e.g. anaspids, furcacaudiforms) can be homologized to pelvic fins owing to their ventrolateral insertion (Wilson, Hanke & Märss, 2007). Gnathostome pelvic fins also have a ventrolateral insertion, in contrast to pectoral fins that generally have a more lateral insertion close to the gill apertures. In this scenario, pelvic fins appeared before pectoral fins (Wilson, Hanke & Märss, 2007). The other scenario is that pectoral fins appeared first among jawless fishes and pelvic fins appeared later among stem gnathostomes (Coates, 1993; 1994; Coates & Cohn, 1998; 1999; Forey & Janvier, 1993; Riley, Cloutier & Grogan, 2017; Ruvinsky & Gibson-Brown, 2000; Shubin, Tabin & Carroll, 1997). This hypothesis is based largely on the observation that the osteostracan paired fins share anatomical and positional similarities with the paired fins of gnathostomes and are therefore interpreted by most authors as their homologs (Forey, 1995; Forey & Janvier, 1993; 1994; Janvier, 2007; Janvier & Arsenault, 1996; Janvier, Arsenault & Desbiens, 2004; Johanson, 2002; Kiaer, 1924; Maisey, 1986; Sansom, 2009; Stensiö, 1927; 1932; 1964; Wängsjö, 1952; Westoll, 1958). Although the latter scenario has been more thoroughly discussed, it does not make explicit claims about the homologies of these elongated ventrolateral fins of some anaspids and thelodonts. One hypothesis is that paired fins first appeared as these elongated ribbon-like structures and were only later modified into narrow-based pectoral and pelvic fins (Larouche, Zelditch & Cloutier, 2017; Tabin & Laufer, 1993). This hypothesis is reminiscent of the lateral fin-fold theory, an evolutionary scenario concerning the origin of the paired fins that Balfour, Mivart and Thacher independently proposed towards the end of the 19th century (Balfour, 1876; 1878; 1881; Mivart, 1879; Thacher, 1877). However, the expected archetypal vertebrate based on the fin-fold hypothesis, combining both median and lateral elongated fin-folds (Jarvik, 1980), has never been found in the fossil record. The contrasting view at the time was that paired fins evolved through the co-option of elements of the gill-arches (Gegenbaur, 1876), a hypothesis that has recently seen some support from molecular data (Gillis, Dahn & Shubin, 2009). Based on our exhaustive review of the literature as well as the mapping of fin characters on a supertree of all fish orders (Larouche, Zelditch & Cloutier, 2017), we find that the evidence that would support a homology claim for the elongated ventrolateral paired fins of anaspids and furcacaudids is tenuous at best. Whether these ribbon-like paired appendages are homologous to the pectoral fins (Gagnier, 1993b; Kiaer, 1924; Robertson, 1938a; 1941; Stensiö, 1927; 1932), or the pelvic fins (Janvier & Arsenault, 2007; Moy-Thomas & Miles, 1971; Wilson, Hanke & Märss, 2007), or both paired fins (Stensiö, 1939), or even whether they are independently derived structures (Coates, 2003; Hopson, 1974; Janvier, 1987; Ritchie, 1964; Robertson, 1941) is impossible to determine given the current evidence.

One hypothesis that would warrant further attention is that in some cases, it is not so much the fins themselves that are homologous across large phylogenetic scales, but rather the fin-forming fields. In support of this hypothesis, studies on several vertebrate models have shown that it is possible to induce the development of additional appendages along the flanks between the fore- and hindlimbs (Cohn, Izpisúa-Belmonte, Abud, Heath & Tickle, 1995; Isaac et al., 1998; Tamura et al., 2001; Tanaka et al., 2000; Tanaka et al., 2002; Yonei-Tamura et al., 2008). Similar methods have also been used to induce the development of an extra limb along the dorsal midline in chick embryos (Tamura et al., 2001; Yonei-Tamura et al., 2008; Yonei-Tamura et al., 1999). These fin-forming fields [or morphogenetic fields *sensu* Gilbert et al. (1996)] could explain how structural similarities can emerge in distinct appendages, more specifically through the redeployment of genetic mechanisms. The structural and functional similarities between the median and paired fins in coelacanths provide another example of the possible redeployment of developmental mechanisms. Ahlberg (1992) hypothesized that these similarities may be owing to a homeotic switch in gene expression whereby paired fin developmental mechanisms were re-expressed in the posterior dorsal and anal fins. Fin-forming fields could also explain how some fins might have evolved more than once independently during the evolutionary history of fishes. Indeed, despite similarities in structure and morphology, the adipose fin has been shown to have evolved independently multiple times within teleosteans (Stewart & Hale, 2013; Stewart, Smith & Coates, 2014). This hypothesis may be extended to other appendages as well: pelvic claspers are considered as a synapomorphy of extant chondrichthyans (Grogan & Lund, 2004; Grogan, Lund & Greenfest-Allen, 2012; Maisey, 1986; Schaeffer & Williams, 1977), but intromittent organs have also been identified in various placoderms (Goujet, 1984; 2001; Miles & Young, 1977; Trinajstic, Boisvert, Long, Maksimenko & Johanson, 2014; Young, 1986) and more recently in the anaspid *Euphanerops* (Chevrinais et al., 2018). Although intromittent organs are present in these disparate taxa, their composition differs. In *Euphanerops*, the intromittent organs are associated with the pelvic girdles despite that pelvic fins are absent (Chevrinais et al., 2018). In placoderms, the claspers are not part of the pelvic skeleton and are interpreted as serial homologues of the pectoral and pelvic fins (Long et al., 2015; Trinajstic, Boisvert, Long, Maksimenko & Johanson, 2014). Lastly, in chondrichthyans, the claspers are a modification of the medial endoskeletal elements of the pelvic fins (O'Shaughnessy, Dahn & Cohn, 2015).

