

# Major issues in the origins of ray-finned fish (Actinopterygii) biodiversity

Lauren C. Sallan<sup>1,2,3,\*</sup>

<sup>1</sup>*Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, U.S.A.*

<sup>2</sup>*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, U.S.A.*

<sup>3</sup>*Michigan Society of Fellows, University of Michigan, Ann Arbor, MI 48109, U.S.A.*

## ABSTRACT

Ray-finned fishes (Actinopterygii) dominate modern aquatic ecosystems and are represented by over 32000 extant species. The vast majority of living actinopterygians are teleosts; their success is often attributed to a genome duplication event or morphological novelties. The remainder are ‘living fossils’ belonging to a few depauperate lineages with long-retained ecomorphologies: Polypteriformes (bichirs), Holostei (bowfin and gar) and Chondrostei (paddlefish and sturgeon). Despite over a century of systematic work, the circumstances surrounding the origins of these clades, as well as their basic interrelationships and diagnoses, have been largely mired in uncertainty. Here, I review the systematics and characteristics of these major ray-finned fish clades, and the early fossil record of Actinopterygii, in order to gauge the sources of doubt. Recent relaxed molecular clock studies have pushed the origins of actinopterygian crown clades to the mid-late Palaeozoic [Silurian–Carboniferous; 420 to 298 million years ago (Ma)], despite a diagnostic body fossil record extending only to the later Mesozoic (251 to 66 Ma). This disjunct, recently termed the ‘Teleost Gap’ (although it affects all crown lineages), is based partly on calibrations from potential Palaeozoic stem-taxa and thus has been attributed to poor fossil sampling. Actinopterygian fossils of appropriate ages are usually abundant and well preserved, yet long-term neglect of this record in both taxonomic and systematic studies has exacerbated the gaps and obscured potential synapomorphies. At the moment, it is possible that later Palaeozoic-age teleost, holostean, chondrosteian and/or polypteriform crown taxa sit unrecognized in museum drawers. However, it is equally likely that the ‘Teleost Gap’ is an artifact of incorrect attributions to extant lineages, overwriting both a post-Palaeozoic crown actinopterygian radiation and the ecomorphological diversity of stem-taxa.

*Key words:* ichthyology, teleost, palaeontology, Palaeozoic, systematics, molecular clocks, diversification, fossils.

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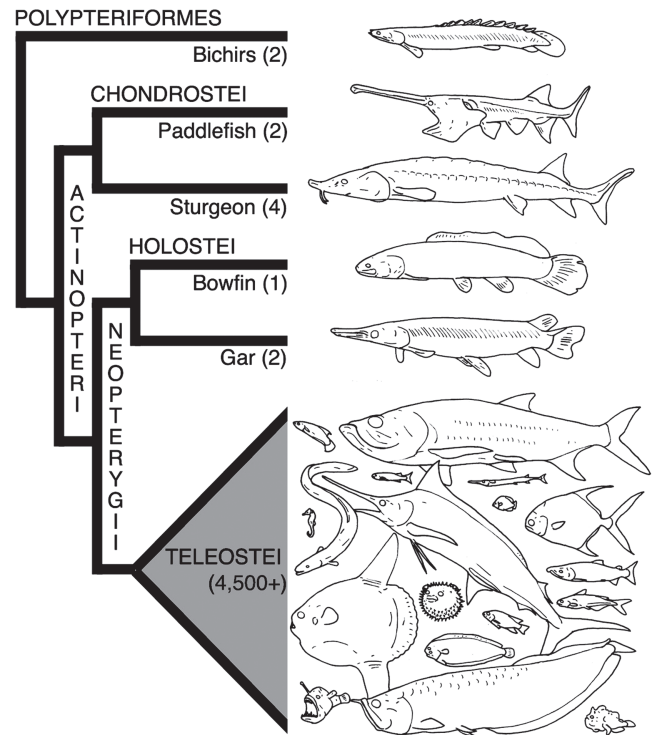
\* Author for correspondence (Tel: (954) 895–9192; E-mail: laurensallan@gmail.com).

## I. INTRODUCTION

Ray-finned fishes (*Actinopterygii*) comprise a major portion of living vertebrate diversity in terms of species count (~32000), total biomass and ecological breadth (Nelson, 2006; Faircloth *et al.*, 2013; Fig. 1). Actinopterygians inhabit every aquatic environment from abyssal plane to montane river to intertidal coastline, and consume resources from microplankton to mammals (Nelson, 2006). These fishes have a long tradition of use in studies of developmental biology (zebrafish, *Danio rerio*; medaka, *Oryzias*; pufferfish, *Takifugu*), population genetics (e.g. three-spine stickleback, *Gasterosteus aculeatus*), ecology (all types), speciation and adaptive radiation (e.g. cichlids, Cichlidae), systematics (e.g. wrasses, Labridae) and biomechanics (e.g. wrasses, Labridae; pufferfishes, Tetraodontiformes) (Webb, 1982; Bell, 1994; Kornfield & Smith, 2000; Streelman & Danley, 2003; Shima & Mitani, 2004; Westneat, 2004; Nelson, 2006). Since actinopterygians are so important in modern science and modern ecosystems, investigation of their evolutionary history is vital for interpreting not only their living biodiversity but also that of vertebrates in general.

Given the numerical dominance of the Actinopterygii in Recent aquatic vertebrate faunas, it is somewhat surprising that the clade was not recognized as a natural group until late in the 19th Century and the exact membership and diagnosis is still under some debate (e.g. Berg, 1940; Nelson, 1969*b*; Jessen, 1973; Patterson, 1973, 1982; Friedman & Brazeau, 2010). Nelson (1969*a*) attributed this uncertainty to neglect in the face of tetrapods, which serve as proxies for human ancestors. However, it is also a consequence of the relative success of actinopterygians, as diverse and divergent groups are hard to define in a way that minimizes exceptions. The 1200 living species of elasmobranch Chondrichthyes (cartilaginous fishes; Nelson, 2006), which are more homogenous in form, have been cited as a group distinct from 'bony fishes' (Osteichthyes) for centuries (e.g. Willughby & Ray, 1686). Yet sharks were repeatedly allied with actinopterygian paddlefishes and sturgeon (Chondrostei; Fig. 1) on the basis of their similarly cartilaginous skeletons and protrusible jaws (e.g. Linnaeus, 1758; Walbaum, 1792, and others cited in Bemis, Findeis & Grande, 1997). Sarcopterygii (lobe-finned fishes), the other crown clade of Osteichthyes (bony fishes; Nelson, 2006), was described relatively recently: the extant lungfish *Protopterus annectens* was named by Owen in 1839, while the 'living fossil' coelacanth *Latimeria chalumnae* was famously discovered a century later (Smith, 1939). This was long after the discovery of other sarcopterygians in the fossil record, setting the stage for recognizing the vast 'rump' of the fishes ('Pisces') as a true group.

A complicating factor is that, for most of the 19th Century, major divisions within the fishes were primarily based on scale morphology and not hypotheses of shared ancestry, a bias rooted in a pre-Darwinian era focused on classification. Agassiz (1833–1844) grouped chondrosteans, some teleosts (e.g. catfishes; Fig. 1), Palaeozoic and Mesozoic actinopterygian fossils, acanthodians, placoderms,



**Fig. 1.** Consensus phylogeny of living actinopterygian clades. Topology based on a survey of molecular and cladistic analyses discussed in the text. Numbers indicate living genera. Drawings represent exemplars of morphological diversity and clades within each group. Basic topology after Grande (2010) and Faircloth *et al.* (2013).

cephalaspid agnathans, lungfishes and other fossil sarcopterygians ('Sauroides') as an order of 'ganoids' defined by enameloid-covered scales. Other ray-finned fishes were divided between the 'ctenoid' and 'cycloid' orders also on the basis of scale morphology (Agassiz, 1833–1844), establishing a squamation classification system still used in textbooks (e.g. Calliet, Love & Ebeling, 1996). Müller (1844, 1846) proposed an alternative taxonomic schema for bony fishes based on ossification: a Chondrostei ('cartilage bone') containing the early 'ganoids,' paddlefishes (Polyodontiformes) and sturgeon (Acipenseriformes), a Holosteii ('whole bone') containing gars (Lepisosteiformes or Ginglymodi), bichirs (Polypteriformes) and eventually bowfins (Halecomorphi or *Amia*, originally assigned to clupeiform teleosts alongside herring; Müller, 1846; Patterson, 1973) and a Teleostei ('perfect bone') containing everything else (Figs 1 and 2). These represent the long-accepted taxonomic divisions within the monophyletic Actinopterygii (Cope, 1887), used within myriad textbooks and field guides (Nelson, 2006). Yet, the fossil and living membership of the Actinopterygii, the basic interrelationships between living groups (Fig. 1), the definitions of those clades and circumstances of their divergence have been the subject of continual controversy and investigation ever since. Here, I review these past and present uncertainties regarding deep branching patterns in ray-finned fishes, the origin of actinopterygian taxonomic

diversity and ecological dominance, and the contributions of molecular, morphological and especially palaeontological data in resolving these issues.

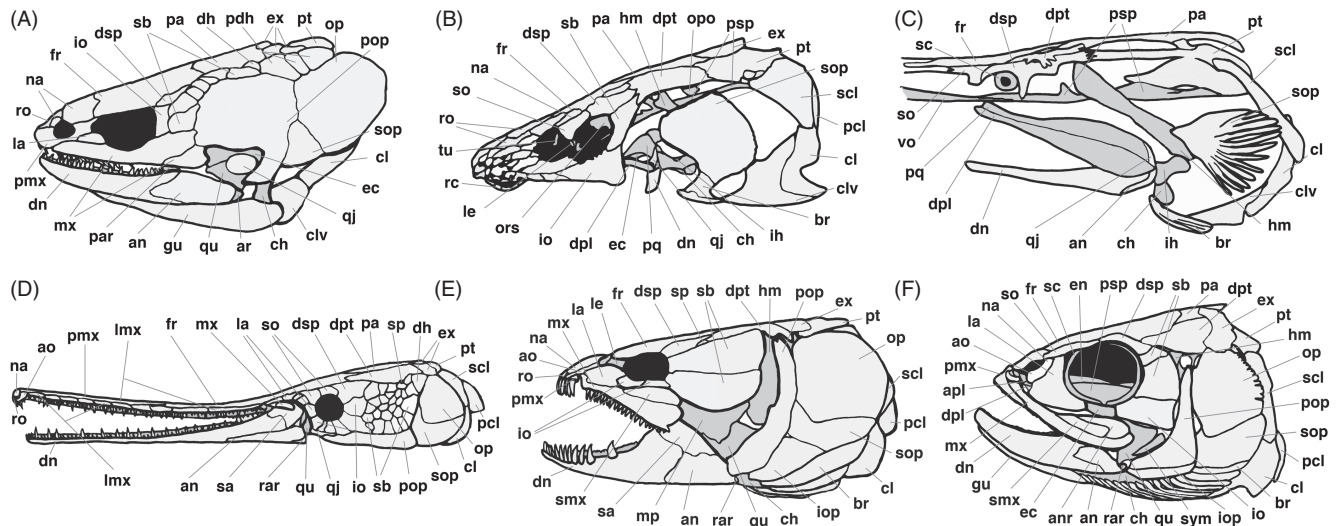
## II. THE BASIC INTERRELATIONSHIPS OF CROWN ACTINOPTERYGII

### (1) Status of the Polypteriformes and the membership of crown Actinopterygii

In Fig. 1 and most recent phylogenies (Hurley *et al.*, 2007; Mickle, Lund & Grogan, 2009; Grande, 2010; Xu & Gao, 2011; Near *et al.*, 2012; Chen *et al.*, 2012*b*; Betancur-R *et al.*, 2013; Broughton *et al.*, 2013; Faircloth *et al.*, 2013; Rabosky *et al.*, 2013), the Polypteriformes (bichirs and ropefishes) are placed as the sister group to all other living actinopterygians, the latter forming a clade known as the Actinopteri (a term originally synonymous with Actinopterygii). This clade is in turn comprised of the Chondrostei, Holostei and Teleostei (Fig. 1). Under this topology, the morphological characters that define crown Actinopterygii would be those shared, at least ancestrally, by the bichirs and all other crown actinopterygians. Historically, determining such diagnostic traits has been somewhat complicated by doubts about the position of the Polypteriformes within Osteichthyes

(Janvier, 1996). This is because of a mix of divergent and derived traits (e.g. axial elongation, multiple dorsal finlets, separation between the maxilla and preoperculum, ossified centra and ribs, apomorphic anamestic bones; Allis, 1922; Markey & Marshall, 2007; Ward & Brainerd, 2007; Suzuki, Brandley & Tokita, 2010) and seemingly primitive or conflicting morphologies (e.g. lobate pectoral fins, spiracles, spiral intestines, diphyccercal tail; White, 1939; Janvier, 1996) within the two living genera *Erpetoichthys* (ropefishes) and *Polypterus* (bichirs) (Fig. 2A).