Another hypothesis that may explain both the disparity in fin configurations and the appearance of novel fins is that fins have a modular organization. Hypotheses of fin modules have already been proposed for both the median and the paired fins. In this context, the appearance of novel or additional fins could be facilitated by the duplication of preexisting fin modules. For the median fins (Figure 2), a dorsal and anal fins module has been proposed based on the observations that these fins share a symmetrical position along the antero-posterior body axis in basal teleosteans and that they show similarities in developmental patterns (Mabee, Crotwell, Bird & Burke, 2002). A caudal fin module has been suggested based on conserved developmental sequences and similarities in plastic responses to differences in flow regimes during ontogeny in the Arctic char (*Salvelinus alpinus*) (Grünbaum, Cloutier & Vincent, 2012). The anterior dorsal fin has been interpreted as a novel fin module in both chondrichthyans (Maisey, 2009) and actinopterygians (Mabee, Crotwell, Bird & Burke, 2002). This anterior dorsal fin module may have evolved multiple times independently. In support of this hypothesis, although the developmental pattern for the anterior dorsal fin of most teleosteans is either bidirectional or directed antero-posteriorly for both radials and fin-rays, it has recently been shown that a third developmental pattern exists, exclusive to the spinous dorsal fin of Atheriniformes, whereby the pterygiophores sequentially develop in a posterior to anterior direction while the fin-rays develop in the opposite direction (Richter & Moritz, 2017). Finally, the adipose fin has also been proposed as a novel fin module that, as previously mentioned, might have evolved more than once (Stewart, 2015; Stewart, Bonilla, Ho & Hale, 2019; Stewart, Smith & Coates, 2014).

Hypotheses of appendage modularity have also been discussed for the paired fins (Figure 3). For instance, developmental and structural similarities between median and paired fins have led some authors to suggest that median fin developmental mechanisms were redeployed laterally, leading to the emergence of the paired appendages (Freitas, Gómez-Skarmeta & Rodrigues, 2014; Freitas, Zhang & Cohn, 2006). Likewise, pectoral and pelvic fins display many developmental and morphological similarities in chondrichthyans, leading to the hypothesis that pectoral fin developmental mechanisms could have been re-expressed in the pelvic fins (Freitas, Zhang & Cohn, 2007; Riley, Cloutier & Grogan, 2017). A paired fins module was further supported by highly significant covariance patterns in their presence/absence across fish orders (Larouche, Zelditch & Cloutier, 2017). Pectoral and pelvic fins can, however, both be individuated as modules hierarchically nested within the paired fins module, based on the observation that they can both be modified or lost independently (Hall, 2010).