As a result of these character combinations, Polypteriformes were first reassigned to the sarcopterygian Crossopterygii by Huxley (1861, Patterson, 1973), having previously been placed within the Holostei, and therefore what would later become the Actinopterygii, on the basis of skeletal ossification (Müller, 1844, 1846). Following the discovery of further fossil actinopterygian material, Polypteriformes were reclassified as Chondrostei, considered a basal and paraphyletic ‘grade’ in such discussions, and hypothesized to be hold-overs from some unknown Palaeozoic forms [Gardiner, 1967*a*; Moy-Thomas & Miles, 1971; Schaeffer, 1973; Nelson, 1994, Noack, Zardoya & Meyer, 1996; see Section II(2)]. However, as detailed below, the record of crown Polypteriformes only extends to the late Cretaceous (Duthiel, 1999; Grandstaff *et al.*, 2012; Broughton *et al.*, 2013) and hypothesized close relationships with various Palaeozoic



**Fig. 2.** Living actinopterygian cranial morphologies. (A) *Polypterus senegalus* (Polypteriformes; after Grande, 2010). (B) *Acipenser brevirostrum* (Acipenseridae: Acipenseriformes: Chondrostei; after Hilton, Grande & Bemis, 2011). (C) *Polyodon spathula* (Polyodontidae: Acipenseriformes: Chondrostei; after Gregory, 1933; Gardiner & Schaeffer, 1989; Grande & Bemis, 1991). (D) *Lepisosteus osseus* (Ginglymodi: Holostei; after Grande, 2010). (E) *Amia calva* (Halecomorphi: Holostei; after Grande & Bemis, 1998). (F) *Elops lacerta* (Elopiiformes: Teleostei; after Diogo, Doadrio & Vandewalle, 2008). Abbreviations: an, angular; anr, anguloretroarticular; ao, antorbital; apl, autopalatine; ar, articular; br, branchiostegal ray; ch, ceratohyal; cl, cleithrum; clv, clavicle; dh, dermohyal; dn, dentary; dpl, dermopalatine; dpt, dermopterotic; dsp, dermosphenotic; ec, ectopterygoid; en, entopterygoid; ex, extrascapular; fr, frontal; gu, gular; hm, hyomandibula; ih, interhyal; io, infraorbital or jugal; iop, interoperculum; la, lachrymal; le, lateral ethmoid; lmx, lachrymaxilla; mp, metapterygoid; mx, maxilla; na, nasal; op, operculum; opo, opisthotic; ors, orbitosphenoid; pa, parietal; par, prearticular; pcl, postcleithrum; pdh, postdermohyal; pmx, premaxilla; pop, preoperculum; pq, palatoquadrate; psp, parasphenoid; pt, posttemporal; qj, quadratojugal; qu, quadrate; rar, retroarticular; rc, rostral cartilage; ro, rostral; sa, supra-angular; sb, suborbital; sc, sclerotic plate; scl, supracleithrum; smx, supramaxilla; sp, sphenotic; so, supraorbital; sop, suboperculum; sym, symplectic; tu, tabular; vo, vomer.

fishes have not been supported morphologically or phylogenetically (e.g. *Cornuboniscus*: White, 1939; Gardiner & Schaeffer, 1989; the Tarrasiiformes or Tarrasiidae: Taverne, 1996; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Sallan, 2012). This ‘chondrostean’ affinity was discussed simultaneously with the acceptance of a polypteriform clade (also called Cladistia and Branchiopterygii) on equal standing with a monophyletic Chondrostei by other workers (see Goodrich, 1928; Patterson, 1982; Noack *et al.*, 1996). However, the divergent and/or ‘primitive’ nature of this independent group, branching just off the base of the actinopterygian tree, cast its affinity into doubt once again. The Polypteriformes were widely suggested to represent a third osteichthyan clade (Langler, Bardach & Miller, 1962; Jessen, 1973; Bjerring, 1985; Meyer & Zardoya, 2003) or members of the Sarcopterygii, sister group to lungfish, coelacanth and tetrapods (Nelson, 1969a). Broughton *et al.* (2013) recently pointed out that these hypotheses were never subject to direct testing, and thus cannot yet be entirely excluded from consideration. This assertion is despite the fact that their own molecular analysis, which included sarcopterygian outgroups, strongly supported an actinopterygian Polypteriformes (Broughton *et al.*, 2013).

Some older molecular trees have disputed the placement of Polypteriformes in Fig. 1, but these tend to be based on dubious sources such as mitochondrial and ribosomal DNA, involve few taxa (particularly actinopterygians) or genes, and/or use novel methods of tree construction which have not subsequently been adopted by the wider community. These studies do not provide a unified or even majority rule alternative to the standard topology, but rather a variety of placements for the bichirs and ropefishes. Polypteriformes have been found as sister group to teleosts to the exclusion of chondrosteans (Mallatt & Winchell, 2007), chondrosteans to the exclusion of other actinopterygians (Steinke, Salzburger & Meyer, 2006; Li, Lu & Orti, 2008), lungfishes (Arnason, Gullberg & Janke, 2001), coelacanth (Stuart, Moffett & Leader, 2002; Yu *et al.*, 2007), tetrapods (a ‘Crossopterygii’ position; Steinke *et al.*, 2006; Raincrow *et al.*, 2011), an actinopteran–coelacanth clade (Rasmussen, Janke & Arnason, 1998; Rasmussen & Arnason, 1999), a coelacanth–chondrichthyan–actinopteran clade (Arnason *et al.*, 2001) and even Osteichthyes and Chondrichthyes (Arnason *et al.*, 2004). The vast majority of these same trees (except Li *et al.*, 2008) show other anomalies, such as a polyphyletic Sarcopterygii (Rasmussen *et al.*, 1998; Rasmussen & Arnason, 1999; Stuart *et al.*, 2002; Mallatt & Winchell, 2007; Yu *et al.*, 2007), a monophyletic ‘Pisces’ (jawed non-tetrapods; Arnason *et al.*, 2004; Rocco *et al.*, 2004; Yu *et al.*, 2007), a chondrichthyan–actinopteran clade (Arnason *et al.*, 2001) and even a chondrichthyan–coelacanth clade (Mallatt & Winchell, 2007). Finally, some gene trees in the same studies conflict in their placement of Polypteriformes and other taxa (e.g. Steinke *et al.*, 2006; Raincrow *et al.*, 2011). Indeed, better vetted and sampled molecular analyses based on whole mitochondrial genomes (Noack *et al.*, 1996), more slowly evolving, dependable nuclear sequences and ever greater numbers of genes and

taxa (Inoue *et al.*, 2001, 2003, 2005, 2009; Venkatesh, Erdmann & Brenner, 2001; Zardoya & Meyer, 2001; Kikugawa *et al.*, 2004; Hurley *et al.*, 2007; Azuma *et al.*, 2008; Alfaro *et al.*, 2009; Santini *et al.*, 2009; Setiamarga *et al.*, 2009; Inoue, Donoghue & Yang, 2010; Near *et al.*, 2012; Chen *et al.*, 2012b; Betancur-R *et al.*, 2013; Broughton *et al.*, 2013; Rabosky *et al.*, 2013) and ultra-conserved elements (Faircloth *et al.*, 2013) have converged on the placement of Polypteriformes in Fig. 1.

Many scaled molecular trees show a relatively long branch subtending the living Polypteriformes, indicating greater amounts of sequence change since divergence than related lineages (Venkatesh *et al.*, 2001; Inoue *et al.*, 2003, 2009; Arnason *et al.*, 2004; Mallatt & Winchell, 2007; Suzuki *et al.*, 2010; Broughton *et al.*, 2013). Therefore, the non-actinopterygian status of Polypteriformes in some more recent, limited studies (e.g. Suzuki *et al.*, 2010; Raincrow *et al.*, 2011) might stem from convergence in sampled sequences rather than shared ancestry. This could be caused by the limited number of base-pair changes available, long-branch attraction (Felsenstein, 2004) between highly divergent taxa (see the high levels of substitution in lungfishes and Polypteriformes in Suzuki *et al.*, 2010), unusually large sequence divergence artificially pushing the group away from its relatives and towards the base of the tree or, alternatively, retention of ancestral sequences and conflicting genetic signals (e.g. similarity in *HoxD1* between *Polypterus* and tetrapods in an analysis where all other sequences matched Fig. 1; Raincrow *et al.*, 2011). Ultraconserved nuclear elements actually show very little sequence divergence in Polypteriformes relative to time since origination (Faircloth *et al.*, 2013), indicating that other results may be reflective of changes in ‘junk’ sequences or unrepresentative sampling.

Cladistic studies also support a crown Actinopterygii containing Polypteriformes (e.g. Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Cloutier & Arratia, 2004; Gardiner, Schaeffer & Masserie, 2005; Hurley *et al.*, 2007; Mickle *et al.*, 2009; Swartz, 2009; Xu & Gao, 2011), usually on the basis of diagnostic skeletal characters first used by Patterson (1982) and amended by Gardiner (1984). These include the presence of ganoine on the scales and dermal bones, scales with anterodorsal processes and distinct pegs and sockets, teeth with acrodin caps, a dentary enclosing the mandibular canal, a single hyomandibular joint, a pectoral fin with propterygium, a pelvic fin supported by a plate and two series of radials, a dermohyal, the absence of a squamosal, a jugal pitline, a parasphenoid with an ascending process and a posterior stem, a neurocranium with an autosphenotic and an enlarged opisthotic, a presupracleithrum, a postacleithrum and a median rostral enclosing the ethmoid commissure (Patterson, 1982; Gardiner, 1984). A total-group Actinopterygii in which Polypteriformes branches off above various actinopterygian stem-clades was defined by Friedman & Brazeau (2010) through comparison between Silurian and Devonian taxa designated as ray-finned fishes, sarcopterygians, acanthodians and stem-osteichthyans. Their synapomorphies for this more

inclusive clade are a basicranium bearing midline canal for the dorsal aorta, a narrow interorbital septum, vateritic statoconia, a propterygial canal, distinct radials supporting the anteriormost median fins, caudal radials which are shorter than the combined length of the haemal arch/spines (although these structures are not preserved in most early taxa; L. C. Sallan, personal observations), an opening in the anterior portion of the palatoquadrate, absence of jugal canal (see jugal pitline trait in Patterson, 1982) and acrodin caps (used to designate the crown elsewhere; Patterson, 1982; and noted to be absent in the Devonian taxon *Cheirolepis*, the sister group to the crown in other studies; Coates, 1999; Gardiner & Schaeffer, 1989). Polypteriformes possess all these synapomorphies except for the propterygial canal, which was therefore designated an actinopteran trait in the original cladistic study by Patterson (1982), and in most subsequent actinopterygian classification scheme. However, as the canal was present in the stem-actinopterygian *Cheirolepis* and all other stem-actinopterygians, and therefore was likely present in the Polypteriform ancestor (see Gardiner, 1984; Fig. 3).

## (2) Actinopteran interrelationships: ancient fish or new fins?

The Actinopteri, all living ray-finned fishes excluding *Polypterus* and *Erpetoichthys*, were diagnosed by Patterson (1982) as sharing the following skeletal characters: fringing fulcra on the leading edges of the fins, pseudoprismatic ganoine, a supra-angular on the lower jaw, a perforated propterygium surrounded by the bases of the pectoral lepidotrichia, a spiracular canal, a lateral cranial canal, three ossifications of the hyoid bar. Gardiner (1984) added an ascending process of the parasphenoid reaching the spiracular canal, a pectoral girdle with a distinct middle section and a distinct dermopterotic formed by fusion of the primitive inter- and supratemporals in the skull roof.

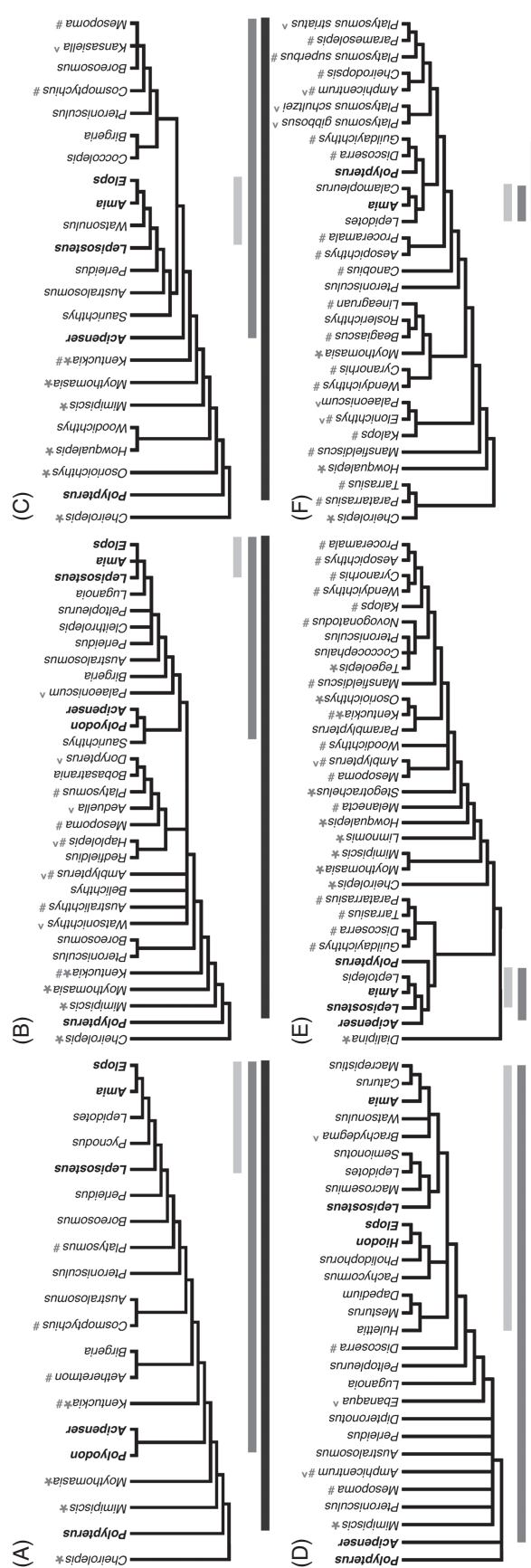
The interrelationships of the major divisions within the Actinopteri were previously a topic of debate among molecular systematists. Some molecular studies over the last decade supported the existence of an 'Ancient Fish Clade' (AFC; Holostei and Chondrostei) as sister group to the Teleostei (Inoue *et al.*, 2003, 2005, 2010; Near & Miya, 2009; mitochondrial data in Hurley *et al.*, 2007), a hypothesis first raised in a mitochondrial analysis by Lecointre *et al.* (1994) and given wider notice by Venkatesh *et al.* (2001). However, the AFC clade was likely caused by long-branch attraction and/or choice of sequences in those studies. For example, one gene tree (*sox11*) generated by Hoegg *et al.* (2004) showed an *Acipenser*–*Lepisosteus* (chondrostean–ginglymorph; Fig. 2B, D) clade, yet two other sequences and the concatenated dataset favoured the topology in Fig. 1. In addition, while a mitochondrial tree produced by Hurley *et al.* (2007) recovered the AFC, concatenated nuclear data recovered a Neopterygii ('new fin'; Fig. 1). All more recent molecular analyses based on different sequences have supported the existence of the latter clade (see below; Crow *et al.*, 2006; Azuma *et al.*, 2008; Raincrow *et al.*, 2011; Near *et al.*, 2012; Betancur-R *et al.*, 2013; Broughton *et al.*, 2013; Faircloth *et al.*, 2013; Rabosky

*et al.*, 2013), including studies (Inoue *et al.*, 2009; Saitoh *et al.*, 2011) by many of the same authors who previously found molecular support for the AFC (Inoue *et al.*, 2001, 2003, 2005).

Nearly all previous hypotheses of morphological transformation (e.g. Gardiner, 1967*a,b*; Patterson, 1973) and all cladistic analyses (e.g. Patterson, 1982; Olsen, 1984; Gardiner & Schaeffer, 1989; Olsen & McCune, 1991; Coates, 1998, 1999; Arratia, 2001; Cloutier & Arratia, 2004; Gardiner *et al.*, 2005; Hurley *et al.*, 2007) have favoured a monophyletic Neopterygii. The exception was a qualitative hypothesis by Jessen (1973) that placed the Chondrostei with the teleosts based on presumed similarities in shoulder girdle morphology alone, in a study that also treated Polypteriformes as a separate osteichthyan clade. By contrast, there has never been a published morphological argument in support of an AFC. Hurley *et al.* (2007) found that enforcing an AFC topology in cladistic analysis of extant taxa produced a tree 16 steps longer than the 80 step cladogram containing Neopterygii, and found just a single (unpublished) synapomorphy to support such a clade. However, as statistical tests could not reject the AFC clade, the authors concluded that the signal in the nuclear data was just too weak to resolve the backbone of the actinopteran tree (Hurley *et al.*, 2007), even though Bayesian support was much higher for Neopterygii. Alternatively, Grande (2010) suggested that the AFC arose from some quirk of earlier molecular systematic usage rather than real signal in the sequences. It is also possible that there was greater sequence divergence within teleosts than among non-teleosts for some of the genes used in earlier studies, perhaps related to the teleost-specific whole-genome duplication event (Amores *et al.*, 1998; Hoegg *et al.*, 2004; Crow *et al.*, 2006; Hurley *et al.*, 2007; Inoue *et al.*, 2010), which may have overwhelmed the neopterygian signal in earlier studies. This general point is raised again in relation to support for the Holostei below.

## (3) The Halecostomi-Holostei morphological controversy

The Neopterygii were defined by Patterson (1973) based on the following character states: reduction of the axial lobe so that caudal lepidotrichia extend beyond it, lepidotrichia in the dorsal portion of the caudal fin equal in length to those in the ventral portion, median lepidotrichia equal in number to supports, premaxilla with an internal nasal process, a coronoid process off the articular of the lower jaw, a vertical suspensorium, a preopercular with a narrow dorsal limb, a symplectic coming off the hyomandibula, a consolidated dentition on the upper pharynx, and a clavicle represented by a few plates on the anterior portion of the cleithrum or lost altogether. Gardiner (1984) amended this list to contain a distinct quadratojugal, antorbitals, a dermal basipterygoid process, an opercular process on the hyomandibula, separation between the palatoquadrate and dermal cheek bones, and separation between the maxilla and preopercular (a mobile maxilla). Grande (2010) added three additional characters that he recovered as nominally



**Fig. 3.** Cladograms containing Palaeozoic and recent actinopterygians. Bold taxa are living forms and grey marks indicate the age of Palaeozoic fossil taxa: \* for Devonian, # for Mississippian Carboniferous and Δ for Pennsylvanian Carboniferous–Permian. Unmarked fossil taxa are Mesozoic. Bottom bars indicate extent of crown clades: dark grey for crown Actinopterygii, medium grey for crown Neopterygii, and light grey for crown Cosmopterygii. (A) Gardiner (1984), with *Bigania* equivalent to the Mississippian taxon *Aelheretmon* and *Australosomus* equivalent to the Mississippian fish *Cosmopterygius*. (B) Gardiner & Schaeffer (1989). (C) Coates (1999). (D) Hurley *et al.* (2007). (E) Cloutier & Arratia (2004). (F) Mickle *et al.* (2009).

holostean: dichotomization of all caudal lepidotrichia, a supra-angular (an actinopteran trait in Patterson, 1982) and presence of fringing fulcra on the upper and lower margins of the caudal fin. This last trait is hard to differentiate from the presence of fulcra on the extended axial lobes of chondrosteans and fossil actinopterans (Patterson, 1982; Lauder & Liem, 1983; Gardiner & Schaeffer, 1989) that appear to extend only to the level of the distalmost caudal fin (L. C. Sallan, personal observations)

The interrelationships of major lineages (lepisosteids, *Amia*, teleosts; Figs 1 and 2D–F) within the Neopterygii has become an even more contentious subject among morphological systematists than the membership of Actinopterygii (see Patterson, 1973; Arratia, 2001; Grande, 2010; Lopez-Arbarelo, 2012). While the Holostei and Teleostei designations coined by Müller (1844, 1846) came into widespread use in subsequent classification schema, Patterson (1973) pointed out that they fell out of favour in the first half of the 20th Century, before the advent of cladistic methods. The Holostei and Teleostei were then poorly diagnosed and treated as evolutionary ‘grades,’ or polyphyletic transformational series as with the Chondrostei as discussed in Section II(1), rather than natural groups (see Berg, 1940; Schaeffer, 1955; Gosline, 1971, Patterson, 1973). The latter descriptive trend is illustrated by the attribution of various early Mesozoic and late Palaeozoic fossil taxa to a ‘Subholostei’ (Romer, 1945, Schaeffer, 1955), representing a grade of transitional taxa connecting the ‘palaeoniscoid’ [or Palaeozoic actinopterygian; see Section III(3)] and Holostean conditions (Schaeffer, 1955).

The earliest character-based morphological analyses supported a monophyletic Holostei (see Discussion in Patterson, 1973) containing lepisosteids and *Amia* (Fig. 2D, E). However, Patterson (1973) and most subsequent cladistic workers generated character sets and trees that split the Holostei (e.g. Patterson, 1973; Lauder & Liem, 1983; Gardiner, 1984; Olsen, 1984; Janvier, 1996; Bemis *et al.*, 1997; Grande & Bemis, 1998; Arratia, 1999, 2001; Coates, 1999; Cloutier & Arratia, 2004; see Grande, 2010, p. 804 for a full list of papers). These proposed that either the Ginglymodi (lepisosteid gars and their relatives; Olsen, 1984; Olsen & McCune, 1991; Fig. 2D) or the Halecomorphi (*Amia* or bowfin and its relatives; Patterson, 1973 and all other such studies; Fig. 2E) are the extant sister group of teleosts. The ginglymodian–teleost arrangement was supported by a single character (detachment of the symplectic from the jaw joint, leading to a single jaw articulation; Olsen, 1984; Olsen & McCune, 1991). This was counted as a loss near the Ginglymodi crown in gar–teleost cladograms (Olsen, 1984; Olsen & McCune, 1991), a state change supported by a recent review of the gar fossil record by Grande (2010). Grande (2010, p. 804) also asserted that the double-jointing of halecomorph and teleost jaws was a derived and homoplastic condition, arising in slightly different form in some potential stem-neopterygians (e.g. *Pteronisculus*: Olsen, 1984; for possible phylogenetic placement see Hurley *et al.*, 2007 and Fig. 3). Most convincingly, Grande (2010)

attempted to replicate Olsen’s (1984) results using a corrected matrix and recovered a monophyletic Holostei.

The *Amia*–teleost clade, Halecostomi, proposed by Patterson (1973) was based on multiple shared traits, including median neural spines, epibranchials bearing uncinat processes, a large posterior myodome, a large post-temporal fossa, a supramaxilla and loss of a distinct quadratojugal (see Grande, 2010, p. 810 for discussion; Fig. 2E, F). Subsequent cladistic analyses (Gardiner, 1984; Coates, 1999) recovered additional synapomorphies, such as pre-ethmoids, an intercalar with membranous outgrowths, a post-temporal process, an absence of lateral gulars and a dermal basiptyergoid process. Many accounts put emphasis on two traits in particular: a mobile maxilla and an interoperculum (Patterson, 1973; Lauder & Liem, 1983; Gardiner, 1984; Bemis *et al.*, 1997), both used as neopterygian characters elsewhere (Gardiner, 1984; Gardiner & Schaeffer, 1989; Hurley *et al.*, 2007; see Grande, 2010, for review).

Cladistic analyses favouring a gar–teleost clade had previously suggested that secondary loss of the interoperculum was an apomorphy of the ginglymodian crown (Olsen, 1984; Olsen & McCune, 1991). A recent survey of fossil gars by Grande (2010) has supported this hypothesis with evidence for an interoperculum, and a mobile maxilla, in the Mesozoic gar *Obaichthys* and other fossil taxa. A cladistic analysis (Grande, 2010) based on this information, involving re-examination of all extinct and extant fossil Ginglymodi, ‘resurrected’ the Holostei based on the following characters: median rostral reduced to a tube, fusion between the occipital condyle and first two vertebrae, loss of the pterotic, a paired vomer, a compound coronoid process (i.e. made of multiple bones), a supra-angular bone (thought by Grande, 2010, to be a potential neopterygian character, but listed as actinopteran trait elsewhere: Patterson, 1982, and Gardiner & Schaeffer, 1989), paired and median neural spines in the tail (as opposed to just median spines in teleosts; Patterson, 1973), dichotomization of all caudal lepidotrichia (alternatively a neopterygian trait lost in teleosts; Grande, 2010), fringing fulcra on the upper and lower caudal fins [another possible neopterygian, or even actinopteran, trait lost in teleosts, see Sections II(2–4); Grande, 2010], anterior and posterior clavicle remnants, four hypobranchials, a premaxilla bearing a nasal process sutured to the frontals and a dermal sphenotic. Holostei have been recovered in a follow-up study (Xu & Wu, 2011) that coded further early ginglymorph and stem-neopterygian taxa for many of Grande’s (2010) characters. However, Neopterygii were collapsed to a trichotomy in a subsequent analysis containing extra ginglymodian fossils but the same characters (Xu & Gao, 2011). A previous analysis by Cavin & Suteethorn (2006), focusing on many of the same Mesozoic taxa as these other studies, had reached this result even before Grande’s (2010) challenge to the halecostome consensus.

Hurley *et al.* (2007) independently found support for the Holostei in an analysis that included many of the same extinct relatives used by Grande (2010) and others, as well as the earliest fossil to be attributed to the

Halecomorpha in that study, *Brachydegma* from the Permian of Texas, and the earliest fossil interpreted as having an *Amia*-teleost-style interoperculum, the designated stem-neopterygian *Discoserra* from the Mississippian of Montana. There, Holostei was supported by a combination of three non-unique character states rather than the assortment of synapomorphies in Grande's (2010) holostean-specific study: a tapering antorbital with the slender anterior process and a triradiate canal, a short, tubular rostral (as in Grande, 2010), and an optic tectum not larger than the telencephalon (Hurley *et al.*, 2007). Because of the homoplastic nature of these traits, it is perhaps not surprising that a simultaneous morphological analysis of only extant taxa, based on the same coding, recovered a Halecostomi clade (Hurley *et al.*, 2007). These mixed results suggest, as in Grande's (2010) study, that some of the confusion about neopterygian interrelationships stems from a lack of appropriate and necessary information about character states in fossil fishes.

A Bayesian analysis of nuclear sequence data also performed by Hurley *et al.* (2007) rejected the Holostei, with an *Amia*-teleost clade receiving minimal support (posterior probability 51; Hurley *et al.*, 2007). However, at time of writing, this represents the only molecular analysis to recover separate ginglymodian and halecostome clades. Nearly all other molecular studies undertaken since the beginning of such analyses have overwhelmingly supported a monophyletic Holostei, often with strong bootstrap values and posterior probabilities (e.g. Normark, McCune & Harrison, 1991; Noack *et al.*, 1996; Zardoya & Meyer, 2001; Meyer & Zardoya, 2003; Kikugawa *et al.*, 2004; Crow *et al.*, 2006; Azuma *et al.*, 2008; Inoue *et al.*, 2009; Santini *et al.*, 2009; Setiamarga *et al.*, 2009; Near *et al.*, 2012; Betancur-R *et al.*, 2013; Broughton *et al.*, 2013; Faircloth *et al.*, 2013; Rabosky *et al.*, 2013; also reviewed in Grande, 2010, p. 803). This includes all studies favouring the AFC over the Neopterygii (Lecointre *et al.*, 1994; Inoue *et al.*, 2001, 2003, 2005, 2010; Venkatesh *et al.*, 2001; Near & Miya, 2009) and many recovering alternative placements of Polypteriformes (Steinke *et al.*, 2006; Li *et al.*, 2008; Raincrow *et al.*, 2011), suggesting very strong signal. This overwhelming consensus among molecular trees, as opposed to the uncertainty which remains in morphological surveys, may be because the split between the Ginglymodi and Halecomorpha is significantly more recent than their divergence with Teleostei, as some relaxed molecular clocks seem to suggest [e.g. Cretaceous *versus* Triassic in Santini *et al.*, 2009; Permian *versus* Mississippian in Broughton *et al.*, 2013, see Section III(1); Table 1]. Alternatively, greater sequence change occurs along the common holostean branch than along the terminal branches, as some scaled molecular trees indicate (e.g. Inoue *et al.*, 2003, 2009). Thus, long-branch attraction and/or convergence in sequences cannot overwhelm the holostean signal or otherwise induce the same uncertainty found in the morphological data.