Molecular mechanisms have been described that support these scenarios of modular duplication. For example, during median fin development, dorsal and anal fins have been shown to share similarities in gene expression patterns in the catshark (Freitas, Zhang & Cohn, 2006) and the zebrafish (Crotwell, Clark & Mabee, 2001; Crotwell, Sommervold & Mabee, 2004). For the paired fins, Tabin & Laufer (1993) hypothesized that the Hox genes controlling fin patterning in the pelvic fins were re-expressed in the pectoral fins in the lineage leading to tetrapods, thereby explaining structural similarities in paired fins in sarcopterygians. Moreover, two genes involved in fin positioning during development are *Tbx5* for the pectoral fins and *Tbx4* for the pelvic fins (Gibson-Brown et al., 1996). One hypothesis is that these two genes could have evolved through the duplication of a *Tbx4/5* gene that controlled the position of the ancestral paired fin (Agulnik et al., 1996; Hadzhiev et al., 2007; Onimaru & Kuraku, 2018; Ruvinsky & Gibson-Brown, 2000; Tanaka et al., 2002). As previously mentioned, some authors have also proposed that the origin of the paired fins can be explained by the lateral redeployment of developmental mechanisms originally associated with the median fins (Crotwell, Clark & Mabee, 2001; Crotwell & Mabee, 2007; Freitas, Gómez-Skarmeta & Rodrigues, 2014; Freitas, Zhang & Cohn, 2006; Letelier et al., 2018). This hypothesis is supported by the similarities in molecular signaling pathways between developing median and paired fins (Abe, Ide & Tamura, 2007; Freitas, Gómez-Skarmeta & Rodrigues, 2014; Freitas, Zhang & Cohn, 2006).

CONCLUSION

In this paper, our main objective was to review the diversified fin configurations that occurred throughout the evolutionary history of fishes and to infer homologies wherever possible. We found that the disparity in fin number, position, structure and function greatly complicates not only interpreting fin homologies, but even formulating an all-encompassing definition of the term "fin." Based on the distribution of fin presence/absence on a supertree and the fin morphologies that are known for the most basal vertebrates, we favour a more conservative scenario where both median and paired fins first appeared as elongated structures that were later modified into shorter-based fins. We also suggest that it may be useful to discuss fin homologies in the context of fin-forming fields. Within this framework, median appendages would have appeared from a unique field of competence first positioned throughout the dorsal and ventral midlines, which was then redeployed laterally leading to the appearance of paired appendages. However, we realize that the available data is not sufficient to rule out other interpretations. We can only hope that future discoveries, whether developmental or palaeontological, will bring additional evidence leading to the resolution of this historical debate.

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Conflict of interest

The authors have no conflict of interest to declare.

Data availability

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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Tables

TABLE 1 Summary of how fins have been "defined" historically. See text for references.

Years of birth-death	Author	Homology criteria	Elements of the definitions
384-322 BC	Aristotle	Functional	Fins are organs of locomotion and differences in fin configurations relate to differences in swimming style.
1507-1566	Guillaume Rondelet	Functional	Fins are functionally important to fish as are wings to birds; fins differ widely among species in their shapes, sizes, colors, positions and structures. However, Rondelet classifies all aquatic animals as fishes (e.g. sea turtles, marine mammals, crustaceans, mollusks).
1517-	Pierre	Functional	Belon also compares fins to bird wings and classifies

1564	Belon		aquatic animals such as dolphins and hippopotami as fishes.
1733-1821	Antoine Goüan	Structural, functional and topological	True fins are composed of rays or spines united by a membrane. Fins are functionally used either as oars or rudders. Goüan distinguishes fins based on their position on the body; he also developed an elaborate descriptive terminology for each of the median and paired fins taking into account their position, size, shape, structure and number.
1756-1825	Bernard-Germain de Lacépède	Structural, functional and topological	Fins are usually composed of a membrane supported by skeletal supports. Yet some structures lacking either a membrane or fin-rays/spines should still be considered as fins owing to their position and function. Lacépède highlights the great disparity in the number of fins that can be present.
1769-1832	Georges Cuvier	Structural, functional and topological	Pectoral fins correspond to the limbs of other vertebrates. Median fins can be identified based on their position and are used as keels or rudders of a boat. Cuvier also describes the internal skeletal structures of the median and paired fins.
1804-1892	Richard Owen	Structural, functional and topological	The paired fins are homologous to the limbs of other vertebrates; both are supported by inverted arches, respectively the scapular and pelvic arches. The pectoral fins are involved in raising and depressing the body during locomotion, the pelvic fins prevent rolling, the caudal fin acts as a propeller, and the anal fin acts as a keel.
1825-1895	Thomas Henry Huxley	Structural and topological	The paired fins are homologous to the limbs of other vertebrates, although the elements of the internal skeleton only imperfectly corresponds to those of tetrapods. Median and paired fins can be recognized