It appears likely that Holostei do comprise a true clade, and that further morphological investigation will bear this out. However, a monophyletic Halecostomi still has a longer

history of cladistic support compared with the Holostei, and so further morphological analyses will be required to determine the sequence of character-state changes particular to the holosteans and more exact diagnoses for the earliest members of the clade (Grande, 2010; Lopez-Arbarello, 2012). Grande (2010, p. 805) asserted that previous morphological support for the Halecostomi was caused, at least in part, by confirmation bias among workers following on Patterson (1973) and using his characters. Lopez-Arbarello (2012) further suggested that a halecostome topology was in many cases caused by incorrect assumptions of polarity and homology from overdependence on character states in living representatives of Teleostei and Ginglymodi relative to fossil taxa. Alternatively, it is possible that *Amia* and teleosts do share a greater number of characteristics, but this similarity is due to greater retention of primitive neopterygian states in those lineages relative to living Ginglymodi (Grande, 2010), or extensive parallelism driven by shared selective pressures (Patterson, 1973; Abouheif, 2008), rather than a sister-group relationship. More work on fossil taxa will be needed to settle this disjunct between the strong molecular and weak morphological signals.

#### (4) Defining the Teleostei

Implicit in the cladistic halecostome/holostean controversy is the existence of a monophyletic Teleostei. However, character-based definitions for the crown clade remain sparse and conflicting because of the broad diversity of living forms (Nelson, 2006; Fig. 1) and uncertainties surrounding the identity of living and fossil sister taxa (see Nelson, 1969*b*; Arratia, 2001). Many classification schemes, such as Berg (1940); Greenwood *et al.* (1966); Nelson (1969*b*); Greenwood, Miles & Patterson (1973) and Grande (2010), simply do not diagnose the Teleostei even when discussing the relationships of defined teleost subgroups. Patterson (1977) performed the first cladistic analysis of living and Mesozoic teleosts, which defined crown Teleostei on the basis of a caudal skeleton bearing uroneurals and seven epurals, mobile premaxillae separated by the rostral, a parasphenoid bearing a foramen for the internal carotid and fusion between the propterygium and primary pectoral lepidotrichium (a modification of the actinopteran association between these structures; Patterson, 1982). However, subsequent analyses have not reached a consensus about this list of traits and their exact appearance along the stem. Arratia (1999) found just one unique synapomorphy of the crown: a quadrate with a 'long' posteroventral process. However, a follow-up study by the same author (Arratia, 2000) recovered this as characteristic of the total group, alongside propterygial fusion and a mobile premaxilla, while the crown was delineated by the presence of three epibranchials and a craniotemporal muscle (the latter not directly observable in fossils). Hurley *et al.* (2007), in an analysis focusing on neopterygian patterns rather than teleost interrelationships, recovered yet another distinct osteological synapomorphy for the crown: an intercalary with 'extensive' membranous outgrowths lateral to the jugular. This is a positional modification of a character found by Gardiner



Table 1. Mean divergence date estimates from molecular clock studies

Crown node	Faircloth <i>et al.</i> (2013) <sup>a</sup>	Betancur-R. <i>et al.</i> (2013)	Broughton <i>et al.</i> (2013)	Near <i>et al.</i> (2012)	M. Chen <i>et al.</i> (2012a) <sup>b</sup>
Osteichthyes	NA	425 (~440–420)	427 (~440–420)	NA	424 (386–466)
Actinopterygii	420	383 (~390–380)	384 (~390–370)	405 (383–434)	331 (277–386)
Actinopteri	367	350 (~385–320)	355 (~390–325)	398 (363–428)	NA
Polypter.	NA	NA	39 (~70–10)	11 (6–16)	NA
Chondrostei	327	NA	133 (~150–130)	NA	NA
Neopterygii	361	323 (~355–290)	328 (~365–310)	361 (332–394)	NA
Holostei	296	268 (~295–245)	269 (~300–245)	271 (248–312)	NA
Teleostei	269	283 (~315–260)	284 (~320–250)	307 (286–333)	179 <sup>c</sup> (129–226)
<b>Crown node</b>	Saitoh <i>et al.</i> (2011)	Alfaro <i>et al.</i> (2009)	Santini <i>et al.</i> (2009)	Inoue <i>et al.</i> (2009) <sup>b, d</sup>	Setiamarga <i>et al.</i> (2009)
Osteichthyes	436 (420–458)	428 (418–463)	423 (418–435)	437 (420–460)	428 (419–442)
Actinopterygii	405 (393–418)	298 (284–362)	299 (284–337)	407 (393–418)	~410 (400–420)
Actinopteri	377 (358–391)	270 (238–321)	271 (244–302)	365 (318–362)	~380 (370–395)
Polypter.	57 (44–73)	NA	NA	~65 (50–80)	~75 (55–95)
Chondrostei	192 (147–235)	~100 (20–195)	~85 (28–155)	~175 (140–220)	~210 (170–250)
Neopterygii	355 (333–373)	231 (225–268)	230 (225–243)	340 (318–362)	364 (346–378)
Holostei	NA	NA	~130 (40–237)	~315 (295–350)	~345 (320–365)
Teleostei	317 (295–337)	204 (179–230)	193 (173–214)	295 (272–319)	289 (269–310)
<b>Crown node</b>	Azuma <i>et al.</i> (2008) <sup>b, e</sup>	Hurley <i>et al.</i> (2007) <sup>b</sup>	Yamanoue <i>et al.</i> (2006) <sup>f</sup>	Inoue <i>et al.</i> (2005) <sup>f</sup>	<b>Range of means</b>
Osteichthyes	428 (417–448)	Not reported	470 (415–524)	451 (413–494)	423–500
Actinopterygii	~417 (395–430)	436 (398–483)	NA	415 (374–448)	298–436
Actinopteri	~380 (360–395)	367 (346–390)	NA	376 (337–413)	270–398
Polypter.	~80 (70–90)	90 (68–117)	NA	68 (54–85)	11–90
Chondrostei	~210 (165–260)	217 (176–257)	NA	145 (108–186)	~100–355
Neopterygii	360 (339–376)	349 (324–377)	390 (340–442)	NA (AFC)	230–390
Holostei	~340 (315–420)	328 (299–358)	NA	NA'	~130–~345
Teleostei	~320 (300–345)	300 (271–329)	NA	334 (295–372)	179 <sup>c</sup> –334

Dates in million years ago (Ma), rounded to nearest whole million years (My).

Dates marked ~ are estimated from published figures where exact dates are not reported.

Dates in parentheses are 95% confidence intervals as reported by original authors.

AFC, Ancient Fish Clade topology; NA, not available.

<sup>a</sup>Dates from pre-publication Arkiv version.

<sup>b</sup>Dates from topology containing Holostei and/or Neopterygii.

<sup>c</sup>Date based on split between *Medaka* and *Takifugu*, not origin of crown Teleostei.

<sup>d</sup>Dates using 12tr<sub>n</sub> dataset.

<sup>e</sup>Dates from analysis without biogeographic constraints on cichlid divergences.

<sup>f</sup>Dates from dataset 2 containing all nuclear sequences and RNA.

(1984) to define the Neopterygii. However, Hurley *et al.* (2007) found five additional unique traits defining various levels within total group Teleostei, all previously used for the crown in those other studies mentioned above.

Despite the difficulties in defining teleosts morphologically, all molecular studies support a monophyletic living Teleostei (e.g. Inoue *et al.*, 2001, 2003, 2005, 2009; Venkatesh *et al.*, 2001; Yamanoue *et al.*, 2006; Hurley *et al.*, 2007; Azuma *et al.*, 2008; Santini *et al.*, 2009; Setiamarga *et al.*, 2009; Saitoh *et al.*, 2011; Near *et al.*, 2012; Chen *et al.*, 2012b; Betancur-R *et al.*, 2013; Broughton *et al.*, 2013; Faircloth *et al.*, 2013; Rabosky *et al.*, 2013). In such studies, crown teleost monophyly is strongly supported by a whole-genome duplication event along their stem (Amores *et al.*, 1998; Hoegg *et al.*, 2004; Crow *et al.*, 2006; Hurley *et al.*, 2007; Santini *et al.*, 2009; Inoue *et al.*, 2010). It is possible that this characteristic of the teleost crown might have biased support for the Holostei over the Halecostomi (or other options) and an AFC over

a Neopterygii in some previous studies, as noted briefly in the previous section. That is, the relaxation of selective constraint inherent in having built-in redundancy could have led to increased molecular differentiation and rates of sequence change in the individual copies of teleost genes. This would obscure close relationships with other actinopterygian lineages which lack this material. In nuclear studies based on fewer genes, this might result in a holostean clade containing those neopterygians (Ginglymodi; Halecomorphi), or AFC clade containing those actinopterygians, which retain a version of the sequence similar to that present in the last common ancestor of total group teleosts, but is not intact in any living member of the crown clade. Such a possibility bears further exploration. One solution would be to compare neopterygian sequences *a priori* to sequences related to genes exhibiting the least amount of change or retaining ancestral function, and only use such data from around such ultraconserved elements (UCEs) in future molecular phylogenies. Indeed, a

recent analysis by Faircloth *et al.* (2013) has done exactly this, using UCEs and associated sequences, many of which are not expressed, to recover the Polypteriformes (Chondrostei (Holostei + Teleostei)) topology presented in Fig. 1.

These kinds of considerations may serve some role in resolving the remaining conflicts between molecular and morphological analyses discussed above. With their greater sampling of characters (e.g. base pairs: Wiley *et al.*, 2011; Chakrabarty, 2010), phylogenetic hypotheses derived from large molecular datasets are more likely to be reflective of the real divergence patterns than those derived from smaller morphological matrices. Morphological phylogenies may be impacted by homoplasy induced by the common physical demands of shared ecological roles [see Section III(5–6)] to a greater extent than molecular studies are affected by convergence or overwriting of base-pair changes. More thorough, targeted morphological surveys are likely required to bring group definitions and cladistic outcomes in line with the overwhelming support for a consensus topology presented by molecular systematics. However, as shown above, molecular topologies produced by different workers often conflict [compare Near *et al.* (2012) and Betancur-R *et al.* (2013), and the AFC with neopterygian solutions]. In such cases, morphological characters, and potential synapomorphies, can be used in a total evidence approach to select among the different options, favouring solutions that can be best supported by fossil and living forms. Such synapomorphies are required to estimate divergence dates, as calibration fossils cannot be identified accurately without them. Greater sampling of calibration fossils belonging to crown groups tends to lead to better agreement between estimated divergence dates and fossil first appearances (e.g. various acanthomorph clades in Near *et al.*, 2013), while estimates for parts of the tree and time intervals with few calibrated nodes (e.g. the basic divergences in Fig. 1 which took place in the Palaeozoic–early Mesozoic) tend to be very discordant with both the fossil record and other sets of estimated dates [see Section III(1–2) and Table 1], obscuring the exact conditions surrounding the origins of major groups.

### III. SOURCES OF UNCERTAINTY IN THE ORIGINS OF MODERN GROUPS AND FORMS

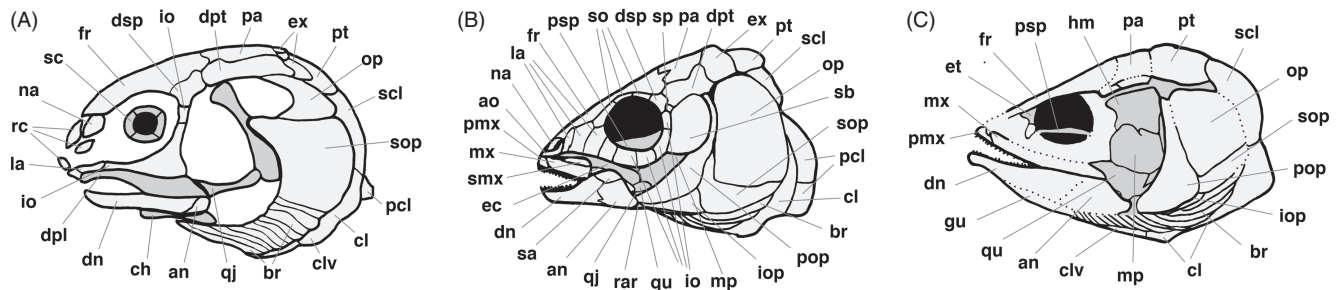
#### (1) Hypotheses of actinopterygian diversification and dominance

The basic topology in Fig. 1 might suggest that the Polypteriformes, Chondrostei, Holostei and Teleostei make nearly equal contributions to modern actinopterygian biodiversity. However, the genera counts and exemplar taxa in the same figure tell a different story. Teleosts comprise more than 99% of Recent actinopterygian taxonomic and ecomorphological diversity (Nelson, 2006). Non-teleosts are represented by a handful of genera which might be termed ‘living fossils’, lineages possessed of relatively homogeneous and long-extant morphologies and limited to a few primarily freshwater habitats (Nelson, 2006; Wright, David & Near, 2012; Rabosky

*et al.*, 2013; Figs 1 and 2). As a result, actinopterygian biodiversity has become synonymous with teleosts, and thus most hypotheses as to the origins and causes of ray-finned fish dominance deal only with that group and its component clades [e.g. marine diversity in Carrete, Vega & Wiens (2012); coral reef diversity in Bellwood (2003); body size and morphological diversity in Alfaro *et al.* (2009) and Santini *et al.* (2009); taxonomic divergence in Near *et al.* (2012, 2013)].

One widespread narrative for the success of living actinopterygians implicates the aforementioned whole-genome duplication event on the teleost stem (Amores *et al.*, 1998; Taylor *et al.*, 2001; Hoegg *et al.*, 2004; Crow *et al.*, 2006; Santini *et al.*, 2009; Inoue *et al.*, 2010). Many ichthyologists have proposed that this additional genetic material allowed greater variation and thus increased disparity and diversification. This new potential, alongside neopterygian/halecostome/teleost specializations of the jaw and fins (e.g. homocercal tails, mobile maxillae; Schaeffer & Rosen, 1961; Lauder, 1982; Lauder & Liem, 1983; Lopez-Arbarello, 2012; Fig. 2), is said to have permitted the production of new body forms and ecologies. Many of the niche-related ecomorphologies widespread among teleosts are likewise hypothesized to be unavailable to ‘ganoid’ bearing fishes (e.g. maneuverable deep-bodied forms; Goatley, Bellwood & Bellwood, 2010; herbivorous feeders; Bellwood, 2003) or, somewhat alternatively, non-neopterygians (feeding niches; Schaeffer & Rosen, 1961; Lauder, 1982; Lauder & Liem, 1983; Lopez-Arbarello, 2012). However, it should be noted that living chondrosteans, which have both mobile jaws and scaleless bodies (Hilton & Forey, 2011), underwent their own, lineage-specific whole-genome duplication events in the Cenozoic (Crow *et al.*, 2012). Yet these non-teleosts are represented by just six living genera and two general ecotypes (benthic sturgeons and filter-feeding paddlefishes), which date back tens of millions of years before the appearance of additional gene sets (Hilton & Forey, 2011; Crow *et al.*, 2012; Fig. 1).

The signature of heightened actinopterygian diversity is thought to be evident in the ‘Mesozoic Marine Revolution’ (Vermeij, 1977), in which increased marine invertebrate complexity has been linked to the supposed first appearance of durophagous fishes in the later Jurassic and Cretaceous (Brett & Walker, 2002; Stanley, 2007, 2008), with novel morphologies centered in the emergent new teleost clade (Bellwood, 2003). Most living teleost groups first appear in the fossil record around this time (Patterson, 1993; Sepkoski, 2002; Santini *et al.*, 2009; Friedman & Sallan, 2012; Near *et al.*, 2012, 2013), just after occurrence of the potential earliest known crown teleost, the Jurassic *Elopsomolus* (Arratia, 2000; Hurley *et al.*, 2007; Fig. 4C). The oldest known members of the Polypteriformes are found in Cretaceous sediments (Duthiel, 1999; Grandstaff *et al.*, 2012) as are the earliest crown Ginglymodi (Grande, 2010). The earliest acipenseriform chondrosteans are Jurassic (Hurley *et al.*, 2007; Hilton & Forey, 2011; Fig. 4A), while the earliest stem-Ginglymodi are late Triassic in age (Olsen, 1984; Fig. 4B). These first appearances give the impression that



**Fig. 4.** Early members of living actinopterygian clades. (A) The Jurassic acipenseriform chondrosteian *Chondrosteus* (after Gardiner & Schaeffer, 1989; Hilton & Forey, 2011). (B) The Jurassic ginglymodian holostean *Semionotus* (after Olsen & McCune, 1991). (C) The Jurassic elopimorph teleost *Elopsomolos* (after Arratia, 2000). Abbreviations: an, angular; ao, antorbital; br, branchiostegal ray; ch, ceratohyal; cl, cleithrum; clv, clavicle; dn, dentary; dpl, dermopalatine; dpt, dermopterotic; dsp, dermosphenotic; ec, ectopterygoid; et, ethmoid; ex, extrascapular; fr, frontal; gu, gular; hm, hyomandibula; io, infraorbital or jugal; iop, interoperculum; la, lachrymal; mp, metapterygoid; mx, maxilla; na, nasal; op, operculum; pa, parietal; pcl, postcleithrum; pmx, premaxilla; pop, preoperculum; psp, parasphenoid; pt, posttemporal; qj, quadratojugal; qu, quadrate; rar, retroarticular; rc, rostral cartilage; sa, supra-angular; sb, suborbital; sc, sclerotic plate; scl, supracleithrum; smx, supramaxilla; so, supraorbital; sp, sphenotic; sop, suboperculum.

actinopterygians were insignificant components of earlier Mesozoic and Palaeozoic vertebrate biotas, particularly in macroevolutionary studies based on Recent taxa (Inoue *et al.*, 2003; Alfaro *et al.*, 2009; Santini *et al.*, 2009; Carrete, Vega & Wiens, 2012), or that there is a ‘gap’ in the records of modern groups (Near *et al.*, 2012; Table 1). Such conclusions ignore the extensive, well-sampled fossil record of actinopterygians, stretching back nearly 400 million years (Ma) (Gardiner, 1993; Friedman & Sallan, 2012), and the implications of cladistic studies involving fossil taxa, as discussed below.

Recent time-calibrated molecular and fossil-based morphological phylogenies (e.g. Gardiner & Schaeffer, 1989; Coates, 1998, 1999; Gardiner *et al.*, 2005; Inoue *et al.*, 2005, 2009, 2010; Hurley *et al.*, 2007; Near & Miya, 2009; Santini *et al.*, 2009; Near *et al.*, 2012, 2013; Chen *et al.*, 2012b; Broughton *et al.*, 2013; Betancur-R *et al.*, 2013; Fig. 1; Table 1) have pushed many deep actinopterygian branching events back to the Palaeozoic from their previous Mesozoic timepoints. These pre-cladistic Mesozoic dates were based primarily on spindle diagrams and phenetic similarities (e.g. Agassiz, 1833–1844; Schaeffer, 1955; Gardiner, 1967a) as well as first appearances and diversity in the record (e.g. Sepkoski, 2002; Bellwood, 2003). Relaxed molecular clock studies have reconstructed dates for the actinopterygian–polypteriform split ranging from a low mean of 298 Ma (Permian–Carboniferous boundary; Alfaro *et al.*, 2009: origin of crown Actinopterygii; all stage ages from Gradstein *et al.*, 2012) to a high mean of 436 Ma (early Silurian; Hurley *et al.*, 2007; Table 1). The chondrosteian–neopterygian divergence date has a low mean estimate of 270 Ma (early-mid Permian; Santini *et al.*, 2009: origin of crown Actinopteri) and a high mean estimate of around 398 Ma (early Devonian; Near *et al.*, 2012; Table 1). Mean dates for the origin of crown Chondrostei span from around 100 Ma (mid Cretaceous; Santini *et al.*, 2009) to 355 Ma (middle Mississippian; Saitoh *et al.*, 2011; Table 1). The Holostei–Teleostei divergence has been assigned dates

ranging from a mean age of 230 Ma (middle Triassic; Santini *et al.*, 2009: origin of crown Neopterygii; Table 1) to a mean age of 390 Ma (middle Devonian; Yamanoue *et al.*, 2006; Table 1). Crown Holostei (or Halecostomi) has been assigned mean origination dates spanning from around 130 Ma (early Cretaceous; Santini *et al.*, 2009; Table 1) to various Mississippian dates (around 345 Ma for uncalibrated Holostei in Setiamarga *et al.*, 2009; 328 Ma for calibrated Holostei and 344 Ma for calibrated Halecostomi in Hurley *et al.*, 2007; Table 1). Crown Teleostei has been given mean origination dates spanning from 179 Ma (early Jurassic; Chen *et al.*, 2012b) to 334 Ma (middle Mississippian; Inoue *et al.*, 2005). The former date is in line with the age of the earliest known crown taxa (i.e. *Elopsomolos*; Fig. 4C), while earlier dates produce anomalies in the narrative of teleost evolution, as discussed below.

Molecular clock divergence dates, whether or not they allow for variable rates, are influenced by choice of models (Inoue *et al.*, 2010), inclusion of taxa, consensus topology and especially the use and designation of fossil-based calibration points. The distribution, age, and attribution of calibration taxa from the fossil record contributes to the differences in the divergence date estimates listed above. Younger dates often come from studies where the oldest crown-group fossil used in calibrations is Mesozoic: for example, the Permian *Brachydegma* is assigned as a stem-neopterygian in Santini *et al.* (2009) rather than a crown holostean as in Hurley *et al.* (2007). However, Near *et al.* (2012); Betancur-R *et al.* (2013) and Broughton *et al.* (2013) found older dates while similarly reassigning that taxon. Younger dates are also recovered where fossils were not assigned to the relevant node, such as the origin of crown Chondrostei in Santini *et al.* (2009), where the mean divergence date is ~100 million years (My) later than the earliest appearance of Acipenseriformes in the fossil record (Hilton & Forey, 2011). Older divergence dates tend to appear in analyses that assign earlier fossils to shallower branching points and/or use extinct taxa as terminals. Examples include the use of Permian *Brachydegma*

as a halecomorph or crown holostean in Hurley *et al.* (2007), placement of the Mississippian *Discoserra* as sister taxon to the crown Neopterygii in the same study and Near *et al.* (2012), and, previously, AFC and other alternative topologies in which clades are reconstructed to diverge more deeply in the tree (see the Mississippian date for crown teleosts in the AFC tree of Inoue *et al.*, 2005; Table 1).

The very oldest divergence dates generally appear in situations where few non-teleosts are used as terminals or in calibrations, so that the analysis attributes great expanses of time to just a few branches (e.g. Yamanoue *et al.*, 2006; Near *et al.*, 2013; Table 1). This might represent the same phenomenon that causes reported ranges for divergence dates of uncalibrated nodes to be much broader than those anchored by fossil taxa (e.g. a range of ~40 My for a calibrated crown Teleostei node *versus* a range of ~200 My for the uncalibrated crown Holostei in Santini *et al.*, 2009). Such uncertainty renders the divergence dates nearly useless for generating and testing macroevolutionary hypotheses. For, example, a 95% confidence interval of early Mississippian to late Cretaceous for the origin of crown Dipnoi (lungfishes) in Santini *et al.* (2009) spans two geological eras and multiple mass extinction events (Bambach, 2006). As shown in Table 1, disagreement between rate-variable molecular clock analyses based on different fossil calibration sets and trees can result in a similarly large range of mean dates available for hypotheses. Therefore, resolving the interrelationships between fossil and living taxa, and particularly the status of the former as stem or crown members of various clades, is essential for understanding the origins of actinopterygian biodiversity.

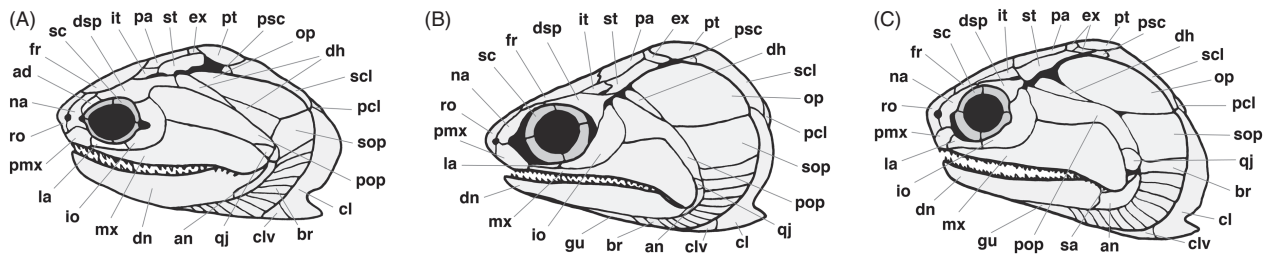
On the whole, origination dates reconstructed from recent phylogenies (Table 1) suggest that the crown groups of all major living actinopterygian divisions, such as the Chondrostei and Teleostei (Fig. 1), existed by the mid-late Palaeozoic, long before their apparent Mesozoic ‘triumph’ and diversification (see Bellwood, 2003) or diagnosable morphological differentiation from other lineages (see fossils listed in Patterson, 1993; Hurley *et al.*, 2007; Santini *et al.*, 2009; Grandstaff *et al.*, 2012). However, these reconstructed divergence dates leave gaps of tens of millions of years and multiple geological periods between the likely origination of the basic actinopterygian divisions and the appearance of crown taxa in the record (see above; Hurley *et al.*, 2007; Grande, 2010; Hilton & Forey, 2011; Grandstaff *et al.*, 2012; Lopez-Arbarello, 2012). Near *et al.* (2012) recently coined the term ‘Teleost gap’ to describe this long-running date discrepancy. The gap has been attributed to fossil sampling issues in the later Palaeozoic and early Mesozoic (Near *et al.*, 2012; Broughton *et al.*, 2013). However, it is important to note that articulated actinopterygian fossils belonging to the stems, if not the crowns, of other groups and more inclusive clades are found in appropriately aged sediments, as discussed in the next sections [Section III(2–5); Gardiner, 1993; Sepkoski, 2002; Sallan & Coates, 2010; Friedman & Sallan, 2012; Broughton *et al.*, 2013]. In any case, Palaeozoic divergences imply that the teleost-specific whole-genome duplication took place long before observed ‘exceptional’

ecomorphological diversification, a phenomenon associated primarily with the Mesozoic-originating clades Ostariophysii and Acanthomorpha in any case (Hurley *et al.*, 2007; Alfaro *et al.*, 2009; Santini *et al.*, 2009; Near *et al.*, 2012, 2013; Broughton *et al.*, 2013; Rabosky *et al.*, 2013).