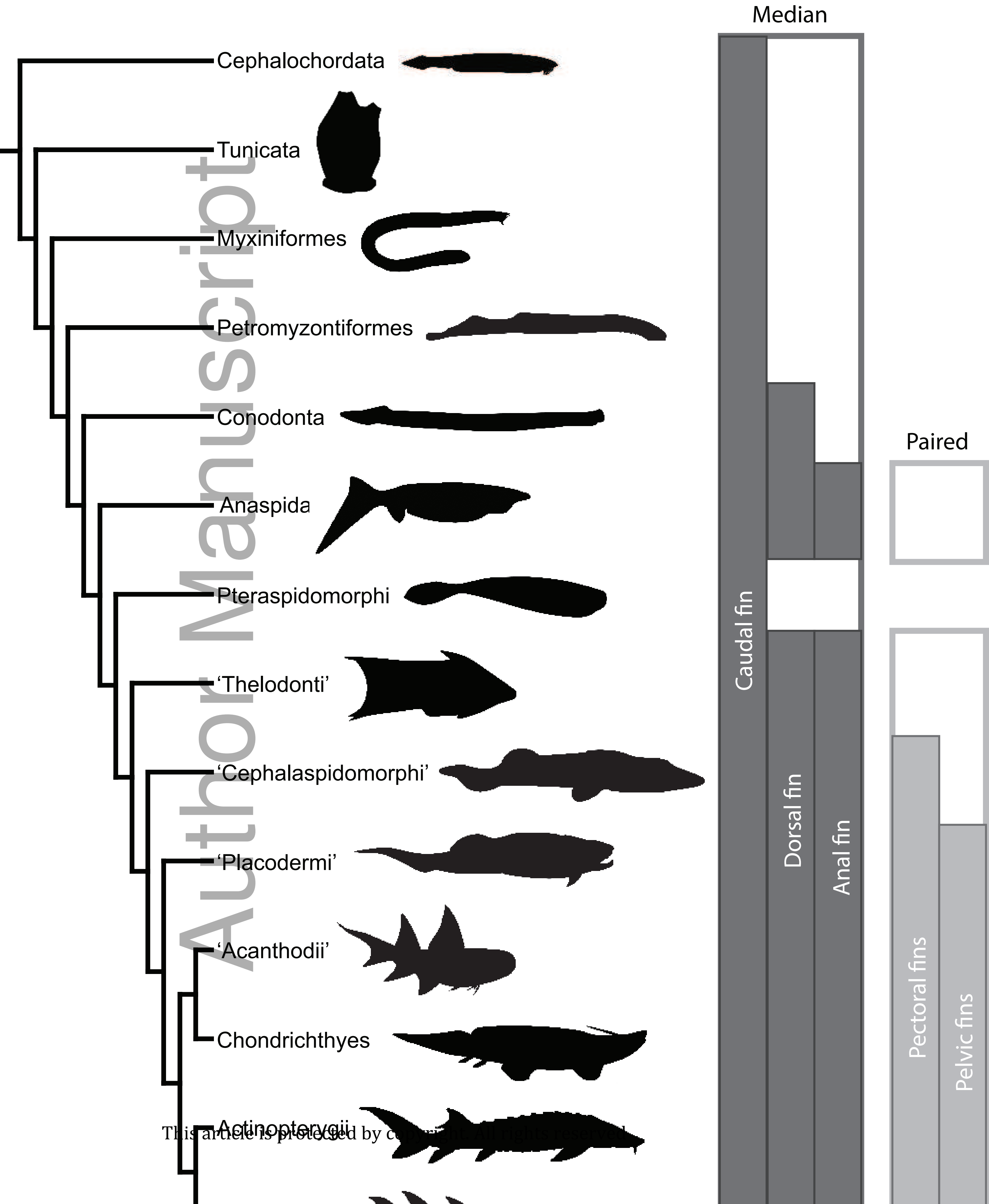
			based on their position.
1868-1946	Edwin Stephen Goodrich	Developmental, structural and topological	Median fins are longitudinal folds that may or may not contain skeletal support structures; paired fins are provided with an internal support structure composed of radials and an endoskeletal arch. Both the median and the paired fins arise from longitudinal folds of skin.