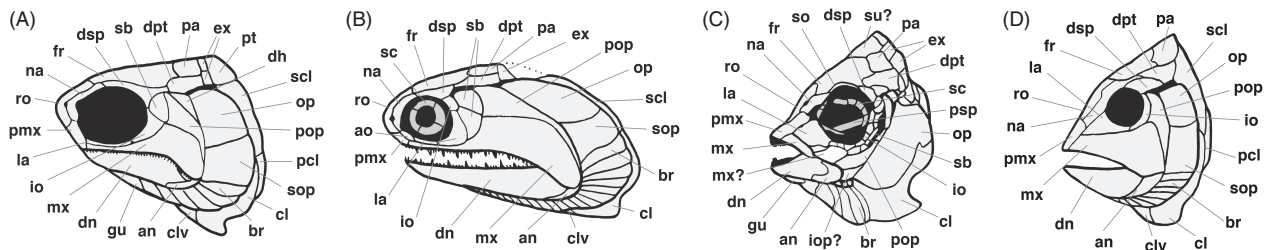
## (2) Divergence dates and the Palaeozoic fossil record

Actinopterygians first appeared in the mid-Palaeozoic, and became very diverse later in the era. The earliest definitive total-group sarcopterygians, the stem-genera *Psarolepis* and *Guiyu* (Zhu, Yu & Janvier, 1999; Zhu *et al.*, 2009), appear in late Silurian sediments of China, setting a minimum date of 420 Ma for the origin of total group Actinopterygii and capping an increasing number of likely osteichthyan remains in later Silurian deposits (Marss, 2001; Botella *et al.*, 2007; Friedman & Brazeau, 2010; Friedman & Sallan, 2012). Presumed Late Silurian and Early Devonian stem-actinopterygian taxa have been named on the basis of ichthyoliths (isolated scales and bones; e.g. *Naxilepis*, *Andreolepis*, *Lingulalepis*, *Dialipina* and *Orvikuina*; Gross, 1968; Schultze, 1968; Wang & Dong, 1989; Marss, 2001) and/or articulated material (e.g. *Dialipina* and *Lingulalepis*; Schultze, 1968; Taverner, 1997; Basden *et al.*, 2000; Schultze & Cumbaa, 2001). The available material exhibits few of the diagnostic characters for total group Actinopterygii, and thus have been hypothesized and/or phylogenetically reconstructed to represent stem-osteichthyans (Basden *et al.*, 2000; Friedman & Blom, 2006; Botella *et al.*, 2007; Swartz, 2009; Friedman & Brazeau, 2010). However, seemingly chimaeric and incompletely diagnostic morphologies may be allowable or even expected in basally branching stem members of any group, so true assignment will require further material and phylogenetic analyses (Friedman & Brazeau, 2010; Davis, Finarelli & Coates, 2012). For example, while scales with pegs and ganoine may be symplesiomorphic for Actinopterygii (Friedman & Brazeau, 2010), the presence of basal fulcra lining the axial lobe – a trait described for the Silurian taxon *Andreolepis* (Chen *et al.*, 2012a) – remains indicative of total group affinity (Patterson, 1982; Gardiner, 1984).

The classic earliest known actinopterygian, *Cheirolepis* (Fig. 5A), appears in Orcadian Lake sediments dating to the Eifelian–Givetian stage boundary, at the midpoint of the Devonian (~387 Ma; Agassiz, 1833–1844; Arratia & Cloutier, 1996; Dineley & Metcalfe, 1999). This suggests an as-yet unexplained lag of around 30 My between the minimum origin of the Actinopterygii and their definitive appearance in the record, initial diversification and/or acquisition of most diagnostic characters. In the later Devonian, actinopterygians are represented by just a dozen fusiform genera and ichthyoliths known from throughout the world (Gardiner, 1993; Arratia & Cloutier, 1996; Swartz, 2009; Sallan & Coates, 2010; Choo, 2011; Fig. 5). However, ray-finned fish diversity was more than an order of magnitude higher in the subsequent Mississippian period (359 to 323 Ma; Gardiner, 1993; Sallan & Coates, 2010).



**Fig. 5.** Devonian actinopterygians. (A) *Cheirolepis* (after Pearson, 1982; Gardiner & Schaeffer, 1989; Arratia & Cloutier, 1996). (B) *Mimipiscis* (after Choo, 2011). (C) *Moythomasia* (after Gardiner, 1984). Abbreviations: ad, adorbital; an, angular; br, branchiostegal ray; cl, cleithrum; clv, clavicle; dh, dermohyal; dn, dentary; dsp, dermosphenotic; ex, extrascapular; fr, frontal; gu, gular; io, infraorbital or jugal; it, intertemporal; la, lachrymal; mx, maxilla; na, nasal; op, operculum; pa, parietal; pcl, postcleithrum; pmx, premaxilla; pop, preoperculum; psc, prescapular; psp, parasphenoid; pt, posttemporal; qj, quadratojugal; ro, rostral; sa, supra-angular; sc, sclerotic plate; scl, supracleithrum; sop, suboperculum, st, supratemporal.



**Fig. 6.** Mississippian actinopterygians. (A) *Mesopoma* (after Coates, 1993). (B) *Nematoptychius* (after Dineley & Metcalfe, 1999). (C) *Discoserra* (after Lund, 2000; Hurley *et al.*, 2007). (D) *Amphicentrum* (after Coates, 1988). Abbreviations: an, angular; ao, antorbital; br, branchiostegal ray; cl, cleithrum; clv, clavicle; dh, dermohyal; dn, dentary; dpt, dermopterotic; dsp, dermosphenotic; ex, extrascapular; fr, frontal; gu, gular; hm, hyomandibula; io, infraorbital or jugal; iop, interoperculum; la, lachrymal; mx, maxilla; na, nasal; op, operculum; pa, parietal; pcl, postcleithrum; pmx, premaxilla; pop, preoperculum; psp, parasphenoid; pt, posttemporal; ro, rostral; sb, suborbital; sc, sclerotic plate; scl, supracleithrum; so, supraorbital; sop, suboperculum, su, supraoccipital.

### (3) The ‘paleoniscoid’ problem

The diverse record of Mississippian and later Palaeozoic actinopterygians (see above; Fig. 6) has been relatively neglected by palaeoichthyologists, to the point that sampling problems can be hypothesized [as Section III(1); Near *et al.*, 2012; Broughton *et al.*, 2013] despite an abundance of specimens in death assemblages and the ichthyolith record. This oversight is evident through comparison to other less abundant and varied vertebrates in the same faunas and Triassic actinopterygians with similar ecomorphologies (e.g. deep-bodied Bobasatiriformes, the fusiform Redfieldiidae and *Pteronisculus*; Nielsen, 1942; Moy-Thomas & Miles, 1971; Gardiner & Schaeffer, 1989), as scans of recent textbooks, the literature and even museum displays will show (Moy-Thomas & Miles, 1971; Carroll, 1988; Long, 1995, 2011; Janvier, 1996; Maisey, 1996; Dineley & Metcalfe, 1999; Benton, 2005; L. C. Sallan, personal observation). Many of the Permo-Carboniferous fishes were last described over 50 years ago, and then only briefly in surveys of specific faunas (e.g. Traquair, 1881; White, 1927; Moy-Thomas & Bradley Dyne, 1938; Gardiner, 1985), whereas in-depth and/or monographic treatment has been given to nearly all Devonian actinopterygians (e.g. Pearson & Westoll, 1979; Gardiner, 1984; Long, 1988; Arratia & Cloutier, 1996; Taverne, 1997; Swartz, 2009), a number of early Mesozoic non-teleost fishes thought to fall on the stems of living clades

(e.g. the Triassic *Pteronisculus* in Nielsen, 1942; early ginglymorphs in Grande, 2010; the acipenseriform chondrostean *Chondrosteus* in Hilton & Forey, 2011), and many other Palaeozoic vertebrates (e.g. *Acanthostega* in Coates, 1996). As a result, the diverse Mississippian–Permian actinopterygian biota and its characteristics are given only brief mentions in many textbooks of vertebrate palaeontology and popular works on fossil fishes, often grouped with Devonian taxa despite greater taxonomic and morphological diversity and/or overshadowed by later, yet similar, forms (Moy-Thomas & Miles, 1971; Carroll, 1988; Gardiner, 1993; Janvier, 1996; Maisey, 1996; Benton, 2005; Long, 2011).

Most Palaeozoic actinopterygians have long been referred to the wastebasket grade ‘Palaeoniscoidea’/‘Palaeonisciformes,’ (see discussions in Watson, 1925; Berg, 1940; Schaeffer, 1955; Berg, Kazantseva & Obruchev, 1967; Moy-Thomas & Miles, 1971; Gardiner & Schaeffer, 1989; Gardiner, 1993; Gardiner *et al.*, 2005), representing the supposed basal condition of ray-finned fishes (Watson, 1925; Berg, 1940). This group was allied with a ‘chondrostean’ grade [as noted in Section II(2)] before the advent of cladistic methods (Traquair, 1887) and was alternatively thought to transition into a ‘subholostean’ or ‘holostean’ grade of actinopterygian evolution in the Mesozoic (Schaeffer, 1955) or give rise to all living lineages (Watson, 1925; Gardiner, 1967a). Watson (1925, 1928) defined Palaeoniscidae as a natural group based on many characters of the neurocranium

and jaw shared by *Cheirolepis*, *Elonichthys* and a few other taxa. Berg (1940) elevated this group to an order, Palaeonisciformes, on the level of the Holostei or Teleostei (which he considered grades) based on the following skeletal characteristics: a myodome (an actinopteran character in Patterson, 1982), a basiptyergoid process, a persistent notochord in the spine (i.e., lack of vertebral centra), an absence of ribs, ganoid scales on the axial lobe, ganoine ornament on the skull, fringing fulcra (another actinopteran trait; Patterson, 1982), branchiostegal rays and a single dorsal fin. This was divided into two suborders: a Palaeoniscoidei with ganoid scales and generally fusiform bodies and a Platysomoidei, consisting of all Palaeozoic deep-bodied taxa incorrectly thought to lack ganoine (see Traquair, 1879; Mickle & Bader, 2009). The two Palaeozoic taxa assigned outside the Palaeonisciformes, the eel-like *Tarrasius* and the enigmatic long-snouted *Phanerorhynchus*, were placed within their own orders defined by their divergent body and fin forms (Berg, 1940).

In subsequent years, platysomoids were also promoted to an order, the Platysomiformes (Moy-Thomas & Miles, 1971). However, just as few clades are found in multiple phylogenies, few new stable multi-generic taxonomic ranks (e.g. families, subclasses) have been erected for Devonian–Permian ‘palaeoniscoids.’ While all recent descriptions have dropped official attribution to this grade, most only make reference to their actinopterygian status (e.g. Mickle & Bader, 2009; Mickle *et al.*, 2009; Mickle, 2011; Broughton *et al.*, 2013) or their hypothesized membership within a crown clade (e.g. Gardiner, 1985; Coates, 1993, 1998, 1999). This makes it difficult to select taxa or characters for phylogenetic analyses and to infer the extent of lineage divergence and structure among early actinopterygians barring their previous inclusion in cladistic analyses.

The taxonomy of Palaeozoic actinopterygians still stretches in many ways back to the seminal work of Agassiz (1833–1844) on fossil fishes, in which the genus *Palaeoniscus* (now *Palaeoniscum*) and a handful of other genera (e.g. *Platysomus*, *Acrolepis*, *Amblypterus* and *Eurynotus*) were diagnosed from basic form and scale ornament. Such brief, shape-based descriptions led to the identification of many additional nominal specimens from multiple intervals and localities, extending some temporal ranges to 100 million years or more and geographic spread to multiple continents despite obvious differences (Gardiner, 1993; Sepkoski, 2002; L. C. Sallan, personal observation). As the broad Agassizian actinopterygian genera were split, they lent their names to equally far-ranging families (Amblypteridae, Acrolepidae) and suborders (the aforementioned palaeoniscoids; Platysomoidea; Traquair, 1879; Moy-Thomas & Miles, 1971). Many species were referred to these groups based on gestalt similarity to a short diagnosis based on the type genus, buttressed by few additional traits (Traquair, 1877–1914, 1879; Moy-Thomas & Miles, 1971).

As discussed in the introduction, Agassiz (1833–1844) assigned most fossil osteichthyans, as well as a few armoured agnathans and acanthodians, to the order of ‘ganoids’ on the basis of scale histology. As teleosts and sarcopterygians were

removed piecemeal by Victorian-era palaeontologists (e.g. Müller, 1844, 1846), ‘ganoid’ came to define all non-teleost actinopterygians, particularly those in the Palaeozoic, such that Traquair (1877–1914) could use the term in his monograph on British Carboniferous ray-finned fishes. Many of these are still referred to as ganoid, along with living non-teleost lineages, although this usage has been dwindling through time (but see Zhao *et al.*, 2008; Frey & Tischlinger, 2012). However, nearly all new Palaeozoic species and undescribed material are still labelled as palaeoniscoid, an adjective used even for early actinopterygians not officially referred to that higher taxon (e.g. Schaeffer, 1955; Poplin & Lund, 2002; Long, Choo & Young, 2008; Mickle *et al.*, 2009; Mickle, 2011). This situation has led to a general impression of a largely natural group, radiation and/or homogeneous grade of Palaeozoic actinopterygians distinct from living forms (see Cloutier & Arratia, 2004; Mickle *et al.*, 2009; Fig. 6C, D), glossing over inherent differences between lineages in terms of diversity, ecology and interrelationships. This is despite the fact Palaeoniscoidea was found to be polyphyletic in the very first cladistic analyses of early actinopterygians (Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989) and almost all the subsequent cladograms discussed above (Fig. 3). Yet, ‘palaeoniscoid’ is still claimed to be a descriptive term, with associated taxa identifiable by their similar body shapes and cranial morphologies (Mickle, 2011; Broughton *et al.*, 2013). As the namesake genus is fusiform, with an oblique suspensorium, immobile jaws, and sharp teeth, other Palaeozoic actinopterygians are presumed to share these features in aggregate, barring marginal lineages such as the deep-bodied platysomoids and eel-like Tarrasiiformes (Berg, 1940; Moy-Thomas & Miles, 1971; Sepkoski, 2002).

#### (4) Interrelationships between early and modern actinopterygians

While the molecular clock estimates presented above (Table 1) favour Devonian–Permian divergence dates in line with recorded increases in actinopterygian diversity, the branches subtending the crowns of the Holostei, Ginglymodi, Polypteriformes, Teleostei, Chondrostei and even Neopterygii remain devoid of Palaeozoic taxa in most cladistic analyses involving both fossil and living actinopterygians (e.g. Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1998, 1999; Lund, 2000; Poplin & Lund, 2000; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Gardiner *et al.*, 2005; Hurley *et al.*, 2007; Mickle *et al.*, 2009; Xu & Gao, 2011; Xu & Wu, 2011; Fig. 3). This is despite the aforementioned abundance of accessible, appropriately aged actinopterygian material (Gardiner, 1993; Dineley & Metcalfe, 1999; Sepkoski, 2002; Sallan & Coates, 2010; Friedman & Sallan, 2012; Sallan & Friedman, 2012). The absence of Palaeozoic stem-taxa obscures the pattern and timing of the origins of major actinopterygian clades and the synapomorphies defining their crowns. It also does little to fill the gaps apparent in molecular phylogenies. One issue is that an inexplicably large portion of previous

cladistic analyses including Devonian actinopterygians either stop at the Devonian–Carboniferous boundary (359 Ma; e.g. Long, 1988; Friedman & Blom, 2006; Long *et al.*, 2008), are constrained to the Palaeozoic (Dietze, 2000; Lund, 2000; Poplin & Lund, 2000; Lund & Poplin, 2002), only include living and/or post-Palaeozoic taxa alongside their Devonian taxa (e.g. Patterson, 1982; Gardiner, 1984; Taverne, 1997) and/or limit their post-Devonian Palaeozoic sample to one or two taxa designated as phylogenetically important *a priori* based on either previous in-depth description, a new included description or use in previous analyses (e.g. Gardiner, 1984; Long, 1988; Taverne, 1996; Schultze & Cumbaa, 2001; Gardiner *et al.*, 2005; Swartz, 2009; Xu & Gao, 2011). These practices are in line with the foci of the fossil fish literature, but have exacerbated the gaps.

A few previous phylogenetic studies used larger numbers of later Palaeozoic taxa, specifically more than two Carboniferous–Permian actinopterygians, alongside representatives of living and Mesozoic actinopterygian clades. Placement of Palaeozoic, particularly Devonian–Carboniferous, actinopterygians within such cladograms falls into two camps: within crown Actinopterygii and Actinopteri (Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Hurley *et al.*, 2007), and outside crown Actinopteri (Cloutier & Arratia, 2004; Mickle *et al.*, 2009). This division reflects two distinct lines of character formulation and taxon selection. The former analyses use many of the synapomorphies for nested actinopterygian/actinopteran/neopterygian clades and other character states proposed to undergo transformation along the stems of living groups by Patterson (1982) and modified by Gardiner (1984) and Gardiner & Schaeffer (1989). These tend to recover almost all actinopterygians, aside from *Cheirolepis* or a few Devonian taxa, within the crown (Coates, 1999; Gardiner *et al.*, 2005; Hurley *et al.*, 2007). The polypteriform stem is naked in all such trees and the Chondrostei similarly lack Palaeozoic branches (Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Gardiner *et al.*, 2005; Hurley *et al.*, 2007; Xu & Gao, 2011). Thus, the vast majority of later Palaeozoic taxa are recovered as either stem-Actinopteri (Gardiner & Schaeffer, 1989; Coates, 1999; Xu & Gao, 2011 based on non-brain characters) or stem-Neopterygii (Gardiner, 1984; Coates, 1999; Hurley *et al.*, 2007, based on all characters).

Gardiner's (1984) (Fig. 3A) cladistic analysis was the first to include early Carboniferous actinopterygians as terminals. These and later Palaeozoic fishes were recovered in stepwise fashion along the neopterygian stem, while Devonian taxa were placed outside the actinopteran crown. Gardiner & Schaeffer's, 1989; Fig. 3B) subsequent study generated a large polytomy containing the origins of most Palaeozoic clades and the crown supported by a single trait: a dermosphenotic overlapping the dermopterotic. This node underlies a naked branch leading to crown Actinopteri, which is characterized by a keystone-shaped dermosphenotic, the 'usual' presence of supraorbitals (likely homoplastic in Palaeozoic actinopterygians) and a 'rudimentary' and distinct posttemporal fossa (Gardiner & Schaeffer, 1989). Whether

or not the Palaeozoic groups branching off this point form a clade exclusive of most living forms, the topology suggests an early Carboniferous–Triassic gap in the record of crown Actinopteri (Gardiner & Schaeffer, 1989; Fig. 3B).

The lack of resolution and absence of more derived Palaeozoic stem-Actinopteri and stem-Neopterygii might be attributable to *a priori* grouping of Palaeozoic taxa based on just a handful of traits, with only the namesake of the group coded into the analysis (Gardiner & Schaeffer, 1989; Fig. 3B). This obscures character conflict and therefore homoplasy, symplesiomorphy and transformational polarity. For example, the *Amblypterus* group (Gardiner & Schaeffer, 1989), named and coded for the Permo-Carboniferous genus (Dietze, 1999) includes two, rather morphologically distinct, earliest Tournaisian (Mississippian) taxa, *Oxypterus* and *Gyrolepidotus* from Bystraya, Russia (Sallan & Coates, 2010). However, the latter fishes are noted by Gardiner & Schaeffer (1989) to retain a primitive pineal opening, as found in the skull roofs of most Devonian taxa (e.g. *Cheirolepis*: Arratia & Cloutier, 1996; *Howqualepis*: Long, 1988; *Stegotrachelus*: Swartz, 2009; *Moythomasia*: Gardiner, 1984; *Mimipiscis*: Gardiner, 1984; Choo, 2011; *Donnrosenia*: Long *et al.*, 2008; *Cuneognathus*: Friedman & Blom, 2006; absent in *Osorioichthys*: Taverne, 1997, and possibly *Tegeolepis*: Cloutier & Arratia, 2004). These fishes are all assigned to other groups in the analysis (Gardiner & Schaeffer, 1989). By contrast, the pineal foramen appears to be absent in nearly all other Palaeozoic taxa [character 21 in Mickle *et al.* (2009); miscoded as present in *Kalops* (Poplin & Lund, 2002); character 50 in Cloutier & Arratia (2004); L. C. Sallan, personal observations], being found only in the earliest Tournaisian, and thus contemporary, *Kentuckia deani* among other post-Devonian actinopterygians (Gardiner, 1984).

In the total evidence cladogram constructed by Coates (1999) based on characters of external morphology, endoskeleton and brain morphology, most Carboniferous–Triassic taxa are resolved as stem-Neopterygii, with the Mississippian fishes *Mesopoma* and *Cosmoptychius* grouped with several Triassic taxa (Node K; Fig. 3C) in a 'palaeoniscid' clade. In the total evidence tree, the clade is characterized by contact between the nasal and dermosphenotic, the presence of suborbitals, and two traits of the posterior myodome: perforation by the facial nerve and an anterior edge marked by a ridge (Coates, 1999). Crown Actinopteri is defined by a dermopterotic (as in the stem-actinopteran node H in Gardiner & Schaeffer, 1989; Fig. 3B), long frontals, fewer than 12–13 branchiostegals, separate openings for the lateral aortae and a posteriorly expanded parasphenoid (Coates, 1999). Interestingly, when novel characters related to brain morphology were excluded from the analysis in order to decrease the number of unknown states, all Palaeozoic taxa fell outside the actinopteran crown (Coates, 1999, fig. 9), despite the lack of recovered brain-related actinopteran synapomorphies in the full analysis. However, Coates (1999) attributes this to uncertainty about the insertion of crown Chondrostei rather than any primitive states within the Palaeozoic taxa.

A newer study by Hurley *et al.* (2007; Fig. 3D) used many of the same characters and recovered nearly all included Palaeozoic taxa, including the Devonian *Mimipiscis*, as stem-neopterygians. The exception was *Brachydegma*, a Permian taxon assigned as a stem-halecomorph on the basis of a supramaxilla, an enlarged median gular, a narrow maxilla with a posterior notch and a dermosphenotic fused to the neurocranium (Hurley *et al.*, 2007). However, it is notable that some more recent molecular clock studies have reinterpreted *Brachydegma* as a stem-neopterygian (e.g. Near *et al.*, 2012) or actinopteran (e.g. Broughton *et al.*, 2013) based on an absence of the aforementioned characters and the synapomorphies of various clades discussed in Section II. In the Hurley *et al.* (2007) topology, Chondrostei and Polypteriformes fall on a trichotomy at the base of the tree (Fig. 3D). The node underlying the total group Neopterygii, including a basal polytomy containing most Palaeozoic taxa, was supported by the presence of a posterior myodome and a surangular on the lower jaw (both actinopteran characters in Patterson, 1982). This polytomy was resolved into a series of staggered dichotomies through reweighting of characters.

An alternative topology in which nearly all Palaeozoic taxa are placed as stem-Actinopterygii was recovered by two cladistic studies largely using the same character set (Cloutier & Arratia, 2004; Mickle *et al.*, 2009; Fig. 6E, F). In these, a designated 'Palaeonisciformi' (i.e. palaeoniscoids/Palaeonisciformes/palaeoniscids) containing nearly all Palaeozoic actinopterygian taxa represented either a distinct clade [Cloutier & Arratia (2004); Fig. 3E; similar to Gardiner & Schaeffer's (1989) clade above] or a more inclusive group of actinopterygians than the Actinopterygii (Mickle *et al.*, 2009; Fig. 3F). While they did not list the synapomorphies of their crown Actinopterygii, Cloutier & Arratia (2004) attributed the derived position of *Polypterus* and *Acipenser* to difficulty in inferring the homology of highly modified morphologies in the living taxa. Thus, the placement of all Palaeozoic taxa outside the crown might be attributable to coding for autapomorphic characters in living taxa, as well as to long-branch attraction due to the large amount of state change involved. A factor here is the exclusion of nearly all post-Mississippian fossil fishes from the analysis, aside from the Mesozoic crown neopterygian *Leptolepis* (recovered as sister taxon to *Amia*; Fig. 3E), the Triassic *Pteronisculus* (recovered in a clade with the Devonian *Tegeolepis*), and the Permian *Amblypterus* (recovered as sister group to a clade of Devonian–Mississippian forms; Fig. 3E; Cloutier & Arratia, 2004). This paucity likely eliminated transitional character states and combinations necessary to relate the living to the long dead and prevented determination of the basic synapomorphies and morphologies defining the crown lineages.

The structure of the cladogram generated by Mickle *et al.* (2009) was also likely affected by both a lack of post-Mississippian fossil fishes and the exclusion of living and Mesozoic Chondrostei and Teleostei (Fig. 3F). While this analysis contained the largest number of Devonian–Mississippian taxa of all studies to date, nearly all of these were excluded from the crown Actinopterygii.

The crown clade was characterized by the addition of infraorbitals (the lachrymal is fourth in a series including the dermosphenotic), a narrow, rectangular dermosphenotic, 'loose' suborbitals, a narrow posterior maxilla, an absent clavicle [a neopterygian crown character elsewhere (Grande, 2010) that is miscoded for *Polypterus* where it is actually present (Claeson, Bemis & Hagadorn, 2007)], a posteriorly expanded parasphenoid (a crown actinopteran character shared by many Palaeozoic taxa such as *Mesopoma* in Coates, 1999) and 'webbed' caudal fin rays (or fully dichotomized, a neopterygian character in Grande, 2010). The only Palaeozoic taxa within crown Actinopterygii were the Guildayichthyiformes (e.g. *Discoserra*), recovered as stem-Polypteriformes rather than stem-Neopterygii as in Hurley *et al.* (2007). The total group Polypteriformes was supported by the absence of an antorbital [symplesiomorphic for many Mississippian actinopterygians; see Gardiner & Schaeffer (1989); and the primitive state of actinopteri in Gardiner (1984), where the antorbital is a neopterygian synapomorphy], numerous serial nasals (absent in more recent descriptions of *Discoserra*; Hurley *et al.*, 2007), serial postspiraculars (also absent in *Discoserra*; Hurley *et al.*, 2007), marginal dentition (a primitive character for crown gnathostomes, perhaps representing reversals here) and the presence of dorsal ridge scales (a symplesiomorphy found in many of the included Carboniferous taxa; see figures in Moy-Thomas & Miles, 1971). Paleonisciforma, a clade containing the crown and all Carboniferous taxa, is defined by characters considered to be actinopteran by Patterson (1982): a median rostral and a distinct inversion of the caudal scales (a hinge line). It appears that exclusion of most early actinopterygians from the crown by Mickle *et al.* (2009; Fig. 3F), and the placement of *Discoserra* as a polypteriform, seems more attributable to miscoding and reconstructed reversals between symplesiomorphic and homoplastic character states than actual interrelationships.