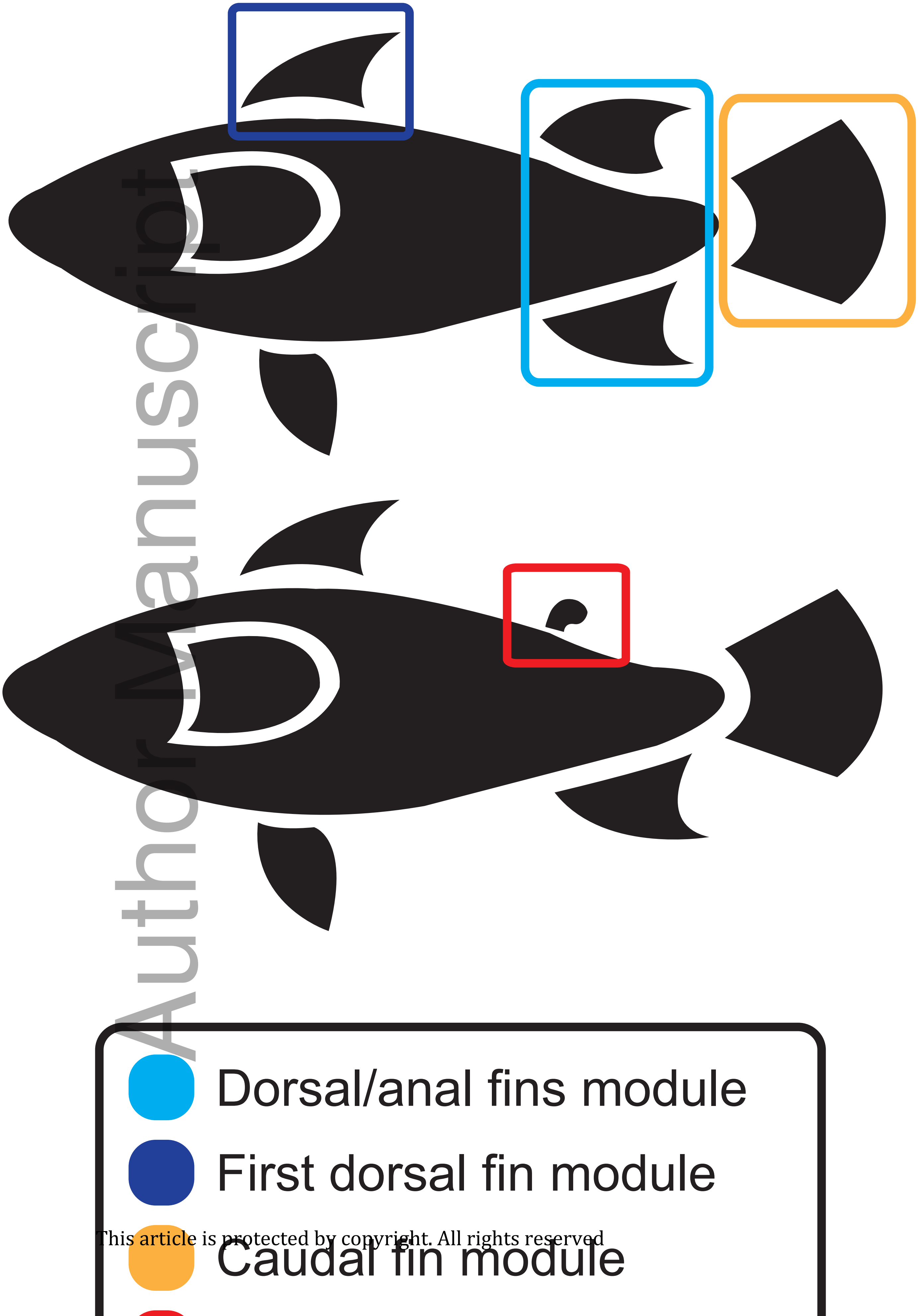
Figure legends

FIGURE 1 Simplified phylogeny of fishes showing the distribution of median and paired fins. The topology summarizes the results of the supertree analysis in Larouche, Zelditch & Cloutier (2017). The presence of median and paired fins in at least some members of each taxonomic group are represented by the boxes with dark and light grey outlines, respectively. The filled boxes represent the presence of median and paired fins that can confidently be homologized to those of gnathostomes.

FIGURE 2 Hypothesized median fin modules. A dorsal and anal fins module has been proposed based on their symmetrical positioning relative to the antero-posterior body axis and on developmental similarities. A caudal fin module has been proposed based on conserved developmental mechanisms across species. The anterior dorsal and the adipose fins have both been interpreted as novel fin modules. See text for references.

FIGURE 3 Hypothesized paired fin modules. The pectoral and pelvic fins have both become individuated as modules based on the fact that they can be modified or lost independently. However, strong covariation patterns in their presence/absence at a macroevolutionary scale suggest that they may be nested within a larger paired fins module. See text for references.


Median
Paired
Cephalochordata
Tunicata
Myxiniformes
Petromyzontiformes
Conodonta
Anaspida
Pteraspidomorphi
'Thelodonti'
'Cephalaspidomorphi'
'Placodermi'
'Acanthodii'
Chondrichthyes
Actinopterygii
Caudal fin
Dorsal fin
Anal fin
Pectoral fins
Pelvic fins


Dorsal/anal fins module
First dorsal fin module
Caudal fin module

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