One potential source of conflict in the placement of Palaeozoic actinopterygians in relation to the crown is choice of characters. Cloutier & Arratia (2004; Fig. 3E), and to a much lesser extent Mickle *et al.* (2009; Fig. 3F), used many of the same, particularly neurocranial, characters and states serving as synapomorphies for the nested crown clades in analyses by Patterson (1982); Gardiner (1984; Fig. 3A), Gardiner & Schaeffer (1989; Fig. 3B) and Coates (1999; Fig. 3C). However, the former analyses added dozens of characters constructed to capture variation in the external morphology of Palaeozoic fishes. These focused on variation in the composition of the dermal skull (e.g. several ranges of branchiostegal counts, presence and size of antorbitals, dentition) and various morphometrics of the body, dermal bones and fins (e.g. ratio of the size of the posterior portion of the maxilla, relative body depth, relative median fin positions). Single bones informed states for multiple characters (e.g. presence, shape and position of infraorbitals; Cloutier & Arratia, 2004; Mickle *et al.*, 2009), limiting variation in taxa lacking such traits. Surveying changes at nodes in Mickle *et al.* (2009) suggests that



the form and multiple presence-based characters heavily informed the resultant cladograms, with many additions and reversals along the branches. This is troubling, as traits contributing body form and fin position and feeding function are more likely to be homoplastic because of their ecological implications (Webb, 1982; Streebman & Danley, 2003; Westneat, 2004; Sallan & Friedman, 2012). Similar functional morphologies have arisen convergently in many extant teleost lineages (Nelson, 2006; Ward & Brainerd, 2007). Thus, the amount of phylogenetic information contained in characters based on these traits is not certain.

It is important to note that few large clades of Palaeozoic actinopterygians are supported in more than one analysis and there is little consensus on their interrelationships (see Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1998, 1999; Dietze, 1999; Lund, 2000; Poplin & Lund, 2000, 2002; Lund & Poplin, 2002; Hurley *et al.*, 2007; Swartz, 2009; Xu & Gao, 2011). In order to resolve the deep branching patterns and origins of major actinopterygian clades, it will be necessary to perform further phylogenetic analyses involving larger numbers of Palaeozoic fishes alongside Mesozoic and living taxa. However, given the state of taxonomy and description for most Palaeozoic actinopterygians, particularly those not included in previous analyses, this will not be not easily accomplished.

### (5) Global events, early ecosystems and gaps in the record

In discussing the plausibility of mid-late Palaeozoic divergence dates for crown clades, it is important to note that the interval is marked by several major mass extinction and other environmental events. Changing ecological and environmental conditions can have a profound impact on diversification by either facilitating or limiting opportunities for divergence, and thus can serve as constraints on the timing of origination of clades. Unfortunately, there is a general lack of palaeobiological and/or macroevolutionary work focusing on Palaeozoic and early Mesozoic actinopterygians, as well as an absence of appropriate taxonomic and ecological databases (Friedman & Sallan, 2012). This is likely both a reflection of the taxonomic and cladistic issues described above and a factor in their persistence.

The Devonian interval contains two major events subsequent to the appearance of the first fossil actinopterygians: the Frasnian–Famennian Kellwasser event (372 Ma) and the end-Devonian Hangenberg event (359 Ma), both of which have documented impacts on marine invertebrate biotas (McGhee, 1996; Caplan & Bustin, 1999; Racki, 2005; Brezinski, Cecil & Skema, 2010). Until recently, it was not known what, if any, impact these biotic events had on vertebrate faunas, yet increased actinopterygian diversity was apparent in the aftermath of the Devonian (Gardiner, 1993; Hallam & Wignall, 1999). Recent analyses of diversity databases have shown that the end-Devonian Hangenberg event coincides with a bottleneck in the evolution of actinopterygians, as well as tetrapods, chondrichthyans, trilobites, eurypterids, and ammonites (Lamsdell & Braddy,

2010; Sallan & Coates, 2010; Sallan *et al.*, 2011; Korn & Klug, 2012; Lerosey-Aubril & Feist, 2012). It is likely that only one or two lineages of each of these pelagic groups made it through the extinction event based on both the record (Lamsdell & Braddy, 2010; Sallan & Coates, 2010; Korn & Klug, 2012; Lerosey-Aubril & Feist, 2012), the phylogenies described above which include modern, Carboniferous and later Palaeozoic taxa (Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1998; Gardiner *et al.*, 2005), and a recent supertree (Sallan & Friedman, 2012). The Hangenberg event itself is followed by a depauperate recovery interval partially coincident with ‘Romer’s Gap’ (Coates & Clack, 1995; Sallan & Coates, 2010). During the early part of this 10–15 million year interval, actinopterygians were homogeneous in form, occupying just a small part of their morphospace (Sallan & Friedman, 2012; L. C. Sallan, personal observations). However, for the first time, actinopterygian specimens are abundant and numerically dominant over other vertebrates at well-sampled faunas, just as in modern faunas (Sallan & Coates, 2010, 2013). This is the start of an adaptive radiation leading to a wide range of new ecomorphologies (Sallan, 2012; Sallan & Friedman, 2012; Sallan & Coates, 2013). In summary, it is probable that the Hangenberg event represents an absolute upper limit on most divergence events within the crown Actinopterygii. However, molecular studies of divergence dates have failed to take this into account, or, indeed, put any constraints based on environmental conditions or global extinction events (e.g. the end-Permian or end-Cretaceous) into their models. Even if Polypteriformes and Chondrostei diverged from Neopterygii in the Mississippian (Fig. 1, Table 1) that does not mean these lineages obtained all of their current diagnostic features at that time. Rather, current synapomorphies, generated from living taxa, might have been gained in a short period of time before the much later appearance of definitive body fossils, their morphological leap triggered by yet another event. The deep separation of crown clades may only be evident in retrospect, now that other large groups are extinct.

### (6) Identifying the crown and the origins of an ecologically modern biota

Reconstructing the origins of present actinopterygian ecological diversity is even more fraught than inferring interrelationships. Biomechanics surveys dating back to Schaeffer & Rosen (1961) have assumed that early actinopterygians could do little more than bite and ram feed. The jaw musculature of ‘palaeoniscoids’ is hypothesized to be limited to a capsule beneath the immobile and tightly sutured dermal bones (Lauder, 1982; Lauder & Liem, 1983; Maisey, 1996; Figs 5 and 6). By contrast, the mobile jaws of crown neopterygians and increased muscle mass permitted a greater number of feeding modes (Schaeffer & Rosen, 1961; Lauder, 1982; Bellwood, 2003; Fig. 2). However, Mississippian actinopterygians display an assortment of dentitions and jaw morphologies, ranging from low mechanical advantage fang-bearing dentaries (e.g., *Acrolepis* and *Nematoptychius*; L. C. Sallan, personal observations; Fig. 6B) to robust mandibles

with tooth plates and denticle batteries (e.g. *Amphicentrum* and *Eurymotus*; Fig. 6D; Traquair, 1879; Bradley Dyne, 1939; Coates, 1988; Sallan & Coates, 2013) to small jaws with multiple rows of pointed symphyseal teeth suited for grazing (e.g. *Discoserra*; Fig. 6C; Lund, 2000; Hurley *et al.*, 2007).

As noted earlier, it has also been suggested that ganoid-scale-bearing fishes were incapable of approximating the divergent body forms and locomotor modes of modern reef fishes because of limited flexibility in trunk and fins (Bellwood, 2003; Goatley *et al.*, 2010), despite the aforementioned deep-bodied ‘platysomoids’ (Traquair, 1879; Moy-Thomas & Miles, 1971) and axially elongated ‘Tarrasiiformes’ (Lund & Poplin, 2002), both hypothesized to be convergent on modern teleost taxa in terms of function (Webb, 1982; Sallan, 2012; Sallan & Coates, 2013), not to mention deep-bodied Triassic ginglymorphs (gars; Xu & Wu, 2011). These assumptions and oversights prevent straightforward characterization of morphological and ecological disparity in Palaeozoic actinopterygians and comparison of early and modern actinopterygian biotas, bolstering aforementioned assertions of teleost exceptionality. However, the great amount of ecological and morphological divergence present in the Palaeozoic and mid-Mesozoic actinopterygians belies explanations related to genome duplication or late Mesozoic ecological drivers. It is also possible that these ecologically diverse Palaeozoic fishes may have delayed the rise of the modern lineages through occupation of niches now filled by teleosts, polypteriformes, holosteans and chondrosteans. Indeed, these extinct groups may have competitively excluded rare members various crown groups until removed by some abiotic or biotic force in the late Paleozoic/early Mesozoic, mirroring the marginalization of actinopterygians before the Hangenberg event (Sallan & Coates, 2010; Sallan & Friedman, 2012). Both of these hypotheses can be tested with more complete ecological and taxonomic data for Palaeozoic and early Mesozoic fishes.

On a that note, looking for teleosts or even chondrosteans in the Palaeozoic may be equivalent to searching for passerines and carnivorans in the Jurassic and Cretaceous. The branching events might be placed there, and there are birds and placental mammals of that age, many of them diverse and approximating passerine and carnivore characters and body plans, but most of these belong to distinct radiations outside the crown (e.g. the enantiornithine birds or multituberculate mammals; Hou *et al.*, 1996; Wilson *et al.*, 2012; J. Mitchell, personal communication). These groups may be considered to branch from the stem of crown birds and mammals, but they are hardly informative in reconstructing the transformation series leading to those clades or dating their origins. Rather, the ecological diversification of these stem clades might have both set the stage for modern radiations or delayed their rise until an abiotic driver took hold. Excessive focus on the origins of modern clades has the potential to obscure the real origins of actinopterygian dominance, an event independent of the relationships of involved taxa, and the exact circumstances and selective pressures behind the rise of living groups.

#### IV. CONCLUSIONS

(1) The interrelationships of the major actinopterygian lineages have been under regular debate, particularly in the morphological literature. However, the molecular consensus is now coalescing around the nested Polypteriformes–Actinopteri, Chondrostei–Neopterygii, and Holostei–Teleostei topology presented in Fig. 1.

(2) There is still a large amount of conflict between molecular and morphological hypotheses, driven by choice of characters, taxa, and genes. Well-sampled molecular phylogenies based on nuclear genes, with their greater range of available characters (base pairs) are more likely to represent the true topology than morphology-based solutions which are prone to ecologically driven homoplasy. However, in the many cases where molecular trees conflict with each other, morphological characters should be used to choose and support a single solution. Thus, either an effort should be made to seek out morphological synapomorphies among both fossil and living fishes to define clades generated through molecular-based efforts, or a total evidence approach should be used from the beginning. At the species, genus and family level molecular and morphological changes are likely to be coincident, even in apparently ecologically static lineages such as gars (Wright *et al.*, 2012).

(3) A source of conflict between molecular and morphological solutions, and between estimated divergence times and the fossil record, is that morphological definitions of many actinopterygian divisions remain elusive. For larger groups such as teleosts, there may be just a few synapomorphies in each analysis, many of which are later found to be homoplastic or in conflict. This is partially attributable to a lack of available transformation series for specific characters or obvious sister taxa. Without robust morphological synapomorphies, calibration fossils cannot be found to date divergences between clades recovered from molecular datasets, confounding analyses of evolutionary rates using such trees. Larger sets of calibration fossils covering a greater proportion of clades are more likely to produce dates in line with the fossil record (as for Acanthomorpha in Near *et al.*, 2013). In addition, as ancestral-state reconstructions based on living species alone are often inaccurate for fish traits across even moderate time spans (Albert, Johnson & Knouft, 2009), fossil/morphological transformation series still provide the best evidence for reconstructing the evolutionary trajectories that led to the foundation of clades.

(4) The ‘Teleost Gap’ (Near *et al.*, 2012), an interval of hundreds of millions of years between Palaeozoic divergence dates taken from molecular clock analyses (Table 1) and the appearance of crown teleosts in the Mesozoic, characterizes the Palaeozoic records of all crown actinopterygian lineages (e.g. Chondrostei; Polypteriformes, Holostei, Neopterygii). While workers have implicated poor sampling as the source of this gap (Hurley *et al.*, 2007; Near *et al.*, 2012; Broughton *et al.*, 2013), the Palaeozoic fossil record is well sampled and contains many *Lagerstätten*. Yet, systematic analyses of

Palaeozoic taxa disagree as to whether crown actinopterygians, stem-neopterygians and/or stem-chondrosteans existed during that era, which complicates selection of calibration fossils in an unappreciated way. This conflict is caused, at least partially, by the arbitrary exclusion of taxa from various relevant timespans in actinopterygian evolutionary history from morphological analyses and the relative neglect of the basic taxonomy and interrelationships of Palaeozoic actinopterygians relative to later taxa. In addition, positive identification of crown and stem fossil taxa is difficult when definitions based on living taxa are in constant flux (see above).

(5) Hypotheses of origination dates need to take into account conditions during projected divergence intervals, including climate change, mass extinction, and ecosystem composition. For example, Devonian (or earlier) origination dates for crown actinopterygian clades are not likely to be correct because of the scarcity of ray-finned fishes of that age and a severe reduction in actinopterygian lineages at the end-Devonian Hangenberg mass extinction.

(6) While identifiable members of the actinopteran or neopterygian crown are currently missing from the Palaeozoic record, the actinopterygian fauna was ecologically robust, approximating Mesozoic and modern diversity in many respects. This diversity might have set the stage for the rise of the crown clades, which are always arbitrarily defined on the small subset of taxa surviving to the present day, or even delayed their rise.

